J. Mar. Biol. Ass. U.K. (2006), **86**, 1407–1419
Printed in the United Kingdom
doi: 10.1017/S0025315406014445

Larval and postlarval development of *Pagurus nigrofascia* (Decapoda: Anomura: Paguridae) reared in the laboratory

Takashi Oba*‡, Kooichi Konishi† and Seiji Goshima*

*Research Faculty of Fisheries Science, Hokkaido University, Minato-cho, Hakodate 041-8611, Japan.
†National Research Institute of Aquaculture, Fisheries Research Agency, Minami-ise, Mie 516-0193, Japan.
‡Corresponding author, e-mail: oba@fish.hokudai.ac.jp

Zoeal, megalopal and first crab stages of *Pagurus nigrofascia* are described and illustrated from laboratory-reared specimens. Larvae were reared at temperatures 6°C, 12°C, 18°C, and 25°C. Survival rates of larvae were considerably higher at 12°C and 18°C, but were low at 6°C and 25°C. Larvae and postlarvae of *P. nigrofascia* can be distinguished from seven morphologically similar species based on adult or larval morphological features. Zoeal stages of this species are distinguished by, for example, setal formulae of maxillule, maxilla and maxilliped 1. The megalopal stage can be identified by the telsonal process, the number of articles of the flagellum of antenna and setal formula on the scaphognathite of the maxilla. Morphological features of *P. nigrofascia* larvae are similar to those of *P. ochotensis*, *P. kennerlyi* and *P. pectinatus*.

INTRODUCTION

Hermit crabs are common components of coastal systems, but the information describing their larvae is still insufficient and therefore, identifying their early life history stages is difficult. *Pagurus* is a major group of hermit crabs and it includes more than 100 species (e.g. Miyake, 1978; Goshima et al., 1996). Larval descriptions of the species of the genus exist, but many are incomplete, especially in the settlement stage, the megalopal, and in the first crab stage. This lack of morphological information could hinder ecological studies of recruitment of hermit crabs.

Pagurus nigrofascia Komai is a common hermit crab species living on the intertidal shores of Japan. Adult morphology was described by Komai (1996) and its reproductive biology was described by Goshima et al. (1996). Adult morphology of *P. nigrofascia* closely resembles *P. samuelis*, *P. filholi*, *P. hirsutiusculus* and *P. venturensis* (Komai, 1996). No morphological and physiological information is available in the literature on the larvae of *P. nigrofascia*.

We describe and illustrate zoeal, megalopal and 1st crab stages of *P. nigrofascia*, and compare the morphological features of *P. nigrofascia* with the four resemblant species mentioned above. We also compare morphological features of *P. nigrofascia* with *P. ochotensis*, *P. kennerlyi* and *P. pectinatus* in detail because larval morphological features of *P. nigrofascia* are very close to them (see Results and Discussion), and we characterize larval morphological features of *P. nigrofascia* among all of these seven species to avoid taxonomic misidentification. Additionally, we show basic developmental data, larval duration and survival at four temperatures to help predict the pelagic period and optimum temperature-range of *P. nigrofascia* larvae for future ecological studies of recruitment.

MATERIALS AND METHODS

Forty ovigerous females of *Pagurus nigrofascia* were collected at Kattoshi, southern Hokkaido, Japan, in January 1999. We kept them individually in 120 ml plastic cylinders containing seawater. The cylinders were placed in an incubator regulated at 12°C, the same as the natural temperature condition in January. We checked for hatching and changed the seawater daily. Zoeae collected from each female were combined and placed in plastic aquaria ($6\times9\times15$ cm; 640 ml). Aquaria, each containing 20 larvae hatched on the same day and 400 ml seawater filtered using 100 μm mesh were placed in incubators preset to reflect the annual temperature-range of the natural habitat, namely, 6°C, 12°C, 18°C, and 25°C (Oba & Goshima, 2004). Five replicates were made for each temperature. We changed the water, provided 1-d-old *Artemia* spp. nauplii as food, and checked for moults and dead individuals every day. The incubators were kept at 12L:12D. We examined five individuals of each stage for description. They were reared in 20 ml plastic bottles individually under 12°C condition. The other rearing procedures were similar to those in the mass culture. Specimens of megalopae for description were collected from females caught in January 2002 and were reared using the same procedures.

The carapace length (CL) of zoea was measured from the tip of the rostrum spine to the posterior margin of the carapace laterally, and the CL of megalopa from the rostrum to mid-posterior point of the carapace dorsally. The shield length (SL) of megalopa and the first crab stage (crab 1) was measured from the rostrum to the posterior margin of the shield. Counts and setal formulae are shown from the proximal to distal end of each segment. Roman numerals designate the dorsal setae on the endopod of maxilliped 1 of zoeal stages. Specimens of

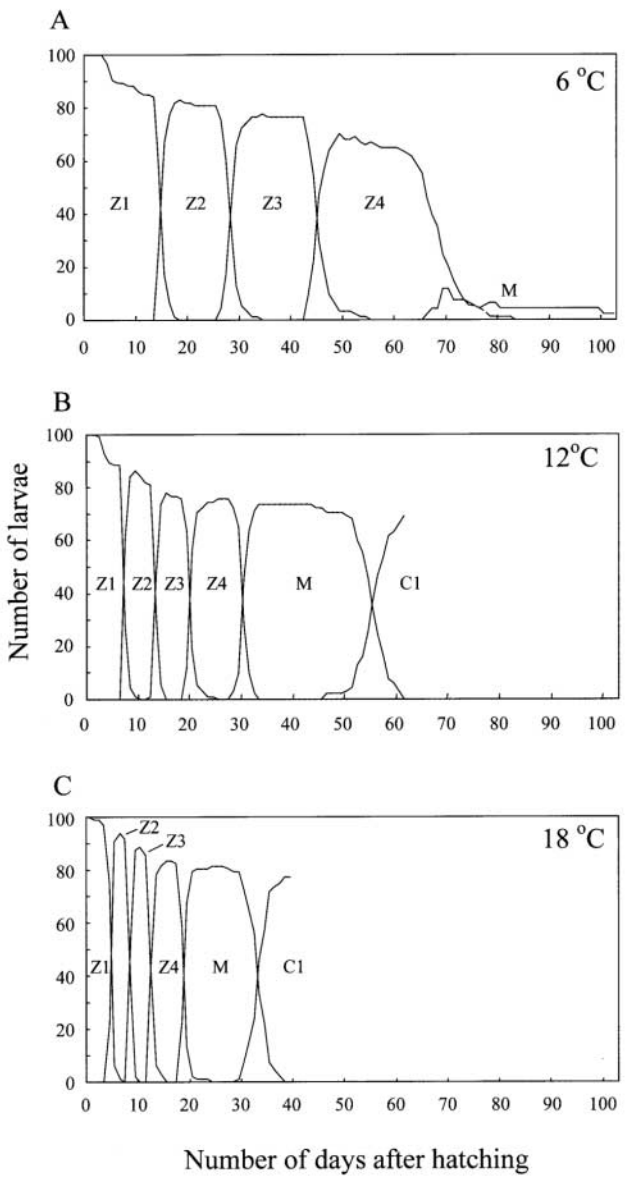

Figure 1. *Pagurus nigrofascia*. Survival and duration of larvae at three temperatures in the laboratory.

all stages of larvae and crab 1 were deposited in the Hokkaido University, Graduate School of Fisheries Science HUMZ-C 02206-02211.

RESULTS

All first zoeae reared at 25°C were dead within two days. At 6°C, larvae developed to megalopae, but no megalopae moulted to crab 1. The larval duration differed between temperatures; larvae developed more quickly as the temperature increased (Figure 1A–C). The larval survival rate at 12°C and 18°C remained high throughout all the developmental stages; the megalopal larval survival rate at 6°C was considerably lower.

DESCRIPTION OF LARVAL AND POSTLARVAL STAGES

First zoea

Size. CL=1.65–1.70 mm; mean=1.68 mm; SD=0.019; N=5.

Carapace (Figure 2A). Surface smooth. Rostrum approximately equal in length to antenna, posterolateral spines short. Eyes sessile.

Pleon (Figure 2B). Five somites and telson. Posterodorsal margin on pleonal somite 1 with no spines; somite 2 with three small pairs; somites 3 and 4 with two pairs; somite 5 with two pairs, outer pair smaller. Posterolateral margins of somites 2–4 with small pair of spines, somite 5 with strong, elongate posterolateral spines; no pleopod buds.

Telson (Figure 2C). Posterior margin with seven pairs of processes: a fused or weakly articulated, naked spine; a minute seta—the so-called 'anomuran hair'; process pairs 3–7 articulated, plumodenticulate spines. Process 4 appreciably longer. Cleft shallow. Anal spine present.

Antennule (Figure 2D). Conical. Peduncle with two aesthetascs and 2–3 setae terminally. Endopod rudiment with one long, plumose seta.

Antenna (Figure 2E). Biramous; endopod fused with protopod, one strong spine at base of endopodal junction. Exopod, inner margin slightly convex with five long plumose setae and distal shorter simple seta.

Mandibles (Figure 2F). Asymmetrical, slightly different in dentition. Incisor processes with strong tooth. Molar processes with several strong teeth, serrate ridges, small teeth and denticles. No palp buds.

Maxillule (Figure 2G). Endopod 3-segmented, with 1, 1, 3 setae, respectively, on segments 1–3. Coxal endite with one simple and four plumose setae marginally, and one or two short simple setae submarginally. Basial endite with two simple setae submarginally and two long, elongate spine-like teeth with several small denticles.

Maxilla (Figure 2H). Endopod slightly bilobed; with two plumose setae and a short simple seta on proximal lobe and four plumose setae on distal lobe. Coxal and basial endites distinctly bilobed; coxal endite with one submarginal and six marginal plumose setae on proximal lobe, one submarginal and three marginal plumose setae on distal lobe; basial endite with one submarginal and four marginal plumose setae on proximal lobe, one submarginal and three marginal plumose setae on distal lobe. Scaphognathite with five marginal plumose setae.

Maxilliped 1 (Figure 2I). Basis with 2+1+1+2+1+3 (occasionally 2) setae ventrally. Endopod 5-segmented, segments 1–4 with 3, 2, 1, 2 setae respectively, ventrally, and 5–8, 7–11, 6–13 and 0 setules, respectively, dorsally. Segment 5 with 4+I plumose setae. Exopod with four terminal natatory setae.

Maxilliped 2 (Figure 2J). Basis with one simple marginal seta in distal half, one simple marginal seta and one marginal spinule. Endopod 4-segmented, segments 1–3 each with one simple seta and one spinule ventrally, and 0, 4–8 and 6–10 setules respectively, dorsally. Segment 4 with 4+I plumose setae. Exopod with four terminal natatory setae.

Maxilliped 3 (Figure 2K). Rudimentary, uniramous, usually with bifurcate tip.

Pereiopods (Figure 2L). Rudimentary, unarmed, visible laterally beneath the carapace.

Second zoea

Size. CL=1.96–2.10 mm; mean=2.04 mm; SD=0.058; N=5.

https://doi.org/10.1017/S0025315406014445 Published online by Cambridge University Press

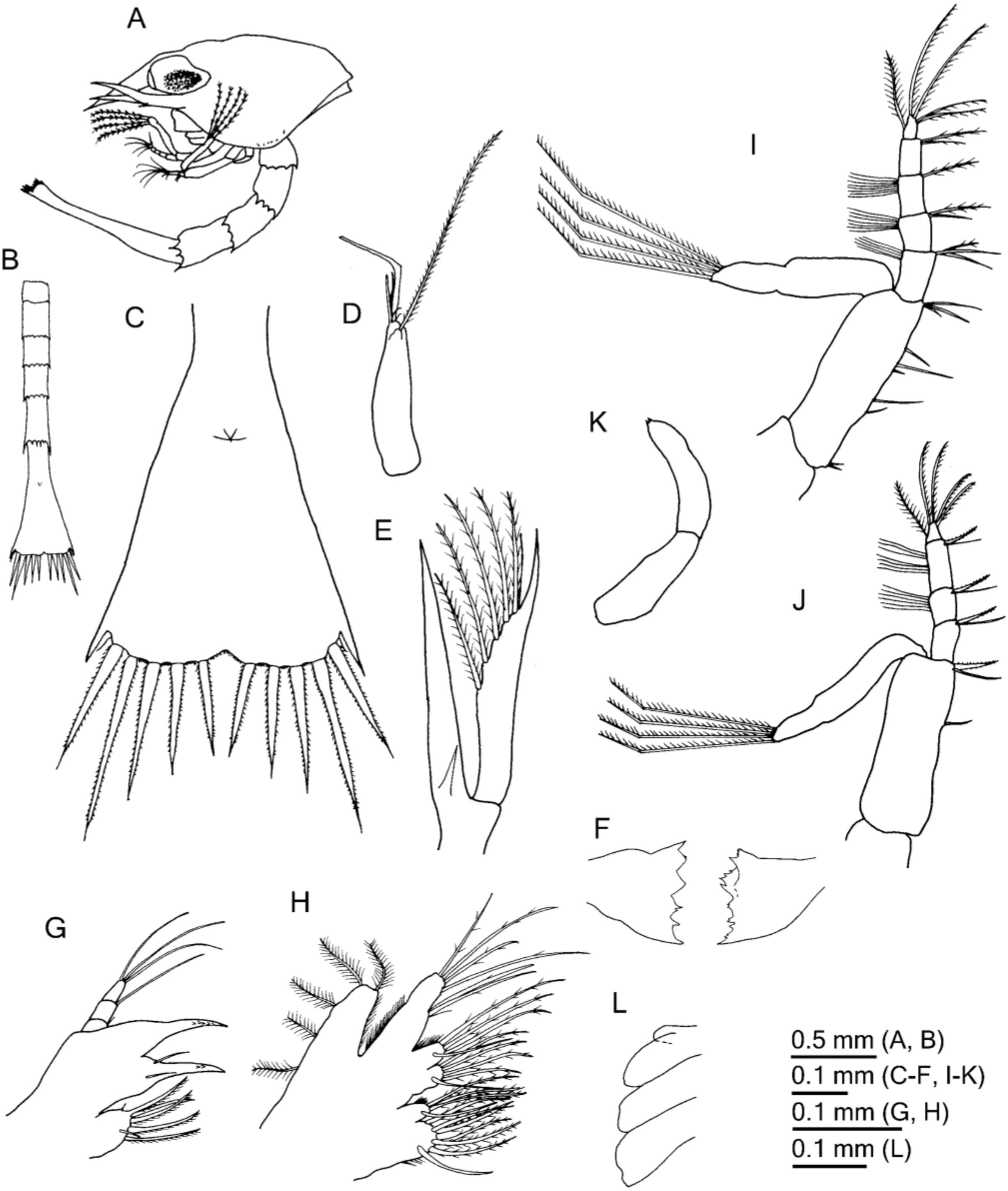

Figure 2. *Pagurus nigrofascia*. First zoea. (A) Lateral view; (B) dorsal view of pleon; (C) telson; (D) antennule; (E) antenna; (F) mandibles; (G) maxillule; (H) maxilla; (I) maxilliped 1; (J) maxilliped 2; (K) maxilliped 3; (L) pereiopods.

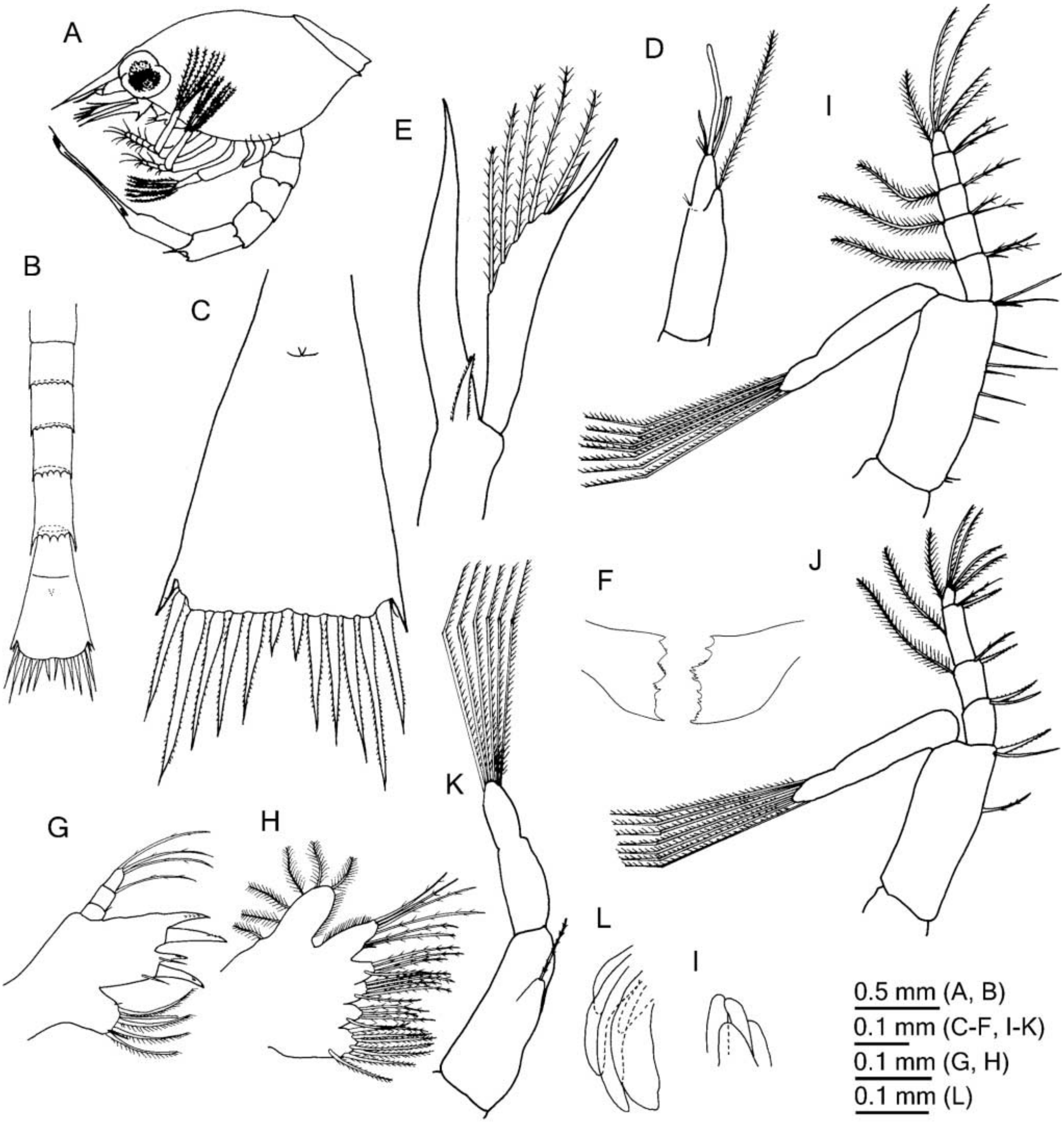

Figure 3. *Pagurus nigrofascia*. Second zoea. (A) Lateral view; (B) dorsal view of pleon; (C) telson; (D) antennule; (E) antenna; (F) mandibles; (G) maxillule; (H) maxilla; (I) maxilliped 1; (J) maxilliped 2; (K) maxilliped 3; (L) pereiopods; (l) pereiopods (ventral view).

Carapace (Figure 3A). Larger, but similar to the previous stage. Eyes stalked.

Pleon (Figure 3B). As in first zoea.

Telson (Figure 3C). Posterior margin with eight pairs of processes; one pair of articulated, plumodenticulate spines innermost in addition to those of first zoea. Anal spine reduced or absent. Otherwise as in first zoea.

Antennule (Figure 3D). Clearly bilobed. Exopod with one long and one or two short terminal aesthetascs, three short marginal setae and 0–3 submarginal setules. Endopod with one long terminal plumose seta.

Antenna (Figure 3E). As in first zoea.

Mandibles (Figure 3F). As in first zoea.

Maxillule (Figure 3G). Basial endite with two simple submarginal setae and four strong teeth alternately fused and articulated, each tooth with several small spines. Otherwise as in first zoea.

Maxilla (Figure 3H). Endopod and coxal and basial endites as in first zoea. Scaphognathite with six or seven short plumose setae.

Maxilliped 1 (Figure 3I). Basis with 2+1+1+2+1+3 setae ventrally. Endopod, 5-segmented with 3+I, 2+I, 1+I, 2, 4+I plumose setae on segments 1–5, respectively. Exopod with seven terminal natatory setae.

Maxilliped 2 (Figure 3J). Basis setation and ventral setal formula of endopod as in first zoea. Dorsal margin of

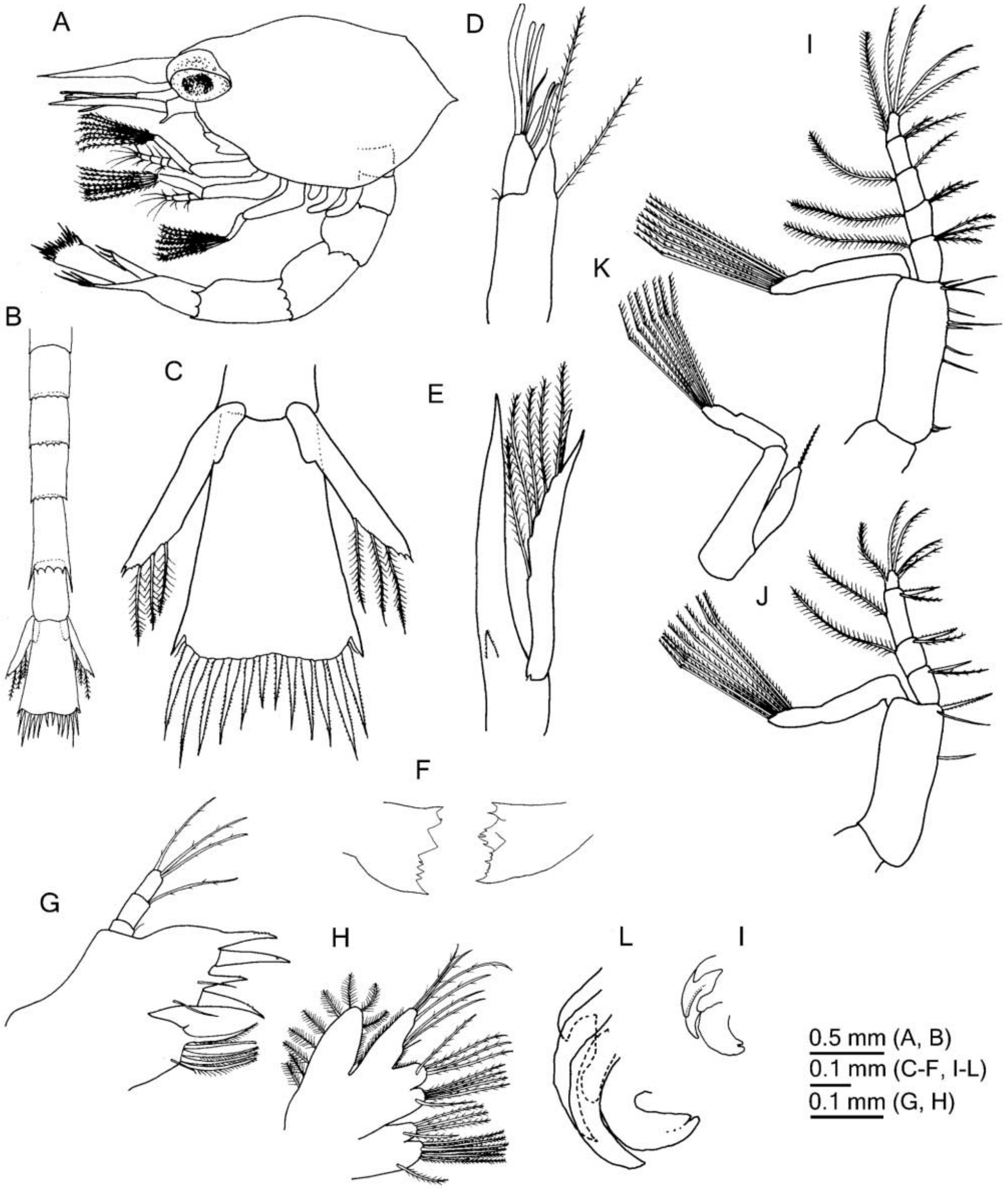

Figure 4. *Pagurus nigrofascia*. Third zoea. (A) Lateral view; (B) dorsal view of pleon; (C) telson; (D) antennule; (E) antenna; (F) mandibles; (G) maxillule; (H) maxilla; (I) maxilliped 1; (J) maxilliped 2; (K) maxilliped 3; (L) pereiopods; (l) pereiopods (ventral view).

endopod with one long plumose seta on segment 2 marginally, and on segment 3 submarginally. Exopod with seven terminal natatory setae.

Maxilliped 3 (Figure 3K). Exopod with six natatory setae. Endopod bud still fused but elongate, with one long terminal plumose seta.

Pereiopods (Figure 3L). Rudimentary and unarmed. Fifth pereiopod bud hidden from view by 1–4 pereiopod buds.

Third zoea

Size. CL=2.44–2.53 mm; mean=2.49 mm; SD=0.052; N=5.

Carapace (Figure 4A). Larger, but similar to second zoea.

Pleon (Figure 4B). Outmost pairs of spines on postero-dorsal margin of somite 2 reduced or absent. Posterolateral spines on somite 5 elongate. Somite 6 delineated from

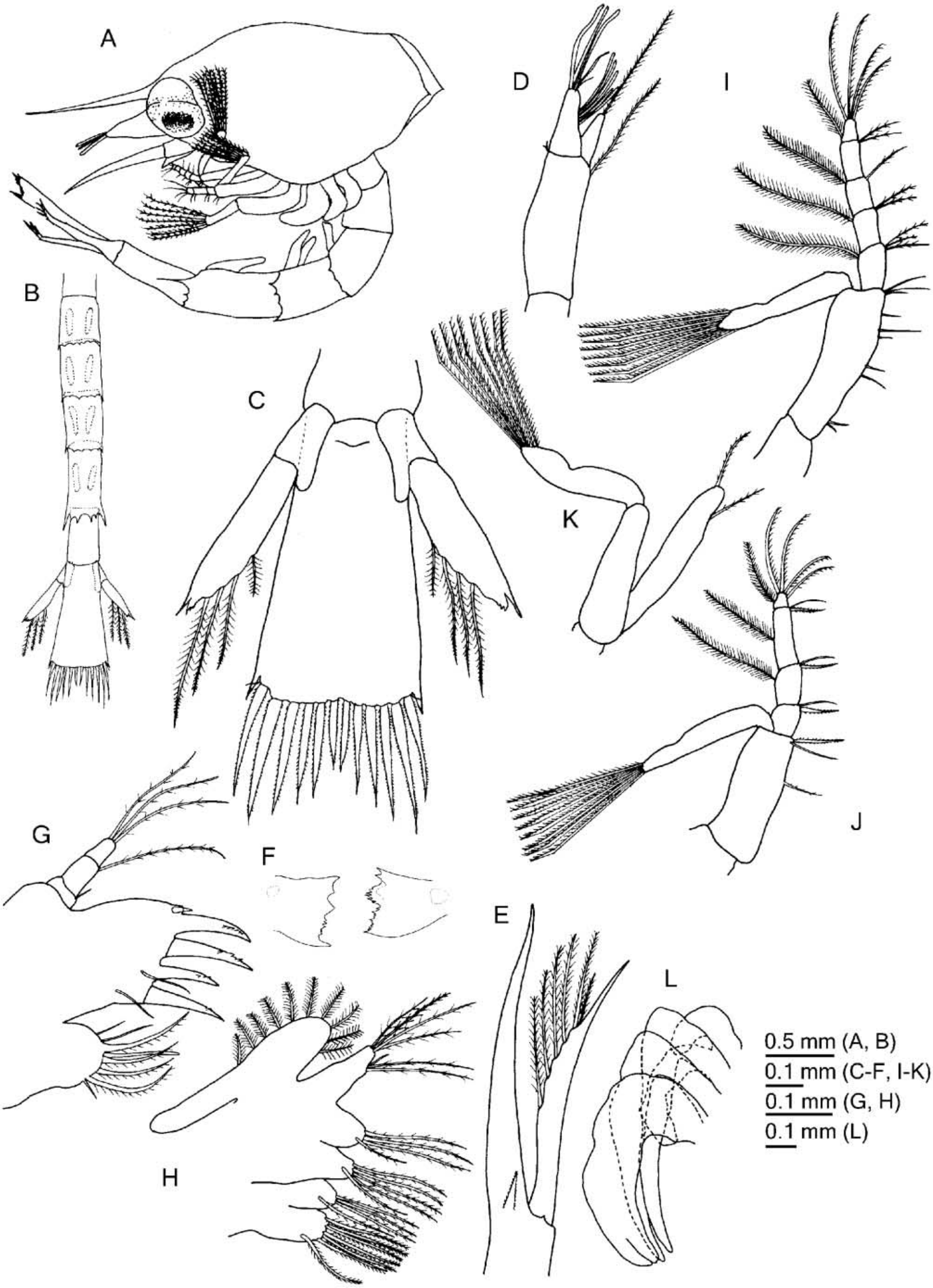

Figure 5. *Pagurus nigrofascia*. Fourth zoea. (A) Lateral view; (B) dorsal view of pleon; (C) telson; (D) antennule; (E) antenna; (F) mandibles; (G) maxillule; (H) maxilla; (I) maxilliped 1; (J) maxilliped 2; (K) maxilliped 3; (L) pereiopods; (l) pereiopods (ventral view).

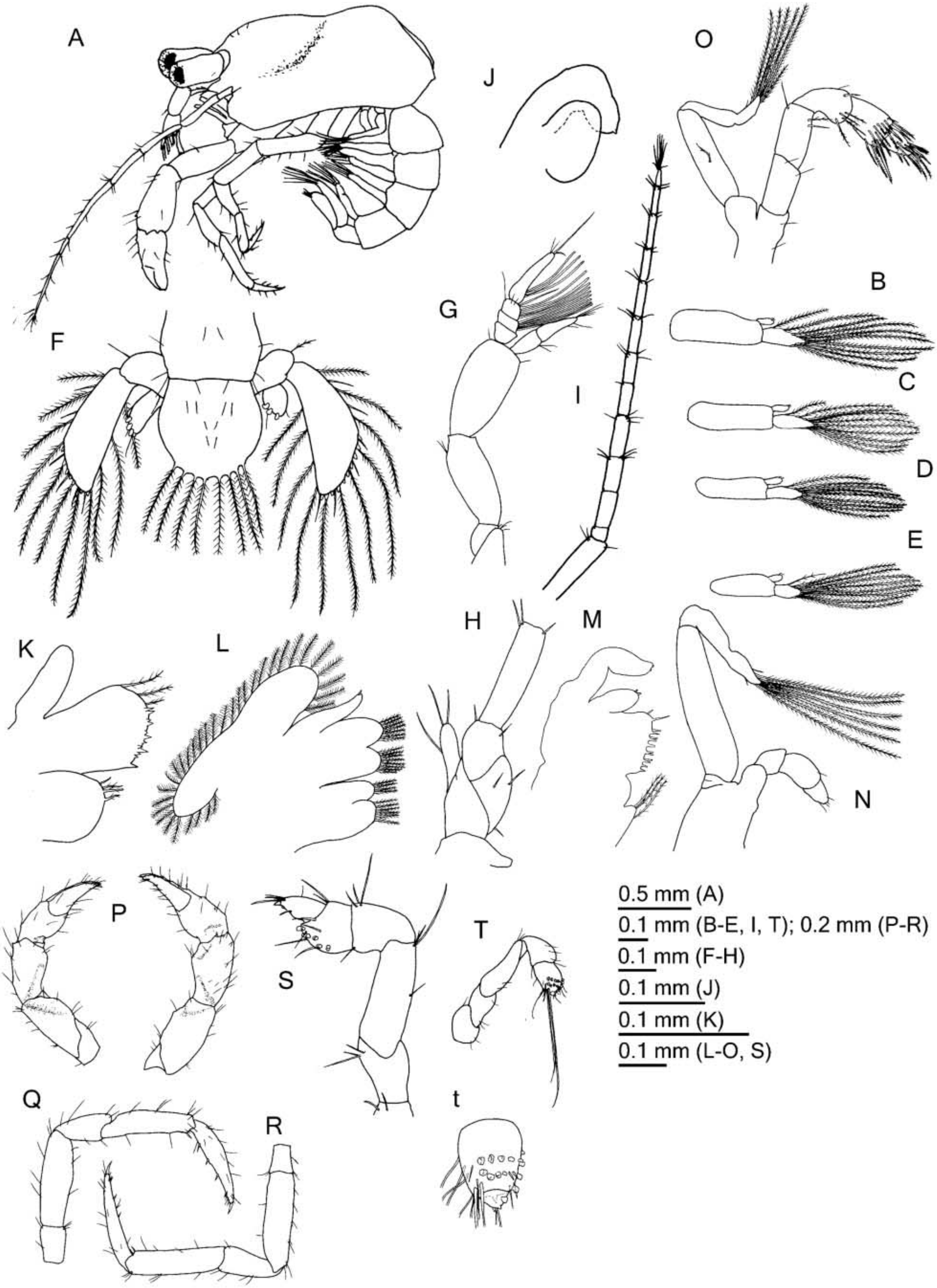

Figure 6. *Pagurus nigrofascia*. Megalopa. (A) Lateral view; (B–E) pleopods 2–5; (F) telson and uropods; (G) antennule; (H) antenna; (I) antennae flagellum; (J) mandible; (K) maxillule; (L) maxilla; (M) maxilliped 1; (N) maxilliped 2; (O) maxilliped 3; (P) chelipeds; (Q) pereiopod 2; (R) pereiopod 3; (S) pereiopod 4; (T) pereiopod 5; (t), detail of dactylus and propodus of the pereiopod 5.

somite 5, posterodorsal margin with no spines. Uropods emerging ventrally from somite 6, with two or three terminal spines and three plumose setae on inner margin. Endopod bud of uropod present.

Telson (Figure 4C). Anal spine absent.

Antennule (Figure 4D). Exopod separated from protopod, with three marginal and two submarginal aesthetascs and two or three terminal setae. Protopod with one or two marginal setules. Endopod with one long plumose marginal seta and one long plumose submarginal seta on endopodal junction.

Antenna (Figure 4E). Small spine at base of exopod.

Mandibles (Figure 4F). As in second zoea.

Maxillule (Figure 4G). As in second zoea.

Maxilla (Figure 4H). Endopod and coxal and basial endite as in second zoea. Scaphognathite with 9–11 short plumose setae.

Maxilliped 1 (Figure 4I). As in second zoea.

Maxilliped 2 (Figure 4J). Basis and endopod setation as in second zoea. Exopod with eight terminal natatory setae.

Maxilliped 3 (Figure 4K). Endopod longer and separated from protopod. Exopod with seven terminal natatory setae.

Pereiopods (Figure 4L). Elongate, pereiopod 1 weakly chelate at tip.

Fourth zoea

Size. CL=2.73–2.94 mm; mean=2.87 mm; SD=0.085; N=5.

Carapace (Figure 5A). Larger, but similar to third zoea.

Pleon (Figure 5B). Naked pleopods on somites 2–5. Somite 6 with 2-segmented uropods. Exopod of uropod with one long terminal spine and two or three small spines, three or four plumose setae on inner margin.

Telson (Figure 5C). As in third zoea.

Antennule (Figure 5D). Endopod elongate. Exopod with three marginal and five submarginal aesthetascs and 1–3 terminal setae. Protopod with 1–4 marginal setules. Otherwise as in third zoea.

Antenna (Figure 5E). As in third zoea.

Mandibles (Figure 5F). Palp bud present, otherwise as in third zoea.

Maxillule (Figure 5G). Endopod as in third zoea. Coxal endite with four plumose, one simple marginal setae and three short simple setae. Basial endite with two simple submarginal setae, four strong teeth alternately fused and articulated, each tooth with several small spines, and zero or one small terminal tooth.

Maxilla (Figure 5H). Endopod and exopod as in third zoea. Posterior lobe of scaphognathite developed. Scaphognathite with 10–14 short plumose setae marginally.

Maxilliped 1 (Figure 5I). Basis and endopod setation as in third zoea. Exopod with eight terminal natatory setae.

Maxilliped 2 (Figure 5J). As in third zoea.

Maxilliped 3 (Figure 5K). Endopod elongate, with one marginal and one submarginal plumose setae. Exopod with eight terminal natatory setae.

Pereiopods (Figure 5L). Development greater than by first to third zoea, but segmentation incomplete and segments indistinct. Pereiopod 1 clearly chelate.

Megalopa

Size. CL=1.37–1.47 mm; mean=1.42 mm; SD=0.035; N=5. SL=0.87–0.91 mm; mean=0.88 mm; SD=0.020; N=5.

Carapace (Figure 6A). Surface smooth. Shield approximately two-thirds total carapace length, usually as long as wide. Rostrum well developed and triangular. Ocular peduncles large, ocular acicles small.

Pleon (Figure 6A). Six somites, with no spines and sparsely covered with short setae. Somite 2–5 each with pair of pleopods. Somite 6 with a pair of uropods.

Pleopods (Figure 6B–E). Biramous, well developed. Exopod of pleopods on pleonal somites 2–5 with 9–11, 9 or 10, 9 or 10, 9 marginal long plumose setae, respectively. Each endopod with two marginal hooks.

Telson and uropods (Figure 6F). Telson with several pairs of short setae, and posterior margin rounded with four pairs of long terminal plumose setae. Uropods approximately symmetrical. Each uropod biramous, protopod with one seta on dorsal surface. Endopods very short, right endopod with two short marginal setae and four or five corneous scales, left endopod with two short marginal setae and three or four corneous scales. Exopods well-developed, right exopod with 8–10 corneous scales on outer margin, and with 8–11 long plumose and 6–8 short simple marginal setae, left exopod with 8–11 corneous scales on outer margin, and with 10–12 long plumose and 5–7 short simple marginal setae.

Antennule (Figure 6G). Biramous. Peduncle 3-segmented. Endopod slender, 2-segmented, with two or three setae on the proximal segment and seven or eight setae on the distal segment. Exopod 4-segmented, segments 2–4 with 5 or 6, 4, 3 aesthetascs, respectively. Segment 3 with four simple marginal setae, one longer, between aesthetascs. Segment 4 longer than total length of segments 1–3, with four terminal setae, one markedly longer.

Antenna (Figure 6H&I). Peduncle 4-segmented, distal segment longer. Flagellum 11 or 12-articulated, each with several short marginal setae. Exopod with two marginal and one submarginal setae.

Mandibles (Figure 6J). Palp greatly developed but unsegmented and with no spines and setae. Mandibular plate simplified.

Maxillule (Figure 6K). Endopod unsegmented. Coxal endite with four or five setae. Basial endite with 2–4 plumose setae and 10–12 minute smooth spines.

Maxilla (Figure 6L). Endopod unsegmented, with one stubby terminal seta. Coxal endite with 4–6 marginal setae on proximal lobe, four marginal setae on distal lobe. Basial endite with 7–9 marginal setae on proximal lobe, 6–8 marginal setae on distal lobe. Scaphognathite well-developed, with 30–36 marginal plumose setae.

Maxilliped 1 (Figure 6M). Endopod unsegmented. Exopod weakly 2-segmented, with 1–7 terminal stubby setae. Coxal endite with 3–4 marginal setae. Basial endite broad, with 13–14 marginal setae.

Maxilliped 2 (Figure 6N). Endopod 4-segmented, segment 4 with 3–5 short terminal setae. Exopod 2-segmented, distal segment with six plumose and two short simple setae.

Maxilliped 3 (Figure 6O). Endopod 5-segmented, all segments with numerous setae, setae of distal and

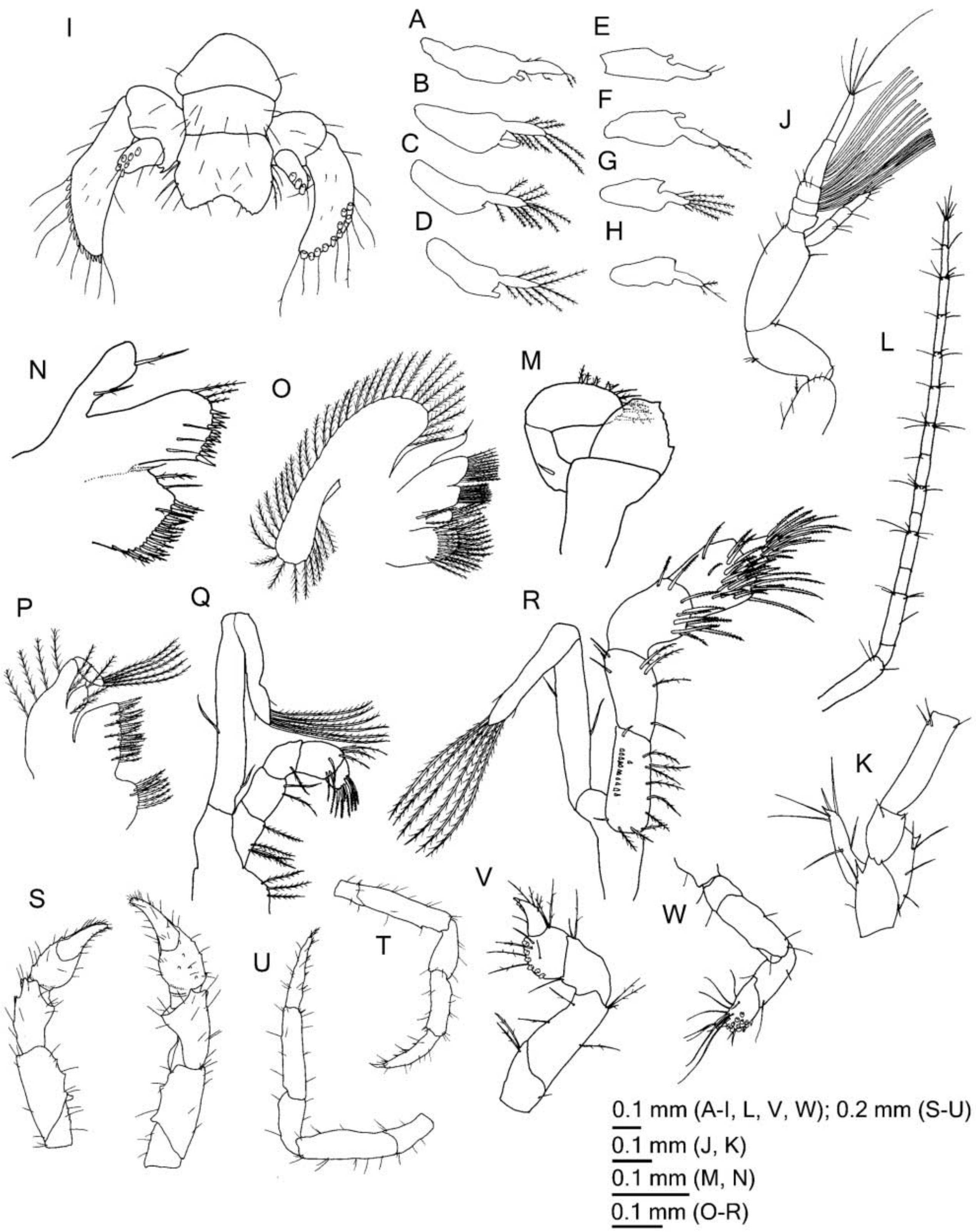

Figure 7. *Pagurus nigrofascia*. Crab 1. (A–D) Left pleopods 2–5; (E–H) right pleopods 2–5; (I) telson and uropods; (J) antennule; (K) antenna; (L) antennae flagellum; (M) mandible; (N) maxillule; (O) maxilla; (P) maxilliped 1; (Q) maxilliped 2; (R) maxilliped 3; (S) chelipeds; (T) pereiopod 2; (U) pereiopod 3; (V) pereiopod 4; (W) pereiopod 5.

https://doi.org/10.1017/S0025315406014445 Published online by Cambridge University Press

Table 1. *Comparison of morphological features of larvae and postlarvae of 8* Pagurus *species.*

Species	*P. nigrofascia*	*P. samuelis*	*P. filholi*	*P. hirsutiusculus*	*P. venturensis*	*P. ochotensis*	*P. kennerlyi*	*P. pectinatus*
References	this study	[1]	[2], [3]	[4]	[5]	[6]	[7]	[8]
Zoea								
Carapace								
posterolateral spines	short	short	short	short	short	short	long	short
Antenna, exopod marginal setae	6	5	6 (Z1)	5 (Z1, Z3, Z4) 5–6 (Z2)	3–4 (Z1 , Z3, Z4) 4 (Z2)	7 (Z1) 8 (Z2–4)	5–6 (Z1, Z2) 6–7 (Z3, Z4)	6
Maxillule, endopod setal formula								
Zoea 1	1, 1, 3	0, 1, 3	1, 1, 3 [3]	0–1, 1, 3	0–1, 1, 3	2, 1, 3	0–2, 1, 3	2, 1, 3
Zoea 2	1, 1, 3	0, 1, 3	–	0, 1, 3	0–1, 1, 3	2, 1, 3	1–2, 1, 3	2, 1, 3
Zoea 3	1, 1, 3	0, 1, 3	–	0, 1, 3	0–1, 1, 3	2, 1, 3	1–2, 1, 3	2, 1, 3
Zoea 4	1, 1, 3	0, 1, 3	–	0, 1, 3	0–1, 1, 3	2, 1, 3	1–2, 1, 3	2, 1, 3
Maxilla, coxal endite proximal lobe setae	6+1	4	5 (Z1) [3]	4 (rarely 3)	4 (Z1, Z2) 5 (Z3, Z4)	7	6–7 (Z1) 6+1 (Z2–4)	6+1
Maxilliped 1								
coxal setae	0	–	–	0	0	–	0	1
basal setae	9–10 (Z1) 10 (Z2–4)	8–9	9 (Z1) [3]	8–9	8–9	9 (Z1) 9–10 (Z2) 10 (Z3, Z4)	8–10	10
Maxilliped 3, endopod setae								
Zoea 1	0	0	0 [3]	0	0	0	0	0
Zoea 2	1	0	–	1	1	1	2	1
Zoea 3	1	1	–	1	1	1	2	1
Zoea 4	2	2	–	2	2	2	3	2
Megalopa								
Telsonal processes	4+4	8	8 [2]	3+3	3+3	8	4+4	4+4
Antennal articles of flagellum	11–12	10	10 [2]	12–13	10	21	14	12
Mandibular exopod	0	4	–	2–4	7–8	6	6	4–5
Maxilla, scaphognathite	30–36	27	–	28–35	32–33	40–41	35–38	37–40
Crab 1								
Antennal articles of flagellum	12–14	–	10 [2]	–	10–11	–	16	–

[1] MacMillan, 1971; [2] Kurata, 1968; [3] Konishi & Quintana, 1988; [4] McLaughlin et al., 1988; [5] Crain & McLaughlin, 1993; [6] Quintana & Iwata, 1987; [7] McLaughlin et al., 1989; [8] Kim & Hong, 2005.
Z1–Z4 indicate first to fourth zoea, respectively.

penultimate segments often serrated. Exopod 2-segmented, proximal segment with one seta medially, distal segment with six plumose and two short simple setae.

Pereiopods (Figure 6P–T). Well-developed, segmented, covered with scattered setae. Right cheliped larger than left cheliped. Pereiopods 2–3 generally similar; dactyls with row of four or five corneous spinules on inner margin; propodi with one or two corneous spinules on ventrodistal margin and often with an additional submarginally spinule. Pereiopod 4 with five or six scales on propodus, dactyls triangular, with two spinules on inner margin. Pereiopod 5 with 13–16 scales and two extremely long setae on propodus, dactyls with two scales terminally.

Crab 1

Size. SL=0.86–0.93 mm; mean=0.90 mm; SD=0.025; N=5.

Carapace. Shield surface with several rows of short simple setae. Rostrum well-developed and triangular, with terminal spinule. Ocular peduncles similar to megalopa, but ocular acicles well-developed and distinct.

Pleon. Six somites and telson. With no spines and with scattered setae on dorsal and lateral surface. Somites 2–5 with a pair of pleopods on ventrodistal margins. Segmentation becoming obscured.

Pleopod (Figure 7A–H). Right pleopods more degenerated than left pleopods. Endopods reduced or often absent. Exopods of right pleopods 2–5 with 0–3, 1–7, 0–9, 0–4 setae, respectively, marginally, whereas exopods of left pleopods 2–5 with 0–7, 9 or 10, 9 or 10, 8 or 9 setae, respectively, marginally.

Telson and uropods (Figure 7I). Telson with scattered pairs of short setae on dorsal surface, and four pairs of small spinules on posterior margin. Terminal edge of telson concave. Left uropod larger than right. Each uropod

https://doi.org/10.1017/S0025315406014445 Published online by Cambridge University Press

biramous. Protopods with scattered setae. Right endopod with two short marginal setae and five or six corneous scales, left endopod with two short marginal setae and 6–8 corneous scales. Right exopod with 11 or 12 corneous scales on outer margin, with 10–12 marginal setae, left exopod with 13–16 corneous scales on outer margin, with 9–12 marginal setae.

Antennule (Figure 7J). Biramous. Endopod 3-segmented, with 2 or 3, 0 or 1, 7 or 8 setae on segments 1–3, respectively. Exopod 5-segmented, with 5–7, 5, 4 aesthetascs on segments 2–4, respectively. Segment 3 with four simple marginal setae, one longer, between the aesthetascs. Segment 5 with four short and one markedly long terminal setae.

Antenna (Figure 7K&L). Peduncle 4-segmented, with spines and with more setae than the megalopa. Flagellum 12–14-articulated, each with several short marginal setae.

Mandibles (Figure 7M). Palp 2-segmented, proximal segment with one short simple seta, distal segment with 9–11 short marginal plumose setae. Mandibular plate margin slightly indentated compared with megalopa.

Maxillule (Figure 7N). Endopod with one marginal and one submarginal setae. Coxal endite with 13–16 marginal or submarginal plumose setae and 1–3 plumose setae on inner margin. Basial endite with two or three plumose setae and 13–16 teeth marginally, three submarginal setae, and one plumose seta on inner margin.

Maxilla (Figure 7O). Endopod with a simple terminal seta. Coxal endite with 7–9 marginal and 11–12 submarginal setae on proximal lobe, four or five marginal and three submarginal setae on distal lobe. Basial endite with 9–11 marginal setae on proximal and distal lobes. Scaphognathite with 35–41 marginal plumose setae.

Maxilliped 1 (Figure 7P). Exopod 2-segmented, proximal segment with 2–4 plumose setae on outer margin and 0–2 on inner margin, distal segment with five plumose terminal setae. Endopod with 0–4 plumose setae. Coxal endite with 7–9 plumose setae, either marginal or submarginal. Basial endite with 12–16 marginal plumodenticulate and 5–9 submarginal plumose setae.

Maxilliped 2 (Figure 7Q). Endopod 5-segmented, with setae as illustrated, setae on segments 4 and 5 serrate. Exopod 2-segmented, proximal segment with one simple seta on inner and outer margin respectively, but sometimes absent, distal segment with five or six long plumose terminal setae and two short simple setae.

Maxilliped 3 (Figure 7R). Endopod with numerous setae compared with megalopa. Segment 1 with crista dentata of 11 or 12 teeth. Exopod 2-segmented, proximal segment with one simple seta on inner and outer margin, distal segment with six long plumose setae and two short simple setae.

Pereiopods (Figure 7S–W). Cheliped with numerous spines compared with megalopa. Merus of each cheliped with one or two strong spines on ventroproximal margin. Pereiopods 2 and 3 as megalopa. Pereiopod 4 with 4–6 scales on propodus, dactyls with 2–4 spinules on inner margin. Pereiopod 5 with 13–19 scales on propodus, dactyls with one marginal and three submarginal scales.

DISCUSSION

Larvae of *Pagurus nigrofascia* had a low survival rate at 6°C and 25°C. We reared ovigerous females at 12°C and transferred newly hatched larvae to each temperature condition within 24 h. Thus the survival of larvae could be influenced by the rapid change in water temperature. This influence would be strong especially at 25°C because larval mortality within the first two days was extremely high, however, at the other temperature conditions, the influence would be less marked because larval early mortalities just after changing water temperature were low. Larvae had a high survival rate until the fourth zoeal stage at 6°C, and almost all died around the moult to megalopa. This suggests that some other factor, for example the sensitivity of fourth zoea or megalopa to low temperature, led to the low survival rate of *P. nigrofascia* larvae at 6°C. Meanwhile the larvae kept at the higher temperatures had higher survival rates. Under natural conditions, *P. nigrofascia* hatches from January to February in Hokkaido (Goshima et al., 1996) and settles in April and May (Oba & Goshima, 2004). The lowest water temperature in this region is about 6°C in February and March, and then the temperature increases to about 10°C in April (Oba & Goshima, 2004). Early stages of zoeae were expected to experience extremely low temperatures (about 6–10°C) but they showed high survival at 6°C until third zoeae. The fourth zoeae and megalopae showed low survival at 6°C, however, water temperature could be expected to rise to about 10°C about the time the larvae were ready to moult to zoeal stage four or megalopae in natural conditions. Possibly the early larval stages are more adapted to tolerate low temperatures and develop to later stages with the increase in water temperature.

Under low temperature conditions, it should take a longer time for larval development thus survival rate of larvae could decrease. Megalopae of hermit crabs, however, need empty shells of gastropods when they settle. Thus, it would be advantageous to acquire empty shells so they can settle earlier than other hermit crabs. Five Paguridae distribute in this study site: *P. nigrofascia*, *P. filholi*, *P. middendorffii*, *P. lanuginosus*, and *P. proximus*. Their larvae settle into the intertidal area from April to December (Oba & Goshima, 2004). *Pagurus nigrofascia* and *P. middendorffii* release zoeae in winter (Wada et al., 1995; Goshima et al., 1996) and recruit into the intertidal shore early in the settlement season (Oba & Goshima, 2004). The benefits of the early settlement to survival could compensate for the effects of their long pelagic period.

The low temperature during the dispersal stage could also affect their spatial distribution. It is difficult to apply the results from laboratory conditions to predict natural events directly, however, we can expect larvae would spend a long time, more than 1–2 months in approximately 6°C temperature conditions as pelagic larvae (Figure 1). The length of time marine invertebrate larvae remain in the pelagic correlates with dispersal distance (e.g. Todd, 1998; Shanks et al., 2003; Siegel et al., 2003), this means larvae of *P. nigrofascia* could have potential to disperse over tens or hundreds of kilometres.

Pagurid larvae may be divided into four groups (A–D) based on morphology (Roberts, 1970). *Pagurus nigrofascia* is assigned to Group A (including *bernhardus*, *pubescens*) which are characterized by: (1) body elongate and telson narrow; (2) lateral spines on pleonal somite 5 elongate; (3) sixth pleonal somite without dorsomedian spine of the fourth zoeal stage; (4) telson process 4 fused and elongate (>1/2 telson width); (5) no setae on endopod of antenna; (6) exopod of antenna straight and narrow (longer than 6×width); (7) less or equal eight setae on inner margin of exopod of antenna; (8) mandibular palp of the fourth zoeal stage present; and (9) no setae on endopod of uropod. However, articulated telson process 4 occurs in some other *Pagurus* species regarded as Group A (e.g. Konishi & Quintana, 1987; Quintana & Iwata, 1987; McLaughlin et al., 1988, 1989; Kornienko & Korn, 2006). As in these species, telsonal process 4 of zoeae in *P. nigrofascia* articulates with the telson.

In this study, we referred and compared larval morphological features of four species in which the adult morphological features closely resemble *P. nigrofascia* (Table 1). Almost all of them are categorized as Group A. Descriptive information is limited for *P. filholi*. It is, however, possible to distinguish *P. nigrofascia* zoeal stages from the other resemblant species by the following morphological features; *Pagurus nigrofascia* has a proximal lobe on the coxal endite of maxilla with six marginal +1 submarginal setae and the basis of maxilliped 1 with ten setae for the second to fourth zoeae (Table 1). These morphological features enable us to distinguish *P. nigrofascia* from many other *Pagurus* species distributed around Japan: *P. middendorffii*, *P. lanuginosus*, *P. brachiomastus*, *P. minutus*, *P. similis* and *P. proximus* (Hong, 1969, 1981; Lee & Hong, 1970; Konishi & Quintana, 1987, 1988; Kornienko & Korn, 2006).

Zoeal morphological features of *P. nigrofascia* are very close to other *Pagurus* species: *P. ochotensis*, *P. kennerlyi* and *P. pectinatus*. We compared and identified them from the *P. nigrofascia* (Table 1). Zoeae of *P. nigrofascia* can be distinguished from *P. ochotensis* by marginal setae on exopod of antenna: five plumose and one simple marginal setae on exopod of antenna on *P. nigrofascia*, but seven plumose setae at first zoea and eight plumose setae for the second to fourth zoeae on *P. ochotensis*. The endopod of the antenna of *P. ochotensis* second to fourth zoeae is clearly longer than the exopod. One seta occurs on the proximal segment of the endopod of maxillule in *P. nigrofascia*, whereas two occur in *P. ochotensis* (Quintana & Iwata, 1987). The difference between *P. nigrofascia* and *P. kennerlyi* is the length of posterolateral marginal spines of carapace. The spines of *P. kennerlyi* are moderately long. From second to fourth zoeae, the numbers of setae on the endopod of third maxilliped differ among species. For the second and third zoeae, *P. nigrofascia* has one terminal seta, whereas *P. kennerlyi* has two. The fourth zoea, *P. nigrofascia* has one terminal and one subterminal seta, whereas *P. kennerlyi* has three terminal setae. Additionally the fourth zoea, *P. nigrofascia* has four or five strong teeth on the basial endite marginally on maxillule, whereas *P. kennerlyi* has six (McLaughlin et al., 1989). *Pagurus pectinatus* has maxilliped 1 with a seta on coxa and maxillule with two setae on proximal segment of endopod. Furthermore in *P. pectinatus* the outermost spine of telsonal process is clearly articulated. The third zoea, *P. nigrofascia* has one plumose seta at endopodal junction of the antennule, whereas for *P. pectinatus* there are two plumose setae there. The fourth zoea, *P. pectinatus* has six marginal teeth on the maxilla as shown in *P. kennerlyi*.

In the megalopal stage, we can identify *P. nigrofascia* among all resemblant species from the morphological features as follows (Table 1). Megalopa of *P. nigrofascia* has telson with four pairs of plumose setae on posterior margin, flagellum of antenna with 11–12 articles, the scaphognathite of the maxilla with 30–36 marginal setae and the palp of mandible with no spines or setae.

In crab 1 stage, just 12–14-articulated flagellum of antenna characterizes *P. nigrofascia* among the resemblant species (Table 1). It could be one of the characteristics for species identification among the invoked species, however, it should be inadequate to characterize *P. nigrofascia* universally in the future. The number of setae, scales, and articles on crab 1 show a larger intraspecific variation, especially of the articles of the antennule flagellum, marginal setae and scales on the exopod of uropod, marginal setae on scaphognathite of the maxilla, and scales of the pereiopod 5 propodus than megalopa. Their ranges overlapped among different species and consequently these characters were more difficult to use for species identification than for the megalopal stage. Adult characters, for example, spine on cheliped, may be more useful for species identification of crab 1, although their morphological features are sometimes unclear. *Pagurus nigrofascia* has chelipeds with one strong spine on the ventroproximal margin of the merus, which is also clear on adult crab *P. nigrofascia* (Komai, 1996) and *P. filholi* (as *P. geminus* McLaughlin, 1976). Morphological features of the cheliped usually show interspecific differences among adult crabs of *Pagurus* species and can be used to distinguish *P. filholi*, for example, from other *Pagurus* species in Japan (Miyake, 1978). As far as comparing with only sympatric species in southern Hokkaido, *P. nigrofascia*, *P. filholi*, *P. middendorffii*, *P. lanuginosus* and *P. proximus*, the merus of cheliped could be one of the characters to distinguish crab 1 of *P. nigrofascia* (T. Oba, personal observation). However, the comparable studies which include descriptions for crab 1 stage are still remarkably few.

Morphological features of *P. nigrofascia* zoea and megalopa are characterized among *Pagurus* species as described above. At present, however, the larval morphological descriptions of *Pagurus* are still inadequate. Furthermore, studies describing the morphological features of crab 1 are still lacking and this lack of data on which to base field surveys precludes the ecological assessment of this important stage in the life cycle, especially for hermit crab communities where there is interspecific competition for resources. Further descriptions for this stage, including any new points of view for species identification, are clearly required.

We thank T. Komai, S. Wada, K. Yoshino, A. Mima, and A.S. Ilano for suggestions on this study. The members of the Benthos Group, Laboratory of Marine Biodiversity, Hokkaido University kindly checked the manuscript and helped us with the field sampling and experiment.

REFFERENCES

Crain, J.A. & McLaughlin, P.A., 1993. Larval, postlarval, and early juvenile development in *Pagurus venturensis* Coffin, 1957 (Decapoda: Anomura: Paguridae) reared in the laboratory, with a redescription of the adult. *Bulletin of Marine Science*, **53**, 985–1012.

Goshima, S., Wada, S. & Ohmori, H., 1996. Reproductive biology of the hermit crab *Pagurus nigrofascia* (Anomura: Paguridae). *Crustacean Research*, **25**, 86–92.

Hong, S.Y., 1969. The larval development of *Pagurus lanuginosus* de Haan (Crustacea, Anomura) reared in the laboratory. *Bulletin of the Korean Fisheries Society*, **2**, 1–15.

Hong, S.Y., 1981. The larvae of *Pagurus dubius* (Ortman) (Decapoda, Paguridae) reared in the laboratory. *Bulletin of National Fisheries, University of Busan*, **21**, 1–11.

Kim, M.H. & Hong, S.Y., 2005. Larval development of *Pagurus pectinatus* (Stimpson) (Decapoda: Anomura: Paguridae) reared in the laboratory. *Invertebrate Reproduction and Development*, **47**, 91–100.

Komai, T., 1996. *Pagurus nigrofascia*, a new species of hermit crab (Decapoda: Amonura: Paguridae) from Japan. *Crustacean Research*, **25**, 59–72.

Konishi, K. & Quintana, R., 1987. The larval stages of *Pagurus brachiomastus* (Thallwitz, 1892) (Crustacea: Anomura) reared in the laboratory. *Zoological Science*, **4**, 349–365.

Konishi, K. & Quintana, R., 1988. The larval stages of three pagurid crabs (Crustacea: Anomura: Paguridae) from Hokkaido, Japan. *Zoological Science*, **5**, 464–482.

Kornienko, E.S. & Korn, O.M., 2006. The larval development of *Pagurus proximus* (Decapoda: Anomura: Paguridae) reared in the laboratory. *Journal of the Marine Biological Association of the United Kingdom*, **86**, 369–381.

Kurata, H., 1968. Larvae of Decapoda Anomura of Arasaki, Sagami Bay-I *Pagurus samuelis* (Stimpdon) (Paguridae). *Bulletin of the Tokai Regional Fisheries Research Laboratory*, **55**, 265–269.

Lee, B.D. & Hong, S.Y., 1970. The larval development and growth of decapod crustaceans of Korean waters. II. *Pagurus similis* Ortman (Paguridae, Anomura). *Publications of the Marine Laboratory, Pusan Fisheries College*, **3**, 13–26.

MacMillan, F.E., 1971. The larvae of *Pagurus samuelis* (Decapoda: Anomura) reared in the laboratory. *Bulletin of the Southern California Academy of Sciences*, **70**, 58–68.

McLaughlin, P.A., 1976. A new Japanese hermit crab (Decapoda, Paguridae) resembling *Pagurus samuelis* (Stimpson). *Crustaceana*, **30**, 13–26.

McLaughlin, P.A., Gore, R.H. & Buce W.R., 1989. Studies on *Provenzanoi* and other Pagurid groups: III. The larval and early juvenile stages of *Pagurus kennerlyi* (Stimpson) (Decapoda: Anomura: Paguridae) reared in the laboratory. *Journal of Crustacean Biology*, **9**, 626–644.

McLaughlin, P.A., Gore, R.H. & Crain, J.A., 1988. Studies on *Provenzanoi* and other Pagurid groups: II. A reexamination of the larval stages of *Pagurus hirsutiusculus hirsutiusculus* (Dana) (Decapoda: Anomura: Paguridae) reared in the laboratory. *Journal of Crustacean Biology*, **8**, 430–450.

Miyake, S., 1978. *The crustacean Anomura of Sagami Bay*. Tokyo: Hoikusha.

Oba, T. & Goshima, S., 2004. Temporal and spatial settlement patterns of sympatric hermit crabs and the influence of shell resource availability. *Marine Biology*, **144**, 871–879.

Quintana, R. & Iwata, F., 1987. On the larval development of some hermit crabs from Hokkaido, Japan, reared under laboratory conditions (Decapoda: Anomura). *Journal of the Faculty of Science, Hokkaido University. Series VI, Zoology*, **25**, 25–85.

Roberts, M.H., 1970. Larval development of *Pagurus longicarpus* Say reared in the laboratory. I. Description of larval instars. *Biological Bulletin. Marine Biological Laboratory, Woods Hole*, **139**, 188–202.

Shanks, A.L., Grantham, B.A. & Carr, M.H., 2003. Propagule dispersal distance and the size and spacing of marine reserves. *Ecological Applications*, **13**, S159–S169.

Siegel, D.A., Kinlan, B.P., Gaylord, B. & Gaines, S.D., 2003. Lagrangian descriptions of marine larval dispersion. *Marine Ecology Progress Series*, **260**, 83–96.

Todd, C.D., 1998. Larval supply and recruitment of benthic invertebrates: do larvae always disperse as much as we believe? *Hydrobiologia*, **375/376**, 1–21.

Wada, S., Goshima, S. & Nakao, S., 1995. Reproductive biology of the hermit crab *Pagurus middendorffii* Brandt (Decapoda: Anomura: Paguridae). *Crustacean Research*, **24**, 23–32.

Submitted 21 March 2006. Accepted 26 September 2006.