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Larval development of *Pandalus gracilis* Stimpson (Crustacea: Decapoda: Pandalidae) reared in the laboratory

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Abstract

The complete larval development of *Pandalus gracilis* Stimpson is described based on larvae reared in the laboratory. The species has four larval stages (stages 1–4) and one postlarval stage (stage 5). The survival rate of the postlarva stage is very high. Of the 40 larvae reared individually, 39 larvae moulted to the postlarva stage within approximately 21 days at a rearing temperature of 15°C. Larval morphological characteristics of the species are described and figured. Larval development of *P. gracilis* is compared with other *Pandalus* and *Pandalopsis* species. Komai (1999) divided species of *Pandalus* into four species groups based on adult morphology. *Pandalus gracilis* belongs to the *P. hypsinotus* group. In this study, using larval characters, the *P. hypsinotus* group can be divided into two groups by the appearance of the mandibular palp and the shape of the telson: the first group contains *P. hypsinotus* and *P. danae*, and the second group contains *P. gracilis*, *P. prensor*, and *P. nipponensis*.

Keywords: Abbreviated form, Crustacea, Decapoda, larval development, morphology, *Pandalopsis*, *Pandalus gracilis*

Introduction

The genus *Pandalus* contains 19 species, which are found at all depths on the continental shelf and slope in the northern hemisphere. Members of this genus are of commercial importance and of scientific interest because of their reproductive patterns. Most species within the genus are protandric hermaphrodites (Holthuis 1980; Komai 1999; Bergström 2000).

Pandalus gracilis Stimpson is usually found in the Korea Strait, East Sea (Japan Sea), Tsugaru Strait, and the Pacific coast of northern Japan at sublittoral to upper slope depths of 30–311 m (Komai 1999). The complete larval development of *Pandalus* has been described for the following 11 species: *P. jordani* by Rothlisberg (1980), *P. eous* by Kurata (1964), *P. borealis* by Haynes (1979), *P. goniurus* by Haynes (1978), *P. stenolepis* by Needler (1938), *P. hypsinotus* by Haynes (1976), *P. danae* by Berkeley (1930), *P. prensor* by

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Mikulich and Ivanov (1983), *P. nipponensis* by Taishaku et al. (2001), *P. platyceros* by Price and Chew (1972), and *P. latirostris* by Kurata (1955); *P. montagui* was described incompletely. However, no descriptions of the larval stages of *P. gracilis* have been published so far.

The present study provides a complete description of the larval development of *P. gracilis* based on laboratory-reared material. Since Berkeley (1930) classified the genera *Pandalus* and *Pandalopsis* based on the adult phase, Komai (1999) indicated that there was a close phylogenetic relationship between the *P. platyceros* group and *Pandalopsis* based on the adult phase. On the other hand, Christofferson (1989) suggested that *Pandalopsis* is a subordinate clade within the genus *Pandalus* by comparing the characters of larval morphology. In this study, we also compare the larvae of *P. gracilis* with those of other *Pandalus* and *Pandalopsis* species.

Materials and methods

An ovigerous female of *P. gracilis* was collected on 10 February 2001 using a shrimp trawl at Yongcho Island (34°30'N, 128°40'E), Tongyeong, Korea. The female was transported to the laboratory and kept in a 4-litre jar with aerated seawater. The diameter of eggs was $1.9\text{--}2.9 \times 1.3\text{--}1.9$ mm. Sixty-eight larvae hatched on 27 April 2001. Of these, 40 larvae were reared individually in 100 ml glass bottles placed in an incubator at 15°C and 33.7 psu. For drawing and descriptions, 28 larvae were reared in a 4-litre jar.

Larvae were fed with newly hatched *Artemia* nauplii each day. Moulting and mortality were recorded daily, and each day all larvae were transferred to fresh containers. At each stage, dead larvae and exuviae were fixed and preserved with 3% buffered formalin.

Four live specimens of each stage were dissected for observation. Drawings were made with a microscope equipped with a drawing tube. Measurements were made to the nearest 0.01 mm as follows: carapace length (CL), from the anterior tip of the rostrum to the postero-median carapace margin; total length (TL), from the anterior tip of the rostrum to the postero-median margin of the telson, excluding telson processes. At least 10 exuviae were measured using a calibrated ocular micrometer. The ovigerous female, the undissected larvae, and dissected appendages are deposited in NFRDI (National Fisheries Research and Development Institute, Busan, Korea).

Results

Duration and survival of the larvae

In the complete larval development of *Pandalus gracilis*, there are four larval stages and one postlarva stage. The duration of each larval stage and survival from an initial 40 larvae is shown in Figure 1. Of the 40 larvae reared individually, 39 larvae moulted to the postlarva stage within approximately 21 days.

Descriptions

Stage 1 (Figure 2). Size: CL=1.39 mm (1.30–1.53 mm); TL=5.72 mm (5.58–5.98 mm). Duration: 3.7 days (3–5 days, $n=40$).

Carapace (Figure 2A, B): rostrum short, spiniform, reaching middle part of eye, directed downward, without teeth. Carapace without spine, posterolateral margin rounded.

Figure 1. *Pandalus gracilis* Stimpson. Survival and duration of larval stages reared under laboratory conditions of 15°C and 33.7‰.

Eyes (Figure 2A, B): sessile at this stage.

Antennule (Figure 2C): uniramous; peduncle with a distal simple seta; flagellum with three aesthetascs distally.

Antenna (Figure 2D): biramous, well-developed. Antennal scale (=exopod) flattened, with 34–35 plumose setae and distolateral spine. Flagellum (=endopod) about five times as long as antennal scale, with numerous segments; each segment bearing from zero to three minute setae.

Mandible (Figure 2E): consisting of incisor and molar processes, without palp.

Maxillule (Figure 2F): coxal endite with three serrate and seven simple setae. Basal endite broad, with 10 simple spines and eight simple setae on mesial margin. Endopod with two short setae.

Maxilla (Figure 2G): bilobed, coxal and basal endites with 9+2 and 7+10 plumose setae, respectively. Endopod unsegmented, with two terminal setae. Exopod (=scaphognathite) with 38 plumose setae.

Maxilliped 1 (Figure 2H): endite with 19 short setae. Endopod unsegmented, with four setae. Exopod long, slender ramus with seven terminal plumose setae, and seven proximolateral plumose setae. Epipod bilobed.

Maxilliped 2 (Figure 2I): endopod four-segmented, with 3, 2, 1, 0 short setae. Exopod longer than endopod, with nine terminal plumose setae. Epipod rounded.

Maxilliped 3 (Figure 2J): endopod three-segmented. Exopod reaching beyond second segment of endopod, with eight terminal plumose setae.

Pereiopod 1 (Figure 2K): biramous, endopod three-segmented, minutely chelate; exopod unsegmented with eight terminal plumose setae.

Pereiopod 2 (Figure 2L, M): biramous, endopod five-segmented, chelate; exopod unsegmented with eight terminal plumose setae. Not symmetrical; left (Figure 2M) longer and thinner than right (Figure 2L).

Figure 2. *Pandalus gracilis* Stimpson, stage 1. (A) Dorsal view (scale bar: ab); (B) lateral view (ab); (C) antennule (ad); (D) antenna (ad); (E) mandibles (ae); (F) maxillule (ae); (G) maxilla (ae); (H) first maxilliped (ae); (I) second maxilliped (ae); (J) third maxilliped (ad); (K) right pereopod 2 (ac); (L–P) left pereopods 1–5 (ac); (Q) telson (ac). Scale bars: 1 mm.

Pereiopods 3–5 (Figure 2N–P): without exopod, seven-segmented as in adult form. Merus and ischium partly fused. All segments with numerous short setae. Each dactylus with three spines. Subdistal spine on lateral margin of merus of pereiopod 4 (Figure 2O).

Gills (Figure 2K–P): arthrobranch absent. Developed pleurobranch present on thoracic somites 4–8. Epipods present on pereiopods 1–4, with two to four setae, respectively.

Abdomen (Figure 2A, B, Q): dorsal surface of each somite smooth, without armature. Sixth somite with pair of blunt posterolateral spines.

Telson (Figure 2A, B, Q): distally rounded; posterior margin with 8+8 plumose setae, and numerous short setae on dorsal side.

Stage 2 (Figure 3). Size: CL=1.45 mm (1.33–1.56 mm); TL=6.56 mm (6.28–6.78 mm). Duration: 4.0 days (3–5 days, $n=40$).

Carapace (Figure 3A, B): rostrum well developed, straight, overreaching anterior margin of eye, about 0.8 times as long as carapace. Dorsal edge of rostrum and anterior part of carapace armed with 10–12 minute teeth. Antennal and pterygostomial spines on anterolateral margin.

Eyes (Figure 3A, B): stalked.

Antennule (Figure 3C): peduncle three-segmented, basal segment with rudimentary stylocerite; inner flagellum two-segmented, with two and three short setae. Outer flagellum four-segmented with 3, 3, 3, 3 aesthetascs on inner margin.

Antenna (Figure 3D): basis with small distolateral spine; antennal scale with 34 or 35 plumose setae.

Mandible (Figure 3E): mandibular palp present, but unsegmented. Incisor and molar processes well developed and distinctly separated by deep cleft.

Maxillule (Figure 3F): coxal endite with 16 serrate setae. Basal endite with 11 simple spines and 20 serrate setae on mesial margin. Endopod with two serrate setae.

Maxilla (Figure 3G): no remarkable change in shape. Coxal endite bilobed, with 9+1 serrate setae. Basal endite bilobed, with 9+16 serrate setae. Endopod unsegmented, with three setae. Scaphognathite with 44 plumose setae.

Maxilliped 1 (Figure 3H): endite with about 50 short setae. Endopod with five setae. Exopod with seven terminal plumose and seven lateral plumose setae.

Maxilliped 2 (Figure 3I): endopod three-segmented; exopod with nine terminal plumose setae.

Maxilliped 3 (Figure 3J): endopod with numerous short setae; exopod shorter than that of stage 1, not reaching middle of first segment of endopod, without terminal plumose setae.

Pereiopod 1 (Figure 3K): endopod four-segmented with numerous short setae; exopod reaching beyond distal margin of ischium.

Pereiopod 2 (Figure 3L): carpus of left pereiopod with five articulations, that of right with three articulations. Ischium, propodus, and dactylus with several short setae. Exopod falling short of distal margin of ischium.

Pereiopods 3–5 (Figure 3M–O): merus and ischium completely segmented.

Gills (Figure 3K–O): no remarkable change.

Abdomen (Figure 3B): fifth and sixth somites with pair of acute posterolateral spines.

Telson (Figure 3A, B, P): slightly longer and more slender than that of stage 1.

Stage 3 (Figure 4). Size: CL=1.65 mm (1.43–1.80 mm); TL=7.80 mm (6.93–8.58 mm). Duration: 5.1 days (4–6 days, $n=39$).

Figure 3. *Pandalus gracilis* Stimpson, stage 2. (A) Dorsal view (scale bar: ab); (B) lateral view (ab); (C) antennule (ac); (D) antenna (ac); (E) mandibles (ad); (F) maxillule (ad); (G) maxilla (ad); (H) first maxilliped (ad); (I) second maxilliped (ad); (J) third maxilliped (ac); (K–O) left pereopods 1–5 (ac); (P) telson (ac). Scale bars: 1 mm.

Figure 4. *Pandalus gracilis* Stimpson, stage 3. (A) Dorsal view (scale bar: ab); (B) lateral view (ab); (C) antennule (ad); (D) antenna (ad); (E) mandibles (ae); (F) maxillule (ae); (G) maxilla (ae); (H) first maxilliped (ae); (I) second maxilliped (ae); (J) third maxilliped (ad); (K–O) left pereopods 1–5 (ac); (P–T) pleopods 1–5 (ae); (U) telson (ac). Scale bars: 2 mm.

Carapace (Figure 4A, B): rostrum almost as long as carapace, and slightly curved upwards. Dorsal margin of rostrum and anterior part of carapace armed with 15–16 teeth; anterior-most tooth well separated from other spines. Ventral margin of rostrum with four teeth. Antennal and pterygostomian spines well developed.

Eyes (Figure 4A, B): no remarkable change.

Antennule (Figure 4C): stylocerite with small distal spine; inner flagellum four-segmented, with zero to five short setae; outer flagellum five-segmented, with 3, 3, 3, 2, 2 aesthetascs on inner margin.

Antenna (Figure 4D): basis with acute distolateral spine; antennal scale with 37–38 plumose setae.

Mandible (Figure 4E): palp three-segmented, distal segment with five serrate setae.

Maxillule (Figure 4F): coxal endite with 14 serrate setae. Basial endite with 10 simple spines and 18 serrate setae on mesial margin. No remarkable change in endopod.

Maxilla (Figure 4G): coxal endite bilobed, with 12+2 serrate setae. Basial endite bilobed, with 10+16 serrate setae. Endopod unchanged. Scaphognathite with 43 plumose setae.

Maxilliped 1 (Figure 4H): endite with about 40 short setae. Endopod with three setae. Exopod with seven terminal plumose and nine lateral plumose setae.

Maxilliped 2 (Figure 4I): endopod four-segmented; exopod with nine terminal plumose setae.

Maxilliped 3 (Figure 4J): exopod rudimentary, small bud-like.

Pereopod 1 (Figure 4K): ischium slightly expanded distoventrally. Exopod rudimentary, small bud-like.

Pereopod 2 (Figure 4L): left carpus with seven articulations and right carpus with four articulations.

Pereopods 3–5 (Figure 4M–O): carpus and merus with subdistal spine on lateral margin.

Gills (Figure 4J–O): well-developed pleurobranch on pereopods 1–5. Arthrobranch bud on thoracic somites 3–5.

Abdomen (Figure 4B): somites 4, 5, 6 with pair of posterolateral spines.

Pleopods 1–5 (Figure 4B, P–T): bilobed buds present on abdominal somites 1–5.

Telson and uropods (Figure 4A, B, U): telson narrow, rectangular shape, armed with two pairs of spines on dorsolateral margin and six pairs of terminal setae. Uropods differentiated; protopod with posterior spine; exopod with blunt spine posterolaterally.

Stage 4 (Figure 5). Size: CL=2.00 mm (1.90–2.08 mm); TL=9.83 mm (9.35–10.28 mm). Duration: 6.2 days (5–8 days, $n=39$).

Carapace (Figure 5A, B): rostrum upcurved distally, about 1.1 times as long as carapace. Dorsal margin of rostrum and anterior part of carapace armed with 15–17 teeth; ventral margin of rostrum with five teeth. One short seta present between tooth and tooth, or not.

Eyes (Figure 5A, B): no remarkable change.

Antennule (Figure 5C): inner flagellum four-segmented, but longer than stage 3. Outer flagellum five-segmented, with 3, 3, 3, 3, 2 aesthetascs on inner margin.

Antenna (Figure 5D): distolateral spine of basis blunt. Antennal scale with 39–40 plumose setae.

Mandible (Figure 5E): palp three-segmented, with 1, 2, 6–7 plumose setae.

Maxillule (Figure 5F): no remarkable change.

Maxilla (Figure 5G): coxal endite bilobed, with 11+2 serrate setae. Basial endite bilobed, with 11+20 serrate setae. Scaphognathite with 44 plumose setae.

Figure 5. *Pandalus gracilis* Stimpson, stage 4. (A) Dorsal view (scale bar: ab); (B) lateral view (ab); (C) antennule (ad); (D) antenna (ad); (E) mandibles (ae); (F) maxillule (ae); (G) maxilla (ac); (H) first maxilliped (ae); (I) second maxilliped (ae); (J) third maxilliped (ad); (K–O) left pereiopods 1–5 (ac); (P–T) pleopods 1–5 (ae); (U) telson (ac). Scale bars: 2 mm.

Maxilliped 1 (Figure 5H): endite bilobed, proximal lobe with eight setae, distal lobe with about 40 setae. Exopod with eight terminal plumose and seven lateral plumose setae.

Maxilliped 2 (Figure 5I): exopod with 10 terminal plumose setae.

Maxilliped 3 (Figure 5J): no remarkable change.

Pereiopod 1 (Figure 5K): no remarkable change.

Pereiopod 2 (Figure 5L): more longer and thinner. Left carpus with 14 articulations and right carpus with six articulations.

Pereiopods 3–5 (Figure 5M–O): no remarkable change.

Gills (Figure 5I–O): rudimentary podobranch on maxilliped 2. Arthrobranch bud on thoracic somites 6, 7.

Abdomen (Figure 5B): several short setae on dorsal side of somites 3–6.

Pleopods 1–5 (Figure 5B, P–T): biramous, longer than those of stage 3, each with zero to three naked setae on distal margin.

Telson and uropods (Figure 5A, B, U): posterior margin of telson rounded, narrower than anterior end, armed with two pairs of dorsolateral spines and five pairs of terminal setae; setae on dorsal side stronger than those of stage 3. Exopod of uropod with acute posterolateral spine.

Stage 5 (postlarva) (Figure 6). Size: CL=2.18 mm (1.80–2.38 mm); TL=11.19 mm (10.63–11.75 mm). Duration: 8.1 days (5–14 days, $n=39$).

Carapace (Figure 6A, B): rostrum upcurved distally, 1.25 times as long as carapace. Dorsal margin of rostrum and anterior part of carapace armed with 16–18 teeth; ventral margin of rostrum with six teeth. One short seta present between tooth and tooth.

Eyes (Figure 6A, B): no remarkable change.

Antennule (Figure 6C): inner flagellum five-segmented; outer flagellum seven-segmented, with 3, 3, 3, 3, 3, 3 aesthetascs on inner margin.

Antenna (Figure 6D): antennal scale with 44–48 plumose setae.

Mandible (Figure 6E): palp three-segmented, with 2–3, 3–4, 9–10 setae.

Maxillule (Figure 6F): endopod with four serrate setae.

Maxilla (Figure 6G): endopod unsegmented, with four setae. Scaphognathite with 61 plumose setae.

Maxilliped 1 (Figure 6H): endopod with 10 setae. Exopod with 10 terminal plumose and 11 lateral plumose setae.

Maxilliped 2 (Figure 6I): exopod with 12 plumose setae.

Maxilliped 3 (Figure 6J): no remarkable change.

Pereiopods 1–5 (Figure 6K–O): general shape unchanged except addition of lateral spines on each merus. Left carpus with 14 articulations and right carpus with seven articulations in pereiopod 2.

Gills (Figure 6I–O): podobranch on maxilliped 2. Well-developed arthrobranch on thoracic somites 3–7. Epipods on thoracic somites 3–7 bearing distal hook.

Abdomen (Figure 6B): no remarkable change.

Pleopods 1–5 (Figure 6P–T): pleopods well developed, each ramus completely separated from protopod except for endopod of pleopod 1, with natatory plumose setae on distal margin. *Appendix interna* present on endopod of pleopods 2–4.

Telson and uropods (Figure 6A, B, U): telson with three pairs of dosolateral spines and three pairs of terminal setae. Exopod of uropod with transverse articulation (diaeresis) from base of posterolateral spine.

Figure 6. *Pandalus gracilis* Stimpson, stage 5. (A) Dorsal view (scale bar: ab); (B) lateral view (ab); (C) antennule (ad); (D) antenna (ad); (E) mandibles (ae); (F) maxillule (ae); (G) maxilla (ae); (H) first maxilliped (ae); (I) second maxilliped (ae); (J) third maxilliped (ad); (K–O) left pereopods 1–5 (ac); (P–T) pleopods 1–5 (ae); (U) telson (ac). Scale bars: 2 mm.

Discussion

In the genus *Pandalus*, the larval development of 11 species have been reported completely and that of one species incompletely. *P. jordani* by Rothlisberg (1980), *P. eous* by Kurata (1964), *P. borealis* by Haynes (1979), *P. goniurus* by Haynes (1978), *P. stenolepis* by Needler (1938), *P. hypsinotus* by Haynes (1976), *P. danae* by Berkeley (1930), *P. prensor* by Mikulich and Ivanov (1983), *P. nipponensis* by Taishaku et al. (2001), *P. platyceros* by Price and Chew (1972), and *P. latirostris* by Kurata (1955) have complete descriptions; *P. montagui* has an incomplete description. There is a wide variation in the number of larval stages within the genus, from 2 to 13 (Table I). *Pandalus gracilis* has four larval stages. Although Bergström (2000) mentioned that most species of *Pandalus* have planktonic larvae which spend their early stages in or near the euphotic zone and then gradually assume a more demersal life with age, *P. latirostris* and *P. prensor* are exceptions from this general pattern. These two shallow water species have large eggs and relatively advanced first larvae with abbreviated development (Kurata 1955; Mikulich and Ivanov 1983). Taishaku et al. (2001) mentioned that *P. nipponensis* also shows “bottom-dwelling behaviour” after hatching with well-developed pereopods. In *P. gracilis*, only 64 larvae were hatched from one ovigerous female. They did not swim in the rearing water; they sank to the bottom of the rearing bottles and remained there, with well-developed pereopods: pereopods 3–5 are segmented as in the adult form. However, they have no pleopods. Mandibular palps are present in the second stage. These traits suggest that the larval development of *P. gracilis* follows the abbreviated pattern and that larvae in the field would stay close to the bottom.

Komai (1999) revised the genus *Pandalus* and divided the species of this genus into four species groups based on adult morphology as follows:

1. *P. montagui* group: *P. montagui*, *P. borealis*, *P. goniurus*, *P. jordani*, *P. tridens*, and *P. eous*.
2. *P. stenolepis* group: *P. stenolepis* and *P. curvatus*.
3. *P. hypsinotus* group: *P. hypsinotus*, *P. danae*, *P. prensor*, *P. gracilis*, *P. gurneyi*, *P. nipponensis*, *P. teraoi*, *P. chani*, and *P. formosanus*.
4. *P. platyceros* group: *P. platyceros* and *P. latirostris*.

We compared characters of *Pandalus* larvae which are known so far (Table I), and there are common characters which can be used to distinguish subgroups within each group (except the *P. stenolepis* group). In the *P. montagui* group, the larvae share poorly developed pereopods. In the *P. hypsinotus* group, pereopods are well developed, but larval pleopods are absent or undeveloped. In the *P. platyceros* group, the larvae have more developed pleopods than those of other groups. The larvae of the *P. stenolepis* group have the same characters as those of larvae of the *P. montagui* group. Komai (1999) mentioned that the adults of the *P. stenolepis* group are placed in an intermediate position between the *P. montagui* and the *P. hypsinotus* groups. Therefore, the characters of the larvae of each group generally support the suitability of Komai's (1999) groups in adult classification.

In addition, using larval characters, Komai's (1999) *P. hypsinotus* group can be divided into two groups: the first group contains *P. hypsinotus* and *P. danae*, and the second group contains *P. gracilis*, *P. prensor*, and *P. nipponensis*. The first group has diagnostic features which differentiate them from the second group as follows: (1) they have five to six larval stages, (2) the shape of the telson is triangular; (3) the number of spines on the telson is 7+7; (4) the mandibular palp appears in the fourth stage, and (5) somite 6 is separated in the second stage. The second group, including the present species, has common characters

Table I. Comparison of the larval characters of *Pandalus* and *Pandalopsis* species.

Species	Egg size (mm)	Larval stage	Characters of stage 1								Earliest stage of				Distribution	References ^a
			Carapace length (mm)	Rostrum spination	Pereopods poorly developed	Laminate expansion		Telson		Mandibular palp	Somite 6 separation	Uropods				
						Third maxilliped	First pereopod	Pleopods	Shape				No. of spines			
Genus <i>Pandalus</i>																
<i>P. montagui</i> group ^b																
<i>P. jordani</i> Rathbun, 1902	1.4 × 0.8	13	1.35–1.72	0	Yes	No	No	a	t	7+7	14	2	3	NP	8, 13	
<i>P. eous</i> Makarov, 1935	ND	7	1.29	0	Yes	No	No	a	t	7+7	7	3	3	NNP	5	
<i>P. borealis</i> Krøyer, 1838	1.2 × 0.9	6	1.96	0	Yes	No	No	a	t	7+7	7	2	3	NA	1, 12	
<i>P. goniurus</i> Stimson, 1960	ND	5	1.21	0	Yes	No	No	a	t	7+7	6	2	3	NNP	7, 11	
<i>P. montagui</i> Leach, 1814	ND	ND	1.16	0	Yes	No	No	a	t	7+7	ND	ND	ND	NA	3, 6	
<i>P. stenolepis</i> group ^b																
<i>P. stenolepis</i> Rathbun, 1902	ND	6	1.20	0	Yes	No	No	a	t	7+7	7?	3	3	NEP	2	
<i>P. hypsinotus</i> group ^b																
<i>P. hypsinotus</i> Brandt, 1851	1.3 × 1.1	6	1.72	0	No	No	No	a	t	7+7	4	2	3	NNP	1, 5, 10	
<i>P. danae</i> Stimpson, 1857	ND	5	1.76	0	No	No	No	a	t	7+7	ND	ND	ND	NEP	1	
<i>P. gracilis</i> Stimpson, 1860	1.9–2.9 × 1.3–1.9	4	1.39	0	No	No	No	a	c	8+8	2	1	3	NWP	This study	
<i>P. prensor</i> Stimpson, 1860	ND	3	1.61	0	No	No	No	u	c	9+9	2	1	3	NWP	14	
<i>P. nipponensis</i> Yokoya, 1933	3.1 × 2.3	4	2.95	0	No	No	No	u	c	23–25	1	1	3	NWP	16	
<i>P. platyceros</i> group ^b																
<i>P. platyceros</i> Brandt, 1851	ND	4	1.27	12–13	No	No	No	b	t	8+8	5	1	3	NEP	1, 9	
<i>P. latirostris</i> Rathbun, 1902	2.6 × 2.0	2	2.97	0	No	No	No	s	t	16+16	3	1	3	NWP	4	
Genus <i>Pandalopsis</i>																
<i>P. coccinata</i> Urita, 1941	ND	3	6.2	13?	No	ND	Yes	b	c	28+28	1	1	ND	NP	5	
<i>P. dispar</i> Rathbun, 1902	ND	5	1.6	WD	No	No	No	b	t	11+12	ND	1	3	NP	17	
<i>P. japonica</i> Balss, 1914	ND	3	2.24–2.43	0	No	No	Yes	b	c	32–39	3	1	3	NP	15	

a, absent; b, biramous bud; c, circular form; NA, northern Atlantic; ND, no data; NEP, northeastern Pacific; NNP, northern North Pacific; NP: northern Pacific; NWP, northwestern Pacific; s, setose; t, triangular form; u, uniramous bud; WD, weak denticles. ^aReferences: 1, Berkeley (1930); 2, Needler (1938); 3, Lebour (1940); 4, Kurata (1955); 5, Kurata (1964); 6, Pike and Williamson (1964); 7, Makarov (1966); 8, Modin and Cox (1967); 9, Price and Chew (1972); 10, Haynes (1976); 11, Haynes (1978); 12, Haynes (1979); 13, Rothlisberg (1980); 14, Mikulich and Ivanov (1983); 15, Komai and Mizushima (1993); 16, Taishaku et al. (2001); 17, Park et al. (2004).

^bKomai (1999).

as follows: (1) they have from three to four larval stages; (2) the shape of the telson is circular; (3) the number of spines on the telson is more than 8+8; (4) the mandibular palp appears from the first to second stages, and (5) somite 6 is separated in the first stage.

In the *P. hypsinotus* group, the larvae of *P. gracilis* are very similar to those of *P. prensor* and *P. nipponensis*. Some morphological differences are found in the following characters: (1) in the first stage, *P. gracilis* has eight pairs of setae on the distal margin of the telson, whereas *P. prensor* has nine pairs and *P. nipponensis* has 23–25; (2) in *P. gracilis*, the pleopods appear in the third stage, whereas these appear in the first stage in *P. prensor* and *P. nipponensis*, and (3) in *P. gracilis* and *P. prensor*, the mandibular palp appears in the second stage, whereas it appears in the first stage in *P. nipponensis*.

Berkeley (1930) classified the genera *Pandalopsis* and *Pandalus* based on their adult phase. According to her classification, *Pandalopsis* has long antennules that are twice as long as the carapace and possess a laminate expansion on the merus of the third maxilliped and the ischium of the first pereopod. Komai (1999) also mentioned that *Pandalus* is immediately distinguishable from *Pandalopsis* in the ventral laminar expansion of the ischium of the first pereopod, which bears spinules ventrally, the slender, conical propodus of the first pereopod, and the greatly unequal second pereopods. However, Christofferson (1989) suggested that *Pandalopsis* is a subordinate clade within the genus *Pandalus*. In this study, we compared larval development in 13 *Pandalus* species with three *Pandalopsis* species (mainly first larval stage). As a result, no diagnostic characters for *Pandalopsis* were observed in the larval phase. *Pandalopsis dispar* has no laminate expansion of the third maxilliped and first pereopod, which Park et al. (2004) noted as a diagnostic feature of *Pandalopsis dispar*. The characters of *Pandalopsis* larvae are similar to those of *Pandalus* as follows: (1) developed pereopods are close to the *P. hypsinotus* and *P. platyceros* groups; (2) the absence of the laminate expansion on the third maxilliped is close to all groups in *Pandalus*; (3) developed pleopods, and (4) the number of setae of the telson is more than eight pairs, which is close to *P. platyceros*. Therefore, *Pandalopsis* and *Pandalus* are not distinguished by larval morphology. This means there is close relation between *Pandalopsis* and *Pandalus*, although Rice (1980) pointed to the potential danger in the uncritical use of larval information for estimating phylogeny in decapods. Further study on the larval development of *Pandalopsis* species and characters of the adult morphology within two genera are required.

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