Larval stages of the Botan shrimp *Pandalus nipponensis* Yokoya, 1933 (Decapoda: Caridea: Pandalidae) under laboratory conditions, with notes on its lecithotrophic development

Hajime Taishaku, Hideo Takeoka and Kooichi Konishi

**Abstract.**—The complete larval development of the Botan shrimp, *Pandalus nipponensis* Yokoya, 1933, is described and illustrated based on laboratory-reared material. Four larval stages (stage 1–4) and two postlarval stages (stages 5, 6) were recognized. The larvae started to feed on *Artemia* nauplii from stage 2. Starved larvae survived until stage 3. According to Gore's (1985) classification of the developmental types of decapods, the development of *P. nipponensis* is of an advanced and lecithotrophic type.

**Introduction**

Nine species of the genus *Pandalus* are known from Japan (Miyake, 1998; Komai, 1999), including five commercially important species: *P. eous* Makarov, 1935, *P. hypsinotus* Brandt, 1851, *P. latirostris* Rathbun, 1902 (= *P. kessleri* Brashnikov, 1907), *P. prenson* Stimpson, 1860, and *P. nipponensis* Yokoya, 1933. These shrimps are distributed in a wide range of depths, from intertidal to deep-sea bottom. Larval development has been documented in detail for four species (Berkeley, 1930; Kurata, 1955; Kurata, 1964; Haynes, 1976; Mikulich & Ivanov, 1983), but only a preliminary report has been published on the Botan shrimp *P. nipponensis* (Yamamoto et al., 1982).

*Pandalus nipponensis* is distributed on the deep continental shelf and slope of the Pacific coast of Japan from Kashimana to Kagoshima Bay at 100–480 m (Komai, 1999). The catch of *P. nipponensis* has declined greatly in recent years (Yamamoto et al., 1982) and, therefore, information on its early life history is required for the analyses of natural populations and management of the species.

The present paper describes the complete larval stages of *P. nipponensis* reared under laboratory conditions and discusses the developmental patterns of *Pandalus* species.

**Material and Methods**

Ovigerous shrimps were collected from Enshu-nada at a depth of 300 m using trawling gear in January 1996. Among them, two females, 36 mm in carapace length, carried 585 and 707 eggs, respectively. They were kept in an aquarium at about 10 °C. The eggs were elliptical; those of the first female measured 3.71 ± 0.15 x 2.41 ± 0.11 mm (10 specimens) and those of the second female 3.13 ± 0.12 x 2.26 ± 0.09 mm. Newly hatched larvae were reared in two polycarbonate tanks each containing five liters of sea water and 10 larvae. They were fed with *Artemia* nauplii and the seawater changed daily. Non-fed larvae were also cultured as a control. They were kept individually in 200 ml vessels, and exuviae were removed immediately after each molt to prevent consumption.

The larvae and exuviae of each stage were fixed by 5% buffered formalin for morphological observation. Dissection and measurement were conducted using an Olympus SZH stereomicroscope with
fine insect pins. Drawings were made with the aid of a drawing tube attached to an Olympus BH-2 microscope. The carapace length (CL) was measured from the tip of rostral spine to the medial posterior margin of the carapace. Most of the terminology for setae follows that of Ingle (1992). All setal arrangements are listed from proximal to distal.

The specimens used in this study are deposited in the Zoological Institute, Faculty of Science, Hokkaido University under registration numbers ZIHU1365-1370 (larvae) and ZIHU 1371 (ovigerous female).

Results

Four larval stages were recognized in *P. nipponensis*. Newly hatched larvae of *P. nipponensis* corresponded to the zoea 1 stage following the definition of zoal larvae (Gurney, 1942; Williamson, 1969), but it has some advanced morphological characters that are normally found in later larval stages in most caridean shrimps, for example the antennule, maxilla, maxilliped 3, pereopods 1–2, pleopods and uropods (Table 1). It is, therefore, hardly acceptable to call these stages as “zoea” in the strict sense. We use the term “stages 1–4” instead of “zoeae 1–4” in this paper. It took about 40 days from hatch-

Table 1. Developmental phase of appendages in the larval stages of *Pandalus nipponensis* Yokoya.

<table>
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<tr>
<th>Appendage</th>
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<td>L</td>
<td>L</td>
<td>L</td>
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<td>Arthrobranchs</td>
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<td>PL</td>
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</tbody>
</table>

L: larval, PL: postlarval.

Description

*Pandalus nipponensis* Yokoya, 1933

Figs. 2–11

Stage 1

Dimension: CL = 2.85±0.07 mm (range 2.70–2.93 mm, 10 specimens).

Carapace (Fig. 2A, A'): Rostrum short, spiniform, directed downward, without teeth. Posterolateral margin rounded. Anterolateral margin with antennal spine. Eyes sessile.

Antennule (Fig. 3A): Uniramous, protopod with a distal plumose seta. Exopod unsegmented process with 3 aesthetascs.
Antenna (Fig. 3E): Biramous, well-developed. Coxa and basis separated and a spine at distalateral corner of basis. Endopod (= flagellum) well developed, much longer than CL. Exopod (= antennal scale or scaphocerite) flattened, with a distalateral spine and 46–47 plumose setae on mesial and distal margins.

Mandible (Fig. 4A): Incisor and molar processes indistinctly separated, armed with several teeth on mesial margin. Palp well developed, but unsegmented.

Maxillule (Fig. 4D): Coxal endite slender, with 1 plumose and 9 simple setae. Basal endite broad, with 2 rows of 14 simple spines and 15 simple setae on mesial margin. Endopod with 3 minute setae.

Maxilla (Fig. 5A): Bilobed coxal and basal endite with 11+2 and 5+9 setae respectively. Endopod unsegmented, with 8 setae. Exopod (= scaphognathite) plate-like, with 53–58 plumose setae.

Maxilliped 1 (Fig. 5D): Protopod bilobed, proximal lobe with 6 setae, distal lobe with 18 setae. Endopod unsegmented, with 7 setae. Exopod with long slender ramus enlarged at base (= caridean lobe), with 6 terminal natatory setae and 11 plumose lateral setae. Epipod bilobed.

Maxilliped 2 (Fig. 6A): Similar to adult form but less setose. Endopod 5-segmented; propodus obliquely articulated to carpus, distal 3 segments with 3, 1, 1, setae respectively, dactylus and propodus with several minute setae. Exopod longer than endopod, with 9 natatory plumose setae terminally. Epipod bilobed.

Maxilliped 3 (Fig. 6D): Endopod 4-segmented. Exopod longer than endopod, with 10 natatory plumose setae distally.

Pereopods (Figs 6J, 7A, 8A, 8D, 8G): Pereopod 1 biramous, endopod 3-segmented, minutely chelate and exopod unsegmented with 10 natatory plumose setae. Pereopod 2 biramous, chelate, left longer than right; endopod 5-segmented; exopod as in pereopod 1. Pereopods 3–5 uniramous, segmented as in adult form.

Abdomen (Fig. 2A): Six somites plus spatulate telson. Dorsal surface of each somite smooth, without armature.

Pleopods (Fig. 2A): Rudimentary small buds on abdominal somites 1–5.

Telson and uropods (Fig. 10A): Telson distally rounded in dorsal aspect, slightly notched posteromedially; posterior margin fringed with 23–25 plumose setae. Rudiments of uropods visible under cuticle on ventral side.

Gills (Fig. 11A): Arthrobranch absent. Pleurobranch present on thoracic somites 4–8, well developed. Epipod present on pereopods 1–4.

Stage 2

Dimension: CL = 3.75 ± 0.14 mm (range 3.45–3.95 mm, 9 specimens).

Carapace (Fig. 2B): Rostrum styliform, distinctly overreaching anterior margin of eye, about 0.8 times as long as carapace; dorsal margin armed with 13–14 minute teeth including 3–5 behind level of posterior margin of orbit, posteriormost one situated on about anterior 0.15 of carapace, none with basal suture; ventral margin armed with 3–5 minute teeth. Antennal and pterygostomian spines on anterior margin.

Antennule (Fig. 3B): Peduncle 3-segmented; proximal segment bearing, small stylocerite with acute tip, concave on outer margin and with about 20 setae on distolateral corner; penultimate segment with 12 setae; distal segment with 6 setae. Inner flagellum (= endopod) 2-segmented with 2, 3 setae respectively; outer flagellum (= exopod) not developed. In some specimens, inner flagellum 3-segmented with 0, 2, 1+3 setae respectively; outer flagellum divided into 4 articles, with 2–4 aesthetascas on each article.

Antenna (Fig. 3F): No major change.

Mandible (Fig. 4B): Incisor and molar processes well separated by deep cleft. Palp 3-segmented, with 0, 0–2, 7 setae.

Maxillule (Fig. 4E): Coxal endite with
17 plumose setae. Basial endite with double row of 14 simple spines and 21 plumose setae on mesial margin. Endopod with 2 plumose setae.

Maxilla (Fig. 5B): Coxal endite with only a few setae. Bilobed basal endite with plumose setae, 15 on proximal lobe, 25 on distal lobe respectively. Endopod unsegmented, with 3 plumose setae.

Maxilliped 1 (Fig. 5E): Protodipod with 2 lobes: proximal lobe with 11 setae, distal lobe with 47–61 setae. Endopod 2-segmented, with 2, 3 setae respectively.

Maxilliped 2 (Fig. 6B): Dactylus and propodus with about 50 and 20 setae respectively.

Maxilliped 3 (Fig. 6E): Endopod 3-segmented. Exopod rudimentary.

Pereopods (Figs 6K, 7B, 8B, E, H): Pereopod 1 and 2 each with rudimentary exopod. Meri of pereopods 3, 4 armed with a subdistal spine and a lateral spine; carpus with a subdistal spine in pereopods 3, 4.

Abdomen (Fig. 2B‘): All somites with setae on ventral margins of pleura.

Pleopods (Fig. 2B‘): Larger than in stage 1, but non-functional.

Telson and uropods (Fig. 10B): Telson fringed with 22 plumose setae. Visible enclosed uropods enlarged.

Gills (Fig. 11B): Arthrobranch bud on thoracic somites 4–6.

Stage 3

Dimension: CL = 5.04±0.10 mm (range 4.9–5.20 mm, 11 specimens).

Carapace (Fig. 2C): Rostrum almost as long as carapace; dorsal margin armed with 16–19 teeth including 4–6 behind level of posterior margin of orbit, anteriormost one situated near apex of rostrum, remotely separated from remainder, posteriormost one situated on anterior quarter of carapace; ventral margin armed with 5–6 teeth.

Antennule (Fig. 3C): Two types recognized: Rudimentary outer flagellum with 6 aesthetascs; elongated, 4-segmented outer flagellum, each segment with 3–5 aesthetascs.

Mandible (Fig. 4C): Palp 3-segmented with 0,1–4,10 setae.

Maxilliped 3 (Fig. 6F): No remarkable change.

Pereopods (Figs 6L, 7C, 8C, F, I): Meri of pereopod 3 armed with a ventral spine, and a subdistal spine in pereopod 5.

Pleopods (Figs 9A–E): Biramous but still not functional.

Telson and uropods (Fig. 10C): Uropods differentiated. Telson widened posteriorly, armed with 1 spine on each side and 9 pairs of terminal setae.

Gills (Fig. 11C): Epipods on pereopods 1, 2 bearing distal hook.

Stage 4

Dimension: CL = 7.12±0.09 mm (range 7.00–7.30 mm, 9 specimens).

Carapace (Fig. 2D): Rostrum slightly curving dorsally, about 1.1 times as long as carapace; dorsal margin armed with 17–19 teeth including 5 behind level of posterior margin of orbit, posteriormost one situated on anterior over 0.25 of carapace, posterior 2 or 3 teeth with basal suture; ventral margin armed with 7–8 teeth.

Maxilliped 3 (Fig. 6G): No major change.

Pereopods: No remarkable change.

Pleopods (Figs. 9F–J): Each ramus incompletely separated from protopod, having natatory setae on distal margin of exopod only in pleopod 2. Appendix internae on endopods of pleopods 2–4 rudimentary.

Telson and uropods (Fig. 10D): Posterior margin of telson narrower than anterior end, bearing 5 pairs of stout spines, and 3 pairs of spines on dorsal side. No remarkable change in uropods.

Gills (Fig. 11D): Two buds of arthrobranchs on thoracic somite 3. Epipod on pereopod 3 bearing distal hook.
Stage 5 (Postlarva 1, decapodid)

Dimension: CL = 7.81±0.46 mm (range 7.13–8.37 mm, 9 specimens).

Carapace (Fig. 2E): Rostrum curved dorsally, about 1.25 times as long as carapace, dorsal margin armed with 17–19 teeth including 5–6 behind level of posterior margin of orbit, posteriormost one situated at point third from posterior margin of orbit, all teeth with basal suture except posteriormost one, ventral margin armed with 8–9 teeth.

Maxillipeds 3(Fig. 6H): No major change.

Pereopods: No major change.

Pleopods (Figs 9K–O): Each ramus completely separated from its protopod except for endopod of pleopod 1, having natatory setae on distal margin. Appendix internae on endopods of pleopods 2–5, each with adhesive hooks.

Telson (Fig. 10E): Posterior border with 4 pairs of stout spines.

Gills (Fig. 11E): Arthrobranchs on thoracic somites with 3–6 lamellate.

Stage 6 (Postlarva 2)

Dimension: CL = 9.51±0.26 mm (range 9.00–9.88 mm, 10 specimens).

Carapace (Fig. 2F): Rostrum with dorsal margin armed 17–20 teeth including 6–7 behind level of posterior margin of orbit, posteriormost on anterior over 0.3 of carapace, ventral margin armed with 8–10 teeth.

Maxillipeds 3 (Fig. 6I): No major change.

Pereopods: No major change.

Pleopods (Fig. 9P): Pleopod 1 completely separated from protopod.

Telson (Fig. 10F): Posterior margin narrower than in stage 5.

Gills (Fig. 11F): Arthrobranch on thoracic somite 7 lamellate. Epipod on pleopod 4 bearing distal hook.

Discussion

Among 19 species known in the genus *Pandalus*, the complete larval development is reported for 10 species (Table 2). There is a wide variation in the number of larval stages, from two to thirteen, within the genus. *Pandalus nipponensis* normally molts to the postlarva 1 after four larval stages (Table 1). Such an abbreviated larval development is also found in *P. latirostris* (two stages), *P. prensor* (three stages) and *P. platyceros* (four stages). Gore (1985) defined two types of abbreviated development: direct development and advanced development. The larval development of *P. nipponensis* belongs to the advanced type of Gore’s classification. The characters of advanced development in the larvae of *P. nipponensis* are recognized in the appendages of stage 1 (Table 1). These are: 1) well developed antennal exopod, 2) presence of mandibular palp, 3) rounded basal endite of maxillule, and 4) unequal pereopod 2. These advanced characters are only observed in the postlarval stages of *Pandalus* species with long term development, as in *P. jordani* (see Rothlisberg, 1980). Besides these, pereopods 3–5 of stage 1 were also well developed and functional, and these appendages lack an exopod. Bottom-dwelling behavior was also observed from stage 1 in *P. nipponensis*.

The larvae of *P. nipponensis* are easily distinguished from those of other congeners by their larger body size and the presence of a mandibular palp in stage 1 (Table 2). On the other hand, the larvae of *P. nipponensis* have two diagnostic features that are in common with *Pandalus* according to Lebour (1940): 1) all walking legs (pereopods 3–5) present at hatching, either rudimentary or functional, and 2) exopods on walking legs 1–2 or 1–3. Komai (1999) noted that one of the adult features of *Pandalus* species is unequal pereopods 2, the left being longer and more slender and bearing more numerous carpal articles, than the right one. In *P. nipponensis*, the asymmetry in pereopods 2 is observed at stage 1. Diagnostic char-
## Table 2. Comparison of the larval characters of *Pandalus* species.

<table>
<thead>
<tr>
<th></th>
<th>Egg size (mm)</th>
<th>Larval stage(s)</th>
<th>Character of Stage 1</th>
<th>Earliest stage of</th>
<th>Depth of habitat(m)</th>
<th>Distribution*</th>
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* Komai (1999), †: from anterior edge of eye to medial posterior margin of carapace.

acters of the pandalid larvae were also reviewed by Kurata (1964) and Konishi (1997). The characters were also observed in *P. nipponensis*: rostrum present from stage 1 and dentate in later stages, and antennular peduncle concave on the outer margins. Komai (1999) revised the genus *Pandalus* and divided the species of this genus into five groups based on adult morphology. *Pandalus nipponensis* is included in the *P. hysinotus* group according to his classification. Four species of this group, which includes *P. nipponensis*, share common characters of pereopods in stage 1 (Table 2). In the other five species of the *P. hysinotus* group, the larval characters have not been reported. At present, however, the presence of the common characters in the pereopods of stage 1 of the above four species may support the suitability of Komai's (1999) division of the genus into five groups.

It has been suggested that *Pandalopsis* is a subordinated clade within the genus *Pandalus* (Christoffersen, 1989; Komai, 1994). Komai (1999) suggested a sister group relationship between *Pandalopsis* and the *Pandalus platyceros* group. The advanced development was observed in two of the species in the *Pandalus platyceros* group: *P. platyceros* (see Berkeley, 1930; Price & Chew, 1967) and *P. latirostris* (see Kurata, 1955) and also in three species of *Pandalopsis*: *P. dispar* (see Berkeley, 1930), *P. coccinata* (Kurata, 1964), and *P. japonica* (see Komai & Mizushima, 1993). However, it is difficult to decide the phylogenetic status of advanced development in the species of *Pandalopsis* and the *Pandalus platyceros* group because of the limited information.

Rabalais & Gore (1985) noted that larger eggs, long incubation period, and advanced morphology is related to the lecithotrophic nature of the larvae. These larvae hatch from large, yolky eggs upon which they depend for nutritional reserves, versus planktotrophic larvae which hatch from small eggs without the energy reserve of yolk and which depend on planktonic prey for energy. The larvae of *P. nipponensis* show lecithotrophic development. The incubation period of eggs of *P. nipponensis* was not clear. The number of eggs in the present ovigerous females (C.L. = 36.4 and 36.9mm) is 1/3 to 1/5 that of *P. jordani* (CL = 18–25 mm) (Modin & Cox, 1967). The mean egg size of *P. nipponensis* was 3.4 x 2.3 mm and this is the largest among those reported for *Pandalus* species (Table 2). *Pandalus nipponensis* larvae began to feed from stage 2 and molt to stage 6 in the present rearing (Fig. 1). The mandibles and the maxillules play an important role in feeding (e.g., Crain, 1999). In the stage 1 of *P. nipponensis*, these mouthparts were less developed than those of stage 2. Namely, the mandible was not separated clearly into incisor and molar processes and the teeth on the mandible and the setae on the basal endite of the maxillule were less numerous than in stage 2. Another example of lecithotrophic development among *Pandalus* species is in *P. latirostris*. This species has large eggs and only two larval stages (Table 2).

The habitat of *P. nipponensis* sometimes overlaps with that of the anomuran lithodid crab *Paralomis hystrix* (De Haan, 1846) and the brachyuran spider crab *Goniopusgettia sagamiensis* (Gordon, 1931). All three species live on the continental shelf break (200–300 m deep), and show lecithotrophic development (Konishi & Taishaku, 1994; Taishaku & Konishi, 2000). It is possible that the lecithotrophic development of these species is related to their habitat. The deep continental shelf lies between productive, nutrient-enriched shelf seas ('neritic' waters) and nutrient-poor abyssal seas (Barnes & Hughes, 1988). The habitat, therefore, may be related to the lecithotrophic larval development of *P. nipponensis*. On the other hand, the shallow-water pandalid *Pandalus latirostris*
also deposits large eggs and shows lecithotrophic development (Kurata, 1955). It can be assumed that the lecithotrophic development of *P. latirostris* results in local dispersal of the larvae because their habitat is restricted to seagrass beds (see Havenhand, 1995). The meaning of lecithotrophic development, therefore, might vary from species to species as a life history strategy. More detailed studies are required to clarify the relationship between the lecithotrophic development and their habitats.

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Fig. 1. A: Growth of larvae and postlarvae of *Pandalus nipponensis* Yokoya. Mean value of carapace length and SD. B: Number of surviving larvae and postlarvae of *Pandalus nipponensis* Yokoya. B': number of surviving larvae and postlarvae of *Pandalus nipponensis* Yokoya under non-feeding condition.
Fig. 2. *Pandalus nipponensis* Yokoya: A–F, carapace of stages 1–6 in lateral view; A', anterior part of carapace in dorsal view, showing short rostrum; B'–F', abdomen of stages 2–6 in lateral view. Scale = 1.0 mm.
Fig. 3. *Pandalus nipponensis* Yokoya: A–D, left antennule of stages 1–4 in ventral view; E–G, left antenna of stages 1–3 in ventral view. Scale = 1.0 mm.
Fig. 4. *Pandalus nipponensis* Yokoya: A–C, mandibles of stages 1–3 in external view; D–F, left maxillule of stages 1–3 in external view. Scale = 0.5 mm.
Fig. 5. *Pandalus nipponensis* Yokoya: A–C, left maxilla of stages 1–3 in external view; D–F, left maxilliped 1 of stages 1–3 in external view. Scale = 0.5 mm.
Fig. 6. *Pandalus nipponensis* Yokoya: A–C, left maxilliped 2 of stages 1–3 in external view, one of natatory setae enlarged in fig. A; D–I, left maxilliped 3 of stages 1–6, stage 1 in mesial view, stages 2–6 in lateral view, only basis in stages 4–6; J–L, left pereopod 1 of stages 1–3, stage 1 in mesial view, stages 2, 3 in lateral view; J'–L', chela of pereopod 1 of stage 1–3 in lateral view. Scales = 1.0 mm for A–L, 0.1 mm for J–L'.
Fig. 7. *Pandalus nipponensis* Yokoya: A–C, left and right pereopod 2 of stages 1–3, stages 1, 2, 3 (right) in mesial view, stage 3 (left) in lateral view. Scale = 1.0 mm.
Fig. 8. *Pandalus nipponensis* Yokoya: A–C, left pereopod 3 of stages 1–3 in lateral view; D–F, left pereopod 4 of stages 1–3 in lateral view; G–I, left pereopod 5 of stages 1–3 in lateral view. Scale = 1.0 mm.
Fig. 9. *Pandalus nipponensis* Yokoya: A–E, left pleopods of stage 3 in lateral view; F–J, left pleopods of stage 4 in ventral view; K–O, left pleopods of stage 5 in ventral view; P, left pleopod of stage 6 in ventral view. A, F, K, P, pleopod 1; B, G, L, pleopod 2; C, H, M, pleopod 3; D, I, N, pleopod 4; E, J, O, pleopod 5. Scale = 0.5 mm.
Fig. 10. *Pandalus nipponensis* Yokoya: A–F, telson of stages 1–6 in dorsal view. Scale = 1.0 mm.
Fig. 11. *Pandalus nipponensis* Yokoya: A–F, right branchial chamber of stage 1–6. Scale = 1.0 mm.