Larval development of the sidestriped shrimp (*Pandalopsis dispar* Rathbun) (Crustacea, Decapoda, Pandalidae) reared in the laboratory

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Abstract—Larval development of the sidestriped shrimp (*Pandalopsis dispar*) is described from larvae reared in the laboratory. The species has five zoeal stages and one postlarval stage. Complete larval morphological characteristics of the species are described and compared with those of related species of the genus. The number of setae on the margin of the telson in the first and second stages is variable: 11+12, 12+12, or 11+11. Of these, 11+12 pairs are most common. The present study confirms that what was termed the fifth stage in the original study done by Berkeley in 1930 was the sixth stage and that the fifth stage in the Berkeley's study is comparable to the sixth stage that is described in the present study. The sixth stage has a segmented inner flagellum of the antennule and fully developed pleopods with setae. The ability to distinguish larval stages of *P. dispar* from larval stages of other plankton can be important for studies of the effect of climate change on marine communities in the Northeast Pacific and for marine resource management strategies.

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Sixteen species of the genus *Pandalopsis* have been recognized in the Southwestern Atlantic and North Pacific Oceans (Komai, 1994; Jensen, 1998; Hanamura et al., 2000). Most members of the genus attain a large body size and are valuable as commercial fishery resources (Holthuis, 1980; Baba et al., 1986). In the North Pacific, *P. dispar, P. ampla, P. aleutica, P. longirostris*, *P. lucidirimicola, and P. spinosior* have been reported. Of these, *Pandalopsis dispar* is an important component of the commercial shrimp fisheries along with several species of the genus *Pandalus.* Commercial landings of shrimp during 1999 totaled approximately 19 million tons (PSMFC, 1999).

Knowledge of the life histories of these species, including the duration and growth of their larvae, is important for stock assessment and management. However, remarkably little is known about their early life histories because most species of the genus live at considerable depths. Of the 16 *Pandalopsis* species, the larvae of only three species have been described partly or completely from plankton samples or from larvae reared in the laboratory. The larvae of *Pandalopsis japonica* were described completely from specimens reared in the laboratory by Komai and Mizushima (1993). Kurata (1964) described the first stage of *P. coccinata* from plankton samples and from larvae hatched in the laboratory. Thatje and Bacardit (2000) assumed that larvae of *P. ampla* occurring in Argentine waters were similar to those of *P. dispar* and *Pandalopsis coccinata*. Berkeley (1930) described four larval stages of *P. dispar* based on samples collected in British Columbia coastal waters. The first stage was obtained from ovigerous females, whereas the larvae of the other stages were separated from plankton samples. In addition, the stage described as the fifth stage was not clearly defined.

In this study, we describe the complete series of larval stages of *P. dispar* using specimens reared in the laboratory.

Materials and methods

Ovigerous females of *Pandalopsis dispar* were collected on 25 March

1999 by using a small shrimp trawl fished at depths of about 40 m near Gabriola Island in the vicinity of the Pacific Biological Station, Nanaimo, British Columbia (latitude 49°13′, longitude 123°55′). Water temperature at the collection site was around 9°C, and salinity was 29.0‰. The females were each kept in a 20-L jar with seawater. The larvae hatched on 1 April 1999. Hundreds of larvae hatched from one female. Of these, one hundred newly hatched larvae were transferred into individual 250-mL jars. To obtain samples for drawing and descriptions, a total of 150 larvae from the female were reared in a 20-L jar. Newly hatched *Artemia* nauplii were used to feed the larvae. We used filtered natural seawater from 40 m depth without adjusting the water temperature or salinity. Water temperature during the rearing experiments ranged from 8.7°C to 12.2°C (mean 10.5°C). Salinity during the rearing experiments ranged from 26.0‰ to 31.0‰ (mean 28.9‰). The water in each jar was changed daily.

All drawings were made with a drawing tube attached to a microscope. Carapace length (CL) was measured with an ocular micrometer from the posterior edge of the orbital arch to the middorsal posterior edge of the carapace. The anatomical terms used in this paper are from Pike and Williamson (1969) and Haynes (1985).

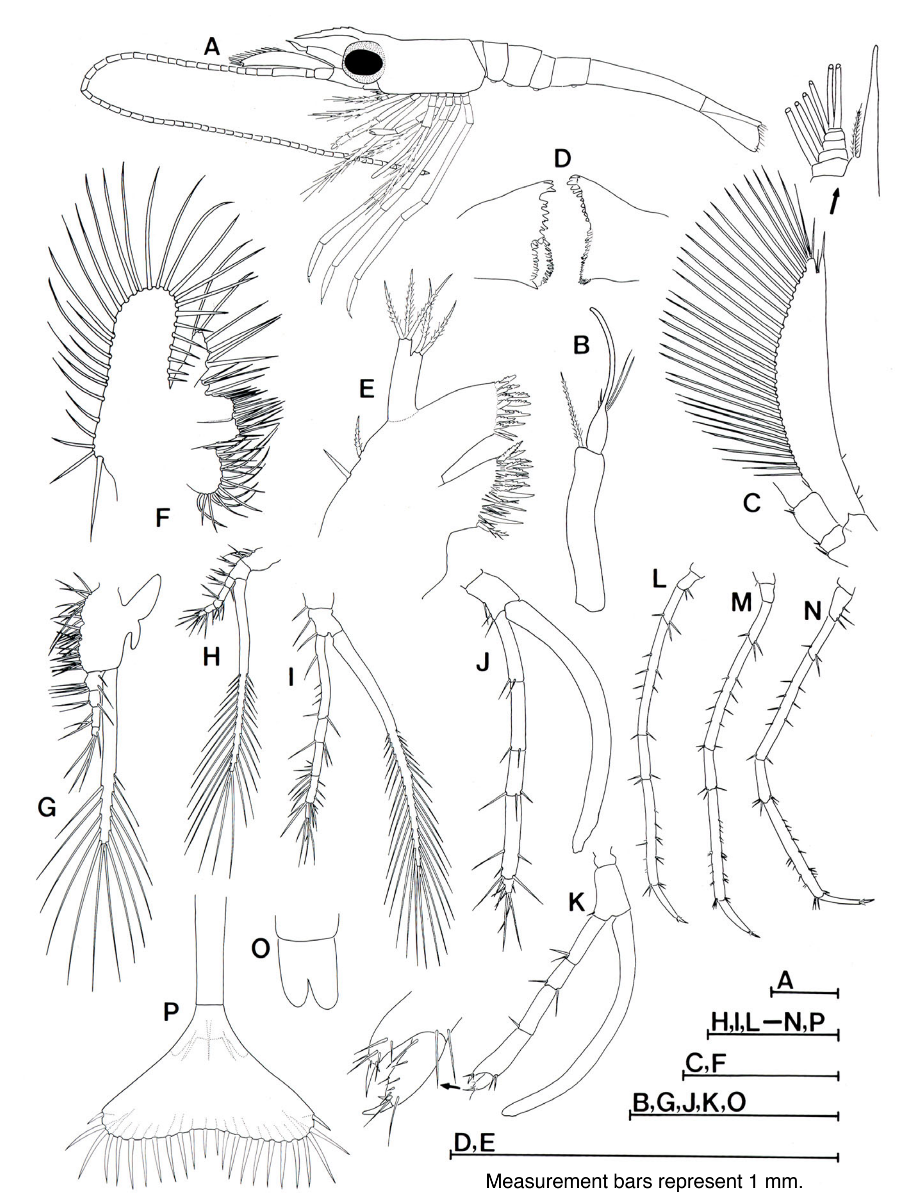


Figure 1

Results

In the complete larval development of *Pandalopsis dispar* there are five zoeal stages. In addition, there is one postlarval stage. The duration of each larval stage and the survival rate of *P. dispar* are shown in Table 1.

Table 1

Duration of each larval stage of *Pandalopsis dispar* at 8.7–12.2°C (mean 10.5°C) and 26.0–31.0‰ (mean 28.9‰). Stage 6 is a postlarval stage.

Stage	Mean duration (day)	Range (day)	Number of larvae observed
1	10.7	9–15	89
2	8.9	8–11	81
3	9.5	8–14	67
4	10	9–12	59
5	10.8	10–13	51
6	10.5	9–12	48

Larval description

First stage

Carapace (Fig. 1A) Carapace length (CL), 1.6 mm (SD: 0.06 mm, n=89); with concave lateral margin; rostrum long, well developed and directed forward and upward; weak dorsal denticles and bare ventral tubercles on rostrum; rostrum about 0.7 times as long as carapace.

Eyes (Fig. 1A) Sessile.

Abdomen (Fig. 1A) 5 somites plus telson.

Antennule (Fig. 1, A and B) Peduncle unsegmented with a strong seta at distromesial margin; outer flagellum with 2+2 short aesthetascs.

Antenna (Fig. 1, A and C) Longer than the whole body length; flagellum segmented throughout its length; outer-distal corner terminated with an acute spine and a minute seta; inner-distal margin 5-segmented with 1, 1, 1, 1, 2 setae; inner margin fringed with 28–29 setae.

Mandible (Fig. 1D) Asymmetrical; without the same arrangement of denticles, however, almost the same size; incisor process not separated from molar process; armed with several teeth on molar part.

Maxillule (Fig. 1E) Coxal and basal endite with serially developed strong spines and multiple setae; endopod with 2+3 terminal setae

Maxilla (Fig. 1F) Palp with 2, 1, 1, 2 setae; coxal endite with 6 distal setae; basal endite with 8 distal setae; broad scaphognathite with narrow posterior lobes having long naked setae.

First maxilliped (Fig. 1G) Endites separated by shallow notch and with multiple setae; bilobed epipod; endopod 4-segmented with 6, 3, 3, 4 setae; exopod with 14 plumose natatory setae; terminal segment with 3 terminal spines and 1 subterminal spine.

Second maxilliped (Fig. 1H) Coxa with 7 setae; basis with 3 setae; no epipod; endopod 5 segmented with 5, 5, 2, 4, 4 setae; exopod with 27 plumose natatory setae.

Third maxilliped (Fig. 1I) Coxa with 1 seta; basis with 2 setae; endopod 5-segmented with various number of setae; exopod with 34–36 plumose natatory setae.

Pereiopods (Fig. 1, J–N) 1st pereiopod (Fig. 1J) not chelate; 3 long terminal spines on dactylus; dactylus short; propodus longer than carpus; exopod without natatory setae; endopod of 2nd pereiopod chelated (Fig. 1K); chela with numerous small spines; ischium and carpus of pereiopods 3–5 (Fig. 1, L–N) longer than 1st and 2nd ones; propodus armed with several minute spines.

Pleopods (Fig. 1O) Bilobed buds, not functional.

Telson (Fig. 1P) Triangular form; broadened at the end, posterolateral margin with 11+12 (12+12, 11+11) marginal spines; each spine with fine hairs.

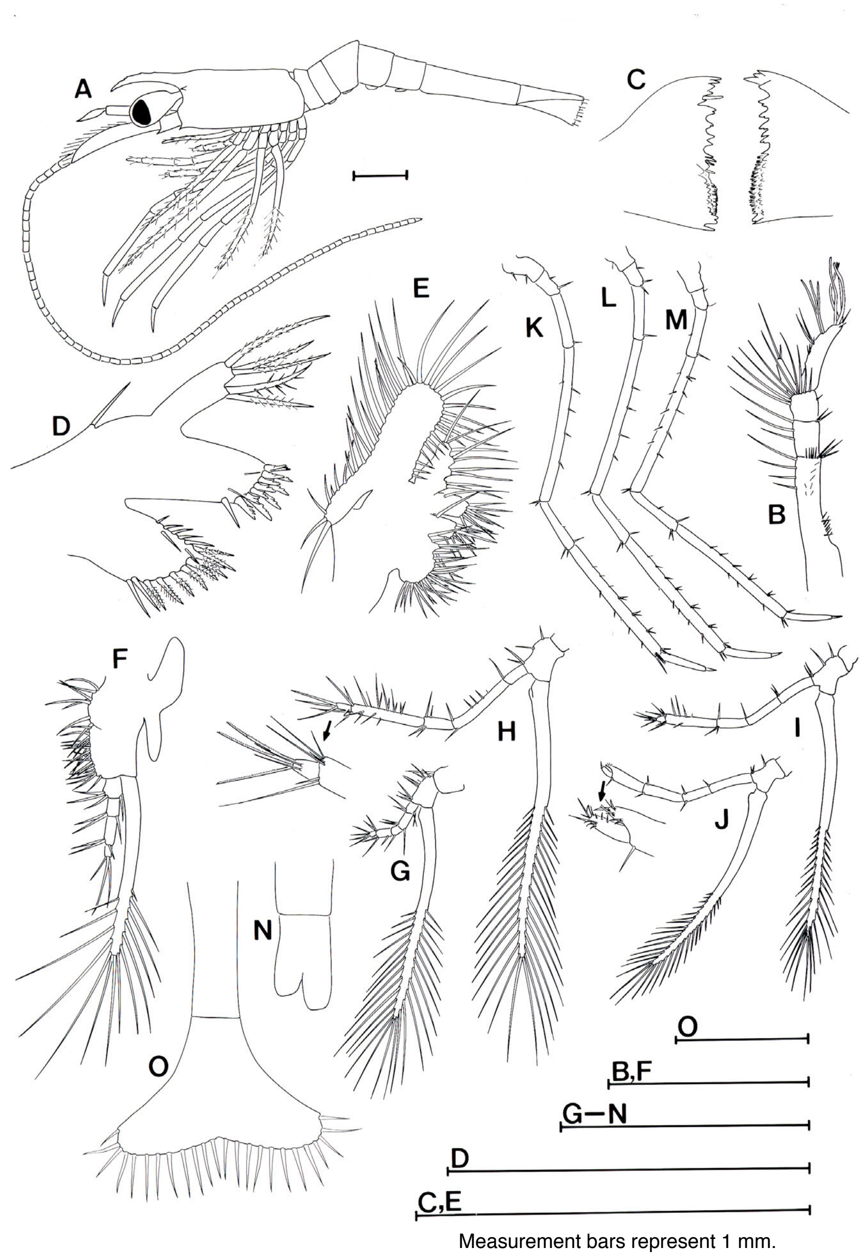


Figure 2

Second stage

Carapace (Fig. 2A) CL, 2.2 mm (SD: 0.11, n=81); rostrum not strongly curved upwards; 5–6 prominent dorsal denticles and 3–4 weak ventral spines; rostrum shorter than carapace; supraorbital spine present.

Eyes (Fig. 2A) Stalked; separated from carapace.

Antenna (Fig. 2A) General shape unchanged; longer than that of 1st stage.

Antennule (Fig. 2B) Peduncle 3-

segmented; inner flagellum with 2 distal setae; outer flagellum with 2, 3, 4, 2 aesthetascs on inner margin.

Mandible (Fig. 2C) General shape unchanged; bigger than that of 1st stage.

Maxillule (Fig. 2D) Coxal and basal endite with serially developed strong spines and multiple setae; endopodite with 2+3 spines; a strong subterminal seta.

Maxilla (Fig. 2E) Palp with 2, 2, 2, 3 setae; broad scaphognathite with narrow posterior lobe having a long naked seta; coxal endite with 6 distal setae; basal endite with 7 distal setae.

First maxilliped (Fig. 2F) Epipod bilobed; endopod with 3+1, 2+1, 2+1, 3 setae; exopod unsegmented with 14 plumose natatory setae.

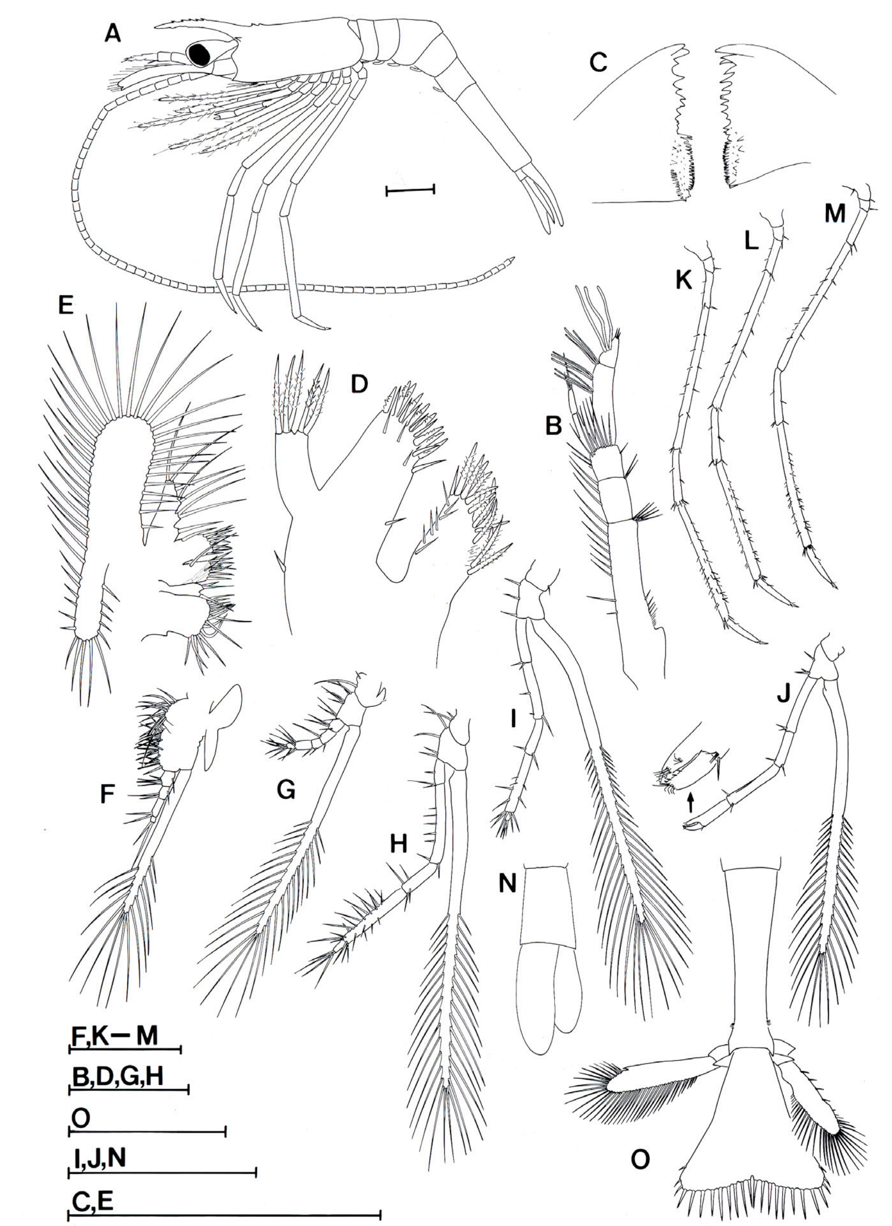
Second maxilliped (Fig. 2G) One long and several intermediate sized spines in basal endite; endopod 5-segmented; exopod with 24 plumose natatory setae.

Third maxilliped (Fig. 2H) Endopod 5-segmented, armed with many spines; exopod of 36 plumose natatory setae.

Pereiopods (Fig. 2, I–M) Not chelate; 1st pereiopod of 4 spines in basal endite; 3 strong and two weak spines in dactylus of 1st pereiopod; general shape unchanged from 2nd pereiopod through 5th pereiopod.

Pleopods (Fig. 2N) Bilobed buds, not functional; no seta and hair on buds; no further development from the 1st stage.

Telson (Fig. 2O) Unchanged.



Measurement bars represent 1 mm.

Figure 3

Third stage

Carapace (Fig. 3A) CL, 2.7 mm (SD: 0.12, *n*=67); longer rostrum than that of 2nd stage; almost 0.9 times as long as carapace; rostrum with 5-6 dorsal spines and 1-2 ventral spines.

Antennule (Fig. 3B) Inner flagellum 2-segmented with 0, 2 setae; outer flagellum 2-segmented with 3+3+3, 3+3 aesthetascs.

Antenna (Fig. 3A) General shape unchanged; longer than 2nd stage.

Mandible (Fig. 3C) Molar and incisor processes present; incisor process with 6-9 teeth; molar process with heavy teeth on biting edge.

Maxillule (Fig. 3D) Palp with 2+3 setae; a small subterminal spine; basal and coxal endite with numerous spines.

Maxilla (Fig. 3E) Protopodite unsegmented; palp with 1, 2, 2, 1+2 setae and with 4 lobes; broad scaphognathite with narrow posterior lobe bearing numerous setae.

First maxilliped (Fig. 3F) Epipod bilobed; endopod 4-segmented with 4, 2, 2, 2 setae; exopod with 15–16 plumose natatory setae;

Second maxilliped (Fig. 3G) Coxal endite with an epipod and a strong spine; endopod 5-segmented with 3, 2, 2, 4, 6 setae exopod with setae.

Third maxilliped (Fig. 3H) Coxal endite with one long and one short spine; basal endite with 2 long and 2 intermediate sized spines; endopod 5-segmented with numerous setae; exopod with 25–26 plumose natatory setae.

Pereiopods (Fig. 3, I–M) General shape unchanged except addition of setae.

Pleopods (Fig. 3N) Buds biramous; much longer than that of 2nd stage.

Uropods (Fig. 3O) Biramous; endopod with a fused spine at distal quarter of outer margin and numerous setae on inner distal margin; exopod with 4 spines on outer margin and numerous setae on inner distal margin.

Telson (Fig. 3O). With 12 pairs of posterolateral spines plus a median spine.

Fourth stage

Carapace (Fig. 4A) CL, 3.1 mm (SD: 0.13, n=59); Rostrum slightly longer than carapace and directed forward; rostrum with 15 dorsal spines and 6 ventral spines.

Antenna (Fig. 4A) General shape unchanged; longer than that of 3rd stage.

Antennule (Fig. 4B) Much longer inner flagellum than that of 3rd stage; inner flagellum about 0.9 times as long as outer flagellum, 2-segmented with 0, 2 setae; outer flagellum 6-segmented with 1, 2, 2, 3, 4 aesthetascs.

Mandible (Fig. 4C) Similar to third stage.

Maxillule (Fig 4D) General shape unchanged except addition of setae on endites.

Maxilla (Fig. 4E) Palp with 3, 2, 2, 3 setae; endites and scaphognathite added numerous setae.

First maxilliped (Fig. 4F) Expod with 15 plumose natatory setae.

Second maxilliped (Fig. 4G) Basal endite with an epipod and a long spine; exopod with 28–29 plumose natatory setae.

Third maxilliped (Fig. 4H) Expopod with 36–37 plumose natatory setae.

Pereiopods (Fig. 4, I–M) Number of spines increased.

Pleopods (Fig. 4N) Lobes much longer than those of third stage.

Uropods (Fig. 4O) Endopod and exopod with numerous setae on inner distal margin.

Telson (Fig. 4O) With 12 pairs of spines on posterolateral margin; a pair of lateral spines at distal third.

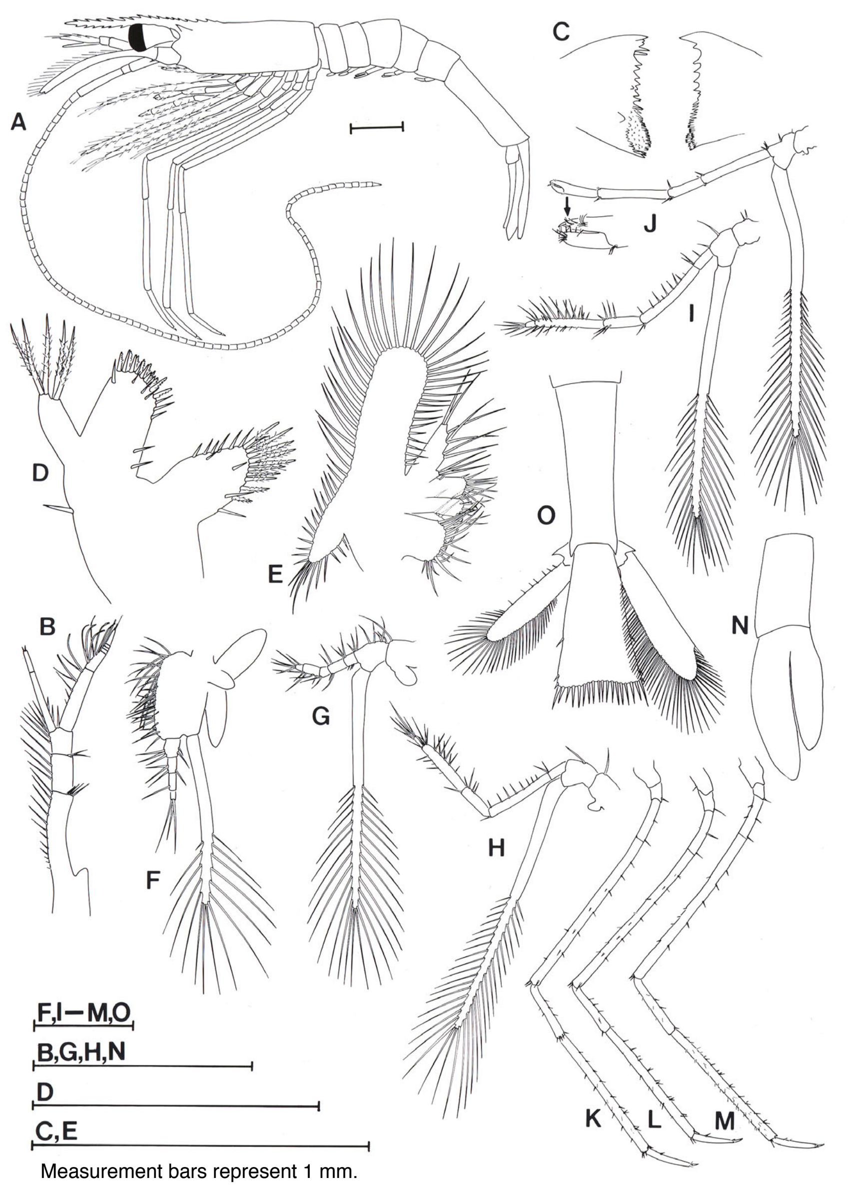


Figure 4

Fifth stage

Carapace (Fig. 5A) CL, 3.6 mm (SD: 0.15, n=51); Rostrum directed forward and upward, slightly longer than carapace; rostrum with 17–18 dorsal spines and 7–8 ventral spines.

Antennule (Fig. 5B) Inner flagellum 3-segmented and about 0.9 times as long as outer flagellum; outer flagellum with 2+2+3+3+3+2+3+5 aesthetascs and distal third 6-segmented.

Mandible (Fig. 5C) More advanced development than that of 6th; not much change in biting surface.

Maxillule (Fig. 5D) General shape unchanged except addition of setae on endites.

Maxilla (Fig. 5E) General shape unchanged.

First maxilliped (Fig. 5F) Exopod with 16 plumose natatory setae.

Second maxilliped (Fig. 5G) Exopod with 31–33 plumose natatory setae.

Third maxilliped (Fig. 5H) Exopod with 46–48 plumose natatory setae.

Pereiopods (Fig. 5, I–M) Ischium slightly expanded in first pereipod.

Pleopods (Fig. 5N) Much more developed than pleopods of 4th stage; exopod with 13, 1 setae; endopod with 6 setae and vestiges of appendix interna.

Uropod (Fig. 5O) Exopod with numerous minute spines on outer margin

Telson (Fig. 5O) Both lateral margins parallel; 19 terminal spines; 2 pairs of lateral spines.

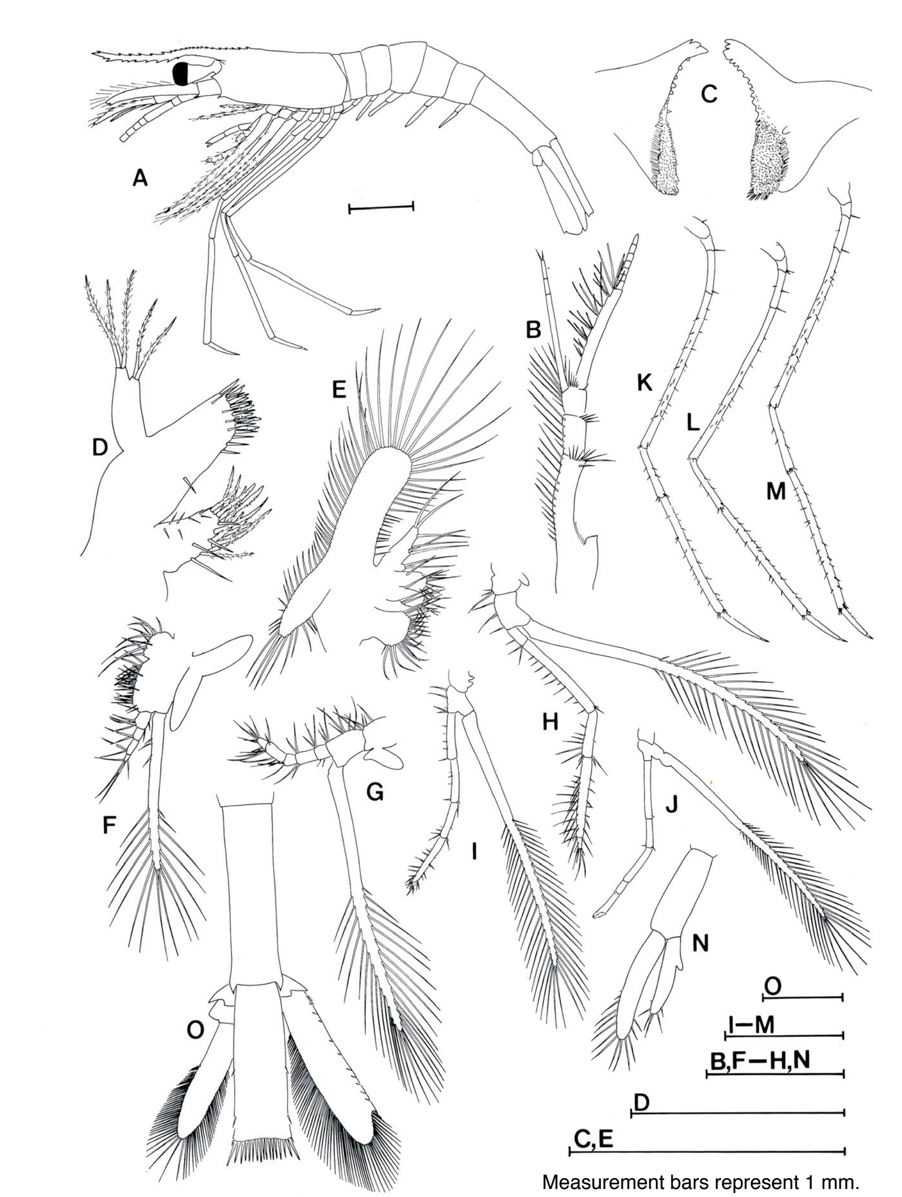


Figure 5

Sixth stage

Carapace (Fig. 6A) CL, 4.0 mm (SD: 0.21, n=48); adult-like.

Antennule (Fig. 6B) Inner flagellum as long as outer flagellum; inner flagellum with multisegments; outer flagellum with numerous segments.

Mandible (Fig. 6C) Incisor part separated from molar process and extended anteriorly.

Maxillule (Fig. 6D) 9 terminal spines on basal endite.

Maxilla (Fig. 6E) Palp with 2, 2, 2, 1+2 spines; broad scaphognathite with narrow posterior lobe bearing 3 long setae.

First maxilliped (Fig. 6F) Exopodite with 4+2, 2, 2 3 long and 1 short spines.

Second maxilliped (Fig. 6G) Basal endite with 2 long spines; vestigial dactylus.

Third maxilliped (Fig. 6H) Propodus armed with many spines; dactylus with 2 spines.

Pereiopods (Fig. 6, I–M) 1st pereipods with subchelated terminal segment; 1st pereiopod with slightly expanded ischium.

Pleopods (Fig. 6N) Endopod and exopod with numerous plumose natatory setae; endopod with epipod almost adult-like.

Uropods (Fig. 6O) Biramous; larger than those of fifth stage; adult-like.

Telson (Fig. 6O) Telson with 20 terminal spines and 4 pairs of lateral spines.

Discussion

The first stage larva of *Pandalopsis dispar* described by Berkeley (1930) is identical to the larva described in the present study. However, we found that she overlooked some important characteristics. She described the first stage larva as having 24 setae on the margin of the telson. We found, however, that the number of setae is variable, and that the larvae have 11+12, 12+12, or 11+11 marginal setae. Of these, 11+12 pairs are more common than the others.

Berkeley (1930) described the fifth stage based on plankton materials. In the present study, what was described by Berkeley (1930) as the fifth stage larva turned out to be the sixth stage because the larvae of this stage have fully developed pleopods. Although the larvae of the fifth stage have somewhat natatory setose on their pleopods, they appear not to be completely functional. Compared to the larvae of *P. japonica*, *P. dispar* has one more stage than that of *P. japonica*. The pleopod development of *P. japonica* from the fourth stage to the fifth stage is very obvious, whereas that of *P. dispar* has another stage and the changes in its features between the fourth and sixth stages are easily seen.

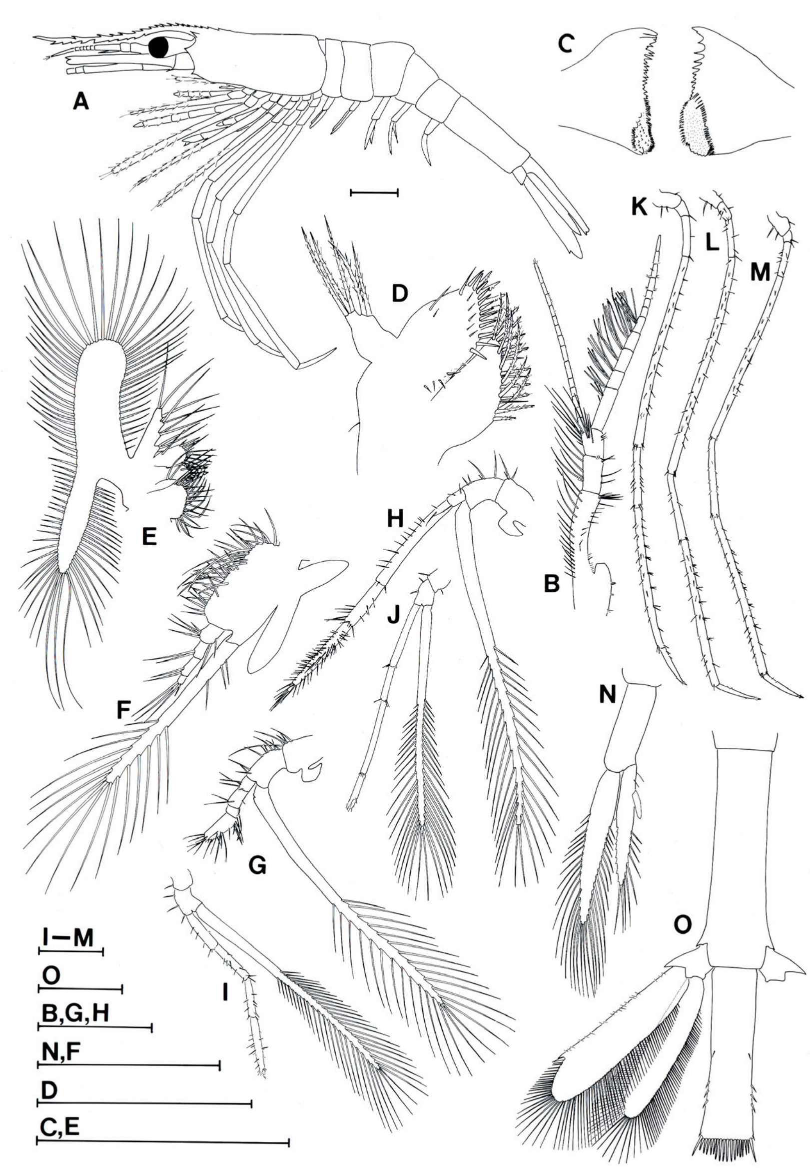
The major characteristics of the six larval stages of *P. dispar* are summarized in Table 2. This table can be used for the identification of the larval stages of this species. Komai (1994) reviewed the morphological characters of the first larval stage of three *Pandalopsis* spp.: *P. dispar, P. coccinata,* and *P. japonica*. The larvae of *P. dispar* at this stage are quite different from those of the other two species. The larvae of *P. dispar* have a triangular telson, whereas those of *P. coccinata* and *P. japonica* have a semicircular telson.

The adults of the genus *Pandalopsis* differ from those of other pandalid shrimps by having a laminated expansion on the first pereiopod (Schmit, 1921; Butler, 1980). This character is also present in larvae of *P. coccinata* and *P. japonica,* whereas it is not present in larvae of *P. dispar*. From the third stage the ischium does indicate expansion, however, it is not distinctive. It is assumed that in *P. dispar,* the expansion should be distinctive after the larval stages.

In *P. coccinata* and *P. japonica* the ischium of the first pereiopod has a laminated expansion; however, in *P. dispar* it has no lamination. The structure of the ischium of the first pereiopod can be a diagnostic feature of *P. dispar* in addition to the shape of the telson.

Interspecific variation in the larval stages of pandalid shrimp is large, ranging from three to thirteen stages (Rothlisberg, 1980; Komai and Mizushima, 1993). Haynes (1980, 1985) assumed that *P. dispar* might have seven pelagic stages, or at least more than four. The present study has determined that *P. dispar* has five zoeal stages prior to the juvenile stage.

Pandalopsis dispar is one of the four principal target species of shrimp trawl fisheries in both offshore and inshore areas of the NE Pacific Ocean (PICES, 2001) but has undergone very large fluctuations in abundance, particularly in Alaska where it was reduced to extremely low levels during the late 1980s and through the 1990s. These fluctuations appear to have been associated first with climate fluctuations (Anderson, 2000), and second with intense harvesting (Oresanz et al., 1998). Anderson (2000) has suggested that pandalid shrimp population changes are one of the early in-



Measurement bars represent 1 mm.

Figure 6

Table 2

Major characters of *Pandalopsis dispar* larvae.

Characters		Larval stage[1] 1	2	3	4	5	6 (postlarva)
Antenna flagellum	Inner	One strong spine	One peduncle with a few small spines	2 segments	2 segments	3 segments	Multisegmented over 14
	Outer	Not segmented	Slightly developed	2 segments	6 segments	7 segments	12 segments
Telson		12+11, 12+12, or 11+11		10 pairs of terminal spines, 2 pairs of uropods	One spine on each midlateral margin	2 spines on each lateral margin	4 spines on each lateral margin
Pleopod development		Wide as much as long	Longer than wide	Almost separated lobes	Longer lobes than those of stage 3	Lobes separated completely with natatory setae	Adult-like, with many natatory setae on both lobes

[1] Eyes of the first stage are sessile on carapace, whereas those of the second and later stages are stalked.

dicators of shifts in marine communities in this region. Orensanz et al. (1998) have suggested it is important to recognize that crustacean stocks can have multiscale spatial structures; species have possibly both widely distributed populations (such as in the oceanic offshore) and populations with discrete and localized distributions (as may occur in the nearshore inlets).

The ability to distinguish the larval stages of *Pandalopsis dispar* from routine plankton samples is therefore of use in studying both these problems of population fluctuations and population distributions. Early identification of trends in strong versus weak year classes can provide rapid indications of possible changes in large-scale climate conditions. Unambiguous identification of planktonic stages of *P. dispar* is also essential for studies of the spatial structure of its populations, for studies of transport pathways and potential mixing rates among populations, and ultimately for understanding the metapopulation structure of these populations. This latter point is critical for the development of improved management approaches, which may include identification of reproductive refugia (Orensanz et al., 1998).

Acknowledgments

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