Bull. Fac. Fish. Hokkaido Univ.
52(2), 61-65, 2001.

Notes on Early Development and Secondary Sexual Characteristics of the Mesopelagic Amphipod *Primno abyssalis* (Hyperiidea : Phrosinidae)

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Abstract

Early development and expression of secondary sexual characteristics of the mesopelagic hyperiid amphipod *Primno abyssalis* (formerly *P. macropa*) from the Oyashio region are described and illustrated. The toothed carpus of peraeopod 5, a marked morphological character of this species, becomes evident at Instar 2. Juveniles in females' marsupia are released into the surrounding water at Instar 3. External sexual characters, such as oostegites for females and extended first antenna for males, become evident from Instar 8 in females and Instar 7 in males. Mature females, characterized by fully developed oostegites larger than the gills, were observed in Instars 13-18. Mature males, characterized by fully extended first antennal flagella, were observed in Instars 10-12.

Key words: Mesopelagic, Amphipod, Early development, Secondary sexual characteristics, *Primno abyssalis*

The amphipod *Primno macropa* was long regarded as monotypic, until its revision by Bowman (1978), who distinguished four species: *P. macropa, P. brevidens, P. latreillei* and *P. johnsoni*). Bowman (1985) further divided *P. macropa* into *P. macropa* and *P. abyssalis*, and a new species, *P. evansi*, was identified by Sheader (1986). *P. macropa* is distributed in the Southern Ocean, and *P. abyssalis* is distributed in the mesopelagic zone of the northern North Pacific and its marginal seas (Bowman, 1985; Vinogradov, 1992).

Primno abyssalis (formerly *P. macropa*) is a carnivore and feeds on euphausiids (Ikeda, 1995). Predators on *P. abyssalis* include salmon (Fukataki, 1967, 1969), walleye pollock (Kooka et al., 1997) and the Japanese common squid (Okiyama, 1965). Despite their possible importance in the trophodynamics of pelagic food webs, little is known about the biology and ecology of *P. abyssalis* (cf. Ikeda, 1995). For hyperiid amphipods, a marked external (=secondary) sexual character of females is the development of oostegites; four pairs of each arise from the posterior inner margin of the coxa of peraeopods 2-5 to jointly form a chamber (=marsupium). The function of the chamber is to retain eggs or newly hatched juveniles (Kane, 1963). The marked external sexual characters of male hyperiids are the extended first or second antenna and the excavated organs on the urosome (Kane, 1963; Sheader, 1981).

Previously, the presence of oostegites and extended first antenna were used as diagnostic features of females and males, respectively, of *Primno abyssalis* by Bowman (1978). Bowman's (1978) description is useful for distinguishing juveniles, adult females and adult males, but there is no information about the early development of this species or about the secondary sexual characters of immature females and males. In the present study, we describe and illustrate the eggs, early juvenile instars, and development of oostegites (in females) and the first antenna (in males) in *P. abyssalis* based on the instar number system established by Ikeda (1995) for this species.

Specimens were collected by oblique tows of bongo nets from about 500-900 m depth to the surface in the Oyashio region within the rectangle defined by 41°30′ to 42°30′ N and 145°00′ to 146°00′ E from July 1996 to July 1998. They were preserved immediately in 10% buffered formalin seawater upon the retrieval of the net for later observations. In the land laboratory, eggs and larvae in the females' marsupia were removed, and immature and mature specimens were sorted for morphological observations under a dissecting microscope fitted with a Nikon Digital Camera E-910.

The eggs are violet and oval. The long and short diameters of the eggs are 0.57 and 0.45 mm, respectively. Eggs are covered with a thin membrane and contain many oil globules of various sizes (Fig. 1A).

At the late embryonic stage, body segments are formed, and appendage rudiments (antennae, peraeopods, pleopods and uropods) are visible through the thin egg membrane (Fig. 1B). The pleopod rami of specimens ready to hatch have one segment (Fig. 2A).

The newly hatched juveniles (Instar 1) are curled strongly and each body segment is slightly developed (Fig. 1C). The number of pleopod rami remains unchanged (2-segmented rami of the next instar are visible

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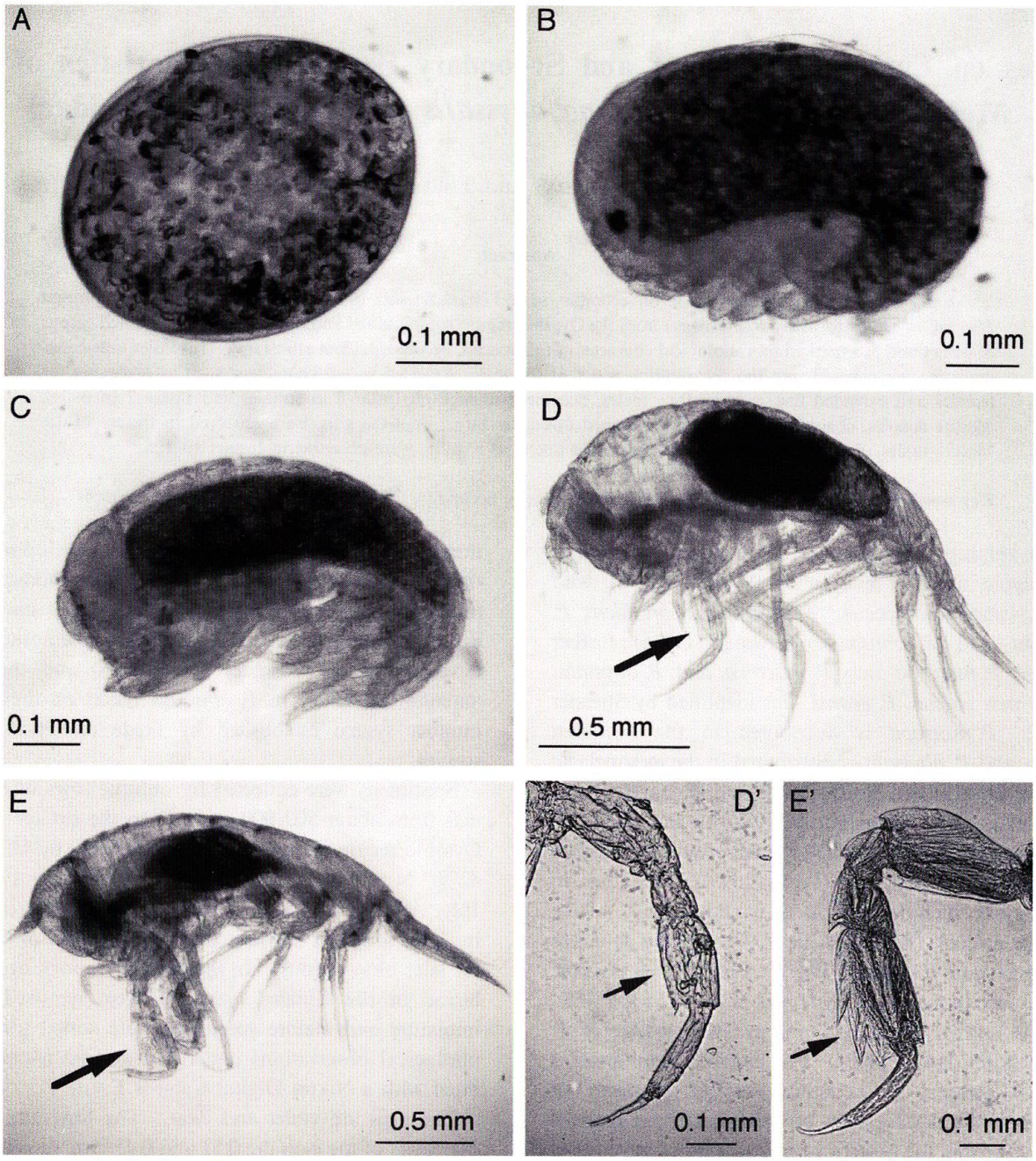

Fig. 1. *Primno abyssalis.* (A) egg containing many oil globules. (B) late embryonic stage. (C) Newly hatched Instar 1 juvenile. (D) Instar 2 juvenile. (D′) The carpus of peraeopod 5 of Instar 2 (allowed in (D′)). (E). Instar 3 juveniles (the first free-swim*m*ing instar). (E′) The toothed carpus of peraeopod 5 or Instar 3 (allowed in (E)).

through the thin cuticle, Fig. 2B). The extended body length (from the base of the first antenna to the distal end of the telson) of Instar 1 is about 1.25 mm. After Instar 1 molts to Instar 2, the body size increases and each appendage becomes more developed. The toothed carpus of peraeopod 5, which is a marked morphological character of the genus *Primno*, starts to develop from Instar 2. The number of segments of pleopod rami increases to two (Fig. 2C). At Instar 3, which is the stage when juveniles are released into the surrounding water, the body extends almost fully, and the development of the appendages, including the toothed carpus, is nearly complete (Fig. 1E). The pleopod rami of Instar 3 have three segments.

Oostegites occur from Instar 8. They are small in Instar 8 females (Fig. 3A), and increase in size gradually through sequential moltings (Fig. 3B). Mature females, which have fully developed oostegites larger than the gill (Fig. 3C), were seen at Instar 13 to 18.

The antennae of males become first evident at Instar 7.

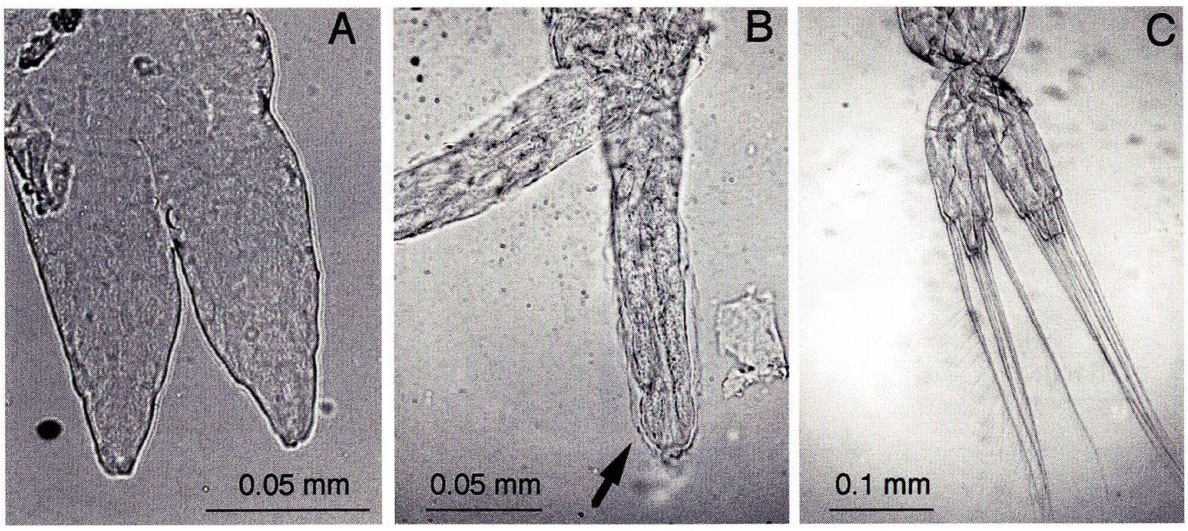

Fig. 2. *Primno abyssalis.* Development (segmentation) of the first pleopod rami. (A) Late embryonic stage. (B) Instar 1.2-segmented rami of the next instar is seen through thin cuticle (allowed). (C) 2-segmented pleopod rami of Instar 2.

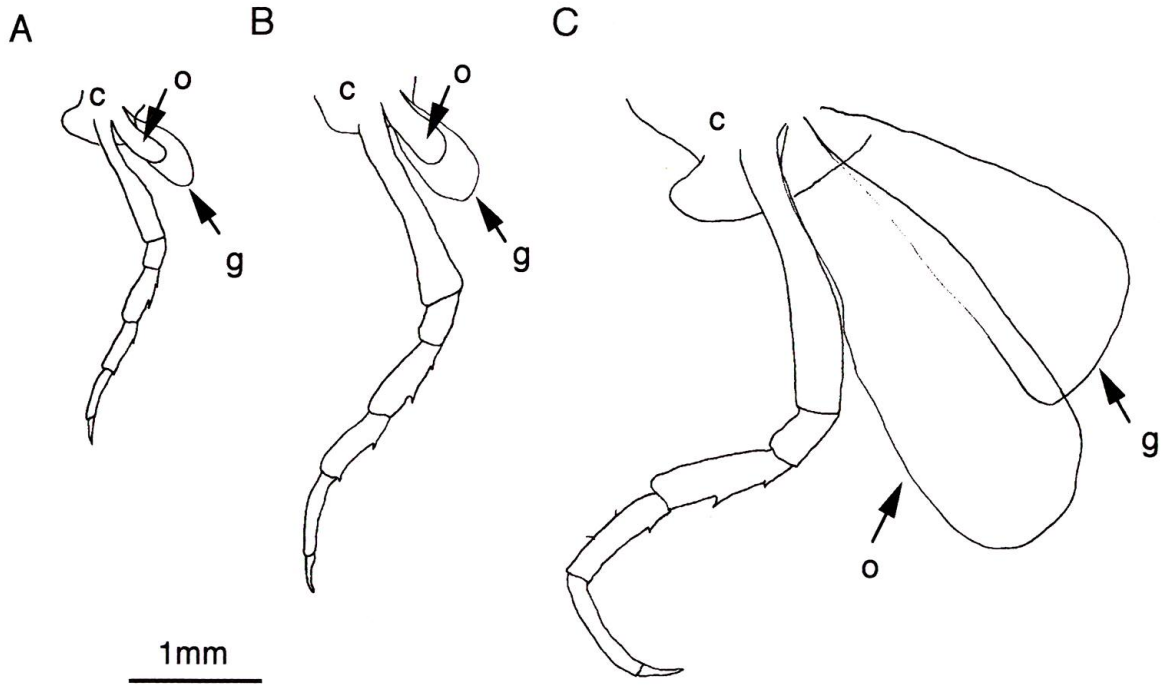

Fig. 3. *Primno abyssalis.* (A)-(C) Development of oostegite (o) and gill (g) on the coxa (c) of right peraeopod 4 through Instar 8 (immature), Instar 11 (immature) and Instar 13 female (mature).

The antennal bases are enlarged but not segmented at Instar 7 (Fig. 4A). In Instar 8 to Instar 9 males, the antennal bases are enlarged further, but the antennal flagella are not yet fully extended (Fig. 4B). Mature males, which have fully extended first antennal flagella and an enlarged spatulate first antennal base with a row of dense seta (Fig. 4C), were identified at Instar 10 to Instar 12.

The morphology of newly hatched juveniles in females' marsupia and the development patterns of oostegites in females of *Primno abyssalis* are almost identical to those of other planktonic hyperiid amphipods such as *Themisto gaudichaudii* (Kane, 1963) and *T. compressa* (formally *T. gaudichaudii* ; Sheader, 1977). A large difference between *Themisto* spp. and *P. abyssalis* is the expression of the secondary sexual characters of males. For *Themisto* spp., the male characters are a long, multi-articulated second antenna, and ex-

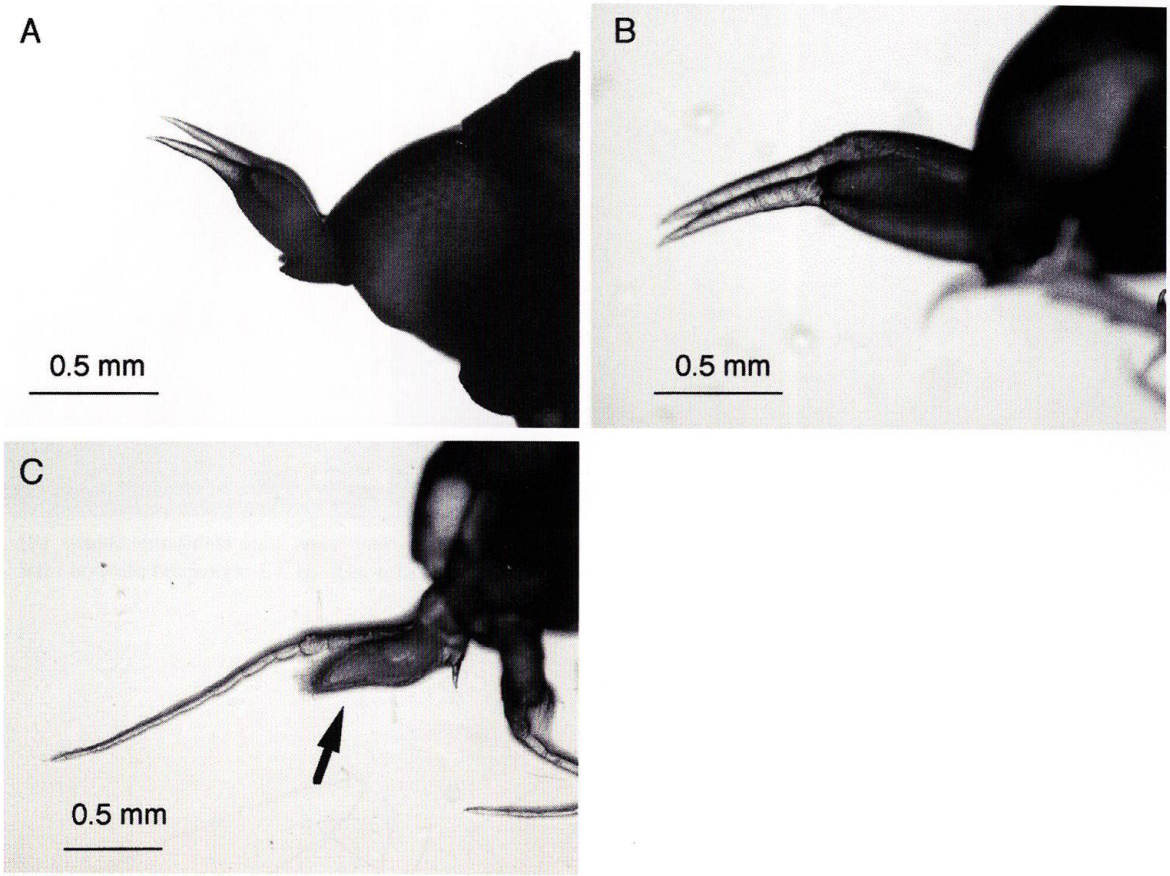

Fig. 4. *Primno abyssalis.* Development of the first antenna in the male. (A) Enlarged antennal bases at Instar 7 (immature). (B) Segmented antennal flagella at Instar 9 (immature). (C) Fully extended antennal flagella, enlarged first antennal base, and bearing a row of dense seta (allowed) at Instar 10 (mature).

cavated organs that develop opposite to one another on the inner margin of the rami of the first pair of urosomes, while mature males of *P. abyssalis* have an extended second antenna, which is shorter than the first antenna, and *P. abyssalis* has no excavated organs on the inner margin of the rami of the first pair of urosomes. The function of the excavated organs in *Themisto* spp. is to transfer sperm bundles to females (Sheader, 1977, 1981). The mating behavior of *P. abyssalis,* including the mechanisms of sperm transfer, has not been explored yet.

Acknowledgment

We are grateful to Dr. A. Tsuda of Hokkaido National Fisheries Research Institute for supplying materials used in this study, and Dr. J.R. Bower for his critical reading of the manuscript.

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