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Abundance, growth and life cycle of the mesopelagic amphipod *Primno abyssalis* (Hyperiidea: Phrosinidae) in the Oyashio region, western subarctic Pacific

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Abstract Abundance and life-cycle features of the mesopelagic hyperiid amphipod *Primno abyssalis* (formerly *P. macropa*) in the Oyashio region, western subarctic Pacific, were investigated using samples collected between July 1996 and July 1998. *P. abyssalis* was collected throughout the entire survey period, with abundance peaks occurring in spring to autumn. While all maturity stages of males and females were observed throughout the study period, the peak reproduction season was in summer. Instar analysis based on the segment number of the pleopod rami indicated that hatched juveniles molted 10 times before becoming adult males and 13 times before becoming adult females. Judging from the dry and ash-free dry weights of each instar, males and females continued to feed throughout the final instar stage. Based on cohort analysis of seasonal samples and laboratory observations on molting frequencies, growth in body length of *P. abyssalis* was linear with time, and estimated generation lengths were 2.3–3.8 years for females and 1.4–1.9 years for males. Brood size of females ranged from 66 to 337 and increased with increasing female body length. Lifetime fecundity, calculated as the sum of six successive broods, was 1,004. Compared with *P. abyssalis* in the southern Sea of Japan, those in the Oyashio region have a larger number of adult instars (six versus five for females, three 3 vs one for males), a lower growth rate (0.014 mm day^{-1} vs 0.021 mm day^{-1}), and mature earlier (instar 13 vs instar 15 for females; instar 10 vs instar 11 for males). These characteristics are considered to be advantageous life-history traits to counteract higher niche competition within the mesopelagic community and higher predation pressure by mesopelagic fishes in the Oyashio region than in the Sea of Japan.

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Introduction

There are six known species of pelagic amphipods in the genus *Primno*: *P. macropa*, *P. brevidens*, *P. latreillei*, *P. johnsoni*, *P. abyssalis*, and *P. evansi* (Bowman 1978; Sheader 1986). *P. macropa* is distributed in the Southern Ocean; *P. brevidens* occurs in temperate waters; *P. latreillei*, *P. johnsoni*, and *P. evansi* occur in tropical to subtropical waters; and *P. abyssalis* occurs in the mesopelagic zone of the northern North Pacific and its marginal seas (Bowman 1985; Sheader 1986; Vinogradov 1992).

Primno abyssalis (formerly *P. macropa*) is a typical carnivore, preying on other zooplankton (Bowman 1985; Ikeda 1995). In turn, it is an important prey of various predators, e.g., salmon, *Oncorhynchus gorbuscha* and *O. masou* (Fukataki 1967, 1969), walleye pollock, *Theragra chalcogramma* (Kooka et al. 1997), the Japanese common squid, *Todarodes pacificus* (Okiyama 1965), Pacific pomfret, *Brama japonica* (Kono 1983) and mesopelagic fishes, such as *Diaphus theta*, *Stenobrachius leucopsarus* (Moku et al. 2000) and *Gonostoma gracile* (Uchikawa et al. 2001). Despite its possibly important role in the pelagic trophodynamics in the northwest Pacific, there is little information presently available on the abundance and life cycle of *P. abyssalis* from areas outside the Sea of Japan (Ikeda 1995). As a habitat of pelagic animals, the Sea of Japan is different from the subarctic Pacific in several respects, including near-zero temperatures in its mid-layers, poor pelagic fauna yet predominance of a few species, and absence of a truly bathypelagic community (Zenkevitch 1963; Vinogradov 1970). Ikeda (1995) suggested a possible reflection of these sets of biotic and abiotic environmental conditions of the Sea of Japan in the life cycle of *P. abyssalis*, but no comparable information from other regions has been available to date.

The present study investigates the abundance, growth, generation length and brood size (BS) of *P. abyssalis* based on the analysis of seasonal samples collected from the Oyashio region, western subarctic Pacific. Laboratory rearing experiments were conducted to confirm the growth pattern derived from seasonal population-structure analysis. Some differences in the life history parameters of *P. abyssalis* living in the Oyashio region and those in the Sea of Japan (Ikeda 1995) are noted and discussed in the light of the environmental dissimilarities between these regions.

Materials and methods

Field sampling

Sixteen seasonal samplings were carried out in the Oyashio region off southeast Hokkaido within a rectangle defined by 41°30′N–42°30′N and 145°00′E–146°00′E (hereafter referred to as "site H"; Fig. 1) on board the F.R.V. "Hokko Maru" and "Tankai Maru" of the Hokkaido National Fisheries Research Institute, and the F.R.V. "Hokushin Maru" of the Hokkaido Fisheries Experimental Station at Kushiro, between July 1996 and July 1998. At each sampling, oblique tows were made with paired bongo nets (mouth opening 70 cm, mesh size 333 μm) from about 500 m (range: 386–900 m) to the surface (Table 1). This depth range sampled the known depth range of *Primno abyssalis* [75–300 m in the Oyashio region (K. Hoshino, personal communication), 200–400 m in the southern Sea of Japan (Ikeda 1995)]. The depth that the net reached was recorded with a depthmeter (Rigosha), and the volume of water sampled was estimated using a flowmeter (Rigosha). Zooplankton samples were preserved immediately in 10% buffered formalin–seawater on board the ship. Temperature and salinity profiles were determined with a CTD system at each net-sampling station.

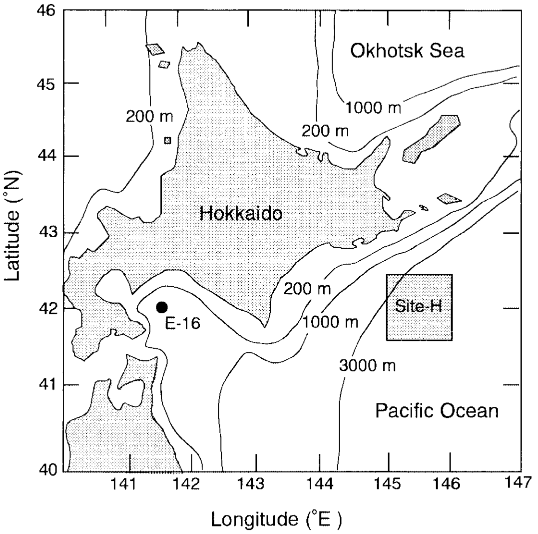


Fig. 1. Location of sampling area (site H, *shaded box*) and station E-16 (*dot*) in the western subarctic Pacific Ocean

Table 1. Sampling data of oblique tows of bongo nets in the Oyashio region from July 1996 to July 1998

Year	Date	Time of day	Maximum net depth m
1996	8 July	23:40–00:31	508
	2 Aug	18:58–19:38	479
	3 Oct	20:12–21:03	No data
	5 Dec	05:15–06:01	488
1997	13 Jan	23:05–23:58	851
	13 Mar	22:13–00:07	574
	15 Apr	20:25–21:30	521
	13 May	00:13–01:00	734
	4 July	01:35–02:26	435
	22 Aug	02:00–02:51	748
	3 Oct	22:49–22:56	685
1998	17 Jan	18:50–20:07	883
	14 Mar	23:06–00:01	386
	19 Apr	20:07–21:07	408
	15 May	18:42–19:41	900
	7 July	02:14–03:00	448

At the land laboratory, the entire zooplankton samples were weighed (wet biomass). *P. abyssalis* specimens were then sorted from the samples and weighed (wet biomass) to calculate the proportion it formed of the total zooplankton biomass.

Maturity stage and size

Amphipods have no larval stage (i.e., hatchlings are morphologically similar to adults; see Hartnoll 1985). The sexual maturity of hyperiid amphipods can be determined from secondary sexual characters, such as the development of oostegites in females, and the extended first or second antenna in males (Kane 1963; Sheader 1981). Previously, the presence of oostegites and extended first antennae was used by Bowman (1978) as a diagnostic feature of mature females and males, respectively, of *P. abyssalis*. Diagnostic features given for mature specimens of *P. abyssalis* by Bowman (1978) were extended to its immature specimens by Yamada and Ikeda (2001). In the present study, we classified the specimens into the following three maturity stages using Yamada and Ikeda's definitions: "juveniles" – no secondary sexual characters evident; "immature adults" – oostegites present on coxae of peraeopods 2–5, but not fully developed beyond the gill (females), or the first antennal bases are enlarged, but the antennal flagellae are not fully extended (males); and "adults" – oostegites become larger than gills (females), or having fully extended first antennal flagellae and enlarged spatulate first antennal base which bear a row of dense setae (males).

Body length (BL; in millimeters) was measured under a dissecting microscope to the nearest 0.05 mm as the maximal distance between the tip of the head to the distal end of the uropod of the straightened body. The wet weight (WW) of each specimen was determined after rinsing briefly in distilled water and blotting on a filter paper. The specimens were subsequently dried at 60°C for 6 h to obtain the dry weight (DW). Ash content was determined by weighing the specimens before and after incinerating at 480°C for 5 h. Ash-free dry weight (AFDW) was computed from DW by subtracting the ash weight.

Instar analysis

For amphipods that lack morphological development stages, the number of segments of the pleopod rami can be used as a marker of instar number. For *P. abyssalis*, the number of segments in the third pleopod rami has been used as the marker of the instar number (Ikeda 1995). Our preliminary examination of the exopod and endopod of the first and third pleopods of 140 specimens of various sizes (BL range 1.3–19.9 mm) revealed that the number of the segments of the exopod was the same for the first and third pleopods. A similar examination of the number of segments of the endopod of the first and third pleopod rami showed a difference of ± 1 compared to the segment count for the exopod of the same specimens. With this limitation in mind, the number of segments of the exopod of the first or third pleopod was used to determine the instar number of *P. abyssalis* in the present study.

Brood size

Female specimens used for counting eggs or early juveniles (instars 1 and 2) in their marsupia were collected at two stations (41°30′N, 147°47′E and 43°01′N, 151°21′E) during 29–30 July 2000, in oblique tows of the bongo nets at night. To avoid possible losses during preservation, eggs and larvae were removed from the females' marsupia immediately after collection and preserved.

Laboratory rearing experiment

Specimens used for the laboratory rearing experiment were collected occasionally from vertical tows (0–500 m) with a ring net (80-cm mouth diameter) or oblique tows (wire length 500 m) with a bongo net at station E-16 (bottom depth about 500 m, Fig. 1) Live specimens were sorted on board, maintained in water at a temperature of about 5°C and transported to the land laboratory. At each sampling, seawater was collected with Van Dorn or Niskin water samplers from 100 m depth and kept in 20-l containers for use in experiments. Live specimens were placed individually in 50–1,000-ml glass containers filled with seawater. Experiments were run in the dark at 2°C. As food, cut whelk (*Neptunea lyrata*) meat was provided in excess in the following experiments. Seawater in the containers was changed every 5–10 days with each new preparation of food. Glass containers were filled with seawater to the top to prevent trapping amphipods at the water surface. The containers were examined daily for molts. Molts, when found, were removed from the container, and the number of the pleopod segments was determined.

Results

Hydrography

Site H is just south of the main stream of the Oyashio Current. Over the study period, surface temperatures ranged from 2°C (March and April 1997, and March 1998) to 16°C (August 1996 and October 1997; Fig. 2). The Oyashio water, characterized by salinities from 33.0 to 33.3‰ and temperature below 3°C (Ohtani 1971), occurred in the upper 150 m from March to April 1997 and in March 1998. Surface temperatures above 10°C were observed in July–October 1996 and June–October 1997, when the thermocline was well established at 20 to 50 m depth. The effect of the Tsugaru Warm Current, which has salinities ranging from 33.7 to 34.2‰ and temperatures over 5°C (Hanawa and Mitsudera 1987), was seen near the 50 m depth in October 1997. Both temperature and salinity below 200 m depth were nearly constant at 2–4°C and 33.5–34.2‰ throughout the entire study period.

Abundance and population structure

Primno abyssalis occurred throughout the entire study period. It was most numerous in July–August 1996

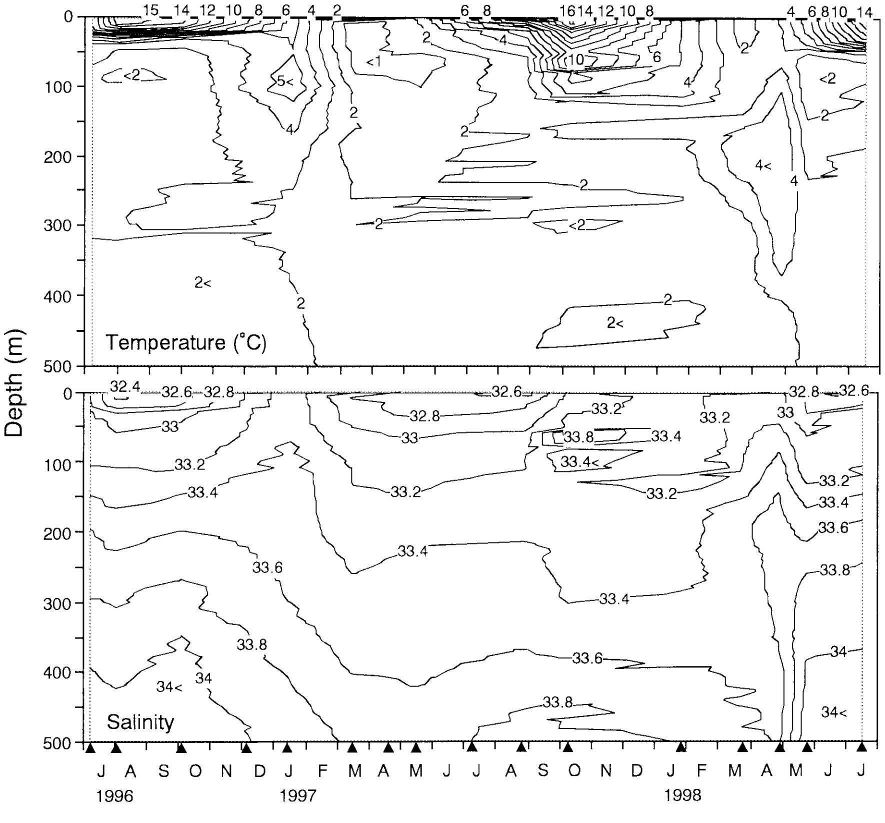


Fig. 2. Temperature (upper panel) and salinity (lower panel) profiles at the sampling station, site H. Sampling dates are indicated by *solid triangles* on the bottom abscissa

(42.1–55.9 individuals m^{-2}), May 1997 (56.7 individuals m^{-2}) and August 1997 (78.5 individuals m^{-2}), and least numerous in March 1998 (9.5 individuals m^{-2}) (Fig. 3A). Seasonal changes in its biomass were similar to the changes in numerical abundance, i.e., highest in July–August 1996 (0.35 g m^{-2}), May 1997 (0.29 g m^{-2}) and August 1997 (0.43 g m^{-2}) and lowest in January 1998 (0.08 g m^{-2}). The mean numerical abundance and biomass of *P. abyssalis* over the entire study period were 31.1 individuals m^{-2} and 0.20 g m^{-2}, respectively. *P. abyssalis* constituted 0.05–0.42% of the total zooplankton biomass, with a grand mean of 0.19% (Fig. 3B).

All maturity stages of *P. abyssalis* were observed throughout the year (Fig. 4). Among them, juveniles constituted 50% or more of the total populations during most seasons, and were especially abundant in May 1997 (86.9%). Female-to-male ratios ranged from 1:0.17 to 1:4 for immature specimens, and 1:0.33 to 1:5 for mature specimens. Mature females and males occurred throughout the year. The minimum maturity size (BL) was 11.9 mm for females (instar 13) and 7.5 mm for males (instar 10). The maximum BL were 19.8 mm (instar 18) for females and 10.4 mm (instar 12) for males.

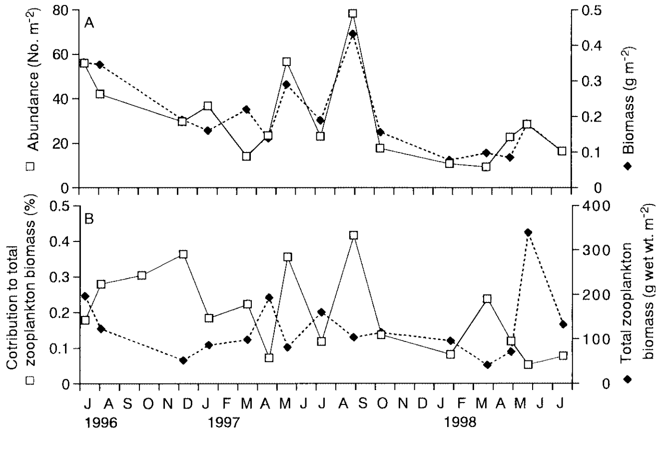


Fig. 3A, B *Primno abyssalis*. Seasonal changes in numerical abundance and biomass (**A**), total zooplankton biomass and its contribution to the total zooplankton biomass (**B**)

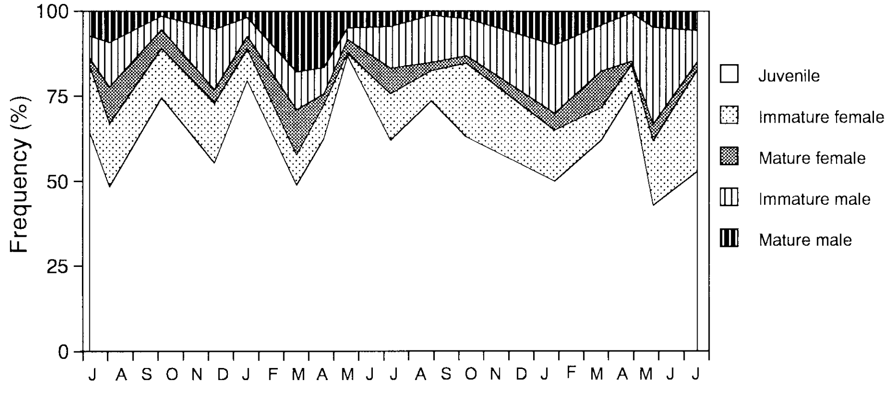
Population growth and generation length

Seasonal sequences in the size–frequency distribution of *P. abyssalis* are shown in Fig. 5. The entire BL range was divided into 0.5-mm increments. The size composition was broad on most sampling dates, with small specimens (BL < 5 mm) forming large proportions of the catches. Because of small sample size (< 201 specimens), accurate modal-size analysis was not possible for each sampling date. To overcome this problem, we divided each year into two periods: one when specimens of < 3 mm BL were abundant (July–October 1996, April–August 1997, and March–July 1998), and one when specimens of < 3 mm BL were scarce or absent (December 1996 to March 1997 and October 1997 to January 1998; Fig. 6). The sampling date of each each set of composite size-distribution data is represented by the mid-point of each designated period. Among the five composite size–frequency distributions thus obtained, a set of two to four cohorts (0+, 1+, 2+ and 3+ year) were identified. The mean BL and its standard deviation were calculated for each cohort (Table 2). The date that juveniles were released from females' marsupia was assigned as 1 January of each year to estimate the juveniles' apparent ages (Table 2). The mean BL of each cohort was then plotted against the apparent age (Fig. 7), showing that the growth in BL (Y, in millimeters) of *P. abyssalis* was linear with time (X, in days), yielding a regression equation: $Y = 0.014X + 0.523$ ($r = 0.988$, $n = 14$, $P < 0.001$). Since juveniles are released from females' marsupia at instar 3 (Yamada and Ikeda 2001), the estimated time to complete one life cycle is 2.3–3.8 years (846–1370 days) for females, and 1.4–1.9 years (527–677 days) for males. For each sex, the shortest life cycle is the development time to the youngest mature instar, and the longest one is the development time to the oldest mature instar.

Body allometry

The BL, WW, DW, AFDW, water content (% of WW) and ash (% of DW) of eggs and all instars of *P. abyssalis* are summarized in Table 3. External sexual characters became evident from instar 7 for males and instar 8 for

Fig. 4. *Primno abyssalis*. Seasonal changes in relative frequency of maturity stages at site H from July 1996 to July 1998



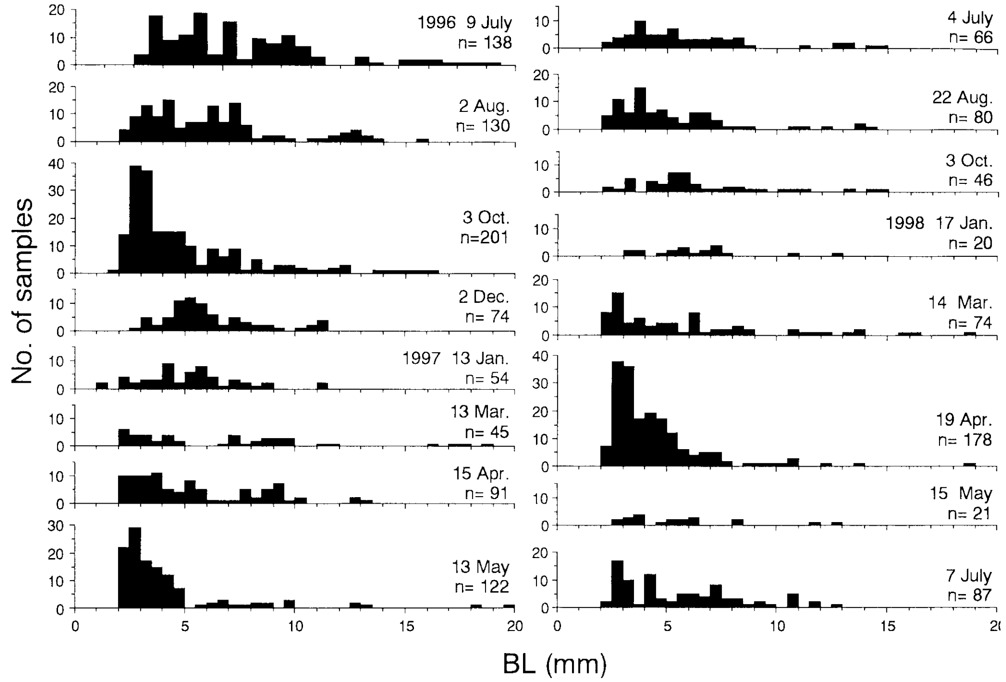


Fig. 5. *Primno abyssalis*. Seasonal sequence in size (*BL* body length, in millimeters) composition at site H, western subarctic Pacific Ocean

females. WW, DW and AFDW all increased as the instar numbers increased.

Water content varied from 69.1% (eggs) to 86.6% (instar-17 females), and ash varied from 11.2% (eggs) to 29.0% (instar-7 juveniles). Linear-regression analysis of water and ash content on instar number (eggs were assigned as instar 0 in this calculation) showed that the water component increased significantly with development ($r=0.75$, $df=23$, $P<0.001$), but no correlation was seen between ash component and instar number ($r=0.067$, $df=23$, $P=0.75$).

The relationships between BL and WW, DW and AFDW were as follows: $WW=0.023BL^{2.88}$ ($r=0.999$, $df=22$, $P<0.0001$); $DW=0.0058BL^{2.711}$ ($r=0.996$, $df=22$, $P<0.0001$) and $AFDW=0.0045BL^{2.716}$ ($r=0.994$, $df=$, $P<0.0001$).

Brood size

BS ranged from 66 to 337 and increased with increasing female BL. This relationship was $BS=27.8BL–281.4$ ($r=0.95$, $n=18$, $P<0.001$; Fig. 8).

The hyperiid amphipod genus *Primno* has been shown to have sequential broodings, each separated by moltings (Sheader and Batten 1995). Using the BS–BL relationship and the BLs of six mature female instars in Table 2, the lifetime fecundity can be calculated as the sum of the six successive broods. The lifetime fecundity of *P. abyssalis* females was thus estimated to be 1,004.

Intermolt period

The intermolt period (IP) recorded for the specimens reared at 2°C was plotted against the pre-molt instar number (Fig. 9). Female and male data could not be separated. The shortest IP, of 40 days, was recorded for instar 6 specimens, and the longest, IP of 90 days, for instar-11 specimens, although IP data were scattered to a large extent at instars 3–7. As a general pattern, IP increased slightly from instar 3 to instar 7, then increased rapidly toward instar 11 (Fig. 9).

The growth pattern in BL from instar 3 to instar 11 was estimated at 2°C, combining the IP data of respective instars (Fig. 9) with mean BL of wild specimens (Table 3). Cumulative IPs were then plotted against the mean BL of each instar (Fig. 7). Regression analysis showed that the growth in BL (Y, in millimeters) was linear with time (X, in days), yielding the regression equation $Y=0.016X+1.877$ ($r=0.989$, $n=9$, $P<0.0001$). Clearly, the estimated growth rate of *P. abyssalis* (slope of the regression line, 0.016 mm day^{-1}) is nearly the same as that derived from cohort analysis (0.014 mm day^{-1}; ANCOVA, $P=0.17$) of seasonal samples (Fig. 7).

Discussion

Seasonal changes in abundance (number) and biomass of *Primno abyssalis* at site H paralleled each other (Fig. 3), with both peaking in midsummer (July–August). While the occurrence of all maturity stages of both sexes throughout the year (Fig. 4) may indicate they reproduce year-round, the greater abundance and predominance of smaller specimens in summer (Fig. 5) suggest that the peak reproduction period at site H occurs in summer. *P. abyssalis* preys largely on planktonic crustaceans (Ikeda 1995). At site H, the biomass of *P. abyssalis* comprised only a small fraction of the total

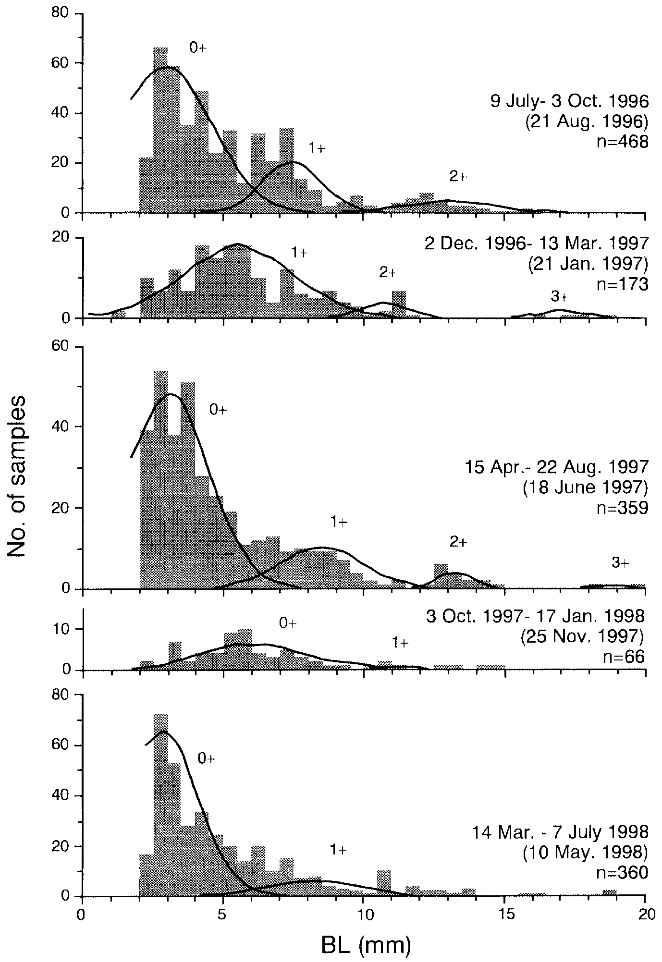


Fig. 6. Composite size–frequency distribution. Cohorts aged 0+, 1+, 2+, and 3+ years old were identified, and newly designated sampling dates are shown in parenthesis. Hypothetical frequency distribution curves are superimposed as *solid lines*

Table 2. *Primno abyssalis*. Age expressed by year and apparent days. Mean body length (*BL*) of cohorts identified in Fig. 6. For the calculation of age, in days, see text

Date	Age (years)	Days after release	BL ± SD mm
21 Aug 1996	0+	233	2.95 ± 1.66
	1+	598	7.45 ± 0.80
	2+	963	13.10 ± 1.76
21 Jan 1997	1+	386	5.51 ± 1.99
	2+	751	10.81 ± 0.80
	3+	1116	17.11 ± 0.93
18 June 1997	0+	168	3.05 ± 1.45
	1+	534	8.51 ± 1.43
	2+	899	13.25 ± 0.67
	3+	1264	18.77 ± 1.25
25 Nov 1997	0+	328	6.11 ± 1.90
	1+	694	11.24 ± 0.69
10 May 1998	0+	129	2.82 ± 1.29
	1+	494	8.12 ± 1.55

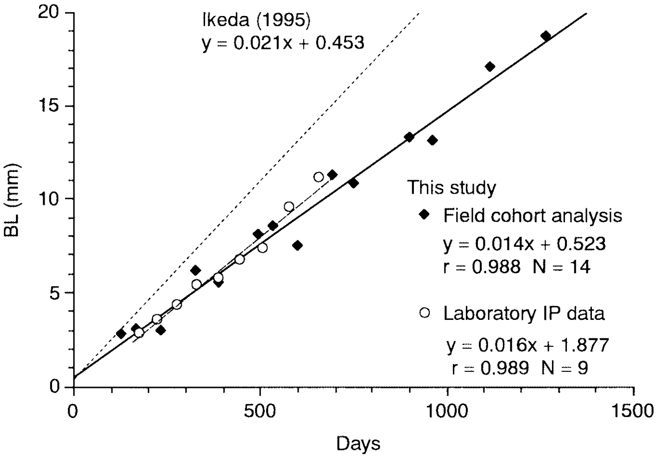


Fig. 7. *Primno abyssalis*. Growth estimated from mean body length and of each cohort at site H given in Fig. 6. Apparent age (days) of each cohort was calculated assuming 1 January to be the date of release from the females' marsupia. Growth estimated from IP data on laboratory-reared specimens in this study (note *X*-axis shifted arbitrarily to facilitate comparison), and Ikeda's (1995) data derived from cohort analysis of field samples from the Japan Sea are superimposed

zooplankton (mean 0.19%; Fig. 3), indicating that the abundance of potential prey crustaceans is unlikely to be related to the increased reproductive activity of this species in midsummer. A close association of hyperiid amphipods with gelatinous zooplankton has been documented (Harbison et al. 1977; Laval 1980; Madin and Harbison 1997). Daniel (1973) observed *Primno* sp. associated with a siphonophore *Abylopsis tetragona*. Williams and Robins (1981) noted a high abundance of a hydromedusa *Aglantha digitale* before the abundance of the amphipod *Themisto* peaked in the North Atlantic Ocean. According to Takahashi and Ikeda (unpublished), the hydromedusa *A. digitale* occurs largely at depth < 500 m and at site H forms a prominent abundance peak in July, 1–2 months prior to the high time of reproduction of *P. abyssalis*, implying a possible association of the reproduction events of these two species at site H.

In the present study, the growth in BL of *P. abyssalis* was postulated to be linear with time both from cohort analysis of seasonal samples and laboratory rearing experiments (Fig. 7). Comparing the two growth equations, it is clear that the growth rates (the slope of the equation) derived from the two methods are very similar to each other (Fig. 7). One other study on the growth and maturation patterns of *P. abyssalis* has been conducted at Toyama Bay, southern Sea of Japan (Ikeda 1995). The life-cycle features of *P. abyssalis* occurring at Toyama Bay and at site H are similar in that the growth in length is linear, males mature earlier than females, and the minimum generation lengths of males (0.8–0.9 years) and females (1.8 years) are identical. However, the two populations differ in several respects (Table 4). First, the overall growth rate in length of the site H population is less than that of the Toyama Bay population (0.021 mm day^{-1}; ANCOVA, $P < 0.0001$). Second, the sizes of eggs and respective instars of site H specimens are smaller than those of Toyama Bay spec-

Table 3. *Primno abyssalis*. Body length (*BL*), wet weight (*WW*), dry weight (*DW*), ash-free dry weight (*AFDW*), water and ash content (%) of eggs and respective instars. Means ± SD (*LD* long diameter; *SD* short diameter for eggs) with the number of replicates in parenthesis

Stage	Instar (number)	BL mm	wet weight mg	DW mg	AFDW mg	Water %	Ash %
Egg	– (9)	LD 0.57 ± 0.01					
		SD 0.45 ± 0.01	0.071 ± 0.03	0.002 ± 0.004	0.020 ± 0.004	69.1 ± 9.5	11.2 ± 3.2
Juvenile	1 (4)	1.25	0.045 ± 0.02	0.016 ± 0.003	0.013 ± 0.003	63.0 ± 8.8	17.5 ± 5.9
	2 (9)	1.78 ± 0.06	0.13 ± 0.03	0.028 ± 0.008	0.023 ± 0.008	77.4 ± 5.6	20.0 ± 7.2
	3 (6)	2.53 ± 0.10	0.32 ± 0.05	0.065 ± 0.018	0.055 ± 0.017	79.4 ± 4.9	16.8 ± 4.9
	4 (8)	1.86 ± 0.05	0.44 ± 0.04	0.074 ± 0.013	0.054 ± 0.012	83.0 ± 2.8	26.7 ± 5.7
	5 (5)	3.57 ± 0.09	0.92 ± 0.10	0.166 ± 0.018	0.120 ± 0.016	81.9 ± 1.0	27.9 ± 2.7
	6 (7)	4.43 ± 0.19	1.80 ± 0.23	0.334 ± 0.025	0.248 ± 0.022	81.3 ± 1.4	25.8 ± 2.5
	7 (5)	5.45 ± 0.07	2.96 ± 0.01	0.475 ± 0.107	0.342 ± 0.113	83.9 ± 3.5	29.0 ± 7.8
Female immature	8 (6)	5.80 ± 0.24	3.92 ± 0.34	0.79 ± 0.14	0.667 ± 0.13	79.9 ± 11	15.9 ± 1.3
	9 (8)	6.76 ± 0.37	5.89 ± 0.71	1.07 ± 0.34	0.864 ± 0.32	82.1 ± 4.5	20.5 ± 5.6
	10 (5)	7.42 ± 0.73	7.53 ± 12.05	1.40 ± 0.55	1.115 ± 0.49	82.0 ± 4.1	21.9 ± 5.9
	11 (6)	9.55 ± 0.70	16.57 ± 4.11	3.56 ± 1.13	3.019 ± 1.03	78.8 ± 4.8	16.4 ± 5.0
	12 (5)	11.14 ± 0.42	25.26 ± 3.34	5.20 ± 1.31	4.34S ± 1.26	79.6 ± 3.2	17.0 ± 3.6
Female mature	13 (5)	12.36 ± 0.36	31.49 ± 4.89	5.21 ± 1.32	4.284 ± 1.21	83.6 ± 2.7	18.3 ± 19
	14 (5)	14.22 ± 0.58	48.33 ± 5.81	8.75 ± 2.62	7.118 ± 2.51	82.2 ± 3.5	19.9 ± 6.2
	15 (7)	14.97 ± 0.95	56.35 ± 6.72	10.85 ± 4.62	8.985 ± 4.00	81.7 ± 4.3	18.0 ± 3.9
	16 (4)	16.90 ± 0.55	81.59 ± 8.71	12.73 ± 2.60	10.242 ± 2.49	84.4 ± 2.6	20.1 ± 3.4
	17 (2)	18.70 ± 0.71	105.14 ± 6.67	14.05 ± 1.76	10.910 ± 1.96	86.6 ± 15	22.6 ± 4.2
	18 (3)	19.70 ± 0.20	123.05 ± 4.09	17.31 ± 4.52	13.912 ± 4.16	86.0 ± 3.3	20.2 ± 5.4
Male immature	7 (5)	4.74 ± 0.47	2.20 ± 0.66	0.34 ± 0.12	0.264 ± 0.10	84.8 ± 2.6	22.1 ± 2.8
	8 (8)	5.63 ± 0.41	3.71 ± 0.94	0.61 ± 0.33	0.491 ± 0.29	84.0 ± 5.2	21.3 ± 4.2
	9 (8)	6.54 ± 0.28	5.35 ± 0.83	0.89 ± 0.23	0.686 ± 0.21	83.3 ± 4.2	23.5 ± 6.7
Male mature	10 (4)	7.90 ± 0.14	7.64 ± 1.17	1.44 ± 0.22	1.131 ± 0.17	80.9 ± 3.3	21.3 ± 2.0
	11 (5)	8.88 ± 0.63	11.66 ± 172	1.97 ± 0.53	1.363 ± 0.45	82.9 ± 4.0	23.0 ± 4.4
	12 (5)	10.00 ± 0.41	17.94 ± 2.54	2.50 ± 0.43	1.804 ± 0.40	86.0 ± 2.5	28.2 ± 5.9

imens. Third, the earliest mature instars in the site H population are 10 for males and 13 for females, compared with 11 for males and 15 for females in the Toyama Bay population.

From studies of the seasonal life cycles of the amphipod *Themisto*, faster growth and rapid maturation of summer populations are thought to be caused by increased water temperature and higher food abundance in that season (Wing 1976; Sheader 1981; Koszteyn et al. 1995). Within the same *Themisto* spp., lower habitat temperature is often associated with longer generation time and greater size (see Ikeda et al. 1992). Site H is slightly warmer (2.8°C, annual mean at 75–300 m depth) and has a higher zooplankton biomass (222 mg m^{-3}, annual mean) than Toyama Bay (temperature: ~1°C;, see Ikeda 1995), zooplankton biomass: 63 mg m^{-3} (Hirakawa et al. 1992). Therefore, observed smaller sizes of specimens and maturation at earlier instars of site H specimens may be attributed to the somewhat warmer habitat temperature there. However, the slower growth rate of *P. abyssalis* at site H cannot be explained by either regional differences in habitat temperature or potential food abundance.

The pelagic community in the Sea of Japan (Toyama Bay) is relatively species-poor (Zenkevitch 1963). The number of species recorded from the Sea of Japan includes 95 copepods (vs 390 in the western North Pacific, including the Oyashio region; Morioka 1980), 10 euphausiids (vs 28 in the western North Pacific; Endo and Komaki 1979), 2 amphipods (vs 26 in the western North Pacific; Irie 1959), and 17 chaetognaths (vs 21 in the western North Pacific; Kitou 1974). The biggest differences in the number of species is seen in micronektonic crustaceans (0 in Toyama Bay vs 49 in the northwest Pacific; Hayashi 1991) and fishes (1 in Toyama Bay vs 75 in the northwest Pacific; Okiyama 1971; Kawaguchi 1974). *P. abyssalis* is a rare component of diets of *Maurolicus muelleri*, the only micronektonic fish in the Sea of Japan (Ikeda et al. 1994), but a common diet component of a number of micronektonic fishes in the Oyashio region (Gordon et al. 1985; Moku et al. 2000; Uchikawa et al. 2001). From these between-habitat dif-

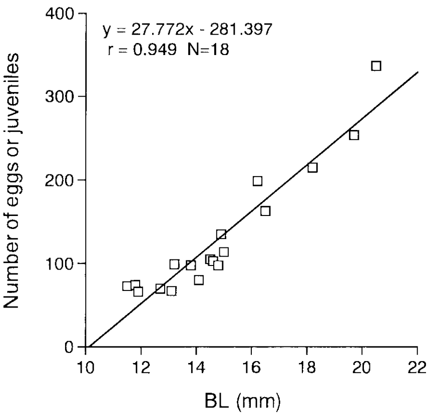


Fig. 8. *Primno abyssalis*. Relationships between brood size (number of eggs or juveniles in marsupium) and body length (*BL*, in millimeters) of females

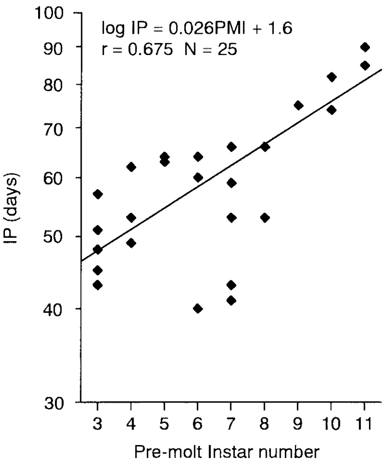


Fig. 9. *Primno abyssalis*. Relationships between intermolt period (*IP*) and pre-molt instar number of specimens raised at 2°C

Table 4. *Primno abyssalis*. Regional comparison of some life-history parameters for the population at site H in the Oyashio region and in Toyama Bay in the Japan Sea

		Site H (this study)	Toyama Bay (Ikeda 1995)
Growth rate (mm day^{-1})		0.014	0.021
Mature instar	Male	10–12	11
	Female	13–18	15–19
Maximum mature size (BL, in millimeters)	Male	10.4	8.5
	Female	19.8	22.0
Generation length (year)	Male	0.9–1.3	0.8
	Female	1.8–3.3	1.8–2.5
Minimum mature size (BL, in millimeters)	Male	7.5	8.1
	Female	11.9	15.8

ferences in species diversity of zooplankton and predation on *P. abyssalis*, it is considered that *P. abyssalis* at site H experiences higher competition for prey from other carnivorous zooplankton and higher predation pressure from micronektonic fishes. The observed slower growth rate, earlier maturation and higher lifetime fecundity (discussed below) of *P. abyssalis* at site H may be advantageous life-history traits offsetting its high mortality and maintaining its populations under such conditions, although the mechanism leading to slower growth rates is currently unknown.

Primno abyssalis at site H had a greater number of mature instars (three for males and six for females) than those at Toyama Bay (one for males and five for females) (Table 4). As noted by Ikeda (1995), the incidence of adult males was very low in Toyama Bay, and therefore increased effort of sampling in future studies may find additional mature instars of males. An apparent advantage of more adult instars of females is the increase in lifetime fecundity, which is an effective strategy to cope with high predation mortality, as discussed above. For *P. abyssalis* in Toyama Bay, Ikeda (1995) observed that after molting, adult males had reduced DW and AFDW, and the DW and AFDW of adult female instars decreased during the final instar stages. Ikeda (1995) interpreted these losses in DW and AFDW as being due to the cessation of feeding in these instars, after which, the energy needed for the production of gonads is supplied in the form of organic matter stored in the body. A similar phenomenon has been reported for the bathypelagic mysid *Gnathophausia ingens* (Childress and Price 1983). Interestingly enough, such reductions in DW and AFDW were not seen in *P. abyssalis* at site H in this study (Table 3). Perhaps, the lack of a reduction in body mass seen for site H specimens indicates their continued feeding, which is needed to compensate for the greater metabolic loss incurred by their slower growth rates.

BS is proportional to female size for many pelagic crustaceans (Mauchline 1988), including epipelagic amphipods such as *Themisto compressa* (formerly *T. gaudichaudii*; Sheader 1977) and *T. japonica* (Ikeda 1991), and mesopelagic amphipods, such as *Primno johnsoni* and *P. evansi* (Sheader and Batten 1995) and *Cyphocaris challengeri* (Yamada and Ikeda 2000). Ikeda (1995) failed to find such a relationship for *P. abyssalis* in Toyama Bay, but this may have been due to egg loss during preservation. In the present study, careful treatment of the specimens (sorted and preserved individually after collection) confirmed this relationship (Fig. 8). The maximum BS (337 eggs) recorded for *P. abyssalis* in this study is less than that of epipelagic *T. japonica* (500), but greater than those of mesopelagic *P. evansi* (80), *P. johnsoni* (100) and *C. challengeri* (65). The lifetime fecundity of *P. abyssalis* estimated here is 1,004, which is much greater than the estimates for *P. evansi* and *P. johnsoni* (326 and 202, respectively; Sheader and Batten 1995), and that for *C. challengeri* (181; Yamada and Ikeda 2000). The mean egg diameter (0.57 mm) for *P. abyssalis* in this study is smaller than those of *P. abyssalis* in Toyama Bay (0.64 mm; Ikeda 1995) and *C. challengeri* (0.63 mm; Yamada and Ikeda 2000), but larger than those of epipelagic *T. compressa* (0.51 mm; Sheader 1977) and *T. japonica* (0.36 mm; Ikeda, unpublished).

Mauchline (1991) reviewed the pattern of reproduction of deep-living crustaceans and fishes in the ocean and noted that the deep species have smaller BS, larger eggs and lower lifetime fecundity than shallow species. The reduced fecundity of deep-living animals is believed to reflect the exponential decrease in predatory pressure that occurs with increasing depth in the ocean. The higher lifetime fecundity of *P. abyssalis* observed in the present study does not follow this pattern; rather, it is an advantageous life-history trait enabling the persistence of the populations under the higher predation pressure in the mesopelagic realm of the Oyashio region.

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