

# Production, metabolism and trophic importance of four pelagic amphipods in the Oyashio region, western subarctic Pacific

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**ABSTRACT:** To estimate the production, metabolism and ingestion of populations of 4 pelagic amphipods (*Themisto pacifica*, *T. japonica*, *Primno abyssalis* and *Cyphocaris challengerii*) in the Oyashio region of the western subarctic Pacific, field time-series data on population structure were combined with laboratory-rearing data. Annual mean biomass,  $B$  ( $\text{mg C m}^{-2}$ ) was 31.2, 19.6, 17.4, and 36.7 for *T. pacifica*, *T. japonica*, *P. abyssalis*, and *C. challengerii*, respectively. Based on size-specific growth rates, annual production,  $P$  ( $\text{mg C m}^{-2} \text{ yr}^{-1}$ ), computed as the sum of somatic growth ( $P_g$ ) and molt production ( $P_e$ ), was 309, 252, 40, and 182, respectively. Annual metabolism ( $M$ ;  $\text{mg C m}^{-2} \text{ yr}^{-1}$ ) was 541, 195, 146, and 258. The annual  $P:B$  ratios indicated that the production potential was greatest for *T. japonica* (11.6), followed by *T. pacifica* (9.1), *C. challengerii* (4.5), and *P. abyssalis* (2.1). Assuming an assimilation efficiency of 0.90, assimilation ( $A = P + M$ ) was converted into ingestion ( $I = A/0.90$ ) for each amphipod. Annual ingestion ( $I$ ;  $\text{mg C m}^{-2} \text{ yr}^{-1}$ ) was 941 for *T. pacifica*, 493 for *T. japonica*, 205 for *P. abyssalis*, and 487 for *C. challengerii*. The total annual ingestion (=predation) of the 4 amphipods ( $1892 \text{ mg C m}^{-2} \text{ yr}^{-1}$ ) equals 0.08% of the non-amphipod zooplankton biomass, or 4.5% of their probable daily production in the Oyashio region of the western subarctic Pacific.

**KEY WORDS:** Metabolism · Production · Predation impact · Amphipod · Zooplankton

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## INTRODUCTION

Pelagic amphipods are primarily carnivores, and are a common component of zooplankton communities in the world oceans (Raymont 1983). Their importance has long been overlooked in the study of energy flow and the cycling of organic matter in pelagic marine ecosystems, partly because of their low contribution to the total zooplankton biomass (usually <0.5%; see Longhurst 1985). However, recent studies have suggested that amphipod populations (mostly *Themisto* spp.) exert significant predation pressure (30 to 70%) on secondary production in the waters around South Georgia in the Southern Ocean (Pakhomov & Perissinotto 1996) and in the southern Japan Sea (Ikeda & Shiga 1999). In the pelagic zone of the Kerguelen

waters in the southern Indian Ocean, *Themisto gaudichaudii* Guérin is reported to have an integral role in zooplankton–sea bird interactions (Bocher et al. 2001).

In the western subarctic Pacific Ocean and neighboring seas, at least 67 pelagic amphipod species occur (Yoo 1970). The 4 most abundant comprise 3 hyperiids (*Themisto pacifica* Bowman, *T. japonica* Bowman, and *Primno abyssalis* Bowman) and 1 gammarid (*Cyphocaris challengerii* Stebbing). In terms of bathymetric distribution, *T. pacifica* and *T. japonica* are epipelagic, and *P. abyssalis* and *C. challengerii* are mesopelagic species (Bowman 1960, 1978, Yoo 1970, Wing 1976). These 4 amphipods are components of the diets of salmon (Fukutaki 1967, 1969, Tadokoro et al. 1996), walleye pollock (Fujita et al. 1995, Kooka et al. 1997, Yamamura et al. 2002), squid (Okiyama 1965), and

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mesopelagic fishes (Beamish et al. 1999, Moku et al. 2000, Uchikawa et al. 2001), suggesting that they are of trophic importance in the pelagic ecosystems of this region. However, reliable data for estimating trophic functions, e.g. production and the predation pressure of these amphipods on other zooplankton, in the western subarctic Pacific are lacking.

As part of a research program to evaluate energy flow and cycling of organic matter in the pelagic ecosystem of the Oyashio region, we investigated the abundance, biomass, growth, metabolism (oxygen consumption, ammonia excretion) and carbon and nitrogen composition of these 4 pelagic amphipods' which are dominant in the Oyashio region (Yamada & Ikeda 2000, 2003, Yamada et al. 2002, 2004). From the results, we calculated their production and metabolism and estimated their predation impact on other zooplankton.

## MATERIALS AND METHODS

**Field sampling and measurements.** We carried out 16 samplings in the Oyashio region, off SE Hokkaido (Site H, Fig. 1) on various cruises in different seasons between July 1996 and July 1998. On each occasion, oblique tows were made at night with paired bongo nets (mouth opening 70 cm, mesh opening 333  $\mu$ m) from about 500 m in depth (range 386 to 900 m) to the surface (Table 1). Zooplankton samples were preserved immediately in 10% buffered formalin–seawater on-board ship. On land, the wet weight (WW) of each zoo-

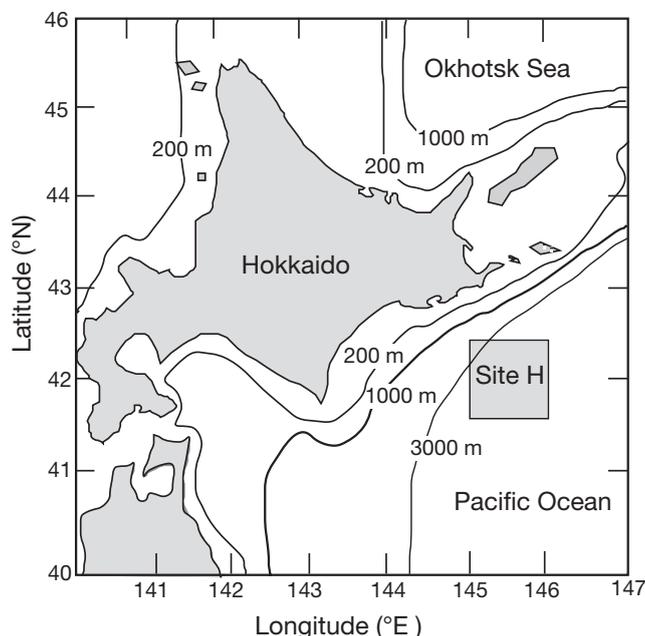


Fig. 1. Location of study area (Site H) in western subarctic Pacific. Bathymetric contours (200, 1000 and 3000 m) are superimposed

Table 1. Sampling data of oblique tows of bongo nets in the Oyashio region from July 1996 to July 1998. nd: no data

Date	Time of day (h)	Max. net depth (m)
1996 8 Jul	23:40–00:31	508
2 Aug	18:58–19:38	479
3 Oct	20:12–21:03	nd
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 Jul	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 Jul	02:14–03:00	448

plankton sample was determined after drying by vacuum filtration and blotting with filter paper (Omori & Ikeda 1984). Possible body shrinkage and underestimation of WW due to formalin preservation (Kapuris et al. 1997) was not taken into account.

All amphipods in the samples were then sorted, into *Themisto pacifica*, *T. japonica*, *Primno abyssalis*, and *Cyphocaris challengerii*. Body length (BL, mm) was measured as the maximal distance between the tip of head to the distal end of the uropod (or telson for *C. challengerii*) of the straightened body. The number of segments in the first pleopod was counted to determine instar stage (see Yamada & Ikeda 2000, Yamada et al. 2002, 2004) for each amphipod (Table 2). In addi-

Table 2. *Themisto pacifica*, *T. japonica*, *Primno abyssalis*, and *Cyphocaris challengerii*. Mean body length (BL) of each instar (after release from female brood pouch) of 4 pelagic amphipods collected from Site H, western subarctic Pacific

Instar no.	BL (mm)			
	<i>T. pacifica</i>	<i>T. japonica</i>	<i>P. abyssalis</i>	<i>C. challengerii</i>
1	1.62	1.59	2.53	3.38
2	1.90	2.40	2.86	4.54
3	2.39	2.68	3.57	5.77
4	2.94	2.86	4.43	7.60
5	3.24	3.56	5.45	9.83
6	4.06	4.07	5.80	11.76
7	4.68	4.79	6.76	13.00
8	5.55	5.59	7.42	13.60
9	6.47	6.40	9.55	14.01
10	7.34	7.19	11.14	14.63
11	7.92	10.07	12.36	
12	9.03	11.37	14.22	
13		12.50	14.97	
14		14.70	16.90	
15		15.22	18.70	
16			19.70	

tion to these seasonal samples, some live specimens of each instar were selected, rinsed briefly with distilled water, and their WW determined. These specimens were then dried at 60°C to obtain dry weight (DW). The dried samples were powdered, and carbon content was determined using an elemental analyzer (Yanaco CHN Coder MT-5). Detailed data on WW, DW, and C for the 4 amphipods have been reported elsewhere (Yamada & Ikeda 2003).

**Growth.** Because of year-round reproduction of these amphipods, tracking the same cohorts to establish their growth patterns is extremely difficult using field population data. Therefore, their growth rates were estimated based on intermolt periods and molt increments of specimens reared in the laboratory. Laboratory conditions often cause reduced growth rates, but their effects on intermolt periods are variable (cf. review of Hartnoll 1982). To minimize laboratory effects, we combined laboratory-obtained intermolt periods with molt increments from field individuals to calculate growth rates. For details see Yamada & Ikeda (2000) and Yamada et al. (2002, 2004).

Specimens used for the laboratory rearing experiment were collected from ca. 500 m depth using ring (mouth opening 80 cm) or bongo nets at Site H or in the adjacent area. Individual live specimens were placed in 50 to 1000 ml glass containers filled with seawater. Experiments were run in the dark at graded temperatures covering the entire range of temperatures encountered by these amphipods (Yamada & Ikeda 2000, Yamada et al. 2002, 2004). Chopped whelk (*Neptunea lyrata*) meat was provided as food. The containers were examined daily for molts which, when found, were removed from the container and the instar determined. Detailed laboratory rearing procedures are reported in Yamada & Ikeda (2000) and Yamada et al. (2002, 2004).

**Metabolism.** A water bottle method (Omori & Ikeda 1984) was used to determine the oxygen consumption rates of the amphipods, i.e. bottles with and without experimental amphipods (100 to 300 ml volume) were prepared simultaneously, and differences in the dissolved oxygen concentration after 24 h incubation in the dark were attributed to respiration. At the end of the experiments, the amphipods were recovered from the bottles, rinsed briefly with distilled water, blotted on filter paper and dried, and their DW determined. For details of metabolic measurements see Yamada & Ikeda (2003).

**Habitat temperature.** To extrapolate laboratory data of growth rates and metabolic rates of the amphipods to the popula-

tions in the field, accurate information on their habitat temperatures was needed. While *Themisto pacifica* and *T. japonica* are known to have an epipelagic distribution and *Primno abyssalis*, and *Cyphocaris challengerii* a mesopelagic distribution, little is known about their diel vertical migration behavior in the Oyashio region across all seasons of the year. Taking into consideration annual ranges of water temperatures in the epipelagic (2 to 18°C) and mesopelagic (2 to 5°C) zones of the Oyashio region, 5°C was taken as a typical temperature encountered by the 4 amphipods in the Oyashio Region.

## RESULTS

### Carbon biomass

The WW of the mixed zooplankton samples was converted to dry weight (DW), and then to carbon weight (C), using appropriate conversion factors for subarctic zooplankton (DW = 0.12 WW and C = 0.47 DW; Kotori 1976). Population biomass was converted to  $\text{mg C m}^{-2}$  by integrating over the sampling depths in Table 1. The mixed zooplankton C ranged from 2307 to 18910  $\text{mg C m}^{-2}$  (March to May 1998) with an annual mean of 7053  $\text{mg C m}^{-2}$  (Fig. 2).

All BL data for each amphipod instar were first converted to WW using the appropriate BL versus WW relationship:  $\text{WW} = 0.029 \text{ BL}^{2.82}$  for *Themisto pacifica*,  $0.036 \text{ BL}^{2.74}$  for *T. japonica* (Y. Yamada & T. Ikeda unpubl. data),  $0.023 \text{ BL}^{2.88}$  for *Primno abyssalis* (Yamada et al. 2002), and  $\text{WW} = 0.027 \text{ BL}^{2.71}$  for *Cyphocaris challengerii* (Yamada & Ikeda 2000). WW was converted to DW using the water content of the 4 amphipods (77.2% for *T. pacifica*, 77.7% for *T. japonica*, 77.4% for *P. abyssalis*, and 80.1% for *C. challengerii*, Yamada &

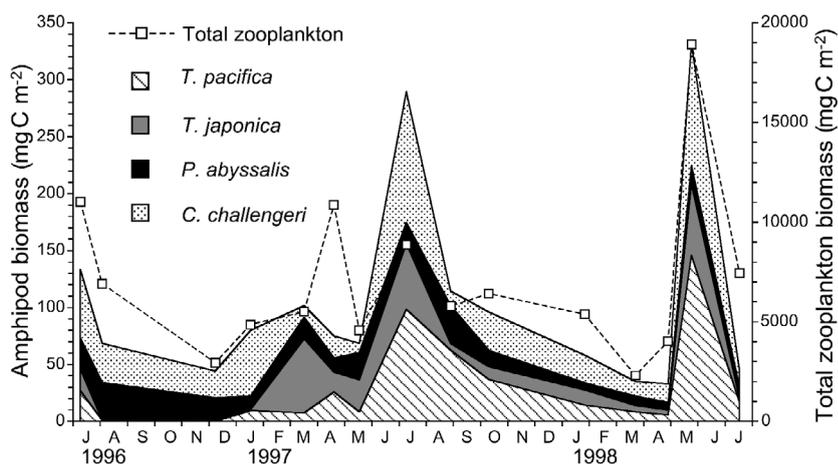


Fig. 2. *Themisto pacifica*, *T. japonica*, *Primno abyssalis*, and *Cyphocaris challengerii*. Seasonal changes in biomass at Site H. Zooplankton biomass is also shown

Ikeda 2003). The DW was then converted to carbon units, using the carbon:DW ratio: 47.9% for *T. pacifica*, 46.3% for *T. japonica*, 54.3% for *P. abyssalis*, and 36.8% for *C. challengerii* (Yamada & Ikeda 2003).

The carbon biomasses of the 4 amphipods varied seasonally from 0.13 to 146, 0 to 65.2, 6.3 to 33.2 and 8.1 to 115 mg C m<sup>-2</sup> for *Themisto pacifica*, *T. japonica*, *Primno abyssalis*, and *Cyphocaris challengerii*, respectively. In general, their biomass was high in spring and summer and low in autumn and winter (Fig. 2). *C. challengerii* was the dominant species (annual mean: 36.7 mg C m<sup>-2</sup>), followed by *T. pacifica* (31.2 mg C m<sup>-2</sup>), *T. japonica* (19.6 mg C m<sup>-2</sup>), and *P. abyssalis* (17.4 mg C m<sup>-2</sup>). The total annual mean biomass of the 4 amphipods was 105 mg C m<sup>-2</sup>, which equals 1.5% of the total zooplankton biomass (7053 mg C m<sup>-2</sup>).

### Production

Since cohorts could not be recognized, with these species apparently reproducing more or less continuously through the year, the 'growth rate method' proposed by Kimmerer (1987, 1990) for continuously reproducing populations at approximate steady state was adopted, since the reproduction mode and size/maturity stage composition of the 4 amphipods met the required conditions (Yamada & Ikeda 2000, Yamada et al. 2002, 2004).

Production (growth) was divided into somatic and molt production. Reproduction (eggs) was not taken into account, since the eggs in the females' marsupium were easily lost during sampling and preservation. The daily somatic production,  $P_g$  (mg C m<sup>-2</sup> d<sup>-1</sup>) by each amphipod population was computed as  $P_g = \sum N_i(CW_{i+1} - CW_i)/D_i$ , where  $CW_i$  is carbon content (mg C) at Instar  $i$ ,  $D_i$  is development time (d) from  $i$  to  $i+1$ , and  $N_i$  is abundance (no. m<sup>-2</sup>) of Instar  $i$  integrated over sampling depths (Table 1). The production of molts,  $P_e$  (mg C m<sup>-2</sup> d<sup>-1</sup>) is given by the equation  $\sum(MDW_i \times N_i \times \alpha/D_i)$ , where  $MDW_i$  is the mean DW [= 0.5(DW<sub>*i*</sub> + DW<sub>*i+1*</sub>)] of each instar, and  $\alpha$  is percent loss in body DW per molt (8.2% for *Themisto pacifica*, 8.7% for *T. japonica*, 8.3% for *Primno abyssalis*, and 8.4% for *Cyphocaris challengerii*; Y. Yamada & T. Ikeda unpubl. data) multiplied by the carbon content of the dried molts (19.8% for *T. pacifica*, 19.9% for *T. japonica*, 19.8% for *P. abyssalis*, and 19.4% for *C. challengerii*; Y. Yamada & T. Ikeda unpubl. data).

The development times of each instar ( $D_i$ ) of the 4 amphipods were calculated using growth equations established by combining the laboratory rearing experiments and field population analyses, i.e.  $Y = 0.039X + 1.37$  for *Themisto pacifica* (Yamada et al. 2004),  $Y = 16.79/[1 + \exp(2.25 - 0.019X)]$  for *T. japonica* (Yamada

et al. 2004),  $Y = 0.014X + 0.52$  for *Primno abyssalis* (Yamada et al. 2002), and  $Y = 15.41/[1 + \exp(1.52 - 0.012X)]$  for *Cyphocaris challengerii* (Yamada & Ikeda 2000), where  $Y$  is body length and  $X$  is days after release from the female marsupium.

Seasonally, somatic production ( $P_g$ ) ranged from 0.01 to 3.66 (annual  $P_g = 284$ ), 0 to 2.56 (228), 0.04 to 0.21 (37), and 0.07 to 1.31 (164) mg C m<sup>-2</sup> d<sup>-1</sup> for *Themisto pacifica*, *T. japonica*, *Primno abyssalis*, and *Cyphocaris challengerii*, respectively (Fig. 3). Molt production ( $P_e$ ) varied from 0.00 to 0.33 (annual  $P_e = 25$ ), 0 to 0.26 (23), 0.00 to 0.02 (3), and 0.01 to 0.16 (18) mg C m<sup>-2</sup> d<sup>-1</sup>, respectively (Fig. 3). As a result,  $P (= P_g + P_e)$  varied from 0.01 to 3.99 (annual  $P = 309$ ), 0 to 2.82 (251), 0.04 to 0.22 (40), and 0.08 to 1.47 mg C (181) m<sup>-2</sup> d<sup>-1</sup>, respectively.

The daily ratio of somatic production to biomass ( $P_g:B$ ) varied from 0.02 to 0.06 (annual mean = 9.1), 0.02 to 0.06 (11.6), 0 to 0.01 (2.1), and 0.01 to 0.02 (4.5) for *Themisto pacifica*, *T. japonica*, *Primno abyssalis*, and

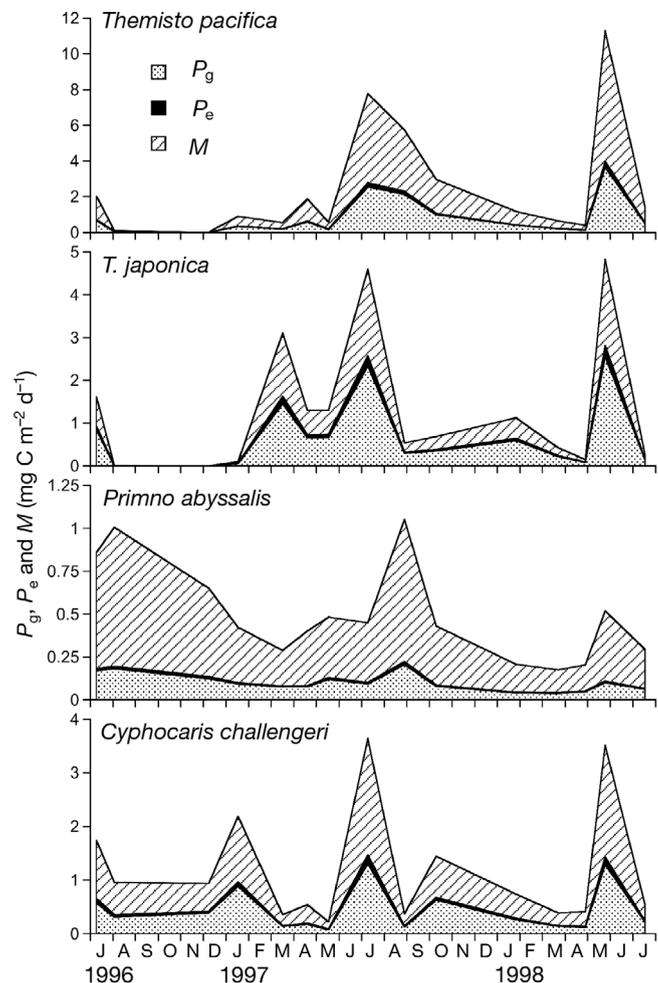


Fig. 3. *Themisto pacifica*, *T. japonica*, *Primno abyssalis*, and *Cyphocaris challengerii*. Seasonal changes in daily somatic production ( $P_g$ ), molt production ( $P_e$ ) and metabolism ( $M$ ) at Site H

*Cyphocaris challengerii*, respectively (Fig. 4, Table 3). The population (=size) index  $B:N$  ( $\text{mg C ind.}^{-1}$ ) ranged seasonally from 0.01 to 0.39, 0.07 to 1.04, 0.04 to 0.78, and 0.06 to 0.85, respectively (Fig. 4). The seasonal pattern of  $B:N$  differed from that of  $P_g:B$ , displaying an opposite trend.

**Metabolism**

Metabolism,  $M$  ( $\text{mg C m}^{-2} \text{ d}^{-1}$ ) is expressed as  $M = 24 \times 10^{-3} \times 0.97 \times 12/24 \times \Sigma(R_i \times N_i)$ , where  $R_i$  is the oxygen consumption rate ( $\mu\text{l O}_2 \text{ ind.}^{-1} \text{ h}^{-1}$ ) at Instar  $i$  (weighing  $\text{MDW}_i$ ), and 24 converts hourly rate into daily rate,  $10^{-3}$  converts  $\mu\text{g}$  to  $\text{mg}$ , 0.97 is a respiratory quotient for detritivores or carnivores (protein metabolism; Gnaiger 1983), and 12/22.4 is the carbon mass (g) in 1 mol of  $\text{CO}_2$  (22.4 l). In general,  $R$  is expressed as a function of body size and temperature. While the temperature which the 4 amphipods encounter in the Oyashio region is difficult to define because they are all (to varying degrees) diel vertical migrators (Yamada & Ikeda 2000, Yamada et al. 2002, 2004, Y. Yamada unpubl. data),  $R$  measured at  $5^\circ\text{C}$  by Yamada & Ikeda (2003) was used in this study on the premise that  $5^\circ\text{C}$  is the mean temperatures that the 4 amphipods encounter in the course of their diel vertical migrations throughout the year. Following Yamada & Ikeda (2003),  $R$  at  $5^\circ\text{C}$  is expressed as  $\ln R = 0.451 + 0.9 \ln \text{MDW}_i$  for *Themisto pacifica*,  $\ln R = 0.102 + 0.9 \ln \text{MDW}_i$  for *T. japonica*,  $\ln R = -0.035 + 0.9 \ln \text{MDW}_i$  for *Primno abyssalis* and  $\ln R = -0.675 + 0.9 \ln \text{MDW}_i$  for *Cyphocaris challengerii*.

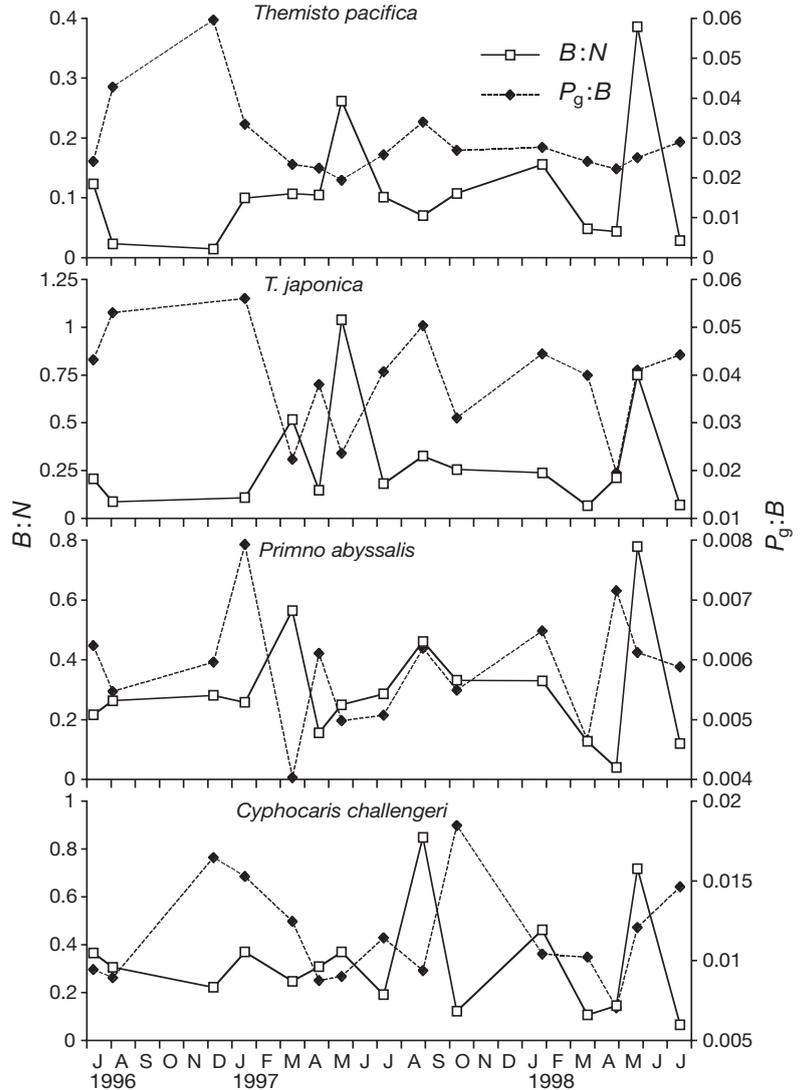


Fig. 4. *Themisto pacifica*, *T. japonica*, *Primno abyssalis*, and *Cyphocaris challengerii*. Seasonal changes in daily somatic production:biomass ( $P_g:B$ ) ratios and population size structure ( $B:N$ ;  $\text{mg C ind.}^{-1}$ ) indices at Site H

Table 3. *Themisto pacifica*, *T. japonica*, *Primno abyssalis*, and *Cyphocaris challengerii*. Summary of annual carbon budgets for populations at Site H, western subarctic Pacific. Data of *T. japonica* in the Japan Sea from Ikeda & Shiga (1999) included for comparison

Parameter	<i>T. pacifica</i>	<i>T. japonica</i>	<i>P. abyssalis</i>	<i>C. challengerii</i>	<i>T. japonica</i> (Japan Sea)
Mean biomass ( $\text{mg C m}^{-2}$ )	31.2	19.6	17.4	36.7	370
Production ( $P = P_g + P_o$ )	309.3	251.5	40.2	182.1	2210
Somatic ( $P_g$ ; $\text{mg C m}^{-2} \text{ yr}^{-1}$ )	284.2	228.1	36.9	164.0	1934
Molt ( $P_o$ ; $\text{mg C m}^{-2} \text{ yr}^{-1}$ )	25.0	23.5	3.3	18.0	176
Metabolism ( $M$ ; $\text{mg C m}^{-2} \text{ yr}^{-1}$ )	541	195	146	258	5878 <sup>a</sup>
Assimilation ( $A = P + M$ )	850	446	186	440	7988
Ingestion ( $I = A/0.904$ )	941	493	205	487	8837
Ratios: $P:B$	9.89	12.79	2.30	4.94	5.71
$P_g:B$	9.10	11.62	2.11	4.47	5.23
$P:M$	0.57	1.29	0.28	0.70	0.36
$P_g:M$	0.53	1.17	0.25	0.64	0.33

<sup>a</sup>Includes DVM (diurnal vertical migration) metabolism ( $1778 \text{ mg C m}^{-2} \text{ yr}^{-1}$ )

Seasonal variation in metabolism ranged from 0.01 to 7.32 (annual  $M = 541$ ), 0.01 to 2.03 (195), 0.13 to 0.83 (146), and 0.14 to 2.18 (258)  $\text{mg C m}^{-2} \text{d}^{-1}$  for *Themisto pacifica*, *T. japonica*, *Primno abyssalis*, and *Cyphocaris challengerii*, respectively (Fig. 3).

### Assimilation

The daily assimilated carbon is defined as  $A = P_g + P_e + M$ , assuming no leakage of soluble organic carbon from the body. The carbon assimilated by the 4 amphipods varied from 0.02 to 11.31 (annual  $A = 850$ ), 0 to 4.83 (446), 0.17 to 1.05 (186) and 0.22 to 3.65 (440)  $\text{mg C m}^{-2} \text{d}^{-1}$  for *Themisto pacifica*, *T. japonica*, *Primno abyssalis*, and *Cyphocaris challengerii*, respectively (Fig. 3).

### DISCUSSION

In the Oyashio region, a phytoplankton (diatom) bloom occurs in April and/or May. It is an annual event, although its magnitude varies considerably between years (range = 2 to 13  $\text{mg chlorophyll a m}^{-3}$ , cf. Saito et al. 2002). In response to the bloom, zooplankton biomass (mostly large grazing copepods such as *Neocalanus* spp. and *Eucalanus bungii*) increases in the mixed layer (upper 10 to 50 m) and forms an annual peak in May or June to July (Saito et al. 2002, Kobari et al. 2003). Since the present study sampled zooplankton from much deeper depths (400 to 900 m; Table 1), the seasonal pattern of the total zooplankton biomass (Fig. 2) is less marked than that reported previously.

The  $P:B$  ratio (often equivalent to the  $P_g:B$  ratio) is an appropriate basis upon which to compare the production potential of various invertebrates, and has been shown to be a function of body size (Banse & Mosher 1980), i.e. the greater the size, the lower the  $P:B$  ratio. Of the 4 amphipods studied, *Cyphocaris challengerii* was most abundant (annual mean biomass = 37  $\text{mg C m}^{-2}$ ), followed by *Themisto pacifica* (31  $\text{mg}$ ), *T. japonica* (20  $\text{mg}$ ), and *Primno abyssalis* (17  $\text{mg}$ ). Nevertheless, *T. pacifica* had the greatest annual somatic

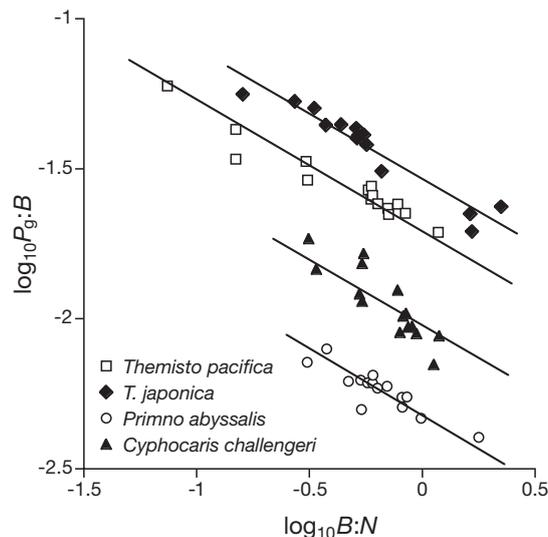


Fig. 5. *Themisto pacifica*, *T. japonica*, *Primno abyssalis*, and *Cyphocaris challengerii*. Relationships between daily somatic production to biomass ratios ( $P_g:B$ ) and population size structure index ( $B:N$ ) of 4 amphipods at Site H

production (284  $\text{mg C m}^{-2} \text{yr}^{-1}$ ), followed by *T. japonica* (228), *C. challengerii* (164), and *P. abyssalis* (37) (Table 3). Therefore, the annual  $P_g:B$  was greatest in *T. japonica* (11.6) and least in *P. abyssalis* (2.1), with *T. pacifica* (9.1) and *C. challengerii* (4.5) intermediate. The plot of  $\log_{10}(P_g:B)$  for each amphipod against  $\log_{10}(B:N)$  for each sampling date showed clearly that  $P_g:B$  decreased as  $B:N$  increased (Fig. 5). The correlation coefficients ( $r$ ) for  $P_g:B$  versus  $B:N$  fit to the linear regression model were highly significant for all 4 species ( $r = -0.882$  to  $-0.963$ , all  $p < 0.001$ ), indicating that seasonal variations in  $P_g:B$  were largely due to variations in the size index  $B:N$ .

The slopes of the  $P_g:B$  versus  $B:N$  regression lines ranged from  $-0.601$  (*Cyphocaris challengerii*) to  $-0.357$  (*Themisto pacifica* and *Primno abyssalis*). As the between-species differences were not significant (the 95% confidence intervals overlapped, see Table 4), the common slope (mean  $b$ -value) was computed as  $-0.437$  and was used to recompute the intercept value ( $a$ ) of the regression line for each species (Table 4). The thus

Table 4. *Themisto pacifica*, *T. japonica*, *Primno abyssalis*, and *Cyphocaris challengerii*. Regression statistics of  $P_g/B$  on  $B/N$  (both daily) (Fig. 5). Regression model adopted is  $\log_{10}P_g:B = a + b \log_{10}B:N$ . Since differences in slope ( $b$ ) between the 4 species are insignificant, common  $b$  was computed as  $-0.437$ . Intercepts ( $a$ ) are for regression lines adjusted to common slope

Species	n	$B:N$	$P_g:B$	$B$ (95% CI)	$a$ for $b = -0.437$	$r$
<i>Themisto pacifica</i>	15	$0.112 \pm 0.098$	$0.029 \pm 0.010$	$-0.357$ ( $-0.417$ to $-0.297$ )	$-1.707$	0.963
<i>T. japonica</i>	14	$0.301 \pm 0.039$	$0.039 \pm 0.011$	$-0.432$ ( $-0.515$ to $-0.350$ )	$-1.534$	0.957
<i>Primno abyssalis</i>	15	$0.297 \pm 0.006$	$0.006 \pm 0.001$	$-0.357$ ( $-0.472$ to $-0.243$ )	$-2.321$	0.882
<i>Cyphocaris challengerii</i>	15	$0.323 \pm 0.012$	$0.012 \pm 0.003$	$-0.601$ ( $-0.793$ to $-0.409$ )	$-2.021$	0.882

recomputed intercept of the  $P_g:B$  versus  $B:N$  regression lines was greatest in *T. japonica* (-1.53), followed by *T. pacifica* (-1.71), *C. challengerii* (-2.02), and *P. abyssalis* (-2.32), while the annual mean  $B:N$  was lowest in *T. pacifica* (0.11), followed by *P. abyssalis* (0.30), *T. japonica* (0.30), and *C. challengerii* (0.32) (Table 4). From these results it is apparent that the relationships between population size-structure and  $P_g:B$  ratio seen in interspecific comparisons differ from those in intraspecific comparisons.  $P_g$  is also affected by development time (see 'Results'), i.e. lower  $P_g:B$  ratios result from longer development time. As mentioned in the 'Introduction', the amphipods studied were epipelagic (*T. pacifica* and *T. japonica*) or mesopelagic (*P. abyssalis* and *C. challengerii*) species. Yamada & Ikeda (2000) and Yamada et al. (2002, 2004) estimated that generation lengths of the latter (1.4 to 3.8 yr for *P. abyssalis*, 1 yr for *C. challengerii*) are greater than those of the former (32 to 224 d for *T. pacifica*, 66 to 358 d for *T. japonica*) (an increase in generation length with increasing depth of occurrence has been reported for various pelagic animals (Mauchline 1991). Therefore, the  $P_g:B$  ratio appears to be influenced by both body size and life-cycle traits in amphipods.

The only comparable information about production of pelagic amphipods presently available is that for *Themisto japonica* in Toyama Bay in the southern Japan Sea (Ikeda & Shiga 1999). According to Ikeda & Shiga (1999), the daily  $P_g$  of *T. japonica* in Toyama Bay is  $5.33 \text{ mg C m}^{-2} \text{ d}^{-1}$ , and its annual mean biomass is  $370 \text{ mg C m}^{-2}$ ; therefore, the annual  $P_g:B$  ratio would be 5.23 (Table 3). In our study, the  $P_g:B$  of *T. japonica* at Site H (11.62, Table 3) was greater than that in Toyama Bay. Comparing the population size structure ( $B:N$ ) for both areas, the annual mean  $B:N$  of *T. japonica* at Site H (0.301, Fig. 4) is lower than that in Toyama Bay (ca. 0.745, Ikeda & Shiga 1999). The data in Fig. 5 indicate that the greater  $P_g:B$  ratio in the Site H population compared to the Toyama Bay population may be related to the smaller body size of the former, which overrides the effect of the somewhat higher temperatures in Toyama Bay (cf. Ikeda & Shiga 1999). However, the metabolic rates for *T. japonica* reported by Ikeda & Shiga (1999) represented routine plus diel vertical migration (DVM) metabolism, whereas only routine metabolism was measured in our study (estimation of DVM metabolism was not possible because of lack of data on the distance of the DVM of these 4 amphipods in the Oyashio region). According to Ikeda & Shiga (1999), DVM metabolism of *T. japonica* migrating 250 m in Toyama Bay accounted for 30% of the total metabolism.

Species-specific differences in body size, generation length and metabolic activity among these 4 pelagic amphipods affect their partitioning of assimilated car-

bon (Fig. 6). Of the assimilated carbon partitioned into somatic growth, molt production and metabolism, the allocation to somatic growth was greatest in *Themisto japonica* (51.1%), followed by *Cyphocaris challengerii* (37.3%), *T. pacifica* (33.4%), and *Primno abyssalis* (19.9%). The allocation of assimilated carbon to molt production comprised but a small fraction (2.9 to 5.3%) of the total assimilated carbon. Therefore, of the 4 amphipods, production potential is greatest in *T. japonica*; this is consistent with the other measures of production potential of the population ( $P_g:B$  ratio, cf. Table 3).

With regard to the trophic importance of pelagic amphipods in pelagic food chains, in the Southern Ocean, Froneman et al. (2000) reported that daily feeding of *Themisto gaudichaudii* accounted for <0.4% of mesozooplankton biomass and <3% of mesozooplankton production in the Prince Edward Archipelago, while in waters around South Georgia this species was reported to feed on up to 70% of the daily secondary production by Pakhomov & Perissinotto (1996). The difference between the 2 studies reflects differences in the abundance of *T. gaudichaudii* between the 2 sites. In contrast to the direct ingestion measurements of Pakhomov & Perissinotto (1996) and Froneman et al. (2000), indirect estimation of ingestion based on assimilated carbon requires 2 additional items of information—the amphipods' assimilation efficiency, and the loss of organic matter from prey during its

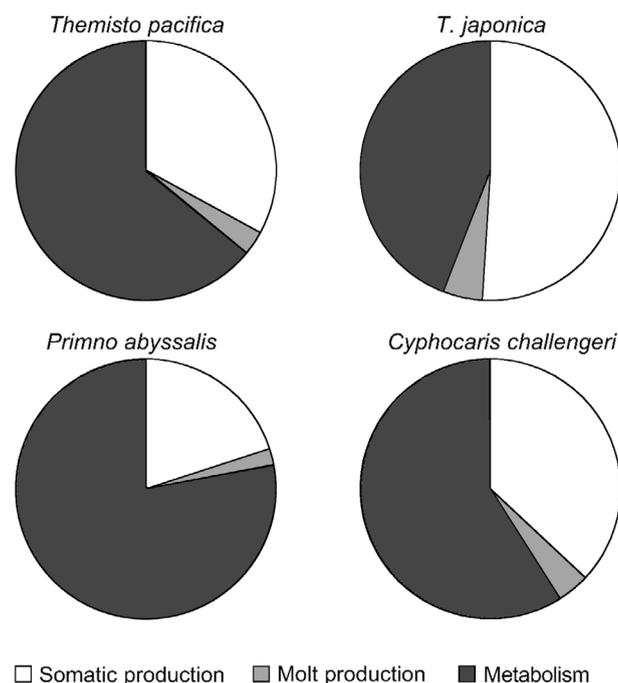


Fig. 6. Partition of assimilated carbon to somatic production, molt production and metabolism by populations of 4 amphipods at Site H

capture and ingestion by the amphipods. With regard to assimilation efficiency, Dagg (1976) reported an efficiency of 90.4% for the benthic–pelagic amphipod *Calliopius laeviusculus*, and this value was used to calculate the carbon ingested from assimilated carbon by the 4 amphipods in the present study. Regarding the loss of organic matter during prey handling, this is known to be significant, with a maximum loss of ca. 40% recorded for the benthic–pelagic amphipod *C. laeviusculus* by Dagg (1974). This pre-ingestive loss is analogous to the ‘sloppy feeding’ of copepods on phytoplankton cells. In a recent review, Møller (2005) considered the loss of organic matter a function of copepod:cell size ratios, whereby loss increases with decreasing ratio. Since nothing is known about possible sloppy feeding by the 4 amphipods in the present study, we did not take this into account in our calculation of their ingestion rates, and therefore the results are possibly underestimates (Table 3, Fig. 7).

The daily predation pressures of the 4 amphipods on zooplankton biomass other than amphipods ranged from <0.01 to 0.11% for *Themisto pacifica*, <0.01 to 0.06% for *T. japonica*, <0.01 to 0.02% for *Primno abyssalis*, and 0.01 to 0.05% for *Cyphocaris challengerii* (Fig. 7). The total daily predation pressure varied irregularly with season, ranging from 0.03 to 0.21%, with an annual mean of 0.08%. The non-amphipod zooplankton biomass was converted to production using the *P:B* of 7.0 reported for copepods on the Scotian Shelf, Atlantic Ocean by McLaren et al. (1989). Using this *P:B* ratio, the daily production of potential prey (or non-amphipod) zooplankton for the amphipods in the Oyashio region was calculated as 135 mg C m<sup>-2</sup> d<sup>-1</sup> (7053 × 7.0/365). The mean daily predation impact of the amphipods (6.5 mg C m<sup>-2</sup> d<sup>-1</sup>) accounted for 4.5% of the daily production of potential prey zooplankton.

Based on the same carbon budget method, Ikeda & Shiga (1999) estimated that the daily predation of *Themisto japonica* equals 6.6 and 30% of the biomass and production of prey zooplankton (copepods and small euphausiids) in Toyama Bay. The greater predation of *T. japonica* in Toyama Bay than in the Oyashio region may largely be due to differences in the population biomass and habitat temperature between these regions, with the extra metabolic costs involved for DVM as a minor component. The annual mean biomass of *T. japonica* in Toyama Bay (370 mg C m<sup>-2</sup>) is nearly 5 times greater than that (105 mg C m<sup>-2</sup>, see Table 3) of the 4 amphipods in the Oyashio region, and

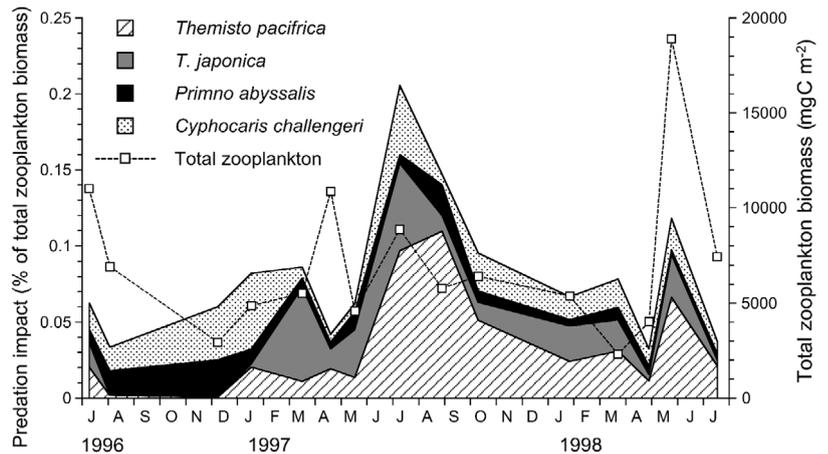


Fig. 7. *Themisto pacifica*, *T. japonica*, *Primno abyssalis*, and *Cyphocaris challengerii*. Estimated predation impact on total biomass of zooplankton other than amphipods at Site H

the habitat temperature in the former region (6 to 15°C) is higher than in the latter (5°C, see ‘Results; Metabolism’). In addition, as the oxygen consumption rate of pelagic amphipods is a function of temperature (cf. Ikeda & Shiga 1999), the higher habitat temperature for the Toyama Bay population of *T. japonica* results in proportionally higher ingestion rates.

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