

Production, metabolism and production/biomass (*P/B*) ratio of *Metridia pacifica* (Crustacea; Copepoda) in Toyama Bay, southern Japan Sea

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Abstract: Population production, metabolism and *P/B* ratio of *Metridia pacifica*, the most abundant copepod in Toyama Bay, southern Japan Sea, were estimated based on biomass and population structure data collected from biweekly sampling from 1 February 1990 through 30 January 1991 (363 days). The annual life cycle of *M. pacifica* in Toyama Bay is characterized by a short growing period in January–April, followed by a long aestivation for the rest of the year. Mean biomass (*B*) over the sampling period was 263 mgC m⁻². Population production during 363 d was calculated as the sum of somatic (*P_g*), molt (*P_e*) and egg (*P_r*) productions, which were 485, 37 and 139 mgC m⁻², respectively (i.e. $P = P_g + P_e + P_r = 661$ mgC m⁻²). Population metabolism (*M*), based on oxygen consumption data, was 3218 mgC m⁻². From these results, mean daily *P/B* and *P/M* ratios were computed as 0.0069 and 0.00057, respectively. Similar calculations for the growing period only (103 d) yielded 334 mgC m⁻² for *B*, 587 mgC m⁻² for *P* (*P_g*: 416, *P_e*: 32, *P_r*: 139), 1584 mgC m⁻² for *M*, 0.0171 for mean daily *P/B* and 0.0036 for mean daily *P/M*. Regional production comparisons imply suppressed production potential of *M. pacifica* in Toyama Bay primarily because of their prolonged aestivation during summer–autumn. The importance of *M. pacifica* in secondary production in Toyama Bay is discussed.

Key words: production, metabolism, *P/B* ratio, *Metridia pacifica*, Japan Sea

Introduction

Metridia pacifica is a medium-sized grazing copepod distributed over the entire subarctic Pacific and its marginal seas (Minoda 1971; Batchelder 1985; Hirakawa & Imamura 1993). Trophic importance and grazing pressure of *M. pacifica* have been estimated as high enough to control phytoplankton standing stock during the unproductive autumn–winter period in the eastern subarctic Pacific (Batchelder 1986). *M. pacifica* is reported as a dietary component of mesopelagic myctophid, gonostomatid and bathylagid fishes in the western subarctic Pacific (Gordon et al. 1985; Moku et al. 2000; Uchikawa et al. 2001). Nauplii of *M. pacifica* are one of the most important prey items of larval walleye pollack (*Theragra chalcogramma*) in the coastal waters of southwestern Hokkaido, the western subarctic Pacific (Nakatani 1995), and the southeastern Bering Sea (Pinchuk & Paul 1998).

In Toyama Bay, southern Japan Sea, *Metridia pacifica* is the major contributor to copepod biomass (annual mean: 36.3%, Hirakawa & Imamura 1993). According to Hirakawa & Imamura (1993), the early nauplii of *M. pacifica* occur in January–February, and develop to copepodite stage 5 by the beginning of April, and to adults in November–December. *M. pacifica* sink to deeper-layers for ‘aestivation’ during summer/autumn, presumably to avoid high temperatures near the surface. While late copepodites (excluding adult males) of *M. pacifica* are known to undergo diel vertical migration (Morioka 1976; Batchelder 1985; Hirakawa 1991; Hattori, 1989) the aestivating population in Toyama Bay exhibits little or no diel vertical migration although no metabolic reduction is apparent (Ikeda & Hirakawa 1998). *M. pacifica* in Toyama Bay has one generation per year, which contrasts with the 3–4 generations per year observed in the eastern subarctic Pacific (Batchelder 1985).

In this study, we integrated information from field surveys and laboratory experiments on *Metridia pacifica* to calculate their population biomass, production (somatic

growth, eggs and molts), and metabolism. The production/biomass and production/metabolism ratios were computed to characterize the production potential of *M. pacifica*. The importance of *M. pacifica* to secondary production in Toyama Bay is discussed.

Materials and Methods

Population data/biomass

Numerical abundance of Nauplius stages 1 and 2 (N1/N2) through N6 and Copepodite stage 1 (C1) through C6 of *Metridia pacifica* was estimated from a series of vertical hauls (500 m to the surface) with twin-Norpac nets at intervals of 2 weeks over nearly one full year (24 dates, February 1990 through January 1991) at an offshore station (37°00'N, 137°14'E) in Toyama Bay (Hirakawa & Imamura 1993). While the N3 were combined with the N1 and N2 and expressed as N1-3 in Hirakawa & Imamura's (1993) data, the N3 is the first feeding stage contributing to population production and is therefore separated in this study (Table 1). Environmental data (temperature, salinity, total net zooplankton biomass) collected concurrently are reported in Hirakawa & Imamura (1993).

Judging from population structure data (Table 1), it is

clear that the growing season for *Metridia pacifica* in Toyama Bay is limited to January–April. In the present calculations of production-related parameters and their ratios, the results from the 'growing' season were separated to gain better insight into the production potential of *M. pacifica*.

Total body length (*BL*, mm) of N3–C6 was determined to the nearest 0.01 mm, using preserved specimens collected during the most abundant season for each stage (December–April) under a compound (for naupliar stages) or dissecting microscope (for copepodites). The diameter (*D*, mm) of spherical eggs and *BL*s of the N1–N2 were determined from laboratory-raised specimens (Hirakawa, unpublished data). These *D* and *BL* data were converted to carbon units (W_c , μg) from W_c to V ($V=(4/3)\pi(D/2)^3$) and W_c to *BL* relationships: $W_c=139V-0.002$ (Huntley & Lopez 1992) for eggs, $W_c=2.58BL^{1.36}$ for nauplii (calculated from the data in Fernandez 1979), and $W_c=3.83BL^{2.46}$ for copepodites (Batchelder 1986). Batchelder's relationship is for *Metridia pacifica* copepodites, but that from Fernandez is for *Calanus pacificus* nauplii which have a similar shape and size to those of *M. pacifica*.

Table 1. Abundance (number per m³, 0–500 m depth) of each developmental stage of *Metridia pacifica*. Blank column=nil.

Year	Date	Stages														Total	
		N1/N2	N3	N4	N5	N6	C1	C2	C3	C4F	C4M	C5F	C5M	C6F	C6M		
1990	1 Feb	15.54	23.32	145.08	18.14	2.59	0.83					0.01		0.01	4.14	1.71	211.37
	14 Feb	26.57	18.55	78.70	43.61	45.11	21.65	4.01	2.41	0.28	0.40	0.26	0.38	6.96	1.70	250.59	
	28 Feb	46.58	11.64	105.97	34.93	11.65	16.77	13.97	29.81	2.15	5.36	0.53	0.92	2.25	2.35	284.88	
	17 Mar	12.66	30.81	62.17	14.86	7.15	9.13	7.70	10.67	3.08	3.64	4.42	10.21	2.41	3.25	182.16	
	3 Apr			1.36					2.72	2.72	2.00	2.23	16.82	14.25	5.09	4.12	51.31
	16 Apr	3.05	6.10	18.29	18.29		8.54	6.10	4.88	1.70	1.96	4.50	5.14	2.54	2.76	83.85	
	1 May	3.41		3.41	0.85				5.33	1.62	2.06	2.89	5.48	2.79	4.06	31.90	
	14 May	3.14	1.35	3.14					0.30	0.55	0.45	3.68	3.33	3.02	4.58	23.54	
	3 Jun			2.16					0.29	0.48		1.44	1.82	6.04	3.84	16.07	
	15 Jun	5.56	0.93	5.56	0.92				0.35	0.26	0.10	1.12	0.87	3.27	2.25	21.19	
	2 Jul		1.21		1.21							0.30	0.81	1.87	1.22	6.62	
	17 Jul											0.05	0.42	1.16	3.12	1.58	6.33
	1 Aug			1.16					0.29			0.95	3.06	3.06	1.75	10.27	
	20 Aug			1.16								1.61	3.07	4.42	1.76	12.02	
	30 Aug											1.37	2.40	3.72	1.42	8.91	
	3 Sep											1.09	2.72	3.45	1.91	9.17	
	17 Sep											1.00	2.00	2.95	1.10	7.05	
	2 Oct											1.09	2.52	3.24	1.75	8.60	
	15 Oct											0.95	2.97	5.47	2.28	11.67	
1 Nov											1.84	4.64	8.33	5.79	20.60		
15 Nov											1.30	0.60	7.90	5.70	15.50		
5 Dec				0.60							1.70	0.05	9.53	7.93	19.81		
1991	16 Jan	26.97	67.15	61.41								0.10	8.64	2.93	167.20		
	30 Jan	28.78	28.78	108.20	27.63	2.87	1.61	0.40	0.40		0.13		0.03	4.79	3.85	207.47	
	Total	172.26	189.84	597.77	161.04	69.37	58.53	34.90	57.45	12.12	16.39	49.28	68.54	109.00	71.59	1668.08	

Stage development time

Preliminary analysis of the development time based on the stage proportions (cf. Miller & Tande 1993) was not successful, largely because of the long sampling intervals of this study relative to the rapid development of *Metridia pacifica* (Table 1). As an alternative, we assumed that seasonal abundance and population structure of *M. pacifica* in Toyama Bay are the same every year (thus disregarding the year), that population growth starts from 16 January (when the N1/2 first occurred, Table 1), and that mortalities between stages are constant. Then, cumulative abundance of each N3–C6 stage (separating females and males for C4–C6) was calculated and the date when 50% of the annual total abundance was reached was used to calculate the apparent development time (*ADT*; d) of that stage since hatching. *ADTs* thus estimated for C5 males and females (99 and 85 d, respectively) are comparable to the results of laboratory rearing of this copepod (80 days at 8°C, Padmavati and Ikeda, unpublished data).

Eggs

Egg production rates of *Metridia pacifica* in Toyama Bay vary seasonally (Hirakawa & Imamura 1993). For the present calculation, their maximum rate of 5.57 eggs female⁻¹ d⁻¹, determined in early March by feeding natural phytoplankton assemblages, was used. A similar egg production rate (6 eggs female⁻¹ d⁻¹) is reported by Batchelder & Miller (1989) for female *M. pacifica* from Station P in the eastern subarctic Pacific. An egg of *M. pacifica* contains 0.2 µg C (Table 2).

Molts

Carbon content of single molts of *Metridia pacifica* was assumed to be 3.8% of body carbon for all development stages, ignoring the effects of temperature, as reported for *Calanus pacificus* (Vidal 1980).

Metabolism

Live C6 females of *Metridia pacifica* were collected from near Toyama Bay in December 1991, placed in 2-l glass containers filled with chilled natural seawater (10°C), and transported to the land laboratory in the dark. Oxygen consumption rates were determined at 0, 4, 8, 12, 16, 20 and 24°C within 5 days after capture, using a water bottle method (Omori & Ikeda 1984). Specimens were acclimated to each experimental temperature for 4–5 h prior to the experiments. For measuring oxygen consumption rates, 8–10 specimens were placed individually into 5-ml glass bottles filled with well oxygenated GF/F filtered seawater for 15 h (12–24°C experiments) or 24 h (0–8°C experiments). For details about the water bottle method with small bottles, see Ikeda & Hirakawa (1998). Subsamples of specimens were freeze-dried to obtain dry weight, and then used for carbon analysis with an elemental analyzer (Yanaco CHN Corder

MT-5).

Oxygen consumption rates (R : µl O₂ specimen⁻¹ h⁻¹) of *Metridia pacifica* are defined as a function of body mass (W_c : µgC) and temperature (T : °C), and expressed as: $\ln R = a + b \ln W_c + cT$, or $R = a' W_c^b \times e^{cT}$, where a , b and c are constants and $a' = e^a$. We determined R only for the C6 females in this study, so the constant $b = 0.780$ for copepods living in the epipelagic realm of the world ocean reported by Ikeda et al. (2001), was used to extrapolate R for N3 through C6 irrespective of temperature. Within a species, temperature-independence of the constant b has been reported for planktonic copepods such as *Diaptomus* spp. (Comita 1968) and *Calanus pacificus* (Vidal 1980).

Habitat temperature

Day/night vertical distribution data for *Metridia pacifica* in June and September 1986 (Hirakawa 1991) and September and November–December 1990 (Hirakawa & Imamura 1993) in Toyama Bay indicate that nocturnal ascent from 300 m depth to the surface occurred in June. In September most of the population was found below 300 m both day and night with no diel vertical movement. November–December is the transitional period from non-migratory to vertical migratory behavior of *M. pacifica*. From these results, combined with seasonal temperature profiles at the station, habitat temperature of *M. pacifica* populations was designated as 10°C (median temperature between the surface and 300 m depth) during the period from December–June, and 0.5°C during the period from July to November for our calculations of metabolism.

Results

Biomass (B)

The results of *BL* measurements and estimated body mass of each developmental stage (W_c : µgC) are summarized in Table 2. Population biomass (B : mgC m⁻³) on a given sampling date can be computed as the sum of W_c of N3–C6, multiplied by the abundance of each stage in Table 1.

Naupliar stages were found only in January–June and were most abundant in January–February. Only C5 and C6 were found during August–December (Table 2). B was high in winter–spring and low in summer and autumn (maximum: 1.242 mgC m⁻³ in April, and minimum: 0.164 mgC m⁻³ in July, Fig. 1), with an integrated mean B over the entire study period (363 d) of 0.525 mgC m⁻³ (or 263 mgC m⁻²). For the growing period only (103 d) mean B was 0.667 mgC m⁻³ (or 334 mgC m⁻²) (Table 3). Biomass stage structure was as follows: mean proportions of the N3–C4, C5 and C6 stages were 8.1, 23.1 and 68.8%, respectively, for the entire survey period, and were 19.7, 34.4 and 45.9%, respectively, for the growing period.

Somatic production (P_g)

Daily somatic production of *Metridia pacifica* on a given sampling date was computed as the sum of daily growth increments of N3–C5, multiplied by the body mass (W_c) and abundance of each stage. Somatic production of C6 (adult) males and females was assumed to be negligible.

Plots of the natural logarithm of W_c of N3–C6 against apparent developmental times (ADT, d; Table 2) yielded instantaneous growth rates (g) for N3 through C5 of 0.056

(i.e. daily growth $G=e^g-1=0.058$), for C5 females to C6 females of 0.0028 ($G=0.0028$), and for C5 males to C6 males of 0.0006 ($G=0.0006$) (Fig. 2).

Daily P_g thus calculated showed a pronounced peak in February (0.018 mgC m⁻³), decreased rapidly to less than 0.001 mgC m⁻³ in June through December, and recovered in January 1991 (Fig. 1). Integrated P_g s over the entire study period (363 d) and growing period (193 d) were 0.969 mgC m⁻³ (or 485 mgC m⁻²) and 0.831 mgC m⁻³ (or 416 mgC m⁻²), respectively (Table 3).

Table 2. Body length (BL) of all developmental stages of *Metridia pacifica* (mean±1SD, the number of specimens is in parenthesis), and estimated carbon content (W_c). Apparent development time (ADT) was estimated designating 16 January as the birth date. See text for details. N=Naupliar, C=Copepodite, F=female, M=male.

Stage	BL (mm)	W_c (μgC)	ADT (d)
Egg	0.14±0.00 (20)*	0.20	
N1	0.17±0.01 (65)	0.23	
N2	0.18±0.02 (65)	0.25	
N3	0.20±0.01 (89)	0.29	13.4
N4	0.26±0.03 (89)	0.41	15.8
N5	0.35±0.03 (89)	0.62	26.4
N6	0.39±0.03 (89)	0.74	24.4
C1	0.55±0.03 (94)	0.88	33.3
C2	0.75±0.03 (66)	1.86	42.1
C3	1.03±0.04 (58)	4.10	41.2
C4F	1.47±0.06 (61)	9.90	64.6
C4M	1.39±0.06 (60)	8.60	53.7
C5F	2.27±0.07 (60)	28.71	84.6
C5M	2.03±0.07 (60)	21.97	99.0
C6F	2.98±0.12 (60)	56.34	323.0
C6M	2.15±0.08 (60)	25.12	323.0

* Diameter

Egg production (P_r)

Within the growing season of *Metridia pacifica* (January–April), the occurrence of early naupliar stages was largely limited to January–February (Table 1), so the repro-

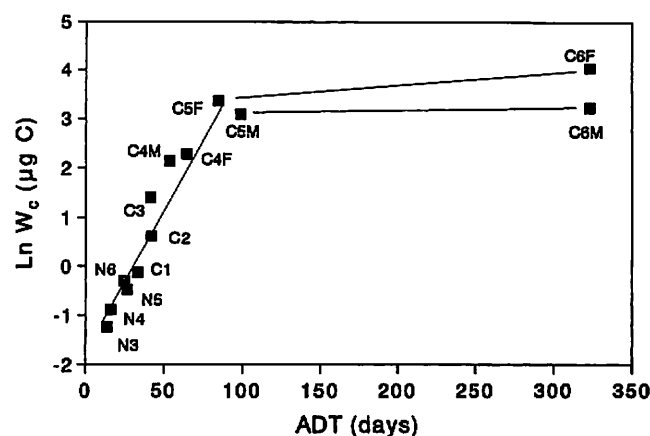


Fig. 2. Relationship between body mass (W_c ; mgC) and apparent cumulative developmental time (ADT; days from the designated birth date, 16 January) of *Metridia pacifica* in Toyama Bay, southern Japan Sea. N=nauplius, C=copepodite, F=female, and M=male.

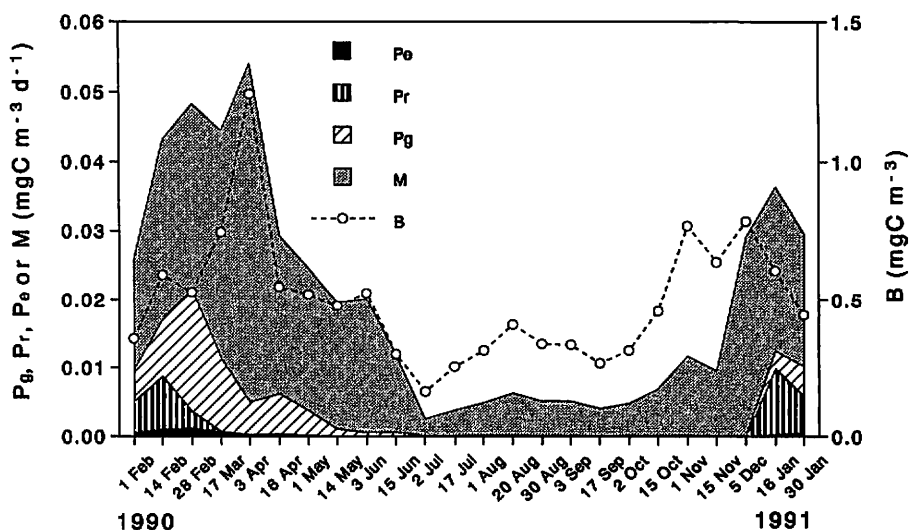


Fig. 1. Changes according to season in daily somatic production (P_g), molt production (P_e), egg production (P_r), metabolism (M) (all mgC m⁻³ d⁻¹) and biomass (B , mgC m⁻³) of the *Metridia pacifica* population in Toyama Bay, southern Japan Sea.

Table 3. Summary of nearly one full year (1 February 1990–30 January 1991) and growing season (1 February–1 May 1990, 16–30 January 1991) carbon budgets for the *Metridia pacifica* population in Toyama Bay. Data are expressed per m^3 and m^2 , the former was multiplied by 500 to obtain the latter.

	Nearly 1 full yr (363 d)		Growing season only (103 d)	
	mgC m^{-3}	mgC m^{-2}	mgC m^{-3}	mgC m^{-2}
Mean Biomass (<i>B</i>)	0.525	263	0.667	334
Production ($P=P_g+P_c+P_r$)	1.322	661 (% of <i>P</i>)	1.173	587 (% of <i>P</i>)
Somatic (P_g)	0.969	485 (73.3)	0.831	416 (70.8)
Molt (P_m)	0.075	37 (5.7)	0.064	32 (5.5)
Egg (P_e)	0.278	139 (21.0)	0.278	139 (23.7)
Metabolism (<i>M</i>)	6.436	3218	3.168	1584
Ratios <i>P/B</i>	2.52 (daily: 0.0069)		1.76 (daily: 0.0171)	
P_g/B	1.85 (daily: 0.0051)		1.25 (daily: 0.0121)	
P/M	0.205 (daily: 0.00057)		0.370 (daily: 0.0035)	
P_g/M	0.151 (daily: 0.00041)		0.262 (daily: 0.0025)	

ductive season of *M. pacifica* was considered to be 60 days for the present calculation. Daily P_r is given as $5.57 \times 0.2 \times N_p$, where N_p is the number of adult females.

Daily P_r ranged from 0.003 to 0.010 $\text{mgC m}^{-3} \text{d}^{-1}$ (Fig. 1), with integrated P_r over the 60 days of 0.278 mgC m^{-3} (or 139 mgC m^{-2}) (Table 3).

Molt production (P_m)

Daily molt production by the population at a given sampling date is given as the sum of $(0.038(W_c/DT))$, where *DT* is the developmental time of each stage. *DT*s of N3–C5 were re-computed from the instantaneous growth rate ($g=0.056$) outlined above substituting W_c data for each stage. The *DT*s of the C6 males and females were derived from the *ADT* data in Table 2.

Daily P_m varied from <0.0001 to 0.0012 mgC m^{-3} (Fig. 1), with integrated P_m s over the entire study period (363 d) and growing period (103 d) of 0.075 mgC m^{-3} (or 37 mgC m^{-2}) and 0.064 mgC m^{-3} (or 32 mgC m^{-2}), respectively (Table 3).

Metabolism (*M*)

The mean body mass of C6 females of *Metridia pacifica* was 0.754 mg (± 0.09 , $N=20$) wet weight or 0.110 mg DW per specimen and the C content was 47.1% (± 2.12 , $N=2$) (i.e. $W_c=51.8 \mu\text{gC}$). Values of *R*s adjusted to $W_c=1 \mu\text{gC}$ ($Adj R: \mu\text{l O}_2 W_c^{-0.780} \text{h}^{-1}$) were plotted against temperature (Fig. 3), indicating that *Adj R* increased exponentially with temperature from 0 to 16°C, then leveled off at 20 and 24°C. Observation of the condition of specimens at the end of the incubation revealed them to be swimming continuously at all temperatures, except at 24°C (all specimens were on the bottoms of the bottles with only feeble movement of their appendages). The regression analysis of the natural logarithm of *Adj R* on temperatures (0 to 16°C) yielded $\ln(Adj R)=0.0957T-5.947$ ($r=0.998$, $df=3$,

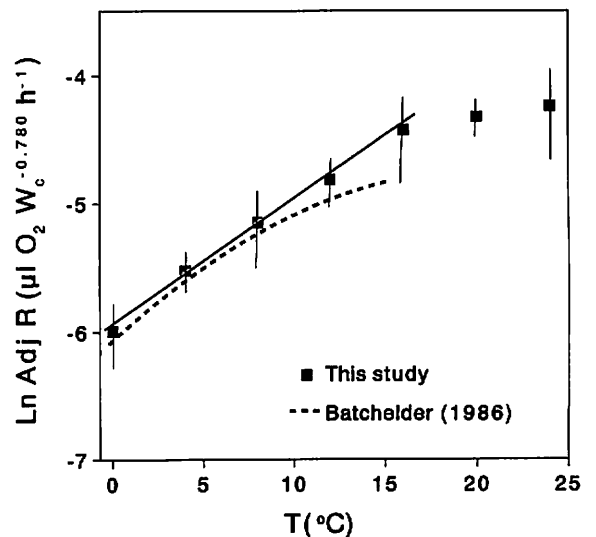


Fig. 3. Relationship between adjusted oxygen consumption rates (*Adj R*; $\mu\text{l O}_2 W_c^{-0.780} \text{h}^{-1}$) and temperature (*T*; °C) of *Metridia pacifica*. Vertical bars denote +1SD on 8–10 replicates. Batchelder's (1986) data are superimposed for comparison.

$p<0.01$), or $R=0.00261W_c^{0.780} \times e^{0.0957T}$. Then, the $R-W_c$ relationship of *M. pacifica* during July through November when $T=0.5^\circ\text{C}$ is expressed as $R=0.0027W_c^{0.780}$, and during December through June when $T=10^\circ\text{C}$ is $R=0.0068W_c^{0.780}$. *R* is converted to daily metabolic carbon loss by multiplying $24 \times 0.97 \times 10^{-3} \times 12/22.4$, where 24 is hours in a day, 0.97 is the respiratory quotient (*RQ*) of protein metabolism (Gnaiger 1983), 10^{-3} is to convert μg to mg, and 12/22.4 is carbon mass in 1 mole of CO_2 . The population metabolism (*M*: $\text{mgC m}^{-3} \text{d}^{-1}$) at a given sampling date was computed as the sum of daily metabolic carbon loss of each N3–C6 stage, multiplied by their abundance as outlined in Table 1.

Daily population *M* ranged from 0.0025 (July) to 0.0505 $\text{mgC m}^{-3} \text{d}^{-1}$ (April) and the general seasonal pattern was very similar to those of *B* and P_g (Fig. 1). Integrated *M* over

the entire study period (363 d) and growing period (103 d) were 6.426 mgC m^{-3} (or 3218 mgC m^{-2}) and 3.168 mgC m^{-3} (or 1584 mgC m^{-2}), respectively (Table 3).

P/B, *P_g/B* and *P_g/M* ratios

Seasonal patterns of daily *P/B*, *P_g/B*, *P/M* and *P_g/M* were similar to those of *B*, *P_g*, *P_e* and *M* in Fig. 1. Integrated *P/B*, *P_g/B*, *P/M* and *P_g/M* were 2.52, 1.85, 0.21 and 0.15, respectively, for the entire survey period (363 d), and were 1.76, 1.25, 0.37 and 0.26, respectively, for the growing period (103 d) (Table 3).

Discussion

The *P/B* (or *P_g/B*) ratio is widely considered to be an appropriate basis for comparing production potential of various invertebrates, and is largely a function of body size (Banse & Moshier 1980), i.e. the greater the size the lower the *P/B*. For marine planktonic copepods, McLaren et al. (1989) estimated production of 10 copepod species over the Scotian Shelf, Northwestern Atlantic, and established the relationship between annual *P/B* ($=P_g/B$ since P_e and P_r were not considered) and adult body mass (*DW*, μg) as $\log_{10}(P_g/B) = 1.92 - 0.30 \times \log_{10} DW$ ($r = 0.78$, $df = 8$, $p < 0.001$, re-calculated from their data in Table 13). As a habitat for boreal copepods, the temperature over the Scotian Shelf (ca. 43°N latitude) is slightly lower than that in Toyama Bay (37°N). Substituting the C6 body mass data ($106 \mu\text{g DW}$) for *Metridia pacifica* in this study, we obtain an annual *P_g/B* of 20.5. Compared with this predicted value, the annual *P_g/B* obtained for *M. pacifica* in this study is 1.86 ($1.85 \times 365/363$) (Table 3), or only one tenth of the predicted value. This anomalously low annual *P_g/B* for *M. pacifica* led us to examine our estimates of their growth rates.

Presently available information about the growth of *Metridia pacifica* is from Vidal & Smith (1986) and Batchelder (1985). Vidal and Smith (1986) followed temporal changes in population structures of *M. pacifica* in the southeastern Bering Sea during the spring season (April–June), and found two prominent abundance peaks of early copepodites, separated by 50–55 days, inferring a generation length of 50–55 days. From these results, combined with body mass data of copepodites, they computed daily growth $G = 0.13 - 0.15$ for C1–C5, which is over two times greater than the present estimates for *M. pacifica* in Toyama Bay ($G = 0.058$ for the N3–C3, $G = 0.0028$ and 0.0006 for the C5 females and C5 males, respectively). Batchelder (1985) sampled over one full year at Station P in the eastern subarctic Pacific, and observed generation repetition of *M. pacifica* every 3–4 months. From the thus obtained generation length of 3–4 months, combined with body mass data for eggs ($0.25 \mu\text{g DW}$) and C6 females ($129 \mu\text{g DW}$) reported by Vidal & Smith (1986), $G = 0.052 - 0.069$ can be derived. This is close to the value

for N3–C4 found in this study (although our *G*s for C5 are still too low). Because of the nature of the data, stage-specific growth rates for *M. pacifica* could not be resolved from the results of either Vidal & Smith (1986) or Batchelder (1985).

Higher growth rates for *Metridia pacifica* in the south-eastern Bering Sea (Vidal & Smith 1986) than those at Station P (Batchelder 1985) and in Toyama Bay (this study) may be interpreted to be due to dissimilar conditions of water temperature and food supply, the two dominant factors affecting growth of copepods (cf. Huntley & Boyd 1984). At both Station P and Toyama Bay, the development of nauplii and early copepodites of *M. pacifica* occur in the upper 200 m, where the water temperature is $5 - 12^\circ\text{C}$ (Batchelder 1985; Hirakawa & Imamura 1993), and phytoplankton food rarely exceeds $1.5 \mu\text{g chlorophyll } a \text{ l}^{-1}$ (or $90 \mu\text{gC l}^{-1}$, assuming C:Chl *a* ratio = 60, cf. Batchelder & Miller 1989). In contrast, water temperature is $3 - 6^\circ\text{C}$ and phytoplankton concentration is as high as $3 - 6 \mu\text{g chlorophyll } a \text{ l}^{-1}$ (or $180 - 360 \mu\text{gC l}^{-1}$) in the southeastern Bering Sea (Vidal & Smith 1986). In the experiments of Batchelder (1986), *M. pacifica* were able to increase their ingestion rates with an increase of food concentrations up to $1000 \mu\text{gC l}^{-1}$. Thus, the greater *G* of *M. pacifica* in the southeastern Bering Sea compared to those at Station P and in Toyama Bay may be explained by an abundant food supply, which is not only high-enough to compensate for the lower water temperature but also accelerates the growth of *M. pacifica*. It is now evident that not only is *P_g* less in Toyama Bay, probably because of the lower food availability, but that this difference is amplified in the annual *P_g/B* calculation by the predominance of non-growing C6 in the population biomass (mean; 68.8% for the entire study period, and 45.9% for the population growing period, see "Results").

Egg (P_r) and molt (P_e) productions of *Metridia pacifica* were 21.0% and 5.6%, respectively, of the total production (*P*) over the entire study period, and these fractions changed slightly when the calculation was made for the growing season only (Table 3). Chisholm & Roff (1990) estimated P_r and P_e to be 44% and 8.4%, respectively, of the total production of tropical neritic copepod assemblages off Kingston, Jamaica. However, Chisholm & Roff (1990) noted that their estimates of P_r were approximations only since the calculation is based on the assumption that eggs are produced at the same instantaneous growth rate as somatic growth. For non-copepod zooplankton in Toyama Bay, P_r and P_e have been estimated as 20.6% and 10.4%, respectively, of *P* for a euphausiid, *Euphausia pacifica*, during their growing season (Iguchi & Ikeda 1999), and P_e as 8.3% of *P* for an amphipod *Themisto japonica* (Ikeda & Shiga 1999).

In an attempt to estimate the grazing impact of *Metridia pacifica* on primary production at Station P, Batchelder (1986) calculated the population metabolism of *M. pacifica*. For this purpose, he established a relationship between oxy-

gen consumption rates and temperatures, combining his own data on *M. pacifica* with those of other workers on the same species and a sibling species *M. lucens*. That relationship and the one obtained in this study are similar within the range of temperature 0–8°C (Fig. 3). From the present results, Q_{10} for oxygen consumption rates is 2.60, which falls within the range of 2.29 (*M. lucens*)–2.69 (*M. longa*) reported on two sibling species of *Metridia* in the Atlantic Ocean by Haq (1967). Population metabolism of *M. pacifica* estimated by Batchelder (1986) at Station P varied with season from 4 to 10 mgC m⁻² as compared with 11 to 25 mgC m⁻² (0.021 to 0.050 mgC m⁻³ × 500 m) during their growing season (January–April, Fig. 1) in Toyama Bay (this study).

From a methodological viewpoint, oxygen consumption rates of *Metridia pacifica* from the water-bottle method employed both in this study and Batchelder's (1986) represent largely the energy required for maintenance (routine metabolism), not the total of maintenance and diel vertical migration (DVM). Energy needed for DVM can be calculated as a function of body mass and the distance of movement of a zooplankton (cf. Torres 1984). As shown by Hattori (1989), only a fraction of the population of late copepodite stages (excluding adult males) of *M. pacifica* undertake DVM, possibly due to individual variations in body condition (i.e. energy content per unit body mass, Hays et al., 2001). Hirakawa (1991) and Hirakawa & Imamura (1993) noted that DVM of *M. pacifica* is a seasonal event in Toyama Bay, and the population in aestivation exhibits little or no DVM. The present lack of quantitative information on these features makes it difficult to calculate the energy required for DVM by *M. pacifica* in Toyama Bay. Studies have shown that the proportion of energy needed for DVM against that for maintenance is 47% in *Euphausia pacifica* (Iguchi & Ikeda 1999) and 30% in *Themisto japonica* (Ikeda & Shiga 1999), both living in Toyama Bay.

In contrast to terrestrial and aquatic benthic invertebrates, few comparisons have been made between population metabolism and population production for marine zooplankton (Humphreys 1979; Banse & Mosher 1980). P/M has been reported as 0.25 for a chaetognath *Sagitta elegans* (Sameoto 1973), 0.36 for *Themisto japonica* (Ikeda & Shiga 1999), and 0.70 (growing season only) for *Euphausia pacifica* (Iguchi & Ikeda 1999). The P/M calculated for *Metridia pacifica* during their growing season (0.39, Table 3) falls within the range of these previous studies. Nevertheless, because of the omission of energy for DVM, the present estimation of M for *M. pacifica* is possibly an underestimate, suggesting possible overestimation of P/M . A marked reduction in P/M from 0.391 during the growing season to 0.214 over the entire survey period is caused by there being little P_g or no P_r during the long aestivation period of *M. pacifica* in Toyama Bay.

The major components of net zooplankton biomass (wet weight) in the top 500 m of the water column in Toyama Bay are euphausiids (31.3%), copepods (28.4%), am-

phipods (17.9%), chaetognaths (11.4%) and others (11.0%) (Hirakawa et al. 1992). Among these, annual P_g has been estimated for *Euphausia pacifica* and *Themisto japonica* (which comprise the bulk of the euphausiids and amphipods, respectively) as 4140 and 1945 mgC m⁻², respectively. From a trophic viewpoint, *Metridia pacifica* and *E. pacifica* may be classified as secondary producers depending on primary production. Our calculation indicates that the contribution of *M. pacifica* to secondary production in Toyama Bay is approximately one tenth that of *E. pacifica*. Compared with *E. pacifica*, the lesser annual mean biomass (263 vs. 1090 mgC m⁻², the latter is from Iguchi & Ikeda 1999) and lower annual P_g/B (1.85 vs. 3.80, the latter is from Iguchi & Ikeda 1999) of *M. pacifica* are responsible for the difference. Iguchi & Ikeda (1999) noted that the P_g/B of *E. pacifica* in Toyama Bay was lower than in the subarctic Pacific because of a long annual non-growing season. This was also the case for *M. pacifica*. Thus, both *E. pacifica* and *M. pacifica* are cold-water species and their production potentials are suppressed by excess warming of the surface layer in Toyama Bay during summer/autumn. A recent study implies that despite their lower biomass (only 1.4% of total net zooplankton) appendicularians are important secondary producers during the warm season, with an annual P_g of 4500 mgC m⁻² and an annual P_g/B ratio of 135 (Tomita et al. 1999). Production calculations for other zooplankton species in Toyama Bay are in progress.

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