

Production, metabolism and *P:B* ratio of *Euphausia pacifica* (Crustacea: Euphausiacea) in Toyama Bay, southern Japan Sea

NAOKI IGUCHI¹ & TSUTOMU IKEDA²

¹Japan Sea National Fisheries Research Institute, 1 Suido-cho, Niigata 951–8121, Japan

²Biological Oceanography Laboratory, Faculty of Fisheries, Hokkaido University, 3–1–1 Minatomachi, Hakodate 041–0821, Japan

Received 8 April 1998; accepted 14 August 1998

Abstract: Production and metabolism of the euphausiid *Euphausia pacifica* in Toyama Bay, southern Japan Sea, were estimated from their population structure data collected at intervals of 2 weeks from February 1990 through January 1991. The *E. pacifica* population in Toyama Bay is characterized by a long non-growing season (August to December) during the year. Production (P) was calculated as the sum of somatic (P_g), molts (P_o) and egg (P_r) production ($P = P_g + P_o + P_r$), and M as the sum of routine metabolism (M_{rn}) and metabolism for diel vertical migration (M_{dvm}). Integrated over the entire sampling period (363 d), P_g , P_o , and P_r were 8.23, 2.41, and 2.45 mgC m⁻³, respectively, and M_{rn} and M_{dvm} were 21.75 and 10.36 mgC m⁻³. Similar calculations for the growing season alone (256 d) yielded P_g , P_o , P_r , M_{rn} , and M_{dvm} of 8.23, 1.24, 2.45, 11.55, and 5.39 mgC m⁻³. Somatic production:biomass ratio ($P_g : B$) was 3.78 for 363 d, and 5.04 for the growing season. Assuming the assimilation efficiency of ingested food to be 0.84, ingestion was computed as 53.82 mgC m⁻³ for 363 d and 34.37 mgC m⁻³ for 256 d (growing season). For the maintenance of growth, metabolism, and reproduction, the population needed to ingest 6.8% of biomass daily from near annual data, and 8.2% of biomass daily from growth season data. The present results are compared with those of previous workers on the same euphausiid in the eastern North Pacific and other euphausiids in the world oceans.

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

Introduction

The euphausiid *Euphausia pacifica* Hansen is distributed widely in the northern North Pacific and its marginal seas, including the Bering Sea, Okhotsk Sea, and Japan Sea (Brinton 1962). In Toyama Bay in the southern Japan Sea, *E. pacifica* is one of the most dominant zooplankton species, comprising approximately 30% (annual mean) of the total zooplankton biomass in the top 500 m (Hirakawa et al. 1992). *E. pacifica* is considered to be a primary herbivore (Ohman 1984) and is preyed upon by common squid *Todarodes pacificus*, Pacific mackerel *Pneumatophorus japonicus*, pink salmon *Oncorhynchus gorbusha*, and Alaska pollack *Theragra chalcogramma* (Nishimura 1957; Watanabe et al. 1958; Okiyama 1965; Fukutaki 1967), and is regarded as an important trophic link in the pelagic

ecosystem of the southern Japan Sea. To understand the quantitative role of *E. pacifica* in the organic matter transfer from the primary production to animals at higher trophic levels, information about the production and cost (metabolism) of this animal is a prerequisite.

According to Iguchi et al. (1993), the life history pattern of *E. pacifica* in Toyama Bay is characterized by a long, growth-halted season (ca. 5 months, from August through December), which is initiated by sinking below the euphotic layer to avoid the high lethal water temperatures (>20°C) during this season. The population returns gradually to the euphotic layer toward mid-winter, when food supply is quite limited. After this long growth stagnation, juveniles grow again from mid-winter and mature in late-winter through spring of the next year when food phytoplankton are most abundant. *E. pacifica* spawn from February to June, and the offspring develop into juveniles (about 10-mm body length) by mid-summer. *E. pacifica* in Toyama

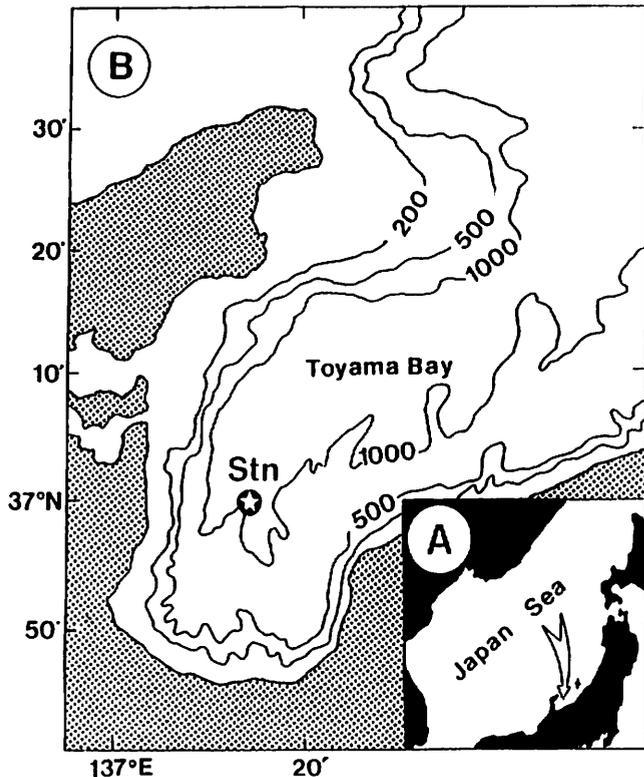


Fig. 1. A. Location of Toyama Bay in southern Japan Sea. B. Sampling station (circled star); 200, 500, and 1000 m depth contours are superimposed.

Bay has one generation per year and its maximum life span is estimated as 21 months. Late larval and postlarval stages of *E. pacifica* undergo a diel vertical migration, which varies in magnitude from 150 to 300 m depending on the development stage and season (Iguchi et al. 1993; Iguchi 1995).

In this study, we estimate the production (somatic, eggs, molts), metabolism (routine and diel vertical migration), and production : biomass ratio ($P : B$ ratio) of the population of *E. pacifica* in Toyama Bay. The results are compared with others for the same species and with other euphausiids from other regions.

Materials and Methods

Population data

A data set consisting of 24 distributions of numerical abundance and body length of *Euphausia pacifica* and its eggs was collected from a series of vertical hauls (500 m to the surface) at intervals of 2 weeks over one full year (February 1990 through January 1991) at an offshore station (37°00'N, 137°14'E) in Toyama Bay (Fig. 1). For these data, the body length (BL: the maximum distance between the tip of the rostrum and distal end of the telson excluding spines) was divided into 1-mm increments (23 size classes over the entire range of <1 to 23 mm BL). The sizes of ca-

lyptopis larvae were <1 to 2 mm, furcilia larvae >2 to 6 mm, and juveniles and adults >6 mm. No separation was made of males and females. Details of these results and environmental data (temperature, salinity, phytoplankton) collected concurrently may be found in Iguchi et al. (1993) and Taniguchi et al. (1997).

Body allometry and carbon content

The relationship between BL (mm) and dry weight (DW, mg) for *E. pacifica* has been established as $DW = 9.954 \times 10^{-4} BL^{3.156}$ (Iguchi & Ikeda 1995). Carbon contents of *E. pacifica* are 37.5% of DW for specimens <2 mm, 42.4% of DW for those 2 to <4 mm, 42.7% of DW for those 4 to <6 mm, 42.4% of DW for 6 to <12 mm, 43.2% for those 12 to <16 mm, 42.9% of DW for those 16 to <19 mm, and 43.1% of DW for those 19 to <23 mm (Iguchi & Ikeda 1998). Carbon contents of eggs and molts of *E. pacifica* are 47.2% (or $2.4 \mu\text{gC egg}^{-1}$) and 23.0% of DW, respectively (Iguchi & Ikeda 1998).

Diel vertical migration and habitat temperature

E. pacifica initiates diel vertical migration from furcilia 3 stage (4 mm), and the magnitude of the vertical migration is estimated as 150 m for furcilia larvae, and 200 m (July through October) to 300 m (the rest of the year) for juveniles/adults in Toyama Bay (Iguchi et al. 1993; Iguchi 1995). Larvae younger than furcilia 3 stay in the top 100 m throughout the day. It has been demonstrated experimentally that growth and metabolism of the amphipod *Themisto japonica*, another extensive diel vertical migrator in Toyama Bay, are under the influence of not extreme but mean temperature experienced during the day (Ikeda 1992). On this premise, the daily mean temperature that migrating *E. pacifica* encounters every day was estimated from day/night vertical distribution patterns of each developmental stage and temperature profiles in June, September, and December 1986 (Iguchi et al. 1993) and March 1993 (Iguchi 1995) as 11°C for the larvae younger than furcilia 3 and 8.1°C for the larvae older than furcilia 3, juveniles and adults in Toyama Bay.

Results

Biomass

The biomass of *Euphausia pacifica* expressed in carbon units (B : mgC m^{-3}) increased gradually from the beginning of the year, forming two peaks in summer (7.85 mgC m^{-3} in August, and 6.40 mgC m^{-3} in September), then decreased toward the end of the year (Fig. 2). From integrated B s over the entire study period (363 d) and growing season (256 d), mean B s were calculated as 2.18 and 1.63 mgC m^{-3} , respectively (Table 1).

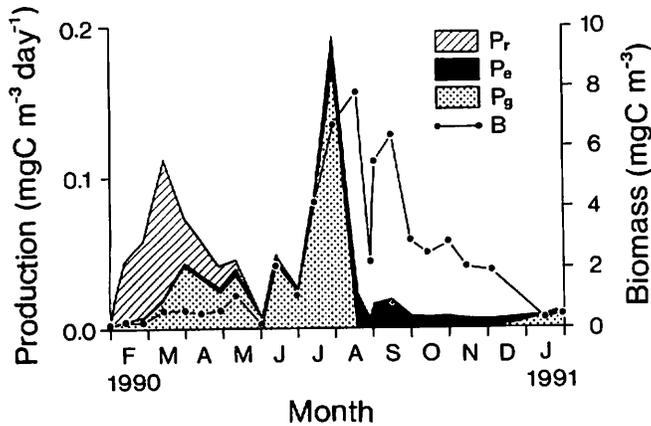


Fig. 2. Seasonal changes in daily production ($\text{mgC m}^{-3} \text{d}^{-1}$) of somatic (P_g), molt (P_e) and egg (P_r), and biomass (mgC m^{-3} , B) of *Euphausia pacifica* population in Toyama Bay, southern Japan Sea.

Somatic production

The somatic production of *E. pacifica* on a given sampling date was computed as the sum of growth increments of 23 size classes multiplied by the abundance of each size class:

$$P_g = \sum_{i=1}^s N_i (CW_{i+1} - CW_i) / D_i,$$

where P_g is the daily somatic production ($\text{mgC m}^{-3} \text{d}^{-1}$), CW_i , CW_{i+1} are carbon weights (mgC) at the beginning and end of the size interval, D_i is the developmental time (d) from CW_i to CW_{i+1} , N_i is the abundance (number m^{-3}) of

each size class, and s is 23. To obtain CW, BL data were converted to dry weight (DW) using the allometric equation, then to C units by multiplying C content data for each BL class mentioned above. D_i was estimated from the natural growth rate of 0.102 mm d^{-1} for <1 to $<10 \text{ mm}$ size classes ($1/0.102=9.80 \text{ d}$ throughout the classes), 0.076 mm d^{-1} for 10 to 23 mm size classes ($1/0.076=13.16 \text{ d}$ throughout the classes), except for the time period August to December when the growth of *E. pacifica* halted (Iguchi et al. 1993).

P_g thus calculated varied greatly with season from zero (August to December) to $0.173 \text{ mgC m}^{-3} \text{d}^{-1}$ (Fig. 2), with an integrated P_g of 8.23 mgC m^{-3} over the entire study period (363 d) and growing season (256 d) (Table 1).

Molt production

The production of molts is given by the equation:

$$P_e = \sum_{i=1}^s \alpha DW_i N_i / IP_i,$$

where P_e is the molt production ($\text{mgC m}^{-3} \text{d}^{-1}$), DW_i is the geometric mean DW of each size-class, N_i is the abundance of each size class, α is the percent loss in body DW per molting (4.0%, Iguchi, unpublished data) multiplied by carbon content of molts (23.0% of DW, Iguchi & Ikeda 1998), and IP_i is the intermolt period (d) of juveniles and adults ($>6 \text{ mm}$) estimated from $\log_{10} IP_i = 0.0321 \text{ BL} + 10^{0.0340 - 0.04357}$ (Iguchi & Ikeda 1995) and BL vs DW allometry mentioned above. IP_i for larvae is 5.5 d at 11°C for <1 to $<4 \text{ mm}$, and 7.4 d at 8°C for 4 to 6 mm specimens, which were estimated from IP data at 8 and 12°C in Ross

Table 1. Carbon budget of *Euphausia pacifica* in Toyama Bay. Calculations were made by integrating over nearly one full year (1 February 1990 through 30 January 1991) and growing season only (excluding the period between 20 August and 5 December 1990). Data are expressed in m^{-3} and m^{-2} ; the former was multiplied by 500 for the latter.

	Toyama Bay (This study)				Northern North Pacific (Lasker 1966)			
	Nearly 1 full year (363 d)		Growing season (256 d)		Nearly 1 full year (363 d)		Growing season (256 d)	
	mgC m^{-3}	mgC m^{-2}	(% of P)	(% of A)	mgC m^{-3}	mgC m^{-2}	(% of P)	(% of A)
Mean biomass (B)	2.18	1090			1.63	816		
Production ($P=P_g+P_r+P_e$)	13.10	6550	(29.0)	(29.0)	11.93	5964	(41.3)	(33.6)
Somatic (P_g)	8.23	4117	(62.9)	(18.2)	8.23	4117	(69.0)	(28.5)
Molt (P_e)	2.41	1206	(18.4)	(5.3)	1.24	621	(10.4)	(4.3)
Egg (P_r)	2.45	1226	(18.7)	(5.4)	2.45	1226	(20.6)	(8.5)
Metabolism ($M=M_{rn}+M_{dvm}$)	32.11	16055		(71.0)	16.94	8471		(58.7)
Routine (M_{rn})	21.75	10875		(48.1)	11.55	5775		(40.0)
Diel vertical migration (M_{dvm})	10.36	5180		(22.9)	5.39	2696		(18.7)
Assimilation ($A=P+M$)	45.21	22604			28.87	14435		
Ingestion ($I=A/0.84$)	53.82	26910			34.37	17185		
$P_g : B$		3.78				5.04		
$P : B$		6.01				7.31		
$P : M$		0.41				0.70		

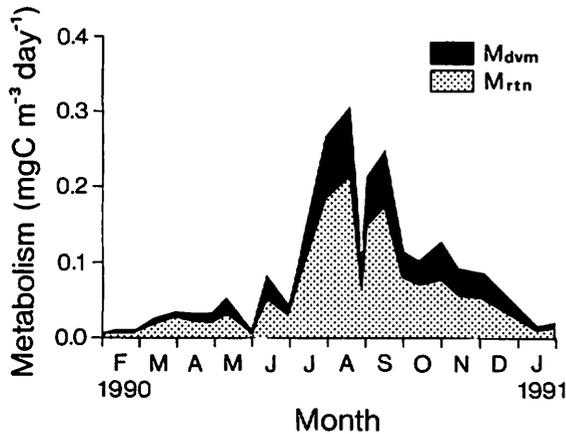


Fig. 3. Seasonal changes in carbon loss ($\text{mgC m}^{-3} \text{d}^{-1}$) due to routine metabolism (M_{rtn}) and diel vertical migration metabolism (M_{dvm}) of *Euphausia pacifica* population in Toyama Bay, southern Japan Sea.

(1981).

P_e fluctuated seasonally, and higher values were seen in the summer season (Fig. 2). The minimum was found in February ($0.0003 \text{ mgC m}^{-3} \text{d}^{-1}$) and maximum in August ($0.024 \text{ mgC m}^{-3} \text{d}^{-1}$), with integrated P_e s over the entire study period (363 d) and growing season (256 d) of 2.41 and 1.24 mgC m^{-3} , respectively (Table 1).

Egg production

The production of eggs was computed by the equation:

$$P_r = ECW_e / D_e,$$

where P_r is the egg production ($\text{mgC m}^{-3} \text{d}^{-1}$), E is the abundance of eggs (number m^{-3}), D_e is the hatching time (2 d at 10°C , Iguchi & Ikeda 1994), and CW_e is the carbon weight of an egg ($2.4 \mu\text{gC}$, Iguchi & Ikeda 1998; Lasker 1966).

Egg production of *E. pacifica* was limited largely to the period from February to May in Toyama Bay (Iguchi et al. 1993), and P_r ranged from 0.004 to $0.057 \text{ mgC m}^{-3} \text{d}^{-1}$. Integrated P_r s over the entire study period (363 d) and growing season (256 d) were the same value of 2.45 mgC m^{-3} (Fig. 2 and Table 1).

Metabolism

The metabolism M ($\text{mgC m}^{-3} \text{d}^{-1}$) was partitioned into two components; routine metabolism (M_{rtn}) and diel vertical migration metabolism (M_{dvm}). M_{rtn} was represented by the mean routine oxygen consumption rates (R : $\mu\text{l O}_2 \text{ indiv.}^{-1} \text{d}^{-1}$) of *E. pacifica* placed in a pressurized (40 atm) and unpressurized (1 atm) annular respirometer by Torres & Childress (1983), combined with the body exponent (0.85) of oxygen consumption rates obtained for an allied species *E. superba* by Ikeda (1984), i.e. $R=1.03\text{DW}^{0.85}$ at 8°C and $R=1.29\text{DW}^{0.85}$ at 11°C ; the latter was computed from the former using the mean $Q_{10}=2.1$ obtained in the same ex-

periment of Torres & Childress (1983). M_{dvm} is the amount of oxygen consumed in the diel vertical migration (R' : $\mu\text{l O}_2 \text{ indiv.}^{-1} \text{km}^{-1}$), which was calculated from the equation of net cost of transport as a function of weight (mg DW) of animals established for pelagic crustaceans ("multiple-paddle" propulsive system as compared with "undulatory" propulsion system of fish): $R'=28.74\text{DW}^{0.72}$ (Torres 1984; the original equation based on energy units was modified using the oxycaloric equivalent of $1 \text{ cal}=208.33 \mu\text{l O}_2$, and water content of *E. pacifica*=80%; cf. Iguchi & Ikeda 1998). R' is independent of temperature in theory (cf. Morris et al. 1990), and is $0.3R'$ for *E. pacifica* furcilia larvae migrating 150 m daily (i.e. 0.3 km for round trip), and $0.4R'$ and $0.6R'$ for juveniles/adults migrating 200 m daily (July through October) and 300 m daily (the other months) in Toyama Bay (Iguchi et al. 1993; Iguchi 1995). The reduced diel vertical migration range of *E. pacifica* during the summer months is due to the high lethal temperature in the top 100 m during this season (Iguchi et al. 1993). Thus, $M_{\text{rtn}}=(1.03 \text{ or } 1.27)\times 24\times 10^{-3}A\sum_{i=1}^s W_i^{0.85}N_i$, and $M_{\text{dvm}}=(0.3, 0.4, \text{ or } 0.6)\times 10^{-3}\times 28.74A\sum_{i=1}^s W_i^{0.72}N_i$, where DW_i is the geometric mean DW of each size class, and A ($0.97\times 12/22.4$) is the conversion factor for oxygen to carbon assuming protein metabolism ($\text{RQ}=0.97$, Gnaiger 1983).

Both M_{rtn} and M_{dvm} thus calculated were the highest in the summer season; the seasonal range was from 0.003 to $0.214 \text{ mgC m}^{-3} \text{d}^{-1}$ for the former and from 0.002 to $0.092 \text{ mgC m}^{-3} \text{d}^{-1}$ for the latter (Fig. 3). Integrated values over the entire study period (363 d) and growing season (256 d) were 21.75 and 11.55 mgC m^{-3} , respectively for M_{rtn} , and 10.36 and 5.39 mgC m^{-3} , respectively, for M_{dvm} (Table 1).

Assimilation and ingestion

The carbon assimilated by *E. pacifica* (A : $\text{mgC m}^{-3} \text{d}^{-1}$) is defined as $A=P+M=P_g+P_e+P_r+M_{\text{rtn}}+M_{\text{dvm}}$, assuming no leakage of soluble organic matter from the body. The amount of ingested carbon (I : $\text{mgC m}^{-3} \text{d}^{-1}$) was computed by adopting an assimilation efficiency value of 84% determined on *E. pacifica* by Lasker (1966), i.e. $I=A/0.84$.

A ranged from 0.008 to $0.459 \text{ mgC m}^{-3} \text{d}^{-1}$, and I from 0.010 to $0.547 \text{ mgC m}^{-3} \text{d}^{-1}$. Integrated values over the entire study period (363 d) and growing season (256 d) were 45.21 and 28.87 mgC m^{-3} , respectively, for A , and 53.82 and 34.37 mgC m^{-3} , respectively, for I (Table 1).

Size structure in production and metabolism

Based on the above results for production and metabolism of the population of *E. pacifica* during growing season, the relative importance of each size class was analyzed (Table 2). Clearly, the larvae were of minor importance based on the results for each of P_g , P_e , M_{rtn} and M_{dvm} (19.9, 6.8, 11.3, and 4.4%, respectively, of each total). The most important size classes are 8 to 12 mm, contributing 50.2, 57.9, 51.0, and 55.8% of the total of P_g , P_e , M_{rtn} , and M_{dvm} , respectively, during this period. The relative biomass (B) of

Table 2. Relative contribution (%) of each size class of *Euphausia pacifica* to mean biomass (B), somatic production (P_g), molt production (P_c), routine metabolism (M_{rm}), and diel vertical migration metabolism (M_{dvm}) achieved during their growing season in Toyama Bay. Developmental stages should be considered as a rough guide.

Development stage	Size class (mm)	% B	% P_g	% P_c	% M_{rm}	% M_{dvm}
Larvae	0-1	0.13	0.9	0.2	0.6	0.0
	1-2	0.28	1.9	0.4	1.0	0.0
	2-3	0.99	5.1	1.3	2.5	0.0
	3-4	1.24	4.4	1.7	2.6	0.0
	4-5	1.45	3.9	1.4	2.2	2.2
	5-6	1.73	3.8	1.7	2.4	2.2
Juveniles	6-7	2.22	4.1	3.4	2.8	4.8
	7-8	3.17	5.0	4.5	3.8	5.3
Juveniles/ subadults	8-9	8.08	11.3	10.7	9.0	11.4
	9-10	11.68	14.6	14.3	12.4	13.0
	10-11	18.59	15.7	21.2	18.8	20.2
Adults	11-12	11.14	8.6	11.8	10.8	11.2
	12-13	7.27	5.1	7.0	6.6	6.5
	13-14	1.96	1.3	1.8	1.7	1.8
	14-15	2.06	1.3	1.7	1.8	2.0
	15-16	1.26	0.7	1.0	1.0	1.1
	16-17	1.50	0.8	1.1	1.2	1.1
	17-18	3.19	1.6	2.1	2.5	2.0
	18-19	7.80	3.7	4.9	6.0	5.5
	19-20	5.22	2.4	3.0	3.9	3.6
	20-21	7.61	3.3	4.1	5.5	5.0
21-22	0.91	0.4	0.5	0.6	0.7	
22-23	0.50	0.2	0.2	0.3	0.4	
Total		100	100	100	100	100

larvae (5.8% of the total) and specimens of 8 to 12 mm (49.5% of the total) correspond roughly to these results. The relative importance of other size classes of 6 to 8 mm and >12 mm is somewhere between those of the <6 mm (larvae) and 8-12 mm (adults) size classes.

Discussion

The growth patterns and production of *Euphausia pacifica* were investigated for the local populations in Saanich Inlet, Canada (Heath 1977) and off Oregon (Mauchline 1977). For the Saanich Inlet population the life span of *E. pacifica* is 19-22 months with stagnation in growth observed during the early seasons of the year (January to April), whereas the off Oregon population grows continuously during its life span of one year. Compared with growth patterns of *E. pacifica* living in these eastern North Pacific regions, those in Toyama Bay are similar to the Saanich Inlet population in terms of the length of life span and the long no-growth period (but its season for the latter is August-December).

Because the seasonal growth patterns of *E. pacifica* vary

regionally, the daily somatic production (P_g) and daily somatic production:biomass ($P_g:B$) ratio during its growing season are considered for meaningful comparison. The daily P_g of the Saanich Inlet population has been calculated as 3.81 mg wet weight (WW) m^{-3} and the daily $P_g:B$ ratio is 0.024 (Heath 1977); the respective figures for the off Oregon population are 0.31 mg DW m^{-3} and 0.024 (Mauchline 1977). To compare with production of *E. pacifica* in Toyama Bay expressed in carbon units, the production expressed by WW or DW was converted to carbon using the rounded conversion factors for this species ($DW=0.2WW$, $C=0.43DW$, cf. Iguchi & Ikeda 1998). The resulting daily P_g is 0.33 mgC m^{-3} for the Saanich Inlet population, and 0.14 mgC m^{-3} for the population off Oregon. Daily P_g computed for the Toyama Bay population during the growing season is 0.032 (=8.23/256) mgC m^{-3} , which is only 10-23% of the daily P_g s of the eastern North Pacific populations. However, the daily $P_g:B$ ratio, which is not affected by the choice of units, of 0.020 (=5.04/256) for the Toyama Bay population is remarkably similar to the 0.024 of the eastern North Pacific populations. Similar daily $P_g:B$ ratios found in the Toyama Bay, Saanich Inlet, and off Oregon populations may be reasonable since daily growth rates of juveniles, which occupy the greatest portion of the populations, from these three regions are identical (about 0.1 mm d^{-1}). From these similar $P_g:B$ ratios, it is clear that the lower daily P_g of the Toyama Bay population is due to its low biomass. Indeed, the mean biomass of the Toyama Bay population during the growing season is 1.63 mgC m^{-3} , which is only 11% of the Saanich Inlet population (15.2 mgC m^{-3} , converted from WW using conversion factors mentioned above) and 29% of the off Oregon population (5.6 mgC m^{-3}).

Despite similar daily $P_g:B$ ratios, the annual $P_g:B$ ratio of *E. pacifica* is variable among the regional populations; i.e. 3.8 (3.8×[365/363]) for the Toyama Bay population (Table 1), 2.6 for the Saanich Inlet population (8.8 given by Heath [1977] is in error since his calculation is from the daily $P:B$ ratio during the growing season multiplied by 365 d, disregarding non-growing seasons of the year), and 8.7 for the off Oregon population (Mauchline 1977). The lower annual $P_g:B$ ratios of the Toyama Bay and Saanich Inlet populations are due to the growth stagnation periods during their one-year cycle. Such regional variations in annual $P_g:B$ ratios within the same species have been reported for other euphausiids, i.e. for *Nyctiphanes simplex* living in western (annual $P_g:B=12.7$, Lavaniegos 1995) and southwestern Baja California (7.0, Gomez-Gutierrez et al. 1996), *Thysanoessa inermis* in the Gulf of St. Lawrence, Canada (ca. 4, Berks 1977) and the east coast of USA and the North Sea (1.3 to 10.4, Lindley 1980), and *Meganycitiphanes norvegica* in the Rockall Trough (4.5, Mauchline 1985) and Lock Fyne, Scotland (1.6 to 2.3, Mauchline 1977).

Production of euphausiids has been estimated as the sum of somatic (P_g), molts (P_c) and eggs (P_e) by several work-

ers. The relative contribution of production of P_g , P_e , and P_r to the total production ($P = P_g + P_e + P_r$) is 69.0:10.4:20.6 for *E. pacifica* in Toyama Bay (growing season data, cf. Table 1) and 30.0:45.5:26.5 in the northern North Pacific (Lasker 1966), 49.6:46.5:3.9 for *E. lucens* in the Benguela Current (Stuart & Pillar 1988), 74.7:23.4:1.9 for *N. simplex* in western Baja California (Lavaniegos 1995), and 62.9:33.7:3.4 for *N. australis* in southeastern Tasmanian water (Hosie & Ritz 1983). Excepting Lasker (1966), who expressed the data in carbon units, all previous measurements were made on a DW basis. Since the carbon content of body, molts, and eggs varies to a great extent, a direct comparison of these DW based results with those of *E. pacifica* expressed in carbon units is not possible. To overcome this problem, the previous measurements were standardized to carbon units by assuming the same carbon content as *E. pacifica* in this study, i.e. 43% of DW for the body (a mean of six size classes), 23% of DW for molts, and 47% of DW for eggs. Thus, standardized $P_g:P_e:P_r$ ratios for carbon are 63.0:31.6:5.4 for *E. lucens*, 83.7:14.0:2.3 for *N. simplex*, and 74.3:21.3:4.4 for *N. australis*. For *E. pacifica*, the present results from growing season data and those of Lasker (1966) are in fair agreement in the proportion of P_r (20.6% vs 26.5%), but are dissimilar in P_g (69.0% vs 30.0%) and P_e (10.4% vs 45.5%). It is considered that Lasker's P_g is underestimated, while P_r is overestimated (see discussion below). Despite this large difference between these two studies in P_r for *E. pacifica*, it is obvious that these P_s (20.6% or 26.5%) of *E. pacifica* are much higher than those of the other three euphausiids (2.3 to 5.4%). While P_r was estimated from the abundance of eggs in the field and egg hatching time in this study, it was from the lifetime fecundity of females (the number of eggs released by females per spawning, multiplied by assumed spawning frequency) in other studies. However, this methodological difference may not be the cause of dissimilar P_s between *E. pacifica* and the other euphausiids, since Lasker's P_r for *E. pacifica* is derived from the latter method. Thus, a comparison of $P_g:P_e:P_r$ ratios presently available suggests that *E. pacifica* is a euphausiid characterized by higher investment of carbon in egg production.

Metabolism has seldom been included in production studies of euphausiids in the past, with the exception of Lasker's (1966) study on *E. pacifica*. Lasker (1966) considered M_{rin} only, but the omission of M_{dvm} in estimating M may not have affected the results seriously, since M_{dvm} is a relatively small fraction of M (32% in the growing season budget; Table 1). Comparing the carbon budget established for *E. pacifica* in this study (growing season) with that of Lasker (1966), it is clear that M is roughly comparable, but P_g in our work is significantly greater than that in his, and the reverse is the case for P_e . Smiles & Percy (1971) and Brinton (1976) have claimed that the *E. pacifica* growth rate (0.021 mm d^{-1}) of *E. pacifica* which Lasker (1966) quoted is too slow, as judged from their observations for field populations (for juveniles, up to 0.1 mm d^{-1}). Lasker

(1966) derived P_e assuming the proportion of body DW lost per molting to be 10%, compared to 4% in this study. Dalpadado & Ikeda (1989) noted a similar discrepancy in the loss of body DW in each molting of *Thysanoessa inermis* (2.1% vs. 5.7% reported by Sameoto 1976), and suggested that residual salts in the molts due to incomplete rinsing in distilled water may be a possible cause for overestimation of molt weight.

Based on the carbon budget, Lasker (1966) estimated the daily cost of growth, molts, and metabolism for *E. pacifica* in the northern North Pacific Ocean to be 5% of their biomass in terms of carbon. Because of his underestimation of P_g and possible overestimation of P_e , Lasker's (1966) estimate for the daily maintenance cost of the species may not be valid. The present results indicate that the daily maintenance cost including growth, molts, metabolism and reproduction of the *E. pacifica* population in Toyama Bay (near annual mean biomass: 2.18 mgC m^{-3}) required 53.82 mgC m^{-3} , which equates to 6.8% ($[53.82 \times 100] / [2.18 \times 363]$) of the biomass. The daily maintenance cost increases to 8.2% ($[34.37 \times 100] / [1.63 \times 256]$) when the calculation was made only for growing season data. It may be argued that inclusion of larvae in this study is an additional cause for higher daily maintenance costs of *E. pacifica*, since the larvae were not considered by Lasker (1966). However, contributions of the larvae to the total P_g , P_e , M_{rin} , and M_{dvm} achieved by the population during the growing season were only 4.4 to 19.9% (Table 2), and thereby cannot be a significant additional cause for the higher daily maintenance cost derived in the present study.

Acknowledgment

We are grateful to Dr C. B. Miller for his critical reading of the manuscript and valuable comments. This is Contribution No. B9802 from the Japan Sea National Fisheries Research Institute.

Literature Cited

- Berkes, F. 1977. Production of the euphausiid crustacean *Thysanoessa raschii* in the Gulf of St. Lawrence. *J. Fish. Res. Bd Can.* 34: 443-446.
- Brinton, E. 1962. The distribution of Pacific euphausiids. *Bull. Scripps Inst. Oceanogr. Univ. Calif.* 8: 51-270.
- Brinton, E. 1976. Population biology of *Euphausia pacifica* off southern California. *Fish. Bull. U.S.* 74: 733-762.
- Dalpadado, P. & T. Ikeda 1989. Some observations on moulting, growth and maturation of krill (*Thysanoessa inermis*) from the Barents Sea. *J. Plankton Res.* 11: 133-139.
- Fukataki, H. 1967. Stomach contents of the pink salmon, *Oncorhynchus gorbuscha* (Walbaum), in the Japan Sea during the spring season of 1965. *Bull. Jpn Sea Reg. Fish. Res. Lab.* 17: 49-66. (In Japanese.)
- Gnaiger, E. 1983. Calculation of energetic and biochemical equivalents of respiratory oxygen consumption, p. 337-345. In *Po-*

- larographic oxygen sensors* (eds. Gnaiger, H & H. Forstner). Springer-Verlag, Berlin.
- Gomez-Gutierrez, J., R. D. Silva & B. E. Lavaniegos 1996. Growth production of the euphausiid *Nyctiphanes simplex* on the coastal shelf off Bahia Magdalena, Baja California Sur, Mexico. *Mar. Ecol. Prog. Ser.* **138**: 309–314.
- Heath, W. A. 1977. The ecology and harvesting of euphausiids in the Strait of Georgia. Ph.D. Thesis, University of British Columbia, 187pp.
- Hirakawa, K., A. Imamura & T. Ikeda 1992. Seasonal variability in abundance and composition of zooplankton in Toyama Bay, southern Japan Sea. *Bull. Jpn Sea Natl Fish. Res. Inst.* **42**: 1–15.
- Hosie, G. W. & D. A. Ritz 1983. Contribution of moulting and eggs to secondary production in *Nyctiphanes australis* (Crustacea: Euphausiacea). *Mar. Biol.* **77**: 215–220.
- Iguchi, N. 1995. Spring diel migration of a euphausiid *Euphausia pacifica* in Toyama Bay, southern Japan Sea. *Bull. Jpn Sea Natl Fish. Res. Inst.* **45**: 59–68. (In Japanese.)
- Iguchi, N. & T. Ikeda 1994. Experimental study on brood size, egg hatchability and early development of a euphausiid *Euphausia pacifica* from Toyama Bay, southern Japan Sea. *Bull. Jpn Sea Natl Fish. Res. Inst.* **44**: 47–55.
- Iguchi, N. & T. Ikeda 1995. Growth, metabolism and growth efficiency of a euphausiid crustacean *Euphausia pacifica* in the southern Japan Sea, as influenced by temperature. *J. Plankton Res.* **17**: 1757–1769.
- Iguchi, N. & T. Ikeda 1998. Elemental composition (C,H,N) of a euphausiid *Euphausia pacifica* in Toyama Bay, southern Japan Sea. *Plankton Biol. Ecol.* **45**: 27–32.
- Iguchi, N., T. Ikeda & A. Imamura 1993. Growth and life cycle of a euphausiid crustacean (*Euphausia pacifica* Hansen) in Toyama Bay, southern Japan Sea. *Bull. Jpn Sea Natl Fish. Res. Inst.* **43**: 69–81. (In Japanese.)
- Ikeda, T. 1984. Sequences in metabolic rates and elemental composition (C,N,P) during the development of *Euphausia superba* Dana and estimated food requirements during its life span. *J. Crust. Biol.* **4** (Spec. No. 1): 273–284.
- Ikeda, T. 1992. Growth and metabolism of the hyperiid amphipod *Themisto japonica* (Bovallius) reared in the fluctuating and constant temperatures in the laboratory. *J. Plankton Res.* **14**: 925–935.
- Lasker, R. 1966. Feeding, growth, respiration, and carbon utilization of a euphausiid crustacean. *J. Fish. Res. Bd Can.* **23**: 1291–1317.
- Lavaniegos, B. E. 1995. Production of the euphausiid *Nyctiphanes simplex* in Vizcaino Bay, western Baja California. *J. Crust. Biol.* **15**: 444–453.
- Lindley, J. A. 1980. Population dynamics and production of euphausiids II. *Thysanoessa inermis* and *T. raschi* in the North Sea and American coastal waters. *Mar. Biol.* **59**: 225–233.
- Mauchline, J. 1977. Estimating production of midwater organism, pp177–215. In *Oceanic Sound Scattering Prediction* (eds. Andersen, N. R. & B. J. Zahuranc). Plenum Press, New York & London.
- Mauchline, J. 1985. Growth and production of Euphausiacea (Crustacean) in the Rockall Trough. *Mar. Biol.* **90**: 19–26.
- Morris, M.J., K. Kohlhage & G. Gust 1990. Mechanics and energetics of swimming in the small copepod *Acanthocyclops robustus* (Cyclopoida). *Mar. Biol.* **107**: 83–91.
- Nishimura, S. 1957. A short note of the feeding of the mackerel in the middle Japan Sea during its over-wintering period. *Jpn. J. Ecol.* **7**: 103–107. (In Japanese.)
- Ohman, M. D. 1984. Omnivory by *Euphausia pacifica*: the role of copepod prey. *Mar. Ecol. Prog. Ser.* **19**: 125–131.
- Okiyama, M. 1965. On the feeding habit of the common squid, *Todarodes pacificus* Steenstrup, in the off-shore region of the Japan Sea. *Bull. Jpn Sea Reg. Fish. Res. Lab.* **14**: 31–41. (In Japanese.)
- Ross, R. M. 1981. Laboratory culture and development of *Euphausia pacifica*. *Limnol. Oceanogr.* **26**: 235–246.
- Sameoto, D. D. 1976. Respiration rates, energy budgets, and molting frequencies of three species of euphausiids found in the Gulf of St. Lawrence. *J. Fish. Res. Bd Can.* **33**: 2568–2576.
- Smiles, M. C. & W. G. Percy 1971. Size structure and growth rate of *Euphausia pacifica* off the Oregon coast. *Fish. Bull. US* **69**: 79–86.
- Stuart, V. & S. Pillar 1988. Growth and production of *Euphausia lucens* in the southern Benguela Current. *J. Plankton Res.* **10**: 1099–1112.
- Taniguchi, A., Y. Nakajima, T. Suzuki, K. Hirakawa, A. Imamura & T. Ikeda 1997. Seasonal variations in the phytoplankton assembly in Toyama Bay, southern Japan Sea. *Bull. Jpn Sea Natl Fish. Res. Inst.* **47**: 33–55. (In Japanese.)
- Torres, J. J. 1984. Relationship of oxygen consumption to swimming speed in *Euphausia pacifica*. II. Drag, efficiency and a comparison with other swimming organisms. *Mar. Biol.* **78**: 231–237.
- Torres, J. J. & J. J. Childress 1983. The relationship of oxygen consumption to swimming speed in *Euphausia pacifica*. I. The effects of temperature and pressure. *Mar. Biol.* **74**: 79–86.
- Watanabe, T., K. Ito, T. Kobayashi, T. Nazumi & S. Yoshioka 1958. A study on the structure of bottom fish communities at trawling ground, off Port Tsuyama in Hyogo Prefecture. *Bull. Fish. Exp. Stn Hyogo-Ken* **9**: 1–20. (In Japanese.)