HOKKAIDO UNIVERSITY

Title	Reproductive and Developmental Characteristics of Three Mesopelagic Paraeuchaeta Species (Copepoda: Calanoida) in the Oyashio Region, Western Subarctic Pacific Ocean
Author(s)	YAMAGUCHI, Atsushi; IKEDA, Tsutomu
Citation	, 53(1), 11-21
Issue Date	2002-03
Doc URL	http://hdl.handle.net/2115/21959
Type	bulletin (article)
File Information	53(1)_P11-21.pdf

Instructions for use

Reproductive and Developmental Characteristics of Three Mesopelagic *Paraeuchaeta* Species (Copepoda : Calanoida) in the Oyashio Region, Western Subarctic Pacific Ocean

Atsushi Yamaguchi[1],[2] and Tsutomu Ikeda[1]

Abstract

Reproductive parameters (egg diameter, brood size) and developmental changes in prosome length (PL), wet weight (WW), dry weight (DW), ash-free dry weight (AFDW) of the three dominant *Paraeuchaeta* species (*P. elongata, P. birostrata, P. rubra*) in the meso- and bathypelagic zone of the Oyashio region were investigated. Among the three copepods, *P. elongata* were characterized by carrying smaller-sized eggs and larger brood size (mean : 26.2 eggs/female) as compared with *P. birostrata* and *P. rubra* which had larger-sized eggs but smaller brood sizes (mean : 7.3-8.5 eggs/female). All relationships between PL and WW, DW, AFDW for copepodid stages of the three species fitted an allometric equation ($Y = a \cdot X^b$) very well ($r^2 = 0.91$-0.99), and the exponent b values varied species-specifically (3.16-3.25 for *P. elongata*, 2.88-2.93 for *P. birostrata*, 2.50-2.93 for *P. rubra*). Between-stage increments for copepodid stages of the three species were identical in terms of PL (10-50%), but those expressed by WW, DW, and AFDW showed a marked increment peak (300-400%) during mid-copepodid stages in *P. elongata* only (<200% in *P. birostrata* and *P. rubra*). Within the species, molt increment in body mass decreased with increasing depth. Through all developmental stages (eggs, nauplii, and copepodids) patterns of change in water contents and organic matter in the body were similar among the three species; the lower water content yet higher organic matter during early developmental stages reflecting the their large accumulation of lipids in the body, and its progressive utilization. The present results are compared with those of other euchaetid copepods in the other regions and discussed in light of possible depth-related food availability in the meso- and bathypelagic realm.

Key words : Mesopelagic, Reproduction, Development, Copepoda, *Paraeuchaeta*

Introduction

Compared with epipelagic copepods, presently available information about biology of meso- and bathypelagic copepods is extremely limited, with a notable exception of the study on euchaetid copepods (*Euchaeta* spp.) living at various bathymetric strata down to 2000 m in the North Atlantic (Mauchline, 1994, 1995, 1998). Copepods in the Family Euchaetidae include the two genera *Euchaeta* and *Paraeuchaeta*, and have common features including carnivorous feeding and sac-spawning (i.e. females carry eggs in egg sacs attached outside of their bodies) (Mauchline, 1998). In the meso- and bathypelagic zones of the subarctic Pacific and its marginal seas, Euchaetid copepods occur with *P. elongata, P. birostrata*, and *P. rubra* (as an exception, only *P. elongata* distributes in the Japan Sea) being the most dominant species (Brodsky, 1950; Park, 1994). Among the three *Paraeuchaeta* spp., *P. elongata* has been studied extensively in the Japan Sea (Morioka,

1975; Ikeda and Hirakawa, 1996), western subarctic Pacific (Ozaki and Ikeda, 1999), and eastern subarctic Pacific (Bollens and Frost, 1991). Laboratory studies of the development of *P. elongata* have been conducted by several workers (Yen, 1983; Bollens and Frost, 1991; Ikeda and Hirakawa, 1996; Ozaki and Ikeda, 1997). Recently, Ozaki and Ikeda (1998) have successfully raised *P. elongata* from eggs through to adults in the laboratory. In contrast to *P. elongata, P. birostrata* and *P. rubra* have been little studied, most of the available information of the latter two species being about their vertical distribution patterns (Minoda, 1971; Sekiguchi, 1975) until the recent works of Yamaguchi and Ikeda (2001).

As part of a research program to evaluate biology of deep-sea zooplankton in the Oyashio region, we have reported seasonal changes in the population abundance (both numbers and biomass), population structure, and the incidence of carcasses and ciliate-infected specimens (Yamaguchi and Ikeda, 2001). Vertical distribution

[1] *Laboratory of Marine Biodiversity, Graduate School of Fisheries Sciences, Hokkaido University*
(北海道大学大学院水産科学研究科多様性生物学講座)
[2] *Present address : Environmental Chemistry Department, Kansai Environmental Engineering Center Co., Ltd., 1-3-5 Azuchi-machi, Chuo-ku, Osaka 541-0052, Japan.*
(現所属 : 〒541-0052 大阪市中央区安土町1-3-5 (株) 関西総合環境センター環境化学部)

patterns at different time scales (diel, seasonal, and ontogenetic) of adults and young copepodid stages of *Paraeuchaeta elongata*, *P. birostrata*, and *P. rubra* in this region, together with between-species trophic features have also reported (Yamaguchi and Ikeda, in this issue). We here report on reproductive and developmental characteristics of these three copepods and discuss the between-species differences in light of possible depth-related food availability in the meso- and bathypelagic realm.

Materials and methods

Specimens

All *Paraeuchaeta* specimens used in this study were those obtained from time-series samplings from 0-2,000 m depth in the Oyashio region, western subarctic Pacific (cf. Yamaguchi and Ikeda, in this issue). In addition to copepodid stages, naupliar stages of *P. elongata* and *P. birostrata* were sorted from samples collected in 5 October 1997. For the nauplii, developmental stages were not identified. For *P. elongata*, there is little difference in length and weights between naupliar stages (cf. Ikeda and Hirakawa, 1996). For egg-carrying females, the number of eggs per brood was counted to define their brood size.

Length and weight measurement

The egg diameter and prosome length (PL) of each copepodid stage [males and females after copepodid 4 stage (C4)], were measured under a Wild dissecting microscope to the nearest 0.01 mm. Wet weight (WW) was determined after rinsing briefly in distilled water and blotting on a filter paper. Then, specimens were dried in a drying oven (60°C) for 5 h to obtain dry weight (DW). To obtain ash-free dry weight (AFDW), ash content (ASH) was determined by weighing the specimens before and after combusting at 480°C for 5h (Omori and Ikeda, 1984). A microbalance (Mettler toledo MT5) was used for weighing to a precision of 1 μg. Water contents (WATER, % of WW) and organic contents (= AFDW, % of DW) were calculated using the following equations: WATER = 100 × (WW-DW)/ WW and AFDW = 100 × (DW-ASH)/DW, respectively.

A power regression model was used to analyze the body allometry; $Y = aX^b$ (or $\log_{10} Y = \log_{10} a + b \cdot \log_{10} X$) where Y is WW, DW or AFDW (all in mg) and X is PL (mm). a and b are fitted constants. Between-stage differences in WATER and AFDW were tested by one-way ANOVA, then significant differences between means were analyzed by Fisher's PLSD. Molt increments between stages in terms of PL, WW, DW or AFDW were computed as; increment (%) = 100 × (postmolt size − premolt size)/premolt size (cf. Mauchline, 1998).

The use of specimens preserved in formalin for WW, DW, and AFDW determinations may not be valid since loss of organic matter could occur during storage (Williams and Robins, 1982; Böttger and Schnack, 1986; Giguère et al., 1989). Nevertheless, the magnitude of error caused by formalin preservations is relatively small and unimportant for broad comparison between stages of both similar and dissimilar species (cf. Gruzov and Alekseyeva, 1970).

Results

Egg and brood size

The results of egg diameter and brood size determinations are summarized in Table 1. The eggs of *Paraeuchaeta elongata* were near spherical in shape, but those of *P. birostrata* and *P. rubra* were oval. The eggs of *P. birostrata* were largest and heaviest, followed by those of *P. rubra* and *P. elongata* (cf. Tables 1-4). Brood size varied little within the species, but it varied greatly between the species. Mean brood size was 26.2 for *P. elongata*, 8.5 for *P. birostrata*, and 7.3 for *P. rubra* (Table 1).

Table 1. Egg diameter, egg volume and brood size (number of eggs per one egg mass) of three *Paraeuchaeta* species in the Oyashio region, western subarctic Pacific Ocean. Note that the shape of eggs was near spherical for *P. elongata*, but oval for *P. birostrata* and *P. rubra*.
n: the number of observations, S: small diameter, L: large diameter.

Species	Egg diameter (μm)			Egg volume (mm³)	Brood size		
	n	Range	Mean ± 1sd		n	Range	Mean ± 1sd
P. elongata	30	400–480	436 ± 24	0.043	20	25–28	26.2 ± 1.2
P. birostrata	30	550–700 (S)	629 ± 51 (S)	0.171	20	8–10	8.5 ± 0.8
		780–850 (L)	813 ± 26 (L)				
P. rubra	30	600–730 (S)	654 ± 44 (S)	0.168	15	6–8	7.3 ± 0.9
		750–780 (L)	764 ± 13 (L)				

Body length and weight

In *Paraeuchaeta elongata*, PL increased with the progress of copepodid stage (Table 2). Weights (WW, DW, and AFDW) decreased from eggs to nauplii, then increased rapidly after the C1. Males were heavier than females in C4 and C5, but lighter than females in C6. The fit of weight-PL data to the allometry equation was very strong ($r^2 = 0.96$-0.99). WATER ranged from 46.8% (of WW) of the egg to 83.6% of the C4F. AFDW ranged from 79.0% (of DW) of the C4M to 93.9% of the egg. The percentage of both WATER and AFDW differed significantly between stages ($p < 0.0001$, one-way ANOVA). Low WATER and high AFDW were characteristic of eggs, nauplii and early (C1-C2) and late (C5-C6) copepodid stages (Fisher's PLSD $p < 0.05$, Table 2). In contrast, mid copepodid stages (C3-C4) exhibited high WATER and low AFDW.

Patterns in development of PL, WW, DW, and AFDW for *Paraeuchaeta birostrata* (Table 3) were near similar to those for *P. elongata*. *Paraeuchaeta birostrata* was longer and heavier than *P. elongata*; the differences in weights were more marked in early development stages (3.1-4.0 times that of *P. elongata* in egg-C1) than in late copepodid stages (1.1-2.1 times that of *P. elongata* in C6). For the stages C4 to C6, the weights of males were consistently less than that of females. Weight-PL relationships were well described by the power regression model ($r^2 = 0.98$-0.99). WATER of *P. birostrata* ranged from 45.8% (of WW) of the egg to 79.8% of the C4F. AFDW ranged from 83.9% (of DW) of the C4M to 94.5% of the egg. Both WATER and AFDW showed significant differences between stages ($p < 0.0001$, one-way ANOVA), and lower WATER and higher AFDW were seen in eggs, nauplii, and early and late copepodid stages (Fisher's PLSD $p < 0.05$, Table 3).

While no PL and weight data were available for the nauplius and C1-C3 of *Paraeuchaeta rubra*, those of their eggs and C4-C6 fell somewhere between those of *P. elongata* and *P. birostrata* mentioned above (Table 4). Patterns of progressive increase in PL, WW, DW, and AFDW with development were consistent with those observed in *P. elongata* and *P. birostrata*. Males were lighter than females in the C6, but were similar to females in the C4 and C5. PL-weight allometries were well described by the power regression model ($r^2 = 0.91$-0.99). WATER ranged from 57.4% (of WW) of the egg to 79.4% of the C4M. AFDW ranged from 83.0% (of DW) of the C4M to 91.2% of the egg. Between stage differences in WATER and AFDW were evident ($p < 0.001$, one-way ANOVA). Further analyses of between-means indicated lower WATER and higher AFDW to be a characteristic of eggs and C6M (Fisher's PLSD $p < 0.05$, Table 4).

Molt increment

Increments between developmental stages of *Paraeuchaeta elongata* showed a decrease in weight for the egg/nauplius (-8% for WW, -50% for DW, and -51% for AFDW, cf. Fig. 1a). There were substantial gains in PL, WW, DW, and AFDW during development from the C1 onward, with a prominent maximum increment of WW (269% to 271%), DW (371-386%), and AFDW (402-417%) for the C4/C5. In contrast to weights, increments in PL were small and relatively constant, ranging from 15% (C5M/C6M) to 46% (C3/C4F). Differences due to sexes were not appreciable, except for the C5/C6. In the C5/C6, increments in PL, WW, DW and AFDW of males were markedly less than those of females.

Increments between stages of *Paraeuchaeta birostrata* were similar to those of *P. elongata* (Fig. 1b); negative gains in weight for the egg/nauplius (-10% for WW, -38% for DW, and -39% for AFDW), extremely smaller weight gains for males (4% for WW, 23% for DW, and 27% for AFDW) than for females (127% for WW, 157% for DW, and 165% for AFDW) at the C6, and relatively constant gains in PLs over the entire developmental stages (range : 12% for the C5M/C6M to 41% for the C2/C3). As a notable difference between the two species, between-stage increments in weights of C2-C5 of *P. birostrata* were less than those of *P. elongata* and lacked the peak as seen at the C4/C5 for the latter species. For *P. birostrata*, between-stage increments in weights were nearly constant from C3 to C6F (127-169% for WW, 157-169% for DW, and 164-171% for AFDW).

Increments between stages for the C4-C6 of *Paraeuchaeta rubra* were identical to those of *P. birostrata* (Fig. 1c). Increments in weights were near constant during C4-C6 (115-163% for WW, 118-171% for DW, and 120-174% for AFDW), with an exception of markedly lower values for the C5M/C6M. Increments in PL were less than for weights, ranging from 20% (C5M/C6M) to 38% (C4F/C5F).

Discussion

Egg and brood size

Mauchline (1995) studied sizes of body, eggs, and spermatophores of 12 bathymetrically partitioned *Euchaeta* copepods in the North Atlantic Ocean and found that the egg diameter of each species increased with increasing depth of occurrence (or, decreasing of temperature since temperature decreases with depth).

Table 2. *Paraeuchaeta elongata.* Summary data of prosome length (PL), wet weight (WW), dry weight (DW), ash-free dry weight (AFDW), water content (WATER, % of WW), and organic content (AFDW, % of DW). Values are mean ± 1sd. The number of replicates is in parenthesis. For analysing body allometry, power regression model $Y = a \cdot X^b$ was used, where Y is WW, DW, or AFDW (mg) and X is PL (mm). Differences between stages in WATER and AFDW were tested by one-way ANOVA and Fisher's PLSD. Any two stages not underscored by the same line are significantly different.

Developmental stage	PL (mm)	WW (mg)	DW (mg)	AFDW (mg)	WATER (% of WW)	AFDW (% of DW)
Egg		0.062	0.033	0.031	46.8	93.9
		(1)	(1)	(1)	(1)	(1)
Nauplius		0.057±0.005	0.017±0.002	0.015±0.002	71.4±2.0	91.3±0.4
		(2)	(2)	(2)	(2)	(2)
C1	0.96±0.05	0.070±0.010	0.019±0.004	0.017±0.004	72.7±5.6	89.2±2.4
	(100)	(34)	(34)	(34)	(34)	(34)
C2	1.34±0.07	0.134±0.022	0.029±0.004	0.025±0.004	78.1±3.6	86.6±2.2
	(100)	(43)	(43)	(43)	(43)	(43)
C3	1.90±0.11	0.429±0.115	0.074±0.029	0.057±0.017	82.7±4.7	79.7±9.3
	(100)	(40)	(40)	(40)	(40)	(40)
C4F	2.78±0.10	1.50±0.35	0.251±0.086	0.203±0.075	83.6±2.4	80.2±3.5
	(100)	(39)	(39)	(39)	(39)	(39)
C4M	2.64±0.14	1.62±0.43	0.278±0.130	0.225±0.120	83.5±3.5	79.0±5.5
	(100)	(41)	(41)	(41)	(41)	(41)
C5F	3.81±0.16	5.56±1.26	1.22±0.49	1.05±0.45	78.6±5.4	84.5±4.4
	(100)	(41)	(41)	(41)	(41)	(41)
C5M	3.80±0.13	5.97±0.97	1.31±0.48	1.13±0.47	78.6±5.6	84.7±5.1
	(100)	(43)	(43)	(43)	(43)	(43)
C6F	4.95±0.24	11.1±1.7	2.09±0.49	1.76±0.47	81.2±3.0	83.6±3.8
	(100)	(44)	(44)	(44)	(44)	(44)
C6M	4.38±0.26	6.89±0.86	1.58±0.32	1.37±0.32	77.0±4.4	86.3±3.2
	(100)	(34)	(34)	(34)	(34)	(34)

Regression statistics					one-way ANOVA	
Constant (a)	0.0632	0.0139	0.0118	df	10	10
Power (b)	3.248	3.167	3.158	F	26	16
r^2	0.991	0.975	0.968	p	<0.0001	<0.0001
				Fisher's PLSD ($p<0.05$)	EN C1 C6M C2 C5M C5F C6F C3 C4M C4F	C4M C3 C4F C6F C5F C5M C6M C2 C1 N E

Table 3. *Paraeuchaeta birostrata.* Summary data of prosome length (PL), wet weight (WW), dry weight (DW), ash-free dry weight (AFDW), water content (WATER, % of WW), and organic content (AFDW, % of DW). Values are mean $\pm$ 1sd. The number of replicates is in parenthesis. For analysing body allometry, power regression model $Y = a \cdot X^b$ was used, where Y is WW, DW, or AFDW (mg) and X is PL (mm). Differences between stages in WATER and AFDW were tested by one-way ANOVA and Fisher's PLSD. Any two stages not underscored by the same line are significantly different.

Developmental stage	PL (mm)	WW (mg)	DW (mg)	AFDW (mg)	WATER (% of WW)	AFDW (% of DW)
Egg		0.195±0.010	0.105±0.007	0.100±0.008	45.8±6.0	94.5±1.0
		(3)	(3)	(3)	(3)	(3)
Nauplius		0.176	0.065	0.061	63.1	93.8
		(1)	(1)	(1)	(1)	(1)
C1	1.33±0.04	0.254±0.016	0.069±0.011	0.061±0.011	73.0±3.7	88.8±2.8
	(50)	(24)	(24)	(24)	(24)	(24)
C2	1.65±0.02	0.446±0.043	0.102±0.013	0.087±0.012	77.1±1.9	84.9±3.1
	(50)	(44)	(44)	(44)	(44)	(44)
C3	2.33±0.06	1.09±0.10	0.223±0.040	0.188±0.037	79.6±2.6	84.3±2.2
	(40)	(44)	(44)	(44)	(44)	(44)
C4F	3.01±0.16	2.93±0.42	0.598±0.159	0.508±0.150	79.8±3.5	84.2±3.6
	(40)	(42)	(42)	(42)	(42)	(42)
C4M	3.10±0.03	2.83±0.46	0.585±0.189	0.497±0.180	79.7±4.4	83.9±4.2
	(40)	(44)	(44)	(44)	(44)	(44)
C5F	4.10±0.14	7.57±1.25	1.61±0.49	1.38±0.47	79.1±4.6	85.2±3.8
	(40)	(43)	(43)	(43)	(43)	(43)
C5M	4.14±0.09	7.42±0.89	1.55±0.43	1.33±0.41	79.4±4.3	84.8±3.5
	(40)	(43)	(43)	(43)	(43)	(43)
C6F	5.68±0.10	17.2±1.3	4.14±0.78	3.66±0.78	75.9±4.1	87.8±2.8
	(50)	(43)	(43)	(43)	(43)	(43)
C6M	4.63±0.17	7.75±0.70	1.90±0.37	1.69±0.36	75.5±4.1	87.7±2.5
	(30)	(31)	(31)	(30)	(31)	(30)

Regression statistics   one-way ANOVA

Constant (a)	0.105	0.0248	0.0213	df	10	10
Power (b)	2.934	2.882	2.888	F	33	12
r^2	0.994	0.991	0.989	p	<0.0001	<0.0001

Fisher's PLSD (p<0.05)   ENC1C6MC6FC2C5FC5MC3C4MC4F   C4MC4FC3C5MC2C5FC6MC6FC1NE

— 15 —

Table 4. *Paraeuchaeta rubra*. Summary data of prosome length (PL), wet weight (WW), dry weight (DW), ash-free dry weight (AFDW), water content (WATER, % of WW), and organic content (AFDW, % of DW). Values are mean ± 1sd. The number of replicates is in parenthesis. For analysing body allometry, power regression model $Y = a \cdot X^b$ was used, where Y is WW, DW, or AFDW (mg) and X is PL (mm). Differences between stages in WATER and AFDW were tested by one-way ANOVA and Fisher's PLSD. Any two stages not underscored by the same line are significantly different.

Developmental stage	PL (mm)	WW (mg)	DW (mg)	AFDW (mg)	WATER (% of WW)	AFDW (% of DW)
Egg		0.158±0.008	0.067±0.002	0.061±0.002	57.4±1.2	91.2±0.02
		(2)	(2)	(2)	(2)	(2)
C4F	2.81±0.07	2.59±0.41	0.561±0.181	0.477±0.173	78.6±4.3	84.1±4.6
	(30)	(39)	(39)	(39)	(39)	(39)
C4M	2.88±0.08	2.51±0.37	0.524±0.153	0.444±0.157	79.4±4.6	83.0±7.8
	(20)	(28)	(28)	(28)	(28)	(28)
C5F	3.87±0.10	6.48±0.96	1.47±0.44	1.28±0.41	77.7±4.6	86.5±3.3
	(20)	(29)	(29)	(29)	(29)	(29)
C5M	3.84±0.06	6.60±0.91	1.42±0.38	1.22±0.36	78.7±4.0	85.5±2.7
	(30)	(38)	(38)	(38)	(38)	(38)
C6F	5.22±0.18	13.9±1.0	3.21±0.65	2.82±0.63	77.0±4.2	87.3±3.1
	(40)	(34)	(34)	(34)	(34)	(34)
C6M	4.62±0.06	6.27±1.23	1.98±0.51	1.77±0.45	68.8±3.1	89.1±2.5
	(4)	(4)	(4)	(4)	(4)	(4)

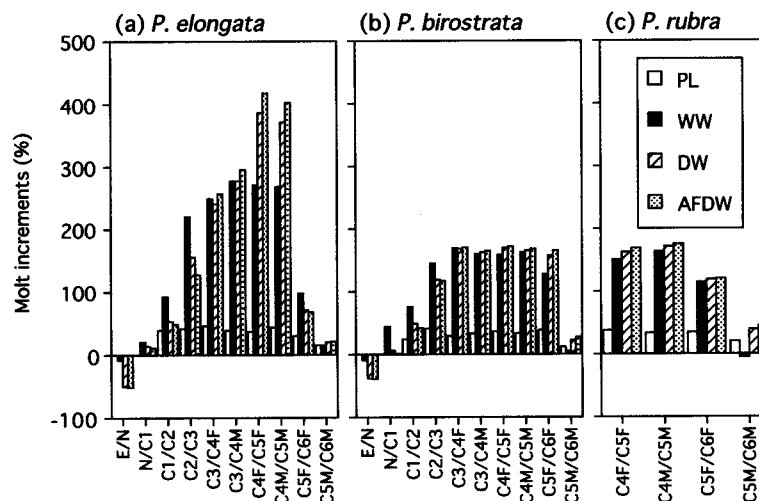| Regression statistics					one-way ANOVA		
Constant (a)	0.193	0.0283	0.0222	df	6	6
Power (b)	2.503	2.854	2.927	F	12	4
r^2	0.909	0.984	0.987	p	<0.0001	<0.001
				Fisher's PLSD ($p<0.05$)	EC6MC6F C5F C4F C5M C4M	C4M C4F C5M C5F C6F C6ME

Fig. 1. Molt increment between consecutive copepodid stages [100×(postmolt size-premolt size)/premolt size] in terms of prosome length (PL), wet weight (WW), dry weight (DW), and ash-free dry weight (AFDW) of *Paraeuchaeta elongata* (a), *P. birostrata* (b), and *P. rubra* (c) (E, egg ; N, nauplius ; C, copepodid ; F, female ; M, male).

The present results on *Paraeuchaeta elongata, P. birostrata,* and *P. rubra* support this Mauchline's (1995) view ; i.e. eggs of shallow-living *P. elongata* were smaller than those of deep-living *P. birostrata* and *P. rubra* (Table 1). The similar egg diameters of the two deep-living species may be due to near identical habitat

temperatures of both species (2.8 and 2.3°C for C6Fs of *P. birostrata* and *P. rubra,* respectively) (Yamaguchi and Ikeda, in this issue).

Brood size of *P. elongata* has been studied at several locations in the subarctic Pacific regions (Lewis and Ramnarine, 1969 ; Morioka, 1975 ; Bollens and Frost,

Table 5. Percentage of egg and egg mass per adult female (C6F) body mass for three *Paraeuchaeta* species as expressed by wet weight (WW), dry weight (DW), and ash-free dry weight (AFDW). Note that data for weights are from Tables 2-4 and those of brood sizes (number of eggs per egg mass) from Table 1. The data for other *Paraeuchaeta* spp. determined by previous workers are also shown for comparison.

Species	Unit	Egg/C6F (%)	Egg mass/C6F (%)	Reference
P. elongata	WW	0.559	14.6	This study
	DW	1.58	41.4	
	AFDW	1.76	46.1	
P. birostrata	WW	1.13	9.64	This study
	DW	2.54	21.6	
	AFDW	2.73	23.2	
P. rubra	WW	1.14	8.30	This study
	DW	2.09	15.2	
	AFDW	2.16	15.8	
P. norvegica	WW	0.2	5.8	Hopkins (1977)
	DW	0.6-0.7	18-23	Nemoto et al. (1976)
	DW	0.83	25.3	Hopkins (1977)
	DW		37	Båmstedt (1979)
P. antarctica	DW	0.17-0.29	15-20	Ward and Robins (1987)
	DW	0.26-0.67	8-23	Alonzo et al. (2000)

1991 ; Ikeda and Hirakawa, 1996 ; Ozaki and Ikeda, 1999). In the eastern subarctic Pacific, *P. elongata* (= *Euchaeta elongata* or *E. japonica*) carries 11-20 eggs per egg mass in Georgia Strait (Lewis and Ramnarine, 1969) and 18.6 (mean) in Dabob Bay (Bollens and Frost, 1991). In the western subarctic Pacific and neighboring marginal seas, the number of eggs per egg mass was recorded as 25 eggs (annual mean) (Morioka, 1975) or 20 (Ikeda and Hirakawa, 1996) in the Japan Sea, and 25.5 Off Cape Esan (Ozaki and Ikeda, 1999). The present results (26.2 eggs) are in general agreement with those reported from the Japan Sea and western Pacific populations. Compared with shallow-living *P. elongata*, brood size of deep-living *P. birostrata* (8.5 eggs) and *P. rubra* (7.3 eggs) were smaller. In the study by Mauchline (1995) mentioned above, he observed a tendency for fewer eggs per brood with increasing depth for 10 *Euchaeta* species, though the relationship was not significant statistically. Fecundity of meso- and bathypelagic zooplankton is known to be less than that of epipelagic species (Mauchline, 1972, 1991).

By combining data on brood size with mass data for eggs, and body-mass data for adult females, the egg production output can be estimated as a percentage of an adult female on the basis of WW, DW or AFDW (Table 5). In terms of WW, a single brood represents a small fraction of a female's body mass (8.3-14.6%). However, in terms of DW and AFDW, it accounts to 15-41% and 16-46%, respectively, of the female's body mass. Within the same species, these large differences originating from the use of WW, DW or AFDW are due

to the dissimilar WATER and AFDW composition of eggs and adult females (cf. Tables 2, 3, and 4). In previous studies based on DW, a single brood mass has been reported to account to 18-23% (Nemoto et al., 1976), 25% (Hopkins, 1977) or 37% (Båmstedt, 1979) of an adult female of *Paraeuchaeta* (= *Euchaeta*) *norvegica*, and 15-20% (Ward and Robins, 1987) or 8-23% (Alonzo et al., 2000) of an adult female of *Paraeuchaeta* (= *Euchaeta*) *antarctica*. All these previous results on *Paraeuchaeta* spp. fall within the range observed for the three *Paraeuchaeta* species in this study.

Taking into account the order of depth-distribution of the three *Paraeuchaeta* species studied here (*P. rubra* > *P. birostrata* > *P. elongata*, cf. Yamaguchi and Ikeda, in this issue), the brood/female mass proportion decreases with depth. Mauchline (1995) calculated brood volume as percent of body volume of adult females of 10 *Euchaeta* species in the North Atlantic, and found the similar trend with depth distribution of each species (though this was not significant statistically). It is noted that brood size alone is insufficient to define the lifetime fecundity of females of euchaetid copepods living at various depth (fecundity=brood size×the number of broods). However, accurate information about the number of broods is presently lacking. Therefore, comparison can not yet be made for example with the extremely high utilization of accumulated body energy for egg production (ca. 60%) known for the bathypelagic mysid *Gnathophausia ingens* (Childress and Price, 1983).

Increment between stages

For developmental stages of various copepods from temperate and boreal seas, increments expressed in proportion to body length or DW fall into a range of between less than zero and 200%, and there are no generalized patterns (Mauchline, 1998). Recent increments data (DW) for tropical inshore water copepods (Webber and Roff, 1995) also fall within that range. These previous data were derived from largely epipelagic copepods, and their possible generalization to meso- and bathypelagic copepods have not been examined.

For mesopelagic euchaetid copepods, Ikeda and Hirakawa (1996) determined the increments in terms of PL, WW, DW, and AFDW for all developmental stages of *Paraeuchaeta elongata* in the Japan Sea and found little gain during naupliar stages, but a substantial gain in weight during C3/C4 (increments in DW and AFDW exceed 400%). While differences in increments between males and females are subtle during C4/C5, for the molt to adults the increment in males is much less than that in females. The present results for *P. elongata* from the Oyashio region are in good agreement with those of Ikeda and Hirakawa (1996), except that the peak increment was found in the C4/C5 transition (Fig. 1), instead of the C3/C4. This discrepancy may be due to dissimilar ontogenetic vertical migration patterns of mid-copepodid stages between the Japan Sea and Oyashio region populations of *P. elongata* (see discussion below).

Between-stage increment patterns of *Paraeuchaeta birostrata* and *P. rubra* are near comparable each other (Fig. 1). Their increment patterns in PL are also similar to that of *P. elongata* ; i.e. near constant over copepodid stages and stable at 10–50%. In terms of weights, negative gains for the E/N and much less gain in males than females at C6 are also seen in both *P. birostrata* and *P. rubra*. However, *P. birostrata* and *P. rubra* are different from *P. elongata* in that the former two species lack a marked increment maximum at mid-copepodid stages, and the overall magnitudes of weight increments during their copepodid stages are much lower (<200% as compared with >400% of *P. elongata*, cf. Fig. 1). For mesopelagic copepods other than *Paraeuchaeta* spp. in the Oyashio region, increment patterns similar to that of *P. elongata* have been observed in *Heterorhabdus tanneri* (Yamaguchi and Ikeda, 2000a) and *Gaidius variabilis* (Yamaguchi and Ikeda, 2000b), and a pattern identical to that of *P. birostrata* and *P. rubra* is found in *Pleuromamma scutullata* (Yamaguchi and Ikeda, 2000a). Thus, information presently available indicates divergent molt increment patterns during the development of copepodid stages in some mesopelagic copepods

as compared with those of epipelagic ones as compiled by Mauchline (1998).

As a possible explanation for differential molt increments observed within the *Paraeuchaeta* species in this study, differences in ontogenetic vertical migration patterns among the three copepods may be considered. This is because food availability for these carnivorous copepods decreases exponentially with increasing depth (cf. Vinogradov, 1968). In the course of development, stages resident at shallower depths are therefore expected to have a better chance of encountering abundant prey animals. Along with prey abundance, temperature changes with depth. However, prey abundance is more important than temperature as a factor affecting the body mass of copepods (cf. Escribano and McLaren, 1992). The relationship between molt increments and depth of occurrence was therefore examined combining the present between-stage increment data for the three *Paraeuchaeta* species with those for stage-specific depth distributions of the same species as reported by Yamaguchi and Ikeda (in this issue). The results of correlation analysis (Table 6) reveal a significant pattern that molt increments expressed by WW, DW, and AFDW (but not PL) of *P. elongata* and *P. birostrata* decrease with increasing depth of occurrence (Fig. 2). This pattern was not seen *P. rubra*, possibly because of their fewer data sets ($n=3$). This close negative correlation between molt increments and the depth of occurrence for *Paraeuchaeta* species may explain why populations of

Table 6. Regression statistics of molt increment between stages (Y=molt increments [PL, WW, DW, or AFDW]) on vertical distribution depth of postmolt stage (X, m) for three *Paraeuchaeta* species. Data on vertical distribution of each stage are from Yamaguchi and Ikeda (in this issue). ns : not significant.

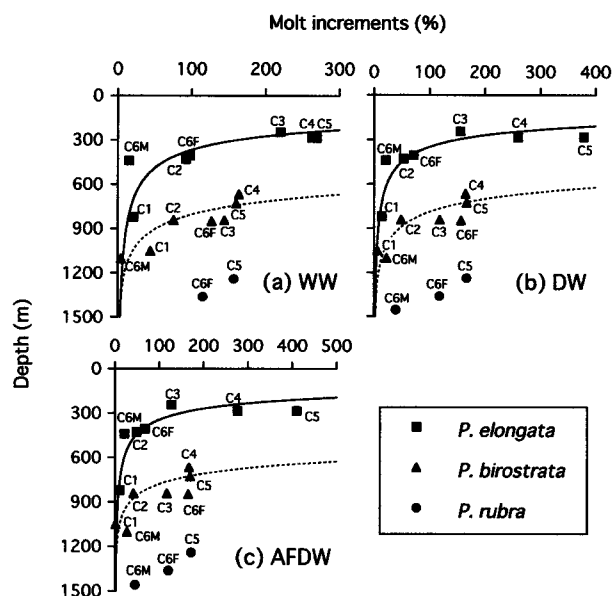| Species	Unit	Regression model $\log_{10} Y = a \cdot \log_{10} X + b$				
		a	b	n	r^2	p
P. elongata	PL	−1.03	4.12	6	0.43	ns
	WW	−2.39	8.14	7	0.68	<0.05
	DW	−2.70	8.86	7	0.78	<0.01
	AFDW	−2.82	9.16	7	0.77	<0.01
P. birostrata	PL	−1.96	7.15	6	0.52	ns
	WW	−5.93	19.23	7	0.68	<0.05
	DW	−5.92	19.14	7	0.70	<0.05
	AFDW	−7.43	23.48	7	0.55	<0.05
P. rubra	PL	−3.26	11.66	3	0.69	−
	WW	−3.33	12.50	2		−
	DW	−8.59	28.84	3	0.86	−
	AFDW	−7.99	27.01	3	0.88	−

Fig. 2. Relationship between vertical distribution depth and molt increment (%) in terms of WW (a), DW (b), and AFDW (c) for each copepodid stage of *Paraeuchaeta elongata* (squares), *P. birostrata* (triangles), and *P. rubra* (circles). Solid and dotted lines indicate fitted regression curves for *P. elongata* and *P. birostrata*, respectively (see Table 6).
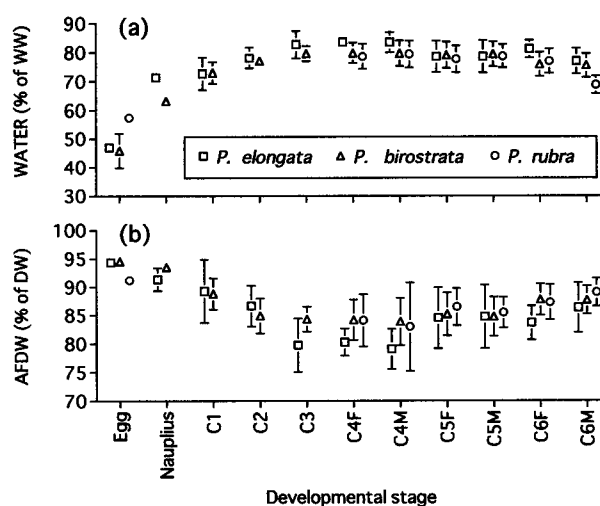

Fig. 3. Developmental changes in water (WATER, % of WW) (a) and ash-free dry weight (AFDW, % of DW) (b) of *Paraeuchaeta elongata* (squares), *P. birostrata* (triangles), and *P. rubra* (circles). Values are annual means. Vertical bars denote 1 standard deviation.

P. elongata in the Japan Sea and Oyashio region have increment maxima between different copepodid stages, as mentioned above. The C3 ascends to shallower depths than the C4 does in the Japan Sea (Morioka, 1975) while the reverse is the case in the Oyashio region (Ozaki and Ikeda, 1999).

Body allometry

While correlations between PL and WW, DW, and AFDW of copepodid stages were very high (r^2=0.91–0.99), the constant b in the allometry equation ($Y = aX^b$) varied among the three *Paraeuchaeta* species; b=3.16–3.25 for *P. elongata*, 2.88–2.93 for *P. birostrata*, and 2.50–2.93 for *P. rubra*, cf. Tables 2, 3, and 4. For other mesopelagic copepods in the Oyashio region, b-values have been reported as 3.46–3.91 for *Heterorhabdus tanneri*, 2.72–3.02 for *Pleuromamma scutullata* (Yamaguchi and Ikeda, 2000a), and 3.14–3.32 for *Gaidius variabilis* (Yamaguchi and Ikeda, 2000b). Mauchline (1998) compiled the relationship between PL and WW for many copepod species (largely shallow-living ones) and noted the range of b-values to be 2.0–4.0. Thus, b-values for *Paraeuchaeta* spp. in this study, and *H. tanneri* and *P. scutullata* as found by Yamaguchi and Ikeda (2000a), fall favorably within the range of many other copepods. Although the data presently available for mesopelagic and bathypelagic copepods are limited, it appears that b-values are quite species-specific

and unrelated to the depth of occurrence of the copepods.

Within the species, the constant b varied to a some degree depending on the choice of weight expression (WW, DW or AFDW), suggesting an influence from changes in water content (WATER, % of WW) and organic matter (AFDW, % of DW) in the course of copepodid development. Changes in WATER and AFDW over the entire developmental stages of *Paraeuchaeta elongata* and *P. birostrata* (egg and C4–C6 only for *P. rubra*) are shown in Fig. 3. Remarkably, the patterns of change for the three species are similar. WATER is lowest in eggs and increases rapidly during development to C3, then decreases gradually toward C6. The pattern of change in AFDW mirrors that of WATER ; it is highest in eggs, decreases toward C3-C4, then recovers gradually at C6. Lower WATER and higher AFDW in the eggs are indicative of a large accumulation of lipids, a character known in deeper-living *Paraeuchaeta/Euchaeta* copepods (Hagen et al., 1995 ; Ikeda and Hirakawa, 1996). Lee et al. (1974) reared *P. elongata* and demonstrated that lipids in eggs (64% of DW) decreased gradually in the course of naupliar development and reached 14% at the C1. Successful development of newly hatched nauplii of *P. elongata* to the C1 without feeding has also been shown by Ikeda and Hirakawa (1996). Other than *Paraeuchaeta/Euchaeta* species, lipid-rich eggs have been reported in a mesopelagic mysid *Meterythrops microphthalma* (Ikeda, 1992a), a bathypelagic mysid *Gnathophausia ingens* (Childress and Price, 1983), and a mesopelagic ostracod *Conchoecia pseudodiscophora*

(Ikeda, 1992b). Recently, Saito and Tsuda (2000) reported lipid-rich eggs of epipelagic copepod *Neocalanus* spp. which reproduce in meso- and bathypelagic zone. Production of energy-rich eggs is believed to result from selection for survival in resource-limited meso- and bathypelagic environments (cf. Mauchline, 1991).

Acknowledgements

We are very grateful to Dr. J.G. Greenwood of the University of Queensland for his critical reading the manuscripts through this series papers (biology and ecology of *Paraeuchaeta*). We thank captains, officers, and crew of T.S. "Oshoro-Maru", T.S. "Hokusei-Maru", R.V. "Tansei-Maru", R.V. "Hokko-Maru", and R.V. "Hokushin-Maru" for their help during the field sampling.

References

Alonzo, F., Mayzaud, P. and Razouls, S. (2000) Egg-production dynamics, biochemical composition and hatching success of the subantarctic copepod *Paraeuchaeta antarctica* : laboratory studies. *Mar. Ecol. Prog. Ser.*, **205**, 219-227.

Båmstedt, U. (1979) Reproductive bioenergetics within the summer and winter generations of *Euchaeta norvegica* (Copepoda). *Mar. Biol.*, **54**, 135-142.

Bollens, S.M. and Frost, B.W. (1991) Ovigerity, selective predation and variable diel vertical migration in *Euchaeta elongata* (Copepoda : Calanoida). *Oecologia*, **87**, 155-161.

Böttger, R. and Schnack, D. (1986) On the effect of formaldehyde fixation on the dry weight of copepods. *Meeresforschung*, **31**, 141-152.

Brodsky, K.A. (1950) Calanoida of the far-eastern seas and polar basin of the USSR. p. 1-442, Strelkov, A.A. (ed.). *Keys to the fauna of the USSR No. 35.* Moskva, Leningrad (English translation, I.P.S.T., Jerusalem, 1967).

Childress, J.J. and Price, M.H. (1983) Growth rate of the bathypelagic crustacean *Gnathophausia ingens* (Mysidacea : Lophogastridae). II. Accumulation of material and energy. *Mar. Biol.*, **76**, 165-177.

Escribano, R. and McLaren, I.A. (1992) Influence of food and temperature on lengths and weights of two marine copepods. *J. exp. mar. Biol. Ecol.*, **159**, 77-88.

Giguère, L.A., St-Pierre, J.-F., Bernier, B., Vézina, A. and Rondeau, J.-G. (1989) Can we estimate the true weight of zooplankton samples after chemical preservation ? *Can. J. Fish. Aquat. Sci.*, **46**, 522-527.

Gruzov, L.N. and Alekseyeva, L.G. (1970) Weight characteristics of copepods from the equatorial Atlantic. *Oceanology*, **10**, 871-879.

Hagen, W., Kattner, G. and Graeve, M. (1995) On the lipid biochemistry of polar copepods : compositional differences in the Antarctic calanoids *Euchaeta antarctica* and *Euchirella rostromagna*. *Mar. Biol.*, **123**, 451-457.

Hopkins, C.C.E. (1977) The relationship between material body size and clutch size, development time and egg mortality in *Euchaeta norvegica* (Copepoda : Calanoida) from Loch Etive, Scotland. *J. mar. biol. Ass. U.K.*, **57**, 723-733.

Ikeda, T. (1992a) Growth and life history of the mesopelagic mysid *Meterythrops microphthalma* in the southern Japan Sea. *J. Plankton Res.*, **14**, 1767-1779.

Ikeda, T. (1992b) Laboratory observations on spawning, fecundity and early development of a mesopelagic ostracod, *Conchoecia pseudodiscophora*, from the Japan Sea. *Mar. Biol.*, **112**, 313-318.

Ikeda, T. and Hirakawa, K. (1996) Early development and estimated life cycle of the mesopelagic copepod *Pareuchaeta elongata* in the southern Japan Sea. *Mar. Biol.*, **126**, 261-270.

Lee, R.F., Nevenzel, J.C. and Lewis, A.G. (1974) Lipid changes during life cycle of marine copepod, *Euchaeta japonica* Marukawa. *Lipids*, **9**, 891-898.

Lewis, A.G. and Ramnarine, A. (1969) Some chemical factors affecting the early development stages of *Euchaeta japonica* (Crustaceana : Copepoda : Calanoida). *J. Fish. Res. Bd. Can.*, **26**, 1347-1362.

Mauchline, J. (1972) The biology of bathypelagic organisms, especially Crustacea. *Deep-Sea Res.*, **19**, 753-780.

Mauchline, J. (1991) Some modern concepts in deep-sea pelagic studies : patterns of growth in the different horizons. p. 107-130, Mauchline, J. and Nemoto, T. (eds.). *Marine Biology, its Accomplishment and Future Prospect.* Hokusen-sha, Tokyo.

Mauchline, J. (1994) Spermatophore transfer in *Euchaeta* species in a 2000 m water column. *Hydrobiologia*, **292/293**, 309-316.

Mauchline, J. (1995) Bathymetric adaptations of life history patterns of congeneric species (*Euchaeta* : Calanoida) in a 2000 m water column. *ICES J. mar. Sci.*, **52**, 511-516.

Mauchline, J. (1998) The biology of calanoid copepods. *Adv. Mar. Biol.*, **33**, 1-710.

Minoda, T. (1971) Pelagic copepoda in the Bering Sea and the northwestern North Pacific with special reference to their vertical distribution. *Mem. Fac. Fish. Hokkaido Univ.*, **18**, 1-74.

Morioka, Y. (1975) A preliminary report on the distribution and life history of a copepod *Pareuchaeta elongata* in the vicinity of Sado Island, the Japan Sea. *Bull. Japan Sea reg. Fish. Res. Lab.*, **26**, 41-56.

Nemoto, T., Mauchline, J. and Kamada, K. (1976) Brood size and chemical composition of *Pareuchaeta norvegica* (Crustacea : Copepoda) in Loch Etive, Scotland. *Mar. Biol.*, **36**, 151-157.

Omori, M. and Ikeda, T. (1984) *Methods in marine zooplankton ecology*. John Wiley & Sons, New York.

Ozaki, K. and Ikeda, T. (1997) The effect of temperature on the development of eggs and nauplii of the mesopelagic copepod *Paraeuchaeta elongata*. *Plankton Biol. Ecol.*, **44**, 91-95.

Ozaki, K. and Ikeda, T. (1998) Development time and generation length of the mesopelagic copepod *Paraeuchaeta elongata* reared in the laboratory. *Plankton Biol. Ecol.*, **45**, 75-78.

Ozaki, K. and Ikeda, T. (1999) Vertical distribution, population structure, and life cycle of the mesopelagic

copepod *Paraeuchaeta elongata* off Cape Esan, southwestern Hokkaido, Japan. *Plankton Biol. Ecol.,* **46**, 48–53.

Park, T. (1994) Geographic distribution of the bathypelagic genus *Paraeuchaeta* (Copepoda, Calanoida). *Hydrobiologia,* **292/293**, 317–332.

Saito, H. and Tsuda, A. (2000) Egg production and early development of the subarctic copepods *Neocalanus cristatus, N. plumchrus* and *N. flemingeri. Deep-Sea Res. I,* **47**, 2141–2158.

Sekiguchi, H. (1975) Seasonal and ontogenetic vertical migrations in some common copepods in the northern region of the North Pacific. *Bull. Fac. Fish. Mie Univ.,* **2**, 29–38.

Vinogradov, M.E. (1968) *Vertical distribution of the oceanic zooplankton.* Izd. Nauka, Moscow (English translation, I.P.S.T., Jerusalem, 1970).

Ward, P. and Robins, D.B. (1987) The reproductive biology of *Euchaeta antarctica* Giesbrecht (Copepoda : Calanoida) at South Georgia. *J. exp. mar. Biol. Ecol.,* **108**, 127–145.

Webber, M.K. and Roff, J.C. (1995) Annual biomass and production of the oceanic copepod community off Discovery Bay, Jamaica. *Mar. Biol.,* **123**, 481–495.

Williams, R. and Robins, D.B. (1982) Effects of preservation on wet weight, dry weight, nitrogen and carbon contents of *Calanus helgolandicus* (Crustacea : Copepoda). *Mar. Biol.,* **71**, 271–281.

Yamaguchi, A. and Ikeda, T. (2000a) Vertical distribution, life cycle and body allometry of two oceanic calanoid copepods (*Pleuromamma scutullata* and *Heterorhabdus tanneri*) in the Oyashio region, western North Pacific Ocean. *J. Plankton Res.,* **22**, 29–46.

Yamaguchi, A. and Ikeda, T. (2000b) Vertical distribution, life cycle and developmental characteristics of mesopelagic calanoid copepod *Gaidius variabilis* (Aetideidae) in the Oyashio region, western North Pacific Ocean. *Mar. Biol.,* **137**, 99–109.

Yamaguchi, A. and Ikeda, T. (2001) Abundance and population structure of three mesopelagic *Paraeuchaeta* species (Copepoda : Calanoida) in the Oyashio region, western subarctic Pacific Ocean with notes on their carcasses and epizoic ciliates. *Plankton Biol. Ecol.,* **48**, 104–113.

Yamaguchi, A. and Ikeda, T. (in this issue) Vertical distribution patterns of three mesopelagic *Paraeuchaeta* species (Copepoda : Calanoida) in the Oyashio region, western subarctic Pacific Ocean. *Bull. Fac. Fish. Hokkaido Univ.*

Yen, J. (1983) Effects of prey concentration, prey size, predator life stage, predator starvation, and season on predation rates of the carnivorous copepod *Euchaeta elongata. Mar. Biol.,* **75**, 69–77.