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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

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Abstract: Abundance and population structure of 3 *Paraeuchaeta* copepods (*P. elongata*, *P. birostrata*, and *P. rubra*) were investigated over one year, based on monthly samplings down to 2000-m depth in the Oyashio region, western subarctic Pacific. Annual mean abundance of *P. elongata*, *P. birostrata*, and *P. rubra* were 597, 516, and 86 indiv. m⁻², respectively. In terms of biomass, these figures equate to 210, 308, and 143 mg DW m⁻², respectively. All copepodid stages occurred throughout the year, except for C1–C3 of *P. rubra* which are distributed below 2000 m depth and were thereby not sampled. In all 3 species, no clear sequence in stage-development was observed from the population structure data, suggesting more or less constant reproduction modes throughout the year. Adult sex ratios (female:male) were biased to females (71% in *P. elongata*, 67% in *P. birostrata*, and 92% in *P. rubra*), reflecting the fact that males are short-lived. No significant correlation was found between the sex ratios and the incidence of spermatophore-attached and egg-carrying females in these *Paraeuchaeta* copepods. Possibly undescribed epizoic ciliates on the *Paraeuchaeta* spp. were noted, and discussed in the light of their possible effect on the copepods. Occurrences of carcasses of various copepodid stages of the *Paraeuchaeta* spp. were also noted. The carcasses outnumbered the living specimens sometimes, and possible causes of the high abundance of *Paraeuchaeta* carcasses in the Oyashio region are discussed.

Key words: mesopelagic, copepods, population structure, parasitic epizoic ciliates, carcasses

Introduction

Three *Paraeuchaeta* species are known to dominate in the subarctic Pacific Ocean: i.e. *P. elongata* (Esterly), *P. birostrata* Brodsky, and *P. rubra* Brodsky (cf. Park 1994). Among the 3 species, the shallow-living *P. elongata* has been studied extensively in the Japan Sea (Morioka 1975; Ikeda & Hirakawa 1996), western subarctic Pacific Ocean (Ozaki & Ikeda 1999), and Dabob Bay in the eastern subarctic Pacific Ocean (Bollens & Frost 1991). Laboratory experiments on the development of *P. elongata* have been

conducted by several workers (Yen 1983; Bollens & Frost 1991; Ikeda & Hirakawa 1996; Ozaki & Ikeda 1997). Recently, Ozaki & Ikeda (1998) have successfully raised *P. elongata* from eggs through to adults in the laboratory. In contrast, *P. birostrata* and *P. rubra* have been little studied, and available information is limited to that concerning their vertical (Minoda 1971; Sekiguchi 1975) and geographical (Park 1994) distribution patterns and their body size and brood size characteristics (Mauchline 1998). Paucity of information about *P. birostrata* and *P. rubra* may partly be due to their distribution being much deeper in the water column than is that of *P. elongata* (cf. Sekiguchi 1975).

As part of a research program to evaluate the biology and ecology of deep-sea zooplankton in the Oyashio region, we

report here on the abundance and population structure of *Paraeuchaeta elongata*, *P. birostrata*, and *P. rubra* based on year-round samples collected from the 0–2000-m depth stratum in the Oyashio region. Additional observations are made on parasite epizootic ciliates, and on the occurrences of carcasses of *Paraeuchaeta*, and their ecological implications.

Materials and Methods

Field samplings

Samples were collected at approximately monthly intervals from September 1996 through October 1997, on board the T.S. *Oshoro-Maru* and T.S. *Hokusei-Maru* of the Faculty of Fisheries of Hokkaido University, R.V. *Tansei-Maru* of the Ocean Research Institute of Tokyo University, R.V. *Hokko-Maru* of the Hokkaido National Fisheries Research Institute, and R.V. *Hokushin-Maru* of the Kushiro Fisheries Experimental Station (Table 1). All samplings were conducted between 41°30′–42°30′N and 145°00′–146°00′E in the Oyashio region off southeastern Hokkaido (hereafter referred to as Site H) (Fig. 1). The Oyashio is a western boundary current of the subarctic circulation in the North Pacific that flows southwestward along the Kuril Islands and Hokkaido until it reaches the east coast of northern Honshu, Japan, where it turns east at about 40°N (cf. Kono 1997). The Site H of this study is located at the southern end of the Oyashio.

Zooplankton were collected with a closing net designed by Kawamura (1989) (60-cm mouth diameter, 0.1-mm mesh) equipped with a Rigosha flowmeter in the mouth of the net, and a TSK Depth Distance Recorder (Tsurumi Seiki, Yokohama, Japan) or RMD Depth meter (Rigosha, Tokyo, Japan). The net was towed vertically at 1 m s^{-1} through five discrete depth strata: 0 m–the bottom of thermocline (Th), Th–250 m, 250–500 m, 500–1000 m, and 1000– ≤ 2000 m (Table 1). Most sampling was conducted at night. After collection, zooplankton samples were preserved immediately in 5% formalin–seawater buffered with sodium tetraborate. Temperature and salinity were determined with a CTD system (Neil Brown, General Oceanics, Miami, USA or Sea Bird Electronics, Washington, USA) at the time of sampling. Chlorophyll-*a* concentration data at Site H were supplied by Drs A. Tsuda, H. Saito, and H. Kasai of the Hokkaido National Fisheries Research Institute.

Identification and enumeration

In the laboratory, *Paraeuchaeta elongata*, *P. birostrata*, and *P. rubra* were sorted from the whole samples under a dissecting microscope and each copepodid stage counted. The abundance of other congeneric *Paraeuchaeta* species was low (<5%). The identification of copepodid stages was based on the descriptions of Campbell (1934) for *P. elongata*. No description is presently available for *P. birostrata*

Table 1. Zooplankton sampling data at Site H (41°30′N–42°30′N, 145°00′E–146°00′E) in the Oyashio region. Discrete sampling strata are: surface–bottom of thermocline (Th), Th–250 m, 250–500 m, 500–1000 m, and 1000– ≤ 2000 m.

Date	Time (Local time)	Vessel
4 September 1996	1827–2023	<i>Oshoro-Maru</i>
19 September 1996	1737–1944	<i>Hokusei-Maru</i>
1 October 1996	2325–0205	<i>Hokusei-Maru</i>
8 December 1996	0110–0248, 0636–0850	<i>Hokushin-Maru</i>
13 January 1997	1000–1200	<i>Hokko-Maru</i>
20 February 1997	0230–0510*	<i>Hokushin-Maru</i>
17 March 1997	0055–0330	<i>Hokko-Maru</i>
11 April 1997	0240–0440, 0820–1030	<i>Hokusei-Maru</i>
6 May 1997	2335–0320**	<i>Hokko-Maru</i>
4 June 1997	1850–2009***	<i>Oshoro-Maru</i>
23 June 1997	2123–2326	<i>Hokusei-Maru</i>
2 July 1997	1953–2208	<i>Hokusei-Maru</i>
17 August 1997	1945–2139	<i>Oshoro-Maru</i>
26 August 1997	1010–1201	<i>Tansei-Maru</i>
5 October 1997	2045–2220, 1505–1715	<i>Hokusei-Maru</i>

Missing strata. * 500–1000 m, 1000– ≤ 2000 m; ** Th–250 m, 250–500 m; *** 1000– ≤ 2000 m.

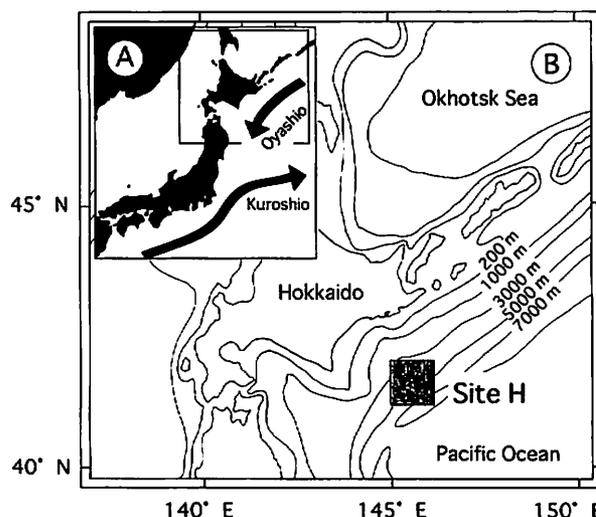


Fig. 1. The Oyashio region in the western subarctic Pacific Ocean (A), and the sampling site ("Site H", shaded) (B). Depth contours (200, 1000, 3000, 5000, and 7000 m) are superimposed in (B).

or *P. rubra* copepodids. To distinguish copepodid 4–5 stages (C4–C5) of the three species, brush-like setae in the ventral margin of the last thoracic segment (*P. elongata*: not present, *P. birostrata*: short and wide, *P. rubra*: long and narrow), and the shape of the distal end of the last thoracic segment (*P. elongata*, sharply elongated; *P. birostrata*, rounded; *P. rubra*, pointed) were used in this study. Based on the presence of the fifth swimming leg (males) or not (females), identification of males and females was made for

C4 to C6. For species identification of C1–C3, the prosome width was useful, i.e. the prosome width of C1–C3 *Paraeuchaeta* species was bimodal throughout the year, and we designated specimens with large width (mean \pm 1SD are 0.52 ± 0.02 mm for C1, 0.64 ± 0.03 mm for C2, and 0.78 ± 0.06 mm for C3) as *P. birostrata*, and those with small width (0.35 ± 0.02 mm for C1, 0.41 ± 0.02 mm for C2, and 0.64 ± 0.03 mm for C3) as *P. elongata*. No C1–C3 of *P. rubra* occurred in the samples; presumably this is due to the deeper distribution of this species (>2000 m) and their species-specific ontogenetic vertical migration pattern (Yamaguchi & Ikeda, unpublished data).

Adult females carrying egg masses or having spermatophore attached were recorded. Egg masses that had been detached from the females were not taken into account because of difficulty in identifying species from which the egg masses were derived. The incidence of dead carcasses, and the presence of parasitic epizoic ciliates, was checked at the same time. Attachment of the stalked epizoic ciliates was largely on the last thoracic segment and the first or second segment of the urosome (Fig. 2A). The morphology of attached ciliates differed among the three species and were categorized as: 'shooting star' in shape with many cilia around the body for those on *P. elongata* (Fig. 2B), 'bell' shaped with many cilia on the tip for those on *P. birostrata* (Fig. 2C), and 'flask' shaped with many cilia on the bottom for those on *P. rubra* (Fig. 2D). Our search of the literature on epizoic ciliates of copepods did not reveal any reports similar to the present forms, which therefore remain unidentified and are possibly new species. Carcasses were easily distinguished from cast molts and live specimens by a partial or near total lack of internal tissues within the central body, and the presence of tissue remnants in appendages (for example, see Fig. 1 of Haury et al. 1995).

Results

Hydrography

Over the study period, surface temperatures ranged from 2°C (March to April 1997) to 18°C (September to October 1996 and 1997) (Fig. 3A). Surface temperatures above 10°C occurred from September to November 1996 and from June to October 1997, when the thermocline was well established at 20–50-m depth. Temperatures below 3°C occurred from February to April 1997, when the top 150 m of the water column was well mixed vertically. Seasonal temperature ranges decreased with increasing depth. Below 300-m depth, temperatures remained below 3.5°C throughout the year.

Surface salinity ranged seasonally from 32.2 to 34.1‰. Relatively high surface salinities (>33.5 ‰) occurred from December 1996 to January 1997 (Fig. 3B). Oyashio Water, characterized by salinities between 33.0 and 33.5‰ and temperatures lower than 3°C (Hanawa & Mitsudera 1987), was observed at 0–150 m from February to April 1997.

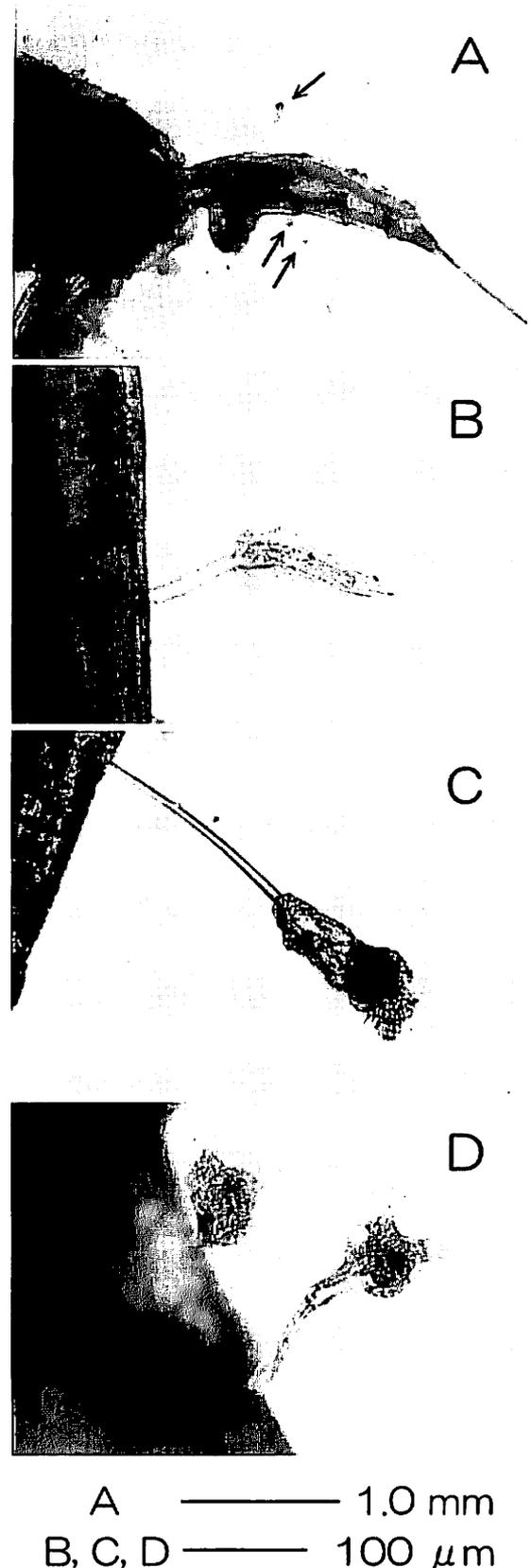


Fig. 2. Epizoic ciliates attached to the urosome of *Paraeuchaeta birostrata* (arrowed) (A). 'Shooting star'-shaped epizoic ciliates on *P. elongata* (B), 'Bell'-shaped epizoic ciliates on *P. birostrata* (C), and 'Flask'-shaped epizoic ciliates on *P. rubra* (D). The scale bars are 1.0 mm for (A) and 100 μ m for (B–D).

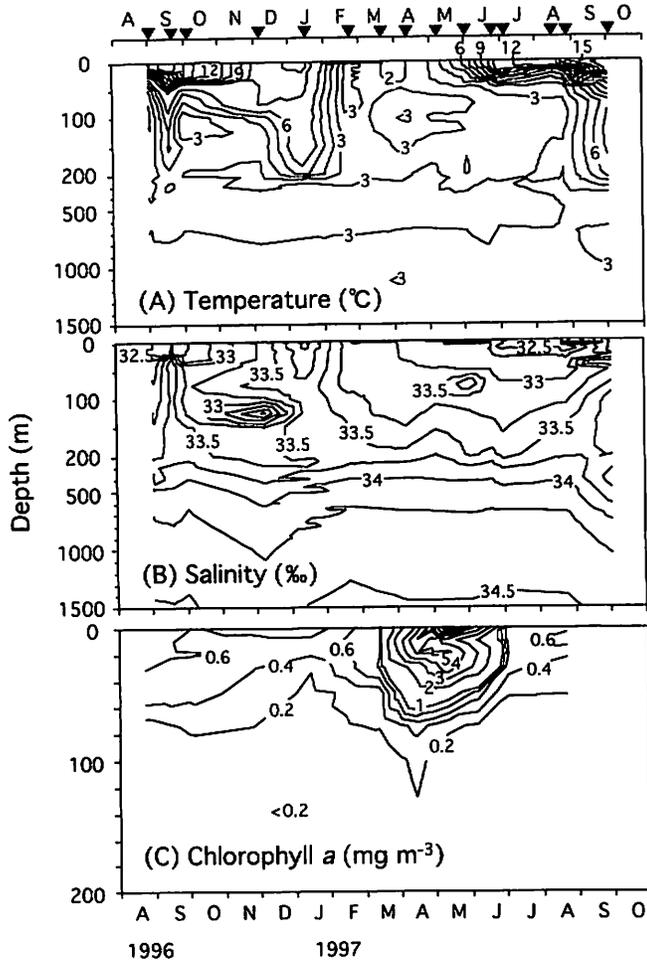


Fig. 3. Seasonal changes in vertical profiles of temperature ($^{\circ}\text{C}$) (A), salinity (‰) (B), and chlorophyll *a* (mg m^{-3}) (C) at Site H. Note the depth scale of (C) is not the same as those of (A) and (B). Solid triangles on top abscissa denote sampling dates.

Less saline water ($<33.0\text{‰}$) recorded near the surface during other months is considered to be derived from the Okhotsk Sea (T. Kono, personal communication). Salinity below 500-m depth changed only slightly throughout the year (range: 34.0–34.5‰).

Phytoplankton biomass, estimated as chlorophyll-*a* concentrations, showed drastic seasonality (Fig. 3C). Chlorophyll-*a* concentrations at the surface were about 0.4 mg m^{-3} from August 1996 to the end of March 1997, then increased rapidly to $>9 \text{ mg m}^{-3}$ in May 1997, where concentrations above 2 mg m^{-3} extended down to 50-m depth. Surface chlorophyll-*a* concentrations decreased to 2 mg m^{-3} by the end of June and were less than 1 mg m^{-3} toward the end of 1997. Chlorophyll-*a* concentrations below 100-m depth were $<0.2 \text{ mg m}^{-3}$ throughout the year.

Abundance and population structure

Paraeuchaeta elongata.—Overall abundance of copepodid stages of *Paraeuchaeta elongata* varied from 331 to 964

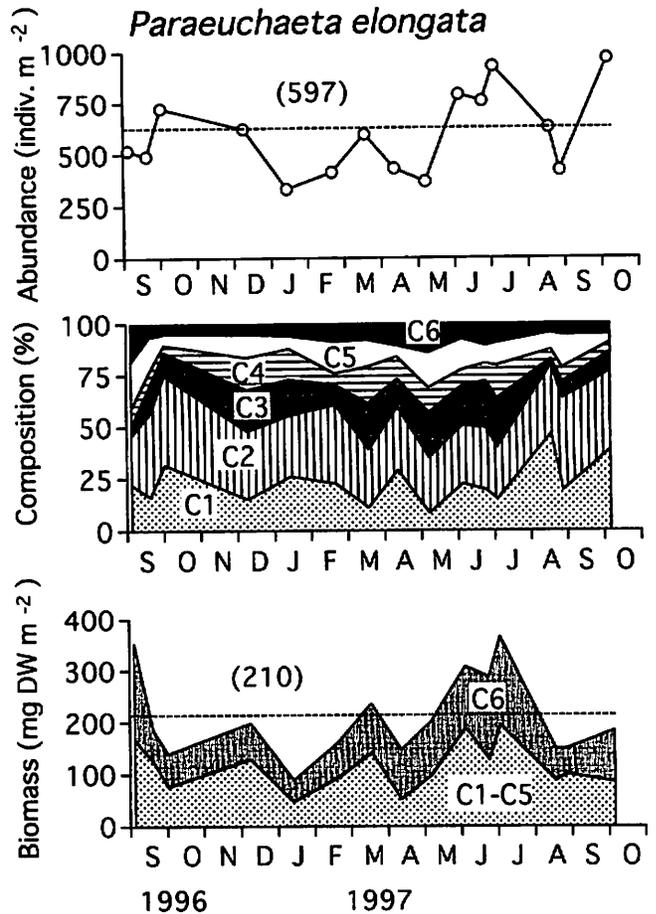


Fig. 4. *Paraeuchaeta elongata*. Seasonal changes in abundance of total copepodids (indiv. m^{-2}) (top), stage composition (%) (middle), and biomass (mg DW m^{-2}) (bottom) at Site H (integrated over 0–2000 m). Horizontal broken lines and associated figures in parentheses in top and bottom panels denote the annual mean.

indiv. m^{-2} throughout the entire study period (annual mean $\pm 1\text{SD}$: 597 ± 200), with irregular maxima in July and October (Fig. 4). All copepodid stages of *P. elongata* occurred throughout the year. Among the copepodid stages, C1 and C2 were most abundant (annual mean percentage abundance was $23 \pm 10\%$ for C1 and $33 \pm 7\%$ for C2). No clear sequence of stage development was traceable. Throughout the entire period, the sex ratio (percentage of females in the total population) ranged between 13.9–74.5% for C4 (annual mean $\pm 1\text{SD}$: $52.4 \pm 13.2\%$), 14.7–69.6% for C5 ($50.6 \pm 15.3\%$), and 29.4–100% for C6 ($71.1 \pm 17.2\%$), and no clear seasonal trend was recognizable (Run-test: *p*, 0.18–0.69, Table 2). Adult females (C6F) with spermatophore attached, or carrying egg masses occurred irregularly, and their percentages of the C6F population ranged between 0–25.0% ($6.6 \pm 8.4\%$) and 0–20.4% ($4.3 \pm 7.8\%$), respectively (Table 2). Abundance data were converted to biomass (mg DW m^{-2}) using previously determined DW data for each copepodid stage (Yamaguchi & Ikeda, unpublished data). Biomass of *Paraeuchaeta elon-*

Table 2. *Paraeuchaeta elongata*. Sex ratios (% of females in the total population), and incidence of spermatophore-attached and egg-carrying C6 females in the total C6 females (%). Seasonality (or non-randomness) was tested by the Run-test at $p=0.05$ level. ns: not significant.

Index	Stage	Range (%)	Annual mean \pm 1SD	Run-test (α)
Sex ratio	C4	13.9–74.5	52.4 \pm 13.2	0.18 ns
	C5	14.7–69.6	50.6 \pm 15.3	0.69 ns
	C6	29.4–100.0	71.1 \pm 17.2	0.50 ns
	C4–C6	50.0–65.5	57.7 \pm 5.1	0.43 ns
Spermatophore attached	C6F	0.0–25.0	6.6 \pm 8.4	0.77 ns
Egg carrying	C6F	0.0–20.4	4.3 \pm 7.8	0.93 ns

gata varied between 89–365 mg DW m^{-2} with season (annual mean \pm 1SD = 210 \pm 82) (Fig. 4, bottom panel). Against the total population biomass, the contribution of C1–C5 biomass was 54.7 \pm 9.1%, and that of C6 was 45.3 \pm 9.1% (annual means).

Paraeuchaeta birostrata.—Overall abundance of copepodid stages of *Paraeuchaeta birostrata* varied between 180–803 indiv. m^{-2} over the study period (annual mean \pm 1SD: 516 \pm 191) (Fig. 5). Seasonally, they were most abundant in June–October. All copepodid stages of *P. birostrata* were found throughout the year, and C2 was the most dominant stage (annual mean percentage abundance was 34 \pm 7%). Throughout the study period, sex ratio ranged between 30.0–86.7% for C4 (annual mean \pm 1SD: 49.1 \pm 18.6%), 17.8–80.6% for C5 (41.3 \pm 15.7%), and 25.0–87.0% for C6 (66.5 \pm 15.3%). No clear seasonal changes in the sex ratio was detected (Run-test: p , 0.14–0.69, Table 3). Throughout the year, the incidence of C6F with spermatophore attached or carrying egg masses showed no seasonal patterns, and their percentages of the C6F population varied from 0–50.0% (10.6 \pm 13.9%) and 0–33.3% (5.1 \pm 11.4%), respectively (Table 3). Seasonal abundance data were converted to biomass (mg DW m^{-2}) using DW data for each copepodid (Yamaguchi & Ikeda, unpublished data), yielding values between 120–487 mg DW m^{-2} (annual mean \pm 1SD = 308 \pm 111) (Fig. 5, bottom panel). The contribution of C1–C5 biomass and C6 biomass to the total population biomass was 53.5 \pm 13.3% and 46.5 \pm 13.3%, respectively (annual means).

Paraeuchaeta rubra.—C1–C3 of *Paraeuchaeta rubra* did not occur in our samples from the upper 2000-m depth layer, because of the deeper distribution (≥ 2000 m) of these stages (Yamaguchi & Ikeda, unpublished data). Total copepodid abundance (C4–C6) of *P. rubra* ranged between 26–166 indiv. m^{-2} (annual mean \pm 1SD: 86 \pm 43) with maxima in July–September (Fig. 6). C4 and C5 dominated in January–May and C6F in June–September. Sex ratio ranged between 18.4–100% for C4 (annual mean \pm 1SD: 57.7 \pm 25.4%), 0–100% for C5 (33.7 \pm 26.9%), and 60.0–100% for

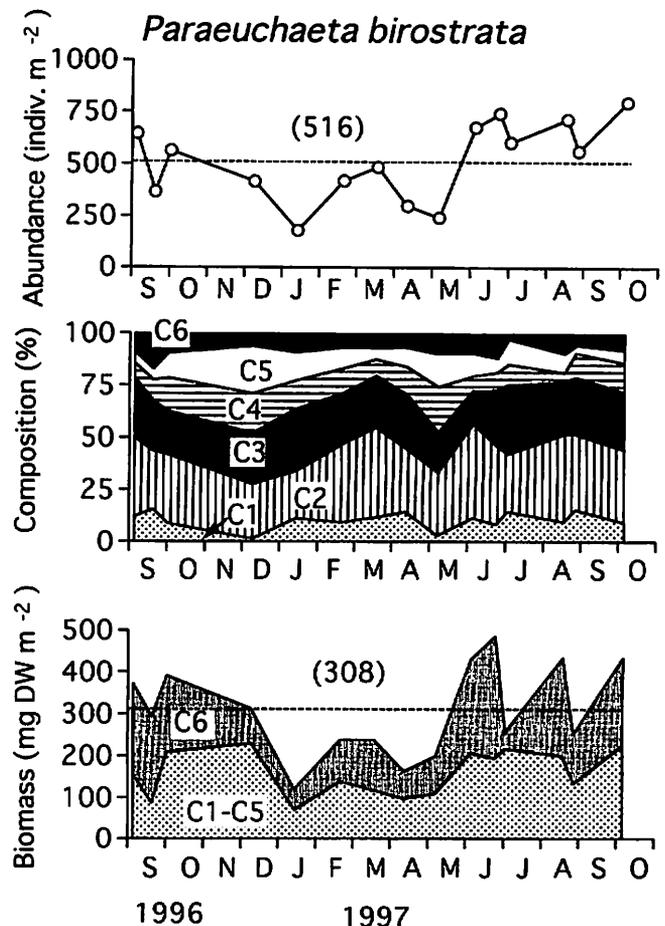


Fig. 5. *Paraeuchaeta birostrata*. Seasonal changes in abundance of total copepodids (indiv. m^{-2}) (top), stage composition (%) (middle), and biomass (mg DW m^{-2}) (bottom) at Site H (integrated over 0–2000 m). Horizontal broken lines and associated figures in parentheses in top and bottom panels denote the annual mean.

Table 3. *Paraeuchaeta birostrata*. Sex ratios (% of females in the total population), and incidence of spermatophore-attached and egg-carrying C6 females in the total C6 females (%). Seasonality (or non-randomness) was tested by the Run-test at $p=0.05$ level. ns: not significant.

Index	Stage	Range (%)	Annual mean \pm 1SD	Run-test (α)
Sex ratio	C4	30.0–86.7	49.1 \pm 18.6	0.69 ns
	C5	17.8–80.6	41.3 \pm 15.7	0.14 ns
	C6	25.0–87.0	66.5 \pm 15.3	0.41 ns
	C4–C6	37.5–68.3	51.5 \pm 8.6	0.41 ns
Spermatophore attached	C6F	0.0–50.0	10.6 \pm 13.9	0.22 ns
Egg carrying	C6F	0.0–33.3	5.1 \pm 11.4	0.29 ns

C6 (91.6 \pm 12.9%), with no clear seasonal patterns (Run-test: p , 0.07–0.77, Table 4). Spermatophore-attached and egg-carrying C6F occurred occasionally, and formed re-

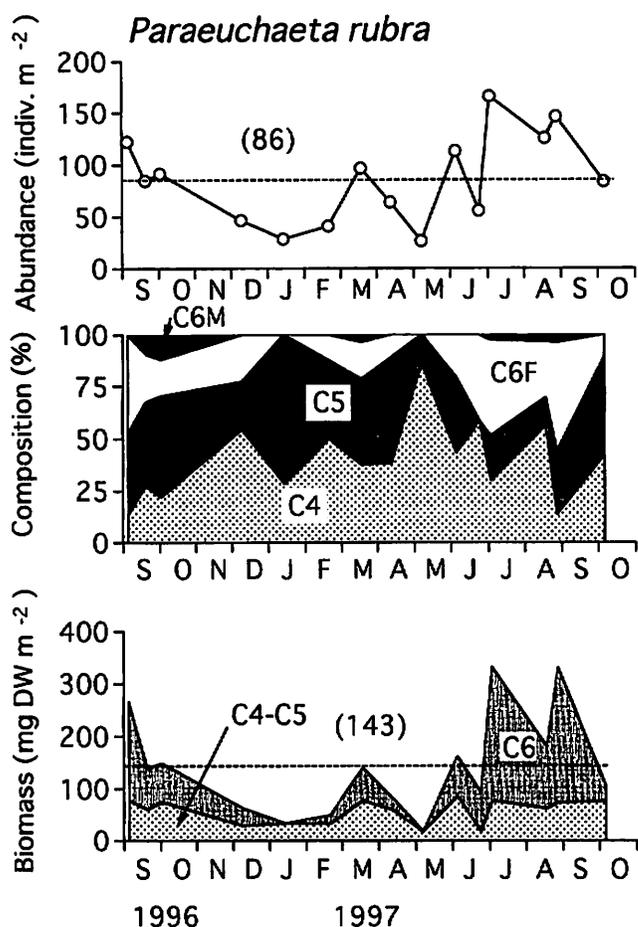


Fig. 6. *Paraeuchaeta rubra*. Seasonal changes in abundance of total copepodids (indiv. m^{-2}) (top), stage composition (%) (middle), and biomass (mg DW m^{-2}) (bottom) at Site H (integrated over 0–2000 m). Horizontal broken lines and associated figures in parentheses in top and bottom panels denote the annual mean.

Table 4. *Paraeuchaeta rubra*. Sex ratios (% of females in the total population), and incidence of spermatophore-attached and egg-carrying C6 females in the total C6 females (%). Seasonality (or non-randomness) was tested by the Run-test at $p=0.05$ level. ns: not significant.

Index	Stage	Range (%)	Annual mean \pm 1SD	Run-test (α)
Sex ratio	C4	18.4–100.0	57.7 ± 25.4	0.77 ns
	C5	0.0–100.0	33.7 ± 26.9	0.07 ns
	C6	60.0–100.0	91.6 ± 12.9	0.15 ns
	C4–C6	28.6–75.0	57.9 ± 12.6	0.43 ns
Spermatophore attached	C6F	0.0–40.6	3.8 ± 10.6	0.12 ns
	Egg carrying	C6F	0.0–50.0	8.2 ± 15.5

spectively 0–40.6% ($3.8 \pm 10.6\%$) and 0–50.0% ($8.2 \pm 15.5\%$) of the C6F population (Table 4). Using known DW data for each copepodid stage (Yamaguchi & Ikeda, unpublished data) abundance data were converted to biomass (mg

DW m^{-2}), yielding values per sample of between 18–331 mg DW m^{-2} (annual mean \pm 1SD = 143 ± 99) (Fig. 6, bottom panel). C4–C5 and C6 biomass contributed $52.5 \pm 26.0\%$ and $47.5 \pm 26.0\%$, respectively, to the total annual population biomass.

Epizoic ciliates and carcasses

Since no seasonal trends in the incidence of epizoic ciliates and carcasses were found (Run-test, $p > 0.05$, Table 5), seasonal data were pooled and summarized in Table 5. For all three *Paraeuchaeta* species, epizoic ciliates were observed only on the C5F/M and C6F (no incidence for C1–C4 and C6M). Among the three species, the incidence of infected specimens was the highest for *P. elongata* C6F, followed by *P. birostrata* C6F and *P. rubra* C6F.

The occurrences of carcasses showed no seasonal pattern, but varied between the species (Table 5). Copepodid stages that occurred as carcasses were C1 and C2 for *Paraeuchaeta elongata*, C1 through C5 for *P. birostrata*, and C4 through C6 (except for males) for *P. rubra*. The abundance of carcasses never exceeded the number of living specimens for *P. elongata*, but sometimes outnumbered those of living specimens for C1 and C3 of *P. birostrata*, and C5F and C6F of *P. rubra* (cf. Table 5). Correlations between the incidence of carcasses of each copepodid stage for these 3 *Paraeuchaeta* species and the respective depths of their distribution (Yamaguchi & Ikeda, unpublished data) were examined. The resultant correlation was significant, implying the incidence of carcasses increases with depth (Table 5).

Discussion

Abundance and population structure

In the subarctic Pacific region, the abundance of *Paraeuchaeta elongata* has been reported as 530 $\text{indiv. (C2–C6) m}^{-2}$ in the 0–500-m water column of Toyama Bay, southern Japan Sea (Ikeda & Hirakawa 1996) and 2009 $\text{indiv. (C4–C6) m}^{-2}$ in the 0–185-m water column of Dabob Bay, eastern subarctic Pacific (Bollens & Frost 1991). Compared with these 2 regions, the present results pertaining to the annual mean abundance of C1–C6 *P. elongata* in the Oyashio region (annual mean \pm 1SD: $597 \pm 200 \text{ indiv. m}^{-2}$ in 0–2000-m water column) are roughly comparable to the results in Toyama Bay, but much lower than those in Dabob Bay. Presently, there is no other information available from the Oyashio region with which to compare the abundances of *P. birostrata* ($516 \pm 191 \text{ indiv. m}^{-2}$) and *P. rubra* ($86 \pm 43 \text{ indiv. m}^{-2}$) as determined in this study. In terms of biomass, *P. elongata* ($210 \pm 82 \text{ mg DW m}^{-2}$), *P. birostrata* (308 ± 111), and *P. rubra* (143 ± 99) exhibit higher values than those known for other mesopelagic copepods such as *Heterorhabdus tanneri* (82 ± 33 , Yamaguchi & Ikeda 2000) and *Pleuromamma scutullata* (111 ± 53 , Yamaguchi & Ikeda 2000) in the Oyashio region, but much less than

Table 5. Incidence of specimens infected with epizoic ciliates (A) and abundance of carcasses (B), both expressed as percentage of living specimens. Seasonalities in the incidences of infected specimens and carcasses were tested by the Run-test at $p=0.05$ level. n : number of specimens observed (ciliate infected) or which occurred (carcasses). —: no occurrence. ns: not significant. Correlation analysis between incidence of infected specimens or carcasses (Y : %) and depth (X : m, Yamaguchi & Ikeda, unpublished data) were made using the model $Y=a \cdot X+b$ (a , b : constants, n : sample size, r : correlation coefficient, p : probability).

Species	Stage	(A) Infected specimens				(B) Carcasses			
		n	Range (%)	Annual mean \pm ISD	Run-test (α)	n	Range (%)	Annual mean \pm ISD	Run-test (α)
<i>P. elongata</i>	C1	—				36	0–59.4	12.8 \pm 16.4	0.65 ns
	C2	—				42	0–37.1	8.2 \pm 12.1	0.42 ns
	C3	—				—			
	C4F	—				—			
	C4M	—				—			
	C5F	1	0–10.5	0.7 \pm 2.7		—			
	C5M	1	0–19.3	1.3 \pm 5.0		—			
	C6F	34	0–100.0	25.1 \pm 30.3	0.10 ns	—			
<i>P. birostrata</i>	C6M	—				—			
	C1	—				26	0–105.0	20.0 \pm 27.8	0.14 ns
	C2	—				101	0–60.6	16.4 \pm 18.0	0.50 ns
	C3	—				75	0–186.6	27.0 \pm 49.1	0.48 ns
	C4F	—				6	0–33.4	4.9 \pm 9.8	0.14 ns
	C4M	—				4	0–33.4	3.1 \pm 9.1	0.50 ns
	C5F	—				2	0–28.0	2.6 \pm 7.5	0.50 ns
	C5M	1	0–11.3	0.8 \pm 2.9		3	0–11.9	0.8 \pm 3.1	0.70 ns
<i>P. rubra</i>	C6F	30	0–46.1	11.7 \pm 13.1	0.41 ns	—			
	C6M	—				—			
	C4F	—				5	0–99.6	12.8 \pm 28.1	0.93 ns
	C4M	—				3	0–35.0	6.6 \pm 12.6	0.93 ns
	C5F	1	0–100.0	6.7 \pm 25.8		4	0–296.3	21.3 \pm 76.3	0.70 ns
	C5M	—				6	0–63.8	4.3 \pm 16.5	0.70 ns
Correlation with depth	C6F	17	0–57.4	7.2 \pm 19.0	0.65 ns	12	0–200.0	23.2 \pm 56.2	0.06 ns
	C6M	—				—			
	a		–0.018			a	0.015		
	b		30.747			b	–2.342		
	n		3			n	14		
	r		0.95			r	0.49		
p		0.21			p	<0.05			

those of large grazing copepods such as *Neocalanus cristatus* (4964) and *N. plumchrus* (2409) in the same region (Kobari & Ikeda 2000).

Meso- and bathypelagic copepods are often characterized by year-round reproduction, with continuous recruitment to adult populations (Mauchline 1998). The present results, showing the presence of all copepodid stages of *Paraeuchaeta elongata* (Fig. 4), *P. birostrata* (Fig. 5), and *P. rubra* (Fig. 6) throughout the year, suggest that this is also the case with these 3 species. The lack of discrete cohorts made it difficult to determine developmental sequences and hence the generation time for any of the species in this study. Nevertheless, *P. elongata* and *P. birostrata* were most abundant in June–September, during which the relative proportions of early copepodid stages in the total was also higher (Figs 2, 3), suggesting that there were moderate spawning peaks. Since development times (as evaluated ex-

perimentally) of eggs and naupliar stages of *P. elongata* at 2–5°C are 22–28 and 24–37 d, respectively (cf. Ozaki & Ikeda 1997), the moderate spawning seasons of these two species may be calculated back to April–July. This estimated moderate spawning peak season is in good agreement with Ozaki & Ikeda's (1999) conclusion (April–June) derived from a seasonal population analysis of *P. elongata* off Cape Esan, located near Site H of this study. While comparable C1–C3 data are not available for *P. rubra*, the similarity of this species seasonal pattern of variation in abundance to those of *P. elongata* and *P. birostrata* (Fig. 6) suggest near synchronized features of the moderate spawning seasons for these 3 species.

Instead of population structure, the frequency of spermatophore attachment to the genital somite of females, and female brood size, may be used to define the major spawning season and to estimate generation length in euchaetid

copepods (Mauchline 1994a). Mauchline (1994a) applied this new method to estimate the generation length of 9 *Euchaeta* species living in meso- and bathypelagic zones in the Northeastern Atlantic. As a result, he successfully estimated 0.5 to 2-year life cycles for 5 species, but failed for the remaining 4 bathypelagic species which did not exhibit pronounced spawning seasons. The present results and those of Mauchline (1994a) suggest that evaluation of life cycle/generation length for those meso- and bathypelagic copepods that are year-round spawners remains an as yet unsolved problem. To overcome this problem, a combination of field population structure data and laboratory rearing data may be a solution, as has been demonstrated by Ikeda & Hirakawa (1996) and Ozaki & Ikeda (1999) in their studies on the life cycle of *P. elongata* in Toyama Bay, southern Japan Sea and off Cape Esan, western North Pacific (near Site H), respectively. According to Ikeda & Hirakawa (1996) and Ozaki & Ikeda (1999), *P. elongata* in both regions has an annual reproductive cycle. No information about the life cycles of *P. birostrata* and *P. rubra* is available at present.

Kouwenberg (1993) hypothesized that adult sex ratios of herbivorous copepods are characterized by a predominance of females, carnivorous ones by near equality of the sexes, and omnivorous ones intermediate between those of herbivorous and carnivorous copepods. Kouwenberg's hypothesis for carnivorous copepods assumes no sexual differences in the feeding activity (a good example of this is *Heterorhabdus tanneri*, cf. Yamaguchi & Ikeda 2000). However, males of euchaetid copepods are known to cease feeding (Campbell 1934), or be shorter-lived than females, which results in typical adult sex ratios (female: male) of 60–80% (Morioka 1975; Hopkins 1982; Ozaki & Ikeda 1999). In the three *Paraeuchaeta* species studied here, adult sex ratios (71% for *P. elongata*, 67% for *P. birostrata*, and 92% for *P. rubra*) were more biased to females. Adult sex ratios of euchaetid copepods are known to greatly influence the incidence of spermatophore-attached or egg-carrying females (Hopkins & Machin 1977; Hopkins 1982; Ward & Robins 1987; Mauchline 1994a). However, in the present study, no significant correlations were found between the frequency of spermatophore-attached or egg-carrying females and sex ratio for any of the 3 *Paraeuchaeta* species. This may be an artifact of the relatively smaller sample size in this study. Multiple placement of spermatophores is documented in some euchaetid copepods (Hopkins & Machin 1977; Ward & Robins 1987) together with spermatophore dimorphism (Ferrari & Dojiri 1987). The 3 *Paraeuchaeta* copepods observed in this study showed neither multiple placement of spermatophores (only one spermatophore) nor spermatophore dimorphism (monomorphism only). Our findings of single placement of spermatophores are consistent with Mauchline's (1994b) view that meso- and bathypelagic euchaetid copepods differ from epipelagic ones in that they attach a single spermatophore to the genital opening of females directly.

Epizoic ciliates

Various bacteria, diatoms, fungi, ciliates, and epicaridean crustaceans have been recorded attached to the body of copepods (cf. review of Ho & Perkins 1985). Infection of copepods by such organisms shows seasonal trends, as has been observed for epizoic ciliates on *Acartia hudsonica* in Long Island Sound (Weissman et al. 1993). Weissman et al. (1993) observed that infection peaked in late spring, with no relation to age or developmental stage of *A. hudsonica*. In contrast, infection by epizoic ciliates on *Paraeuchaeta* was observed to not be related to season, but related to developmental stage (C5 and C6 only, cf. Table 5) in this study. The incidence of epizoic ciliates only on C5 and C6 may be related to the longer intermoult durations of these late stages (cf. Ikeda & Hirakawa 1996; Ozaki & Ikeda 1999). As judged by the incidence of carcasses (Table 5), the ciliates on these late copepodid stages suffer least predation (see below "Discussion-Carcasses"). The effects of epizoic ciliates on the ecology of *Paraeuchaeta* species is unknown. Weissman et al. (1993) noted that ciliate infection led to lower survival rates but normal growth rates of *Acartia nauplii*, while infected adult *Acartia* had lower than average sinking rates. The proportion of infected C6F of *Paraeuchaeta* spp. decreased with increasing depth, but the pattern was not significant statistically ($p=0.21$) (Table 5). The lack of statistical significance may be due to the small data sets ($n=3$).

Carcasses

Occurrence of copepod carcasses has been reported from both meso- and bathypelagic zones of various parts of the world ocean, although the causes of carcass production are not explicitly known (Wheeler 1967; Weikert 1977; Sameoto 1986; Terazaki & Wada 1988; Roe 1988; Haury et al. 1995). It is noted that the most numerous *Paraeuchaeta* carcasses were those of the early copepodid stages, not adults (cf. Table 5). Haury et al. (1995) thought that the copepod carcasses they found over seamounts in the Pacific Ocean resulted from predation, for the following reasons: (1) the damage to many of the carapaces resembled that caused by euphausiids; (2) some vertebrates (fishes) and invertebrates (crinoids, corals, gelatinous zooplankton) ingest whole copepods and egest fragmented or complete exoskeletons identical to those found in their samples. In addition, some carnivorous copepods ingest only parts of large prey animals and the rest is discarded (Mauchline 1998: p. 149). Carcasses of *Paraeuchaeta* species found in the present study were similar to those of *Calanus pacificus*, *Pleuromamma borealis*, and *Metridia pacifica* photographed by Haury et al. (1995), and are therefore considered to result from predation.

Taking into account the depth distribution ranges of the three *Paraeuchaeta* copepods in the Oyashio region (223–458 m for *P. elongata*, 646–963 m for *P. birostrata*, 931–1468 m for *P. rubra*, cf. Yamaguchi & Ikeda, unpublished

data), possible predators on them are myctophid fishes such as *Lampanyctus jordani* (distribution depth: 200–700 m), *Stenobrachius nannochir* (600–700 m), and *Diaphus theta* (20–500 m), all of which are abundant in the Oyashio region (Watanabe et al. 1999). The main diet of these myctophids is copepods and euphausiids, but no *Paraeuchaeta* spp. have been found in the stomachs of these myctophids (Gordon et al. 1985). Among the three *Paraeuchaeta* copepods studied here, a few *P. elongata* (= *P. japonica*) have been observed in the stomachs of some mesopelagic fishes in the Bering Sea (Beamish et al. 1999) and juvenile salmon in the Okhotsk Sea (Volkov 1996). Meso- and bathypelagic decapod shrimps are also possible predators on *Paraeuchaeta* spp. While there is no quantitative information about feeding of decapod shrimps on *Paraeuchaeta* spp. in the Oyashio region, the biomass of decapod shrimps (0.44 g wet weight m⁻², 0–1000 m depth; Aizawa 1974) is appreciably less than that (19 g wet weight m⁻², 20–700 m depth; Watanabe et al. 1999) of the myctophid fishes mentioned above. Information about feeding of meso- and bathypelagic chaetognaths, amphipods, and other copepods on *Paraeuchaeta* spp. is still lacking. In addition to these taxa, recent observations using submersibles have revealed the occurrence of potential predators on *Paraeuchaeta* spp. such as cnidarians and ctenophores from the meso- and bathypelagic zones of the western North Pacific (Hunt & Lindsay 1999).

Among the 3 *Paraeuchaeta* spp. studied here, the incidence of carcasses increased with depth (Table 5). This pattern is also seen within *P. elongata*; C1 and C2 live deeper than C3–C5 (Yamaguchi & Ikeda, unpublished data). Positive correlations between the incidence of *Paraeuchaeta* carcasses (as % of living specimens of each copepodid stage of the 3 species) and their depth distribution (Table 5) may reflect slower decomposition of carcasses in deeper, cooler environments (<3°C below 1000-m depth, cf. Fig. 3) in the Oyashio region. Terazaki & Wada (1988) considered also that the near-zero water temperature of the “Japan Sea Proper Water” is a main factor contributing to the abundance of *Neocalanus* carcasses in the Japan Sea. According to Harding (1973), bacterial decomposition of dead copepods takes 11 d at 4°C in Scotian Shelf waters, and 3 d at 22°C in Sargasso Sea waters. Seki (1965) studied chitin (a major component of copepod exoskeletons) decomposition in seawater, and noted that chitin may be mineralized within 370 d at 5°C and 500 d at 2°C. However, lower temperatures do not explain the reason why C6 carcasses of the three *Paraeuchaeta* species (except for females of *P. rubra*) were absent. Absence of C6 carcasses may be due to their relatively lower abundance, unknown escape mechanism from predators, and possibly faster sinking due to their larger body masses (6.3–17.2 mg wet weight; Yamaguchi & Ikeda, unpublished data).

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