

Vertical distribution, population structure and life cycle of the mesopelagic copepod *Paraeuchaeta elongata* off Cape Esan, southwestern Hokkaido, Japan

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Abstract: Seasonal investigations of the vertical distribution, population structure and reproduction of the mesopelagic copepod *Paraeuchaeta elongata* were conducted from 1994 through 1996 off Cape Esan, southwestern Hokkaido, Japan. Vertical distribution patterns varied with copepodite stage and season. Early-stage copepodites were found at 150–250 m depth, while older copepodite stages were collected near 270-m depth. Seasonal ascent into shallow layers occurred in the copepodite-5 and 6 (adult) stages in spring. The repeated seasonal sequence of population structures in which young copepodites predominated in summer–winter while older stages were most numerous in spring suggests that the life span of *P. elongata* is one year. Judging from the occurrence of young copepodites, reproduction continues throughout the year, with a peak occurring in April to June. The present results are compared with observations on *P. elongata* in the Japan Sea, and other Euchaetidae species from other regions.

Key words: mesopelagic copepod, *Paraeuchaeta elongata*, vertical distribution, population structure, life cycle

Introduction

As a group of pelagic calanoid copepods, the Family Euchaetidae includes medium- and large-sized predatory copepods that inhabit epipelagic to bathypelagic layers. This family has two genera, *Euchaeta* and *Paraeuchaeta*; the former is characterized by medium-sized epipelagic inhabitants and the latter by large-sized meso/bathypelagic inhabitants (Park 1975).

As a species belonging to the Family Euchaetidae, *Paraeuchaeta elongata* (Esterly) is distributed throughout the mesopelagic zone of the North Pacific and its adjacent seas, and is the most abundant species among the known 20 *Paraeuchaeta* species in the northern Pacific (Park 1994). The late copepodite stages of this species prey on small-sized calanoid copepods, such as *Pseudocalanus* adults and *Calanus pacificus* copepodites (Green & Landry 1985; Yen 1983), and their predation pressure is known to significantly affect the distribution patterns of small copepods in Dabob Bay, North East Pacific (Ohman et al. 1983; Ohman

1990). *P. elongata* occurs abundantly in the Japan Sea and off the southeast Pacific coast of Hokkaido, Japan (Morioka 1972, 1975). While the ontogenetic vertical distribution (Morioka 1975) and life cycle (Ikeda & Hirakawa 1996) of this species have been reported for the population in the Japan Sea, information on populations from other regions is extremely limited.

In this study, we report on the seasonal changes in vertical distribution patterns, population structure and life cycle of *P. elongata* in the northwestern Pacific Ocean. Observations on this population are compared with those in the Japan Sea and those for other *Euchaeta/Paraeuchaeta* species in other regions.

Materials and Methods

A series of 17 seasonal samples was collected at a single station (bottom depth: about 500 m, Fig. 1) off Cape Esan, southwestern Hokkaido, during November 1994 through November 1996, using a set of MTD horizontal closing nets (0.33 mm mesh aperture, Motoda 1971). The nets were towed at 12–16 discrete depth horizons between the surface

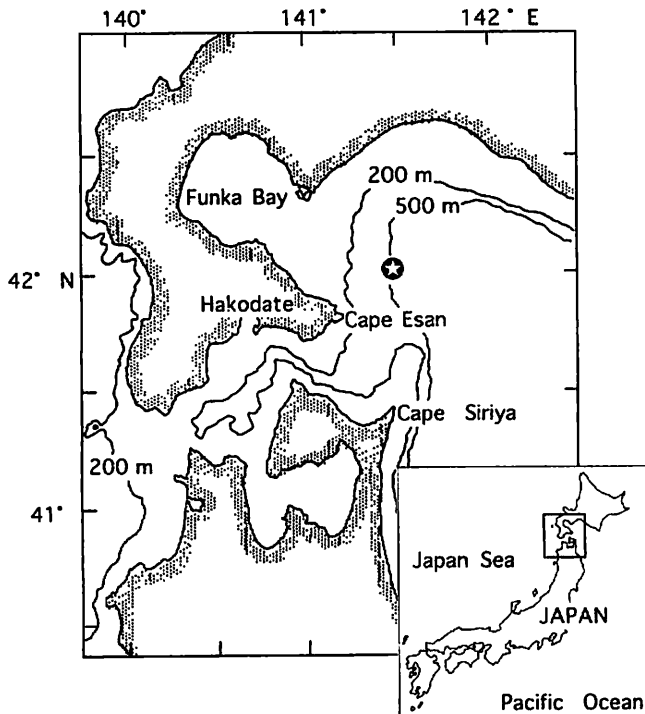


Fig. 1. Sampling station (circled star) off Cape Esan (42°00'N, 141°30'E, depth about 500 m) in southwestern Hokkaido. Depth contours (200 and 500 m) are shown.

and 300 m (only 6 depth horizons between 150 and 300 m were sampled on 2 September 1995). All samplings were conducted during daylight hours (local time: 1100–1400 h). Upon retrieval of the nets, zooplankton samples were preserved immediately in 5% buffered formalin-seawater on board the ship. The volume of water filtered by the nets was determined from the readings of a Rigosha flowmeter mounted on the mouth ring of each net.

All *Paraeuchaeta elongata* copepodites were first sorted from the samples and then separated into each developmental stage under a dissecting microscope. The sexes of copepodites older than the stage 4 (C4) were recorded. Because a 0.33-mm mesh size was used, copepodites younger than the C2 were not effectively collected (body length and width of C1 is 1.37 mm and 0.35 mm, respectively, as compared with diagonal distance of the mesh size of 0.47 mm). A weighted mean depth (WMD) was calculated for each copepodite stage according to the equation given by Frost and Bollens (1992); $WMD = (\sum N_i D_i) / \sum N_i$, where N_i and D_i are the abundance and depth, respectively, at i -m depth.

For the females carrying egg sacs, the number and diameter of eggs in the sacs were determined. Detached egg sacs collected in the samples were also treated in the same way. The occurrence of spermatophores in the females was recorded. The prosome length (from the anterior point of the rostrum to the posterior lateral edge of the last prosome segment) of each copepodite stage and the diameter of eggs were measured under the dissecting microscope to the nearest 0.01 mm. To express catches as the numerical abun-

dance per m², density data (indiv. m⁻³) at each designated sampling depth were integrated over the distance between sampling depths.

Vertical profiles, from the surface to near the bottom, of temperature and salinity were determined with a CTD unit or digital bathythermograph. The temperature-salinity diagram proposed by Hanawa & Mitsudera (1987) was used to classify water mass.

Results

Hydrography

Seasonal features of temperature and salinity are shown in Fig. 2. Three water types were distinguished at the present study site, i.e. those that originated from “Oyashio” Water (low temperature, low salinity), “Tsugaru” Warm Water (high temperature, intermediate salinity), and Cold Lower-Layer Water (low temperature, high salinity). The surface temperature was the lowest (<2°C) in March when Oyashio water first intruded into the top 200 m, and reached an annual maximum (>15°C) in August–September when Tsugaru warm current water occupied the top 200 m. Below 200-m depth, temperature was stable at 2–5°C, except for a rise to about 6°C that occurred during the vertical mixing season (January–March). Salinity ranged from 32.5 to 34.2 except for extremely low values that occurred at the surface during February to June. Excursions of Oyashio-derived water early in the year and of the Tsugaru warm current in summer are regular annual events at the present study site (Hanawa & Mitsudera 1987).

Vertical distribution

Throughout the year, *Paraeuchaeta elongata* copepodites occurred largely at depths greater than 100 m (Fig. 3). The C2 stage (mean WMD=230 m) resided at depths slightly shallower than the C3 (mean WMD=243 m) and C4 (mean WMD=274 m) stages. The C5 (mean WMD=277 m) and C6 (mean WMD=276 m) stages occurred deepest, except during spring, when they ascended to 100–150 m depth. The C4–C6 stage males and females showed no significant differences in their bathymetric distributions, based on analysis of their WMDs ($p > 0.05$, Wilcoxon two-sample test), so data for both sexes were pooled in Fig. 3.

Abundance, sex ratio and reproductive condition

Seasonal abundances of each copepodite stage of *P. elongata* were characterized by the dominance of early copepodite stages (C2–C3) in summer–winter and of the late copepodite stages (C4–C6) in spring (Fig. 4). Repetition of these seasonal population structures in 1995 and 1996 suggests that this species has an annual life cycle. While C6 (adult) females with 1 or 2 spermatophores attached were collected throughout the year, those carrying egg sacs were collected only during April to June in 1995 and in May

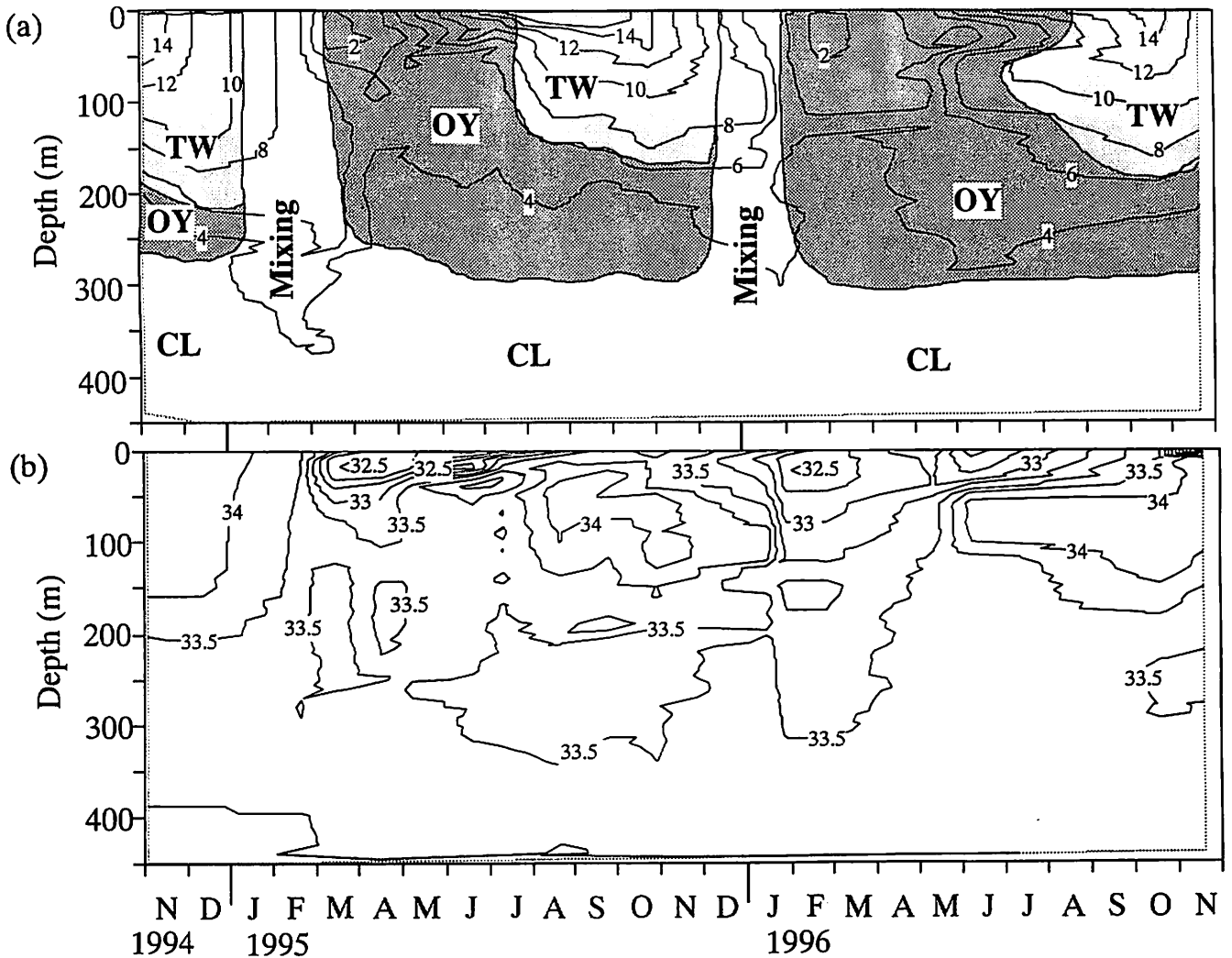


Fig. 2. (a) Temperature ($^{\circ}\text{C}$) and (b) salinity profiles of the water column at the sampling station off Cape Esan, southwestern Hokkaido. Water types: OY; the Oyashio Water, TW; the Tsugaru Warm Water, CL; the Cold Lower-Layer Water are superimposed on the temperature profile.

1996 (Fig. 4). The number of eggs per egg sac varied from 19 to 32 (25.5 ± 2.1 , mean \pm 95% CI), but the egg diameter remained nearly constant throughout the year (0.47–0.48 mm).

Sex ratios (females/males) varied from 0.77 to 1.44 for the C4 stage (mean=1.03), from 0.55 to 2.56 for the C5 stage (mean=1.09), and from 0.55 to 3.60 for the C6 stage (mean=1.55) (Fig. 4).

Body length

Mean prosome length was 1.43 (95% CI: ± 0.01) mm for the C2 stage, 1.97 (± 0.01) mm for the C3 stage, 2.83 (± 0.02) mm for the C4 stage (male and female data were pooled), 4.10 (± 0.02) mm for the C5 stage (male and female data were pooled), and 5.18 (± 0.03) mm for C6 females (Fig. 5). Seasonal prosome length data were divided arbitrarily into March–August (season when old copepodites predominated) and September–February (season

when young copepodites predominated), and differences between these groups were analyzed statistically. As a result, the C2 stage showed no significant size differences between the two periods ($p > 0.05$, t -test), but the C3 to C6 stages were significantly larger in March–August than in September–February ($p < 0.0001$, t -test).

Discussion

Morioka (1975) examined the ontogenetic vertical distribution and reproduction of *Paraeuchaeta elongata* in the southern Japan Sea, and reported that eggs, nauplii and the C1 stage were distributed mainly below 500 m, the C2–C3 stages at 200–400 m, the C4–C5 stages at 300–400 m, and the C6 stage at depths below 500 m. While females carrying eggs were observed throughout the year, the major reproductive season of this species was estimated to occur during summer to fall. Because *P. elongata* has a complex population structure due to continued reproduction

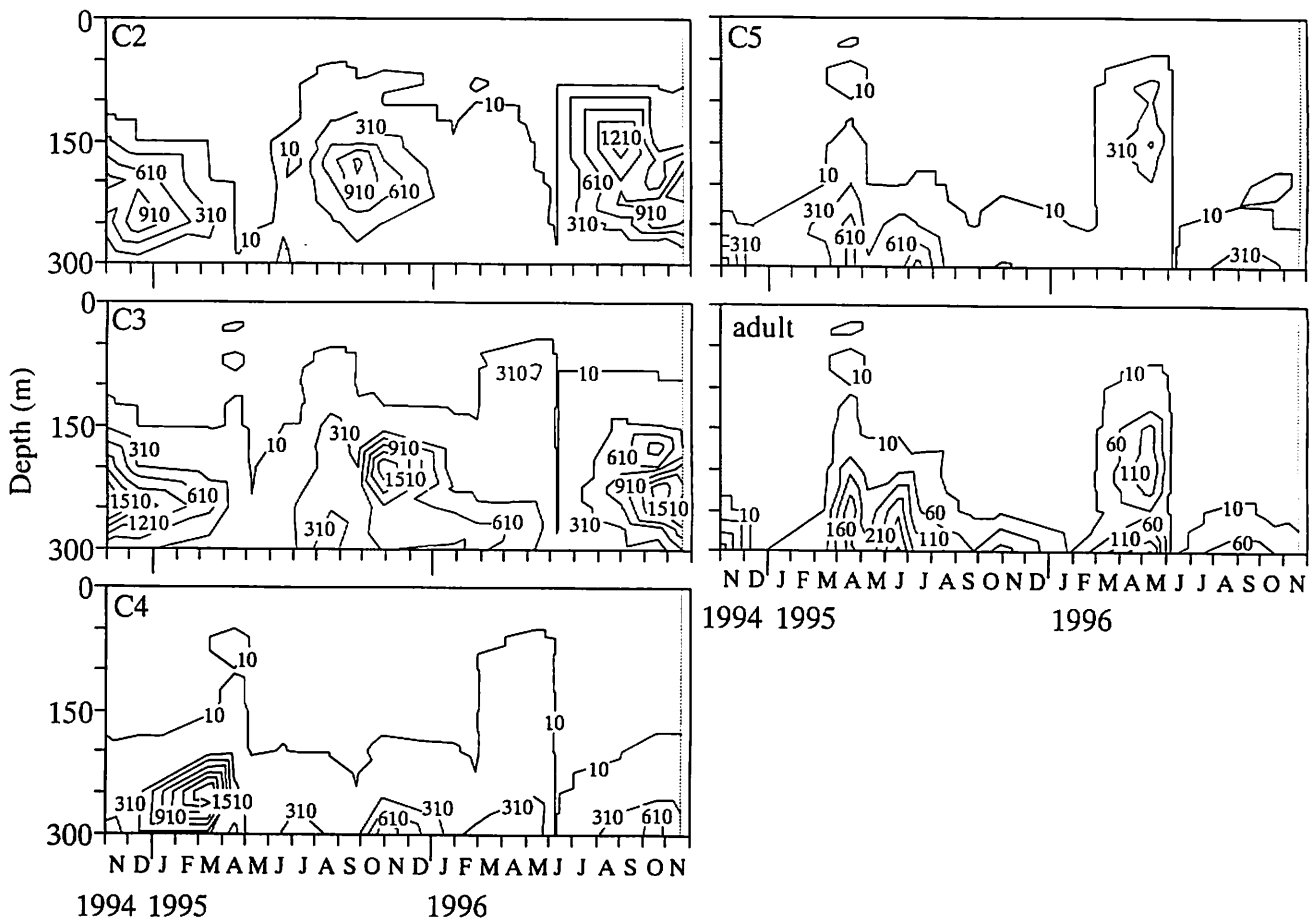


Fig. 3. Seasonal changes in vertical distribution patterns (no. copepods per 1000 m³) of each copepodite stage of *Paraeuchaeta elongata* at the sampling station off Cape Esan, southwestern Hokkaido. Note that the data for females and males are combined for the C4–adults, since no statistical difference was detected between the two ($p > 0.05$ for the all stages, Wilcoxon two-sample test).

throughout the year, Morioka (1975) was unable to identify and trace the growth of cohorts, or to estimate generation length. Since then, Ikeda and Hirakawa (1996) combined their laboratory rearing data with population structure data and concluded that the generation length of *P. elongata* in the southern Japan Sea is 1 year.

The vertical distribution patterns of the C2–C3 stages of *P. elongata* from populations off Cape Esan and from the southern Japan Sea are nearly the same. The C4–C6 stages occurred in the 250–300 m layer off Cape Esan, while they occurred in a deeper layer (300 to >500 m) in the southern Japan Sea. This may be due to the shallower sampling strategy for investigating the former population (0–300 m). In support of this, the highest number of the C5–C6 stages always occurred in the deepest stratum sampled off Cape Esan (Fig. 3). The spring ascent of the C4–C6 stages to the shallow depth observed in the present study was also seen in Morioka's (1975) study.

The main reproductive season is clearly different for *P. elongata* populations off Cape Esan (April–June) and in the southern Japan Sea (August–October) (Table 1). As *P. elon-*

gata is a carnivore, this regional difference in the major reproductive seasons in *P. elongata* may be due to differing abundance cycles of prey (other zooplankton) between these two regions. The annual peak in zooplankton biomass occurs around April off Cape Esan region (Kubo 1993) and during August–September in the southern Japan Sea (Hirakawa et al. 1992). The greater body size of the C3 to C6 stages observed in March–August (Fig. 5) supports the view that food supply was more abundant during this period off Cape Esan. Peaks in spawning and abundance of prey organisms often coincide in marine copepods, especially in herbivorous species (Colebrook 1979; Raymont 1983).

Both the number of eggs per egg sac and the size of the eggs of *P. elongata* off Cape Esan (25.5 eggs, 0.47–0.48 mm) are close to those of the southern Japan-Sea population (25 eggs, 0.45–0.55 mm). For both populations, the female/male ratio was nearly 1 for the C4–C5 stages, but higher (1.6) for the C6 stage (adult), suggesting that adult males do not live as long as females.

Comparison of prosome lengths of *P. elongata* collected

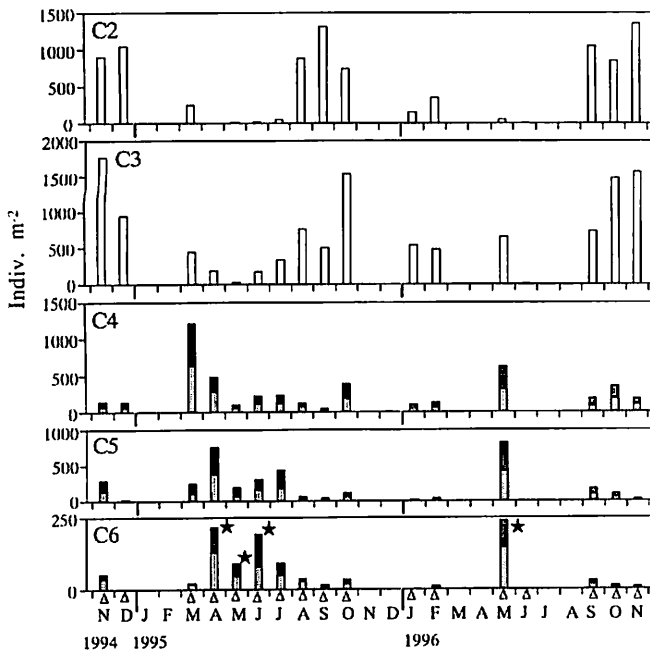


Fig. 4. Seasonal change in abundance of each copepodite stage of *Paraeuchaeta elongata* at the sampling station off Cape Esan, southwestern Hokkaido. C4 to C6 males (dark area) and females (light area) are separated each other. Stars indicate the occurrence of females with attached egg sacs. Δ =sampling dates.

off Cape Esan (this study) and those collected in the southern Japan Sea (Morioka 1975), indicates that the C2 to C4 stages are similar, but the C5–C6 stages off Cape Esan are consistently smaller (Table 1). The body size of marine copepods is affected mainly by habitat temperature and food supply (Mullin & Brooks 1970; Vidal 1980; Klein Breteler & Gonzalez 1988; Uye 1988, 1991; Escribano & McLaren 1992). Taking into account regional differences in the vertical distribution patterns in some stages as mentioned above, the C2–C4 stages' habitat temperatures are nearly identical between the southern Japan Sea (4.0–5.0°C, cf. Morioka 1975) and off Cape Esan (3.9–4.2°C, Fig. 2). However, the C4–C6 stages occur in much colder water (<1.5–2°C) in the southern Japan Sea than off Cape Esan (3.4–3.9°C). Assuming that food is unlimited, larger body size in the C5–C6 stages from the southern Japan Sea may reflect the cooler ambient temperatures. The life cycle of *P. elongata* off Cape Esan appears to be annual, based on seasonal population-structure data (Fig. 4). This result is consistent with the conclusion derived from laboratory rearing data for this species (Ozaki & Ikeda 1998). Ikeda & Hirakawa (1996) have already reported a 1-year life span for the southern Japan-Sea population of this species.

The present results can be put into a wider perspective if compared with observations on Euchaetidae copepods from other regions. Among the Euchaetidae copepods, *Euchaeta norvegica* has been extensively studied in the Atlantic Ocean and is reported to have 2 generations per year in the northeastern Atlantic Ocean (Wiborg 1954; Båmstedt &

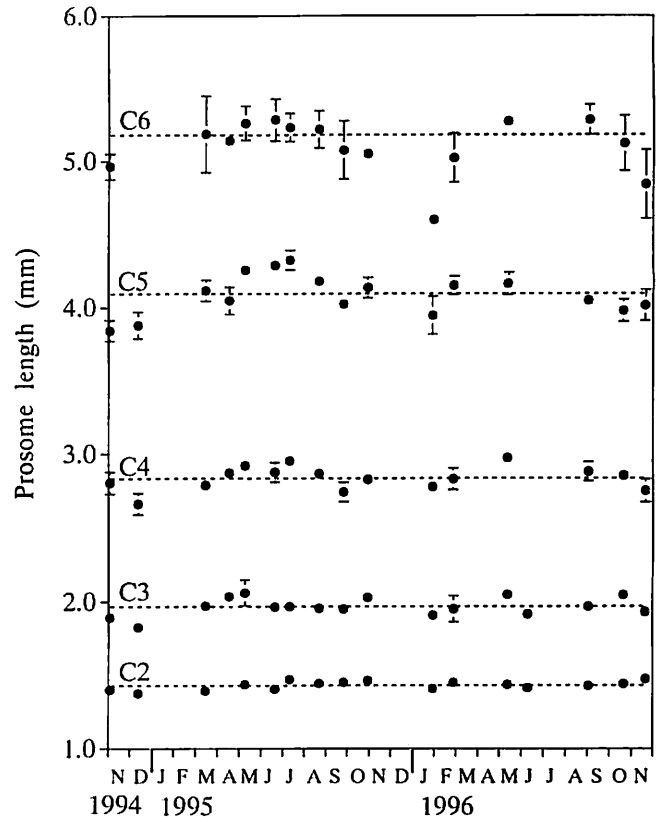


Fig. 5. Seasonal change in prosome length (mm) of each copepodite stage of *Paraeuchaeta elongata* at the sampling station off Cape Esan, southwestern Hokkaido. Vertical bars denote $\pm 95\%$ CI range. Annual means are superimposed by horizontal broken lines for each stage.

Matthews 1975; Bakke 1977; Båmstedt 1979). Mauchline (1994) investigated the generation length of several meso/bathypelagic *Euchaeta* species in Loch Etive and the Rockall Trough, Northeastern Atlantic Ocean. According to his estimates, the number of generations per year is 1 for *E. acuta* and *E. pseudotonsa*, 1 (population in Rockall

Table 1. Comparisons between *Paraeuchaeta elongata* populations in the southern Japan Sea and off Cape Esan for several biological and ecological parameters.

	Southern Japan Sea (Morioka 1975)	off Cape Esan (This study)
Main reproductive season	August–October	April–June
Brood size	2–36 (mean 25.0)	19–32 (mean 25.5)
Egg size (mm)	0.45–0.55	0.47–0.48
Life span	1 year	1 year
Prosome length (mm)		
C2	1.40	1.43
C3	1.80	1.97
C4	2.85 (♀)–2.85 (♂)	2.83 (♀♂)
C5	4.40 (♀)–4.50 (♂)	4.10 (♀♂)
C6	5.30 (♀)	5.18 (♀)

Trough) or 2 (population in Loch Etive) for *E. norvegica*, 2 for *E. gracilis*, and 0.5 for *E. sarsi*. In the Southern Ocean, Ward & Robins (1987) have suggested that the generation time of *E. antarctica* is 0.5 year. Thus, the 1-year generation time for *P. elongata* proposed in the present study falls within the range of 0.5–2 generations per year reported for the other meso/bathypelagic Euchaetidae species studied to date.

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