

Note

Development time and generation length of the mesopelagic copepod *Paraeuchaeta elongata* reared in the laboratory

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Paraeuchaeta elongata (Esterly) is a large, carnivorous calanoid copepod, distributed throughout the mesopelagic zone of the North Pacific and its adjacent seas (Brodskii 1950; Park 1994). This species is a dominant component of the copepod biomass in the southern Japan Sea (Hirakawa et al. 1992) and exerts significant predation pressure on other copepods in the eastern North Pacific (Ohman et al. 1983; Ohman 1986, 1990; Bollens & Frost 1991). Despite its possible importance in the energy-flow and matter cycling in the pelagic ecosystem, information about the development time and generation length of *P. elongata* is currently known only for the local population in the southern Japan Sea (Ikeda & Hirakawa 1996). A major problem associated with life-cycle analyses of *P. elongata* is their continuous reproduction throughout the year (cf. Morioka 1975; Ozaki, unpublished data).

In 1996, we successfully raised copepodite 1 stage (C1) specimens of *Paraeuchaeta elongata* in the laboratory using eggs attached to females collected at a station (42°00'N, 141°30'E) off Cape Esan, northwestern Hokkaido (Ozaki & Ikeda 1997). The C1 specimens thus obtained were reared through to the adult stage (C6). This is the first account of the development time and generation length of a mesopelagic copepod evaluated in the laboratory.

Details of the sampling methods for collecting egg-carrying females off Cape Esan, and the experimental procedures used for raising eggs and

nauplii of *Paraeuchaeta elongata* have been reported elsewhere (Ozaki & Ikeda 1997). Of the C1 specimens raised at 2, 5 and 10°C by Ozaki & Ikeda (1997), only those at 2°C developed successfully to the C6 stage (adult). Specimens grown at 5 and 10°C died after reaching C5 and C3, respectively. Individual copepodites were reared in 200-ml (C1 to C4) or 500-ml (C5 to C6) glass containers. Small live copepods (mostly *Acartia* spp. and *Pseudocalanus* spp.) were provided as food at a concentration of 20 to 30 indiv. per container (=40–150 indiv. l⁻¹). All glass containers were placed in an incubator (2°C), and experiments were run in the dark. The development of individual copepodites was traced by collecting cast molts. Newly molted specimens were transferred into new containers filled with filtered seawater and a new complement of prey organisms. Prosome length of cast molts was measured to the nearest 0.01 mm using a micrometer eyepiece fitted to a dissecting microscope.

Of 55 C1 specimens, four successfully reached C6. Combining the data for naupliar 1 stage (N1) to C1 at 2°C (Ozaki & Ikeda 1997) with the data for stages C2 to C6 at the same temperature (this study) revealed that the highest mortality rate occurred during the development from N1 to N2, and that most mortality was due to failure in molting. Mean copepodite development time ($\pm 95\%$ CI) increased progressively with each stage (Fig. 1); 32.9 (± 1.3) d for C1, 48.1 (± 1.5) d

for C2, 50.7(\pm 3.5) d for C3, 69.8(\pm 3.2) d for C4, and 86.5(\pm 6.5) d for C5 (288 d from C1 to C6). Adding the egg hatching time (27.2 d) and naupliar development time (37.0 d) reported in Ozaki & Ikeda (1997) to this, the life span of *Paraeuchaeta elongata* is estimated to be approximately 352 d at 2°C.

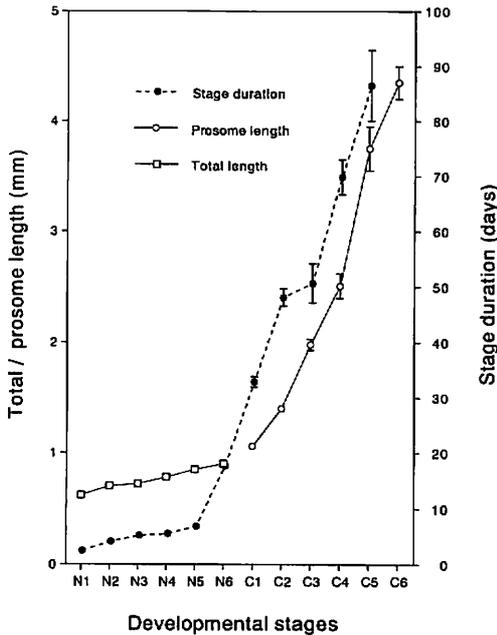


Fig. 1. Stage durations (d) and total (Naupliar 1 to 6) and prosome (Copepodite 1 to 6) length of *Paraeuchaeta elongata* raised in the laboratory at 2°C. Data for nauplii and C1 are from Ozaki & Ikeda (1997). Vertical bars for copepodites' data denote 95% CI. N=Nauplius. C=Copepodite.

The four C6 specimens obtained in this study were all females. In an attempt to obtain fertilized eggs, each female specimen was paired with a male (C6) specimen collected from the field. Dark blue eggs formed in the ovaries of three of the four females, ranging in age from 32 to 38 d. After this time, in two of the females the egg mass moved from the ovary to the end of oviduct in 16 and 18 d, respectively, forming egg sacs. However, no spermatophores were observed attached to the genital segment of the females in this study, suggesting that attempts to fertilize the eggs were unsuccessful. The unfertilized eggs became detached from the females 24 and 25 d after egg-sac formation.

Late copepodites (C4 to C6) of *Paraeuchaeta elongata* raised in the present study were smaller than wild specimens (Table 1). Water temperature and diet (prey quality and quantity) are important factors affecting the size of marine copepods (Mullin & Brooks 1970; Vidal 1980). Within natural temperature ranges, higher temperatures often cause adults to mature at smaller sizes than lower temperatures. However, the present experimental temperature of 2°C is on the lower edge of the habitat temperature range of *P. elongata* off Cape Esan (2°C to <12°C; Ozaki, unpublished data), and therefore low water temperature does not appear to be responsible for the small size of the late copepodites raised in the present study. Small copepods (*Acartia*, *Pseudocalanus*) used as prey for *P. elongata* in this study have been evaluated to be adequate in terms of size and ingestion efficiency for *P. elongata* (Yen 1983). Yen's (1983) results on the functional response of

Table 1. Comparison of prosome length (PL; mm) between laboratory raised and wild copepodites of *Paraeuchaeta elongata*. Mean \pm 95% CI. Difference was tested by Mann-Whitney's *U*-test. *N* represents number of measured specimens.

| Developmental stages | Laboratory-raised | | Wild | | Difference |
|----------------------|-------------------|----------|-----------------|----------|-----------------|
| | PL | <i>N</i> | PL | <i>N</i> | |
| C1* | 1.06 \pm 0.01 | 42 | 1.07 \pm 0.02 | 10 | ns |
| C2 | 1.40 \pm 0.03 | 26 | 1.43 \pm 0.01 | 254 | ns |
| C3 | 1.98 \pm 0.05 | 16 | 1.97 \pm 0.01 | 300 | ns |
| C4 | 2.51 \pm 0.11 | 13 | 2.83 \pm 0.02 | 313 | <i>p</i> <0.001 |
| C5 | 3.75 \pm 0.20 | 4 | 4.10 \pm 0.02 | 299 | <i>p</i> <0.01 |
| C6 | 4.35 \pm 0.15 | 4 | 5.18 \pm 0.03 | 319 | <i>p</i> <0.001 |

* Data from Ozaki & Ikeda (1997).

the feeding of *P. elongata* on *Pseudocalanus* indicate that the concentrations of small copepods used in our experiment (40–150 indiv.l⁻¹) are sufficient to maintain the maximum ingestion rate in *P. elongata*. Thus, neither temperature nor prey-related factors appear to have caused the smaller body size of *P. elongata*. However it is possible that feeding in *P. elongata* was suppressed in the small containers (200–500 ml), since the perception of prey by this copepod is mediated by mechanical or tactile receptors (Yen 1982).

According to Landry (1983) and Klein Breteler et al. (1994) general features of the development pattern of marine calanoid copepods include a relatively shorter pre-feeding naupliar stage, a longer first feeding stage, a C5 stage longer than any previous stage in females, and earlier maturation of males than females. As a result, egg, naupliar and copepodite stage durations account for 4–9%, 30–44% and 48–62%, respectively, of the generation length. Bearing in mind that all these generalizations were made from laboratory experiments on calanoid copepods inhabiting shallow waters, our results for the mesopelagic copepod *Paraeuchaeta elongata* are consistent with these in that the duration of C5 was the longest of the copepodite stages. The relatively short pre-feeding stage and the long first feeding stage, considered to be the C1 stage (cf. Ikeda & Hirakawa 1996), were not clear for *P. elongata*. Differences in development time between males and females could not be tested in this study since no C6 males were available. The relative duration of the egg, naupliar and copepodite stages of *P. elongata* were 7.7, 10.5 and 81.8%, respectively. The relative duration of naupliar stages is much shorter and that of the copepodite stages longer than those of shallow-living calanoid copepods.

Extrapolation of the data generated from laboratory reared zooplankton to field populations requires caution (cf. Paffenhöfer & Harris 1979), particularly for the present experiment, in which a mesopelagic species was confined in a limited volume of water and reared at normal pressure (1 atmosphere). Despite these unnatural conditions, the estimated generation length of nearly one year for *Paraeuchaeta elongata* in the present rearing experiment is consistent with estimates from field population analyses for the same

species inhabiting Toyama Bay (Ikeda & Hirakawa 1996) and off Cape Esan (Ozaki, unpublished data). These results clearly show that laboratory rearing is a feasible and powerful method to help fill the present gap in our knowledge about the development and life spans of mesopelagic copepods.

Acknowledgments

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