

## Note

# The effect of temperature on the development of eggs and nauplii of the mesopelagic copepod *Paraeuchaeta elongata*

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Temperature exerts a significant effect on various biological rate processes. Analyzing a large body of data from the literature, Huntley & Lopez (1992) and Huntley (1996) concluded that the generation period of marine copepods was ultimately controlled by temperature. Copepod development is characterized by 13 stages: egg, 6 naupliar stages and 6 copepodite stages. The relationship between the development time of copepods and temperature has been expressed by the Bělehrádek equation. However, verification of the Bělehrádek function by most previous workers is on small, inshore water copepods and few studies have been made on large oceanic copepods (McLaren 1965; McLaren et al. 1969; Corkett & McLaren 1970; Uye 1988, 1991; Klein Breteler et al. 1995).

*Paraeuchaeta elongata* (Estery) is a large carnivorous calanoid copepod, distributed throughout the mesopelagic zone of the Okhotsk Sea, Bering Sea, Japan Sea and probably the entire northern North Pacific (Brodkii 1950; Park 1995). Compared with the early development of small calanoid copepods from inshore waters, which lay eggs freely into the surrounding water and start feeding at naupliar stage 2 or 3 (cf. Landry 1983; Klein Breteler et al. 1994), *P. elongata* carries eggs in an "egg-sac" attached to the body and none of the naupliar stages feed (Ikeda & Hirakawa 1996). Naupliar development of *P. elongata* relies on lipid reserves in the eggs. Because of their abundance, large size and their

possibly large predation pressure on other copepod populations, egg development and/or naupliar development of this copepod has been studied in some local populations, but only at the temperatures prevailing in each habitat: populations in the southern Sea of Japan at 0.5°C (Ikeda & Hirakawa 1996) and northwestern North Pacific populations at 8 to 12°C (Lewis & Ramnarine 1969; Yen 1983; Bollens & Frost 1991). No data are presently available at intermediate temperatures (between 0.5 and 8°C). The area off Cape Esan, southern Hokkaido, is an ideal study site to fill the temperature gap in the data since *P. elongata* inhabiting this region encounters a temperature range of 2 to  $\leq 12^\circ\text{C}$  (Ozaki, unpublished data). As part of a study evaluating the life cycle of *P. elongata* in the western subarctic Pacific, we determined egg hatching time and naupliar developmental time at 2, 5 and 10°C. The results are discussed in the light of the reproductive strategy of this egg-carrying mesopelagic copepod.

Female specimens of *Paraeuchaeta elongata*, carrying egg sacs, were collected off Cape Esan, southern Hokkaido, on 10 March, 13 May and 10 June 1996 with vertical hauls of an 80-cm ring net or North Pacific Standard net (both 0.33-mm mesh) from near the bottom (ca. 470 m) to the surface. Concurrently, seawater was collected at >50-m depth with 20-liter Van-Dorn bottles or 5-liter Niskin bottles, filtered through GF/F filters, well oxygenated, and used for the following

experiments. Upon retrieval of the net, egg-carrying females and their free eggs presumably being detached during the process of sampling were sorted out immediately, placed in chilled seawater (ca. 5°C) and transported to a shore laboratory. In the shore laboratory, females with egg sacs were placed in a petri dish with a small amount of seawater, and egg sacs were detached carefully by means of a dissecting needle. Egg sacs thus obtained and those already detached were placed individually into 100-ml glass vials filled with seawater, and maintained at 2, 5 or 10°C in the dark.

In the course of the experiments, the state of the glass vials were inspected once a day, and seawater in the vials was changed once a week. Hatched nauplii (Naupliar Stage 1, N1), when found, were counted and transferred to a separate glass vial filled with seawater for observation of the subsequent development of naupliar stages. Egg hatchability was calculated for each egg sac as the percentage of hatched nauplii against the total number of hatched nauplii and dead eggs. Dead eggs were identified easily by the change in color from deep-blue to pale yellow. Development of a batch of the first naupliar stage from each egg sac was traced by collecting discarded molts. Because there were few individuals per batch (<10) and near synchronous development, the development time of each stage was defined as the interval between the date of hatching and first occurrence of new stages. Identification of naupliar and copepodite stages of *P. elongata* was made through reference to Campbell (1934). Body (molt) length of each stage was measured to the nearest 0.01 mm using a micrometer eyepiece fitted to a dissecting microscope.

The number of egg sacs used was 11 for 2°C, 15 for 5°C and 16 for the 10°C experiments. Analysis following the method of Burgis (1970) yielded a hatching time of 27.2 (95% CI: 29.6 to 25.3) days at 2°C, 22.2 (30.1 to 18.6) days at 5°C and 11.8 (14.4 to 10.2) days at 10°C (Fig. 1). Four females formed egg sacs successfully over the course of the present experiment. Egg hatching time measured directly (from egg sac formation to hatching of nauplii) was 23.0 days (95% CI: 23.5 to 22.4) at 5°C, which does not differ appreciably from the 22.2 days estimated by Burgis's method at the same temperature. Egg hatching times shortened progressively as temperature

increased.

Egg hatchability ranged from 11.5 to 69.9% (mean: 42.7%) at 2°C, 4.8 to 66.7% (29.4%) at 5°C, and 9.7 to 80.7% (46.3%) at 10°C. The effect of temperature on hatchability was not significant (one-way ANOVA for arcsin transformed data:  $F_{2,39}=3.547$ ,  $P>0.05$ ), and the grand mean was calculated to be 39.3%. Low hatching success is a consistent feature in previous studies on *Paraeuchaeta elongata* (Lewis et al. 1971; Ikeda & Hirakawa 1996). Acute decompression of eggs when sampling from deep-water and damage caused from the artificial detachment of eggs from females may be considered as possible causes. However, high hatching success, as high as 73% (25 to 100%), has been recorded for the mesopelagic ostracod *Conchoecia pseudodischochophora* collected from a 300 to 500-m depth and treated similarly (Ikeda 1992). Furthermore no detrimental effects to the hatchability owing to artificial detachment of eggs from females is known for the sac-spawning copepod *Pseudocalanus* sp. (Landry 1983).

Over the course of development from N1 to

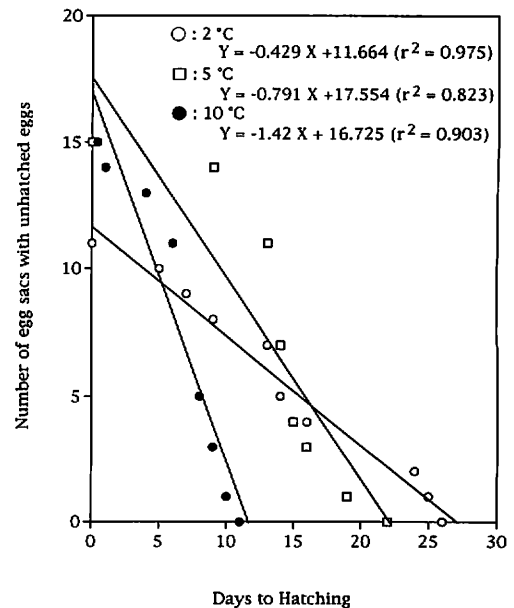


Fig. 1. Egg hatching time of *Paraeuchaeta elongata* estimated from X-intercept of the linear regression of number of egg sacs with unhatched eggs vs. incubation time, assuming that spawning was continuous and the egg sacs were randomly selected (cf. Burgis 1970).

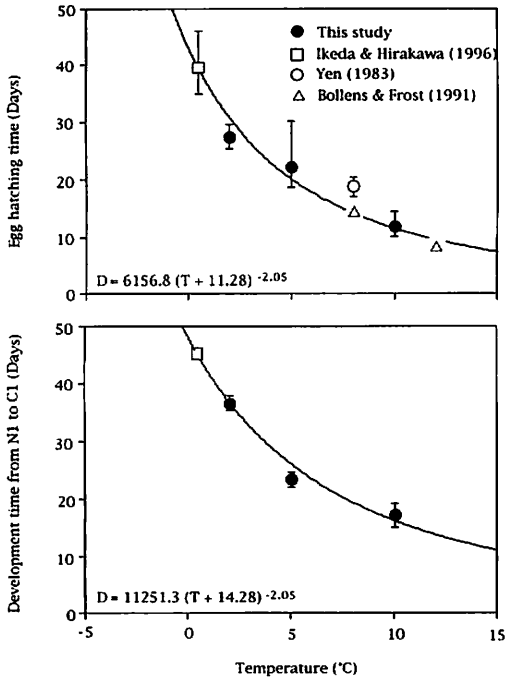
Copepodite Stage 1 (C1), overall mortality was 44% at 2°C, 62% at 5°C, and 84% at 10°C. In Ikeda & Hirakawa's (1996) experiment at 0.5°C, 54% of N1 individuals died before reaching C1. The fact that greatest mortality was recorded at 10°C may imply that while hatching experiment has been done at a temperature as high as 12°C by Bollens & Frost (1991) for the population in the north eastern North Pacific, 10°C is close to the normal upper limit for the local population off Cape Esan. Geographic variations in thermal tolerance have been reported in a euphausiid, *Euphausia pacifica* (Iguchi & Ikeda 1995). The size (body length) of nauplii increased with progress through the developmental stages, despite the fact that there was no gain in wet, dry or ash-free dry weight (Ikeda & Hirakawa 1996). No temperature effect on the size of the naupliar stages was apparent (i.e. overlapping 95% CI). Except for the aberrant data of N1 and N2 raised at 5°C, the development time of naupliar stages shortened with increasing temperature (Table 1). As a result, the newly hatched N1 reached C1 in 37.0 days at 2°C, 23.7 days at 5°C and 17.6 days at 10°C. These results, combined with Ikeda & Hirakawa's (1996) data at 0.5°C (48.5 days), indicate that *Paraeuchaeta elongata* nauplii develop faster as the temperature increases within the range of 0.5 to 10°C.

The Bělehrádek equation is expressed as  $D = a(T - \alpha)^b$ , where  $a$ ,  $b$  and  $\alpha$  are fitted constants,  $D$  is development time (days) and  $T$  is temperature (°C). McLaren et al. (1969) applied the

Bělehrádek function to the egg hatching time of 11 small copepod species belonging to the genera *Calanus*, *Pseudocalanus*, *Acartia*, *Tortanus*, *Metridia*, *Temora*, *Eurytemora* and *Centropages* from arctic to tropical waters and found that the constant  $b$  was essentially the same over all 11 species ( $-2.05$ ). Further study by Corkett & McLaren (1970) revealed that the Bělehrádek functions for egg hatching time and development time from N1 to C1 of the small copepods were identical in terms of having a common  $b$  between species and  $\alpha$  within species. With these results, we set the constant  $b$  at  $-2.05$  and fitted the egg hatching time vs. temperature and naupliar development time vs. temperature relationships of *Paraeuchaeta elongata* to the Bělehrádek equation following the procedure described by Corkett & McLaren (1970). The result is  $D = 6156.8(T + 11.3)^{-2.05}$  for egg hatching time and  $D = 11251.3(T + 14.3)^{-2.05}$  for naupliar development time (Fig. 2). In this calculation, Ikeda & Hirakawa's (1996) data on the southern Japan Sea population at 0.5°C were combined with the present data on the basis of similarities in experimental procedures and egg sizes (egg diameter  $0.46 \pm 0.03$  mm for Cape Esan population,  $0.45$ – $0.55$  mm for southern Japan Sea population; Morioka 1975). Although the egg hatching time at 8°C for Yen (1983) is somewhat higher, those at 8 and 12°C by Bollens & Frost (1991) lie close to the predicted value (Fig. 2, top panel).  $\alpha$  values of these two equations for *P. elongata* are similar, supporting the finding of Corkett &

**Table 1.** Cumulative development time (days after hatching) and body length (mm) of naupliar stages (N1 to N6) and copepodite stage 1 (C1) of *Paraeuchaeta elongata* raised at three temperatures (2, 5 and 10°C). Mean  $\pm$  95% confidence intervals. The replicate number is in parenthesis. PL = Prosome length.

Stage	2°C		5°C		10°C	
	Development time	Body length	Development time	Body length	Development time	Body length
N1	1.5 $\pm$ 1.0 (2)	0.62 $\pm$ 0.01 (21)	2.0 $\pm$ 2.0 (2)	0.61 $\pm$ 0.03 (17)	1.0 $\pm$ 0.0 (3)	0.67 $\pm$ 0.01 (14)
N2	3.5 $\pm$ 1.1 (8)	0.70 $\pm$ 0.01 (37)	3.8 $\pm$ 1.7 (6)	0.69 $\pm$ 0.02 (24)	1.6 $\pm$ 0.3 (13)	0.72 $\pm$ 0.01 (22)
N3	8.3 $\pm$ 1.2 (8)	0.72 $\pm$ 0.01 (50)	7.4 $\pm$ 1.7 (10)	0.74 $\pm$ 0.02 (24)	3.9 $\pm$ 0.2 (11)	0.75 $\pm$ 0.004 (44)
N4	13.9 $\pm$ 1.3 (8)	0.78 $\pm$ 0.01 (58)	12.9 $\pm$ 1.7 (7)	0.79 $\pm$ 0.01 (36)	6.2 $\pm$ 0.3 (10)	0.80 $\pm$ 0.01 (27)
N5	20.1 $\pm$ 0.7 (8)	0.85 $\pm$ 0.01 (42)	15.8 $\pm$ 1.8 (10)	0.83 $\pm$ 0.02 (14)	9.6 $\pm$ 1.2 (7)	0.84 $\pm$ 0.01 (23)
N6	37.0 $\pm$ 1.3 (8)	0.90 $\pm$ 0.01 (30)	23.7 $\pm$ 1.2 (17)	0.89 $\pm$ 0.01 (14)	17.6 $\pm$ 2.0 (8)	0.91 $\pm$ 0.01 (27)
C1	68.0 $\pm$ 2.8 (8)	1.37 $\pm$ 0.01 (41) (PL: 1.05 $\pm$ 0.01)	45.2 $\pm$ 2.8 (15)	1.36 $\pm$ 0.03 (11) (PL: 1.03 $\pm$ 0.02)	31.3 $\pm$ 2.4 (3)	1.36 $\pm$ 0.02 (18) (PL: 1.04 $\pm$ 0.01)



**Fig. 2.** The relationship between egg hatching time and temperature (top), and naupliar development time (N1 to C1) and temperature (bottom) of *Paraeuchaeta elongata* fitted to the Bělehrádek function. Vertical bars represent  $\pm 95\%$  CI.

McLaren (1970) that intraspecific  $\alpha$  values are relatively constant. These results suggest that the relationship between early development and temperature of the mesopelagic copepod *P. elongata* fits the Bělehrádek equation, and equations thus obtained for the egg hatching time and naupliar development of *P. elongata* have common features to those of small copepods from inshore water investigated by previous workers.

Kjørboe & Sabatini (1994, 1995) analyzed the reproductive strategies of egg-sac spawners and broadcast spawners in marine planktonic copepods, and noted that the former were characterized by lower egg mortality, lower egg production rates and longer egg hatching times than the latter, although both reproduction strategies were deemed evolutionarily viable and appear equally fit. Comparisons of the present results on *Paraeuchaeta elongata* with those of the egg-sac spawners (mostly neritic cyclopoids) in Kjørboe & Sabatini (1994, 1995) revealed that naupliar development rates ( $0.023 \text{ stage h}^{-1}$  at  $15^\circ\text{C}$  in the former, extrapolated from the Bělehrádek equa-

tion in the lower graph of Fig. 2 vs.  $0.036 \pm 0.032 \text{ stage h}^{-1}$  at  $15^\circ\text{C}$  in the latter) were similar, while egg hatching times (7.6 days at  $15^\circ\text{C}$ , extrapolated from the Bělehrádek equation in the upper graph of Fig. 2 vs.  $3.88 \pm 2.32$  days) were dissimilar. In contrast to neritic egg-sac spawners, the eggs of *P. elongata* are characterized by their large size (0.46 mm diameter vs. 0.05–0.133 mm diameter, cf. Kjørboe & Sabatini 1994) and they are extremely rich in energy and lipids (Ikeda & Hirakawa 1996), both of which enable the large size of the first feeding stage of *P. elongata*. This kind of reproductive strategy may be particularly advantageous in mesopelagic habitats where food availability is relatively low and the reactive distances of visual predators are greatly reduced because of darkness (cf. Childress & Price 1983).

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