

Effects of temperature on life history traits of *Eodiaptomus japonicus* (Copepoda: Calanoida) from Lake Biwa (Japan)

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Abstract Effects of temperature on life history traits of the dominant calanoid *Eodiaptomus japonicus* were examined to evaluate its population dynamics in Lake Biwa (Japan). Embryonic and post-embryonic development times and reproduction were determined in the laboratory at four temperatures (10, 15, 20 and 25 °C) and under ad libitum food condition. Post-embryonic development time of *E. japonicus* from hatching to adult female decreased with increasing temperature from 67.9 to 15.1 days. Males reached the adult stage 1–6 days earlier than the females. Only 15 % of the individuals survived until the adult stage at 10 °C, while 40 % did so at >15 °C. Egg production also depended on temperature. A power function of temperature on instantaneous growth rate predicted a value of $<0.06 \text{ day}^{-1}$ when water temperature was below 10 °C, suggesting that *E. japonicus* retards its growth during winter. The null value obtained at 8.6 °C for the computed population growth rate supports the idea of an overwintering strategy. Responses of life history traits to temperature suggested that in conditions where there was no food limitation, *E. japonicus* in Lake Biwa would be able to take advantage of the rise of temperature predicted in the context of global climate change.

Keywords Life history traits · Temperature effects · *Eodiaptomus japonicus* · Copepod dynamics · Individual variability

Introduction

Copepods are important components of zooplankton populations and play a critical role in the dynamics of freshwater ecosystems, serving as links between phytoplankton and higher trophic levels in food webs. Understanding the processes that control copepod abundance and production is a major objective in lake ecosystem research (Jiménez-Melero et al. 2005). Growth and productivity are mainly governed by temperature (Bonnet et al. 2009; Halsband-Lenk et al. 2002) and food concentration (Klein Breteler et al. 1995; Ban 1994). Both these factors may affect the life history traits of copepods, consequently affecting community dynamics in aquatic ecosystems.

Lake Biwa is the largest and oldest lake in Japan. Because of its economic importance, it has been subjected to many human activities, with strong impacts on its environment, including eutrophication from the early 1960s to mid 1980s and increasing temperature after 1990 (Hsieh et al. 2010; Kawabata 1987; Yoshida et al. 2001). Despite those variations in the environment, the calanoid copepod *Eodiaptomus japonicus* has dominated the zooplankton for over 50 years (Hsieh et al. 2011). This egg-carrying copepod is an endemic species widely distributed in freshwater bodies in Japan. It has also been shown to dominate zooplankton communities in Lake Ikeda (Japan) (Baloch et al. 1998). In Lake Biwa, maximum abundances have been observed in June, when water temperature ranged between 13 and 18 °C, with densities reaching $19,000 \text{ ind. m}^{-3}$ during the last four decades (G. Dur, unpublished data). Because of its high abundance and

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importance as a food resource for fish (Kawabata et al. 2002), *E. japonicus* plays a key role in the food web of Lake Biwa. However, studies on *E. japonicus* population dynamics are scarce compared to those on counterpart species in European lakes: e.g., *Eudiaptomus gracilis*, *Eudiaptomus graciloides* (Herzig 1983; Jiménez-Melero et al. 2005; Munro 1974). To obtain an idea of how zooplankton populations in Lake Biwa may respond to increasing water temperatures resulting from global warming, it is crucial to study the population dynamics of this most important component in the lake.

Development time, survival, and reproduction are basic life history traits of a copepod, and knowledge of these traits is essential for understanding population dynamics (Jiménez-Melero et al. 2005). Development times (i.e., embryonic and post-embryonic) and survival are known to be strongly affected by temperature (Herzig 1983; Jiménez-Melero et al. 2005, 2007, 2012; Devreker et al. 2007; Bonnet et al. 2009; Chinnery and Williams 2004; Cook et al. 2007). Many studies have also shown that temperature controls copepod egg production (Ban 1994; Halsband-Lenk et al. 2002; Lee et al. 2003; Beyrend-Dur et al. 2009, 2011; Bonnet et al. 2009; Devreker et al. 2009; Jiménez-Melero et al. 2012). Under sufficient food supply, temperature is the main parameter that controls seasonal copepod population dynamics (Halsband-Lenk et al. 2004; Uye 2000). Decrease in development time with increasing temperature has been recognized as a general rule for many organisms (Gillooly 2000; Gillooly et al. 2001), including calanoid copepods (Ban 1994; Beyrend-Dur et al. 2011; Devreker et al. 2004, 2007). Earlier investigation of the development time of *E. japonicus* in situ in Lake Biwa revealed the importance of food limitation (Kawabata 1989a). Whereas Kawabata (1989a) observed the development of selected developmental stages under natural conditions, here we studied the effect of temperature under controlled environments on all life stages: development, growth, survival, and reproduction. We subsequently computed individual and population growth rates to evaluate adaptation to temperature. The experimental protocol used was based on individual observations, allowing for quantification of individual variability and fitting of moulting rate distributions (Beyrend-Dur et al. 2011; Devreker et al. 2004, 2007; Jiménez-Melero et al. 2005; Souissi and Ban 2001). Individual observations can further be used for calibration of individual-based models (Dur et al. 2009).

Methods

Field collection and stock cultures

E. japonicus females with egg-sacs were sorted from zooplankton samples collected with vertical plankton net

hauls (ring diameter, 45 cm; mesh size, 200 μm) from 30 m to the surface at a sampling site situated in the north basin of Lake Biwa (35°19'27"N, 136°11'44"E) on 12 September 2011 and 17 August 2012. Copepods were then cultivated in four 1-L jars filled with autoclaved filtered (Whatman GF/F; porosity, 0.47 μm) tap water as stock cultures. The cultures were maintained at 15 °C under a photoperiod of 12L:12D with a light intensity of 15.4 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Such conditions were found to be optimal for development. Copepods were fed with $\sim 10^5$ cells ml^{-1} of a 1:1 fresh algal mixture of *Chlamydomonas reinhardtii* (IAM, C-9) and *Cryptomonas tetrapyrenoidosa* (NIES, 282). Fresh food suspensions were provided every 2 days. Algal cultures were grown in 1-L flask under a photoperiod of 12L:12D with a light intensity of 125 $\mu\text{mol m}^{-2} \text{s}^{-1}$. For the experiments, we used individuals cultivated in the laboratory for at least two or three generations to avoid biases due to inherent wild population variability (Laabir et al. 1995).

Experimental conditions

In Lake Biwa, the temperature range encountered by *E. japonicus* populations varies between 5 and 25 °C [Shiga Prefectural Fisheries Experiment Station (SPFES), unpublished data]. Consequently, we used four representative temperatures: i.e., 10, 15, 20, and 25 °C. For the experiments, individuals were acclimatized at each of these temperatures, initially in sterilized filtered tap water, and then fed in excess (5×10^4 cells ml^{-1}) with the same algal mixture used for the stock cultures. Food was provided once a day. Water was changed every 2 days at 10 and 15 °C and once a day at 20 and 25 °C. Frequency of water renewal was adapted to limit bacterial growth and keep water clean from waste matter produced by the copepods themselves. All experiments were conducted under the same light conditions as those of the stock cultures.

Post-embryonic development time experiment

For each experimental condition, we sorted 36–86 newly hatched nauplii (within 12 h) from more than six females acclimatized at each temperature and placed them individually in a 10-mL well of a culture plate at the same temperature as those of the mother. Subsequently, development was followed from first naupliar (N1) to adult stage. Each individual was observed under a dissecting microscope (Olympus, SZX12) twice a day at 10 and 15 °C, and four times a day at 20 and 25 °C, to check for exuviae or dead animals. Time zero was defined as the time when the N1 stage hatched from the egg. Stage duration represents the inter-moult duration calculated from the age of moulting from the developmental stage i to $i + 1$ for each individual.

Reproduction experiments

In experiments to determine reproductive traits, we followed the same protocol used by Beyrend-Dur et al. (2011). At each of the four temperatures, more than 500 N1s isolated from the stock cultures were reared in 1-L jars with the same food supply and under the same photoperiod and light intensity as those of the stock culture. When individuals reached the fifth copepodid (C5) stage, a female and male pair was transferred to a 30-mL vial filled with the same food suspension as that of the post-embryonic development experiments. Reproductive parameters were recorded daily until the death of the females. Duration from moulting to adult female until death was expressed as female longevity. Dead males were removed and replaced by a male from the stock culture acclimatized at the same temperature. The culture medium and algal food were exchanged in the same manner as in the experiments on post-embryonic development time.

We determined the following reproductive parameters: clutch size (CS, eggs per clutch); hatching success (HS, percentages of number of nauplii hatched to number of eggs in a clutch); embryonic development time (EDT, time taken from egg laying to hatching of the nauplius); inter-clutch duration (ICD, time between spawning of clutch “ x ” and spawning of clutch “ $x + 1$ ”); latency time (LT, time between hatching or fall of clutch “ x ” and spawning of clutch “ $x + 1$ ”); and egg production rate (EPR, number of eggs produced by a female per day) calculated from clutch size/ICD in each clutch. A few clutches including unfertilized eggs, i.e., presenting no delimitation of the egg membranes ($\ll 3.9$ % of total clutches produced), were not taken into account for the estimation of hatching success.

Measuring body size

The prosome length was measured with an eyepiece micrometer under a dissecting microscope as body size of the exuviae during development from first copepodid (C1) to pre-adult C5 stages. Using exuviae is a very convenient method to distinguish individual stages and to measure the body size of these live small animals (Twombly and Burns 1996; Lee et al. 2003). The adult prosome lengths were determined after death on individuals preserved in neutral 5 % formalin.

Data and statistical analysis

Relationship between development time and temperature

The relationship between development time (DT , days) and temperature (T , °C) was described by the most frequently used equation in the literature, Bělehrádek’s function:

$$DT = \lambda(T - a)^b \quad (1)$$

where λ , a and b are fitted constants. The values of λ and a were estimated with a non-linear analysis using least squares as a loss function in the curve fitting tool box of MATLAB 7.8 software (The MathWorks Inc 2009). According to McLaren et al. (1969) b was fixed at -2.05 .

Individual variability and moulting probabilities

To predict the moulting probability from one developmental stage group to the next, the cumulative proportion of individuals moulting from one stage group to the next was plotted against individual development time. We constructed four additional groups of post-embryonic developmental stages for the copepod, as suggested by Souissi and Ban (2001): early (N1–N3) and late (N4–N6) naupliar stages, and early (C1–C3) and late (C4–C5) copepodid stages to avoid the irregular distribution of developmental stages. We fitted a gamma density function (GDF) (Souissi and Ban 2001) to the data, using the *gamcdf* [x/α , β] function included in the curve fitting toolbox of MATLAB 7.8 software (The MathWorks Inc 2009) to obtain estimates of the maximum likelihood and confidence bounds of the GDF parameters: i.e., α the shape parameter and β the scale parameter.

Somatic growth

The effect of temperature on somatic growth was determined from the C1 to adult stages. The body dry weight (W , μg) was calculated from the prosome length (PL , mm) using the following exponential equation (Kawabata and Urabe 1998):

$$W = e^{(2.59 \ln PL + 2.6995)}$$

Body dry weight was then used to estimate the growth rate of *E. japonicus* at each experimental temperature. The log-transformed body weight was plotted against cumulative development time. Then the natural log-transformed growth rate was fitted to a linear function of temperature. The slope is the instantaneous growth rate (g , day^{-1}) at each temperature.

Life table analysis of population growth

The population growth rate (r , day^{-1}) was derived from Euler–Lotka’s equation and calculated iteratively:

$$\sum_{x=i_a}^{\omega} l_x m_x e^{-rx} = 1$$

where i_a is the age at maturity, l_x is the proportion of individuals surviving at day x , m_x is the number of

offspring produced by a female at day x , and ω is female longevity.

Individual variability of fecundity

Individual fecundity variability (cumulative number of eggs produced by a female in its lifetime) was estimated with the coefficient of variation (CV) at each temperature tested. CV was calculated as follows:

$$CV = \sigma/\mu \times 100$$

where μ is the mean value of the parameter and σ is standard deviation.

Comparison between temperature treatments

Differences between four temperature conditions in growth and reproductive parameters were tested using the non-parametric Kruskal–Wallis test for independent data with the significance level set at $p < 0.05$. When the test resulted in a significant difference, the post hoc Tukey–Kramer test was conducted. All statistical analyses were performed with MATLAB 7.8 software (The MathWorks Inc 2009).

To test the differences of stage duration between temperatures, generalized linear models (GLM) are commonly used

(Jiménez-Melero et al. 2007). Here, a log-linear model was employed for testing the main effects and different interactions among temperature, stage and survival. This log-linear model included three main effects (stage, temperature and survival), three two-variable interactions (stage \times temperature, stage \times survival, and temperature \times survival), and three-variable interactions (stage \times temperature \times survival). The variable ‘stage’ had 11 categories (N1–C5), the variable ‘temperature’ had four categories (10, 15, 20 and 25 °C), and the variable ‘survival’ had two categories (alive and dead). The saturated (full) model included all main effects, all two-way interactions, and the three-way interactions. The fit of each model was based on observed data and fitted cell frequencies. SPSS software (IBM Inc 2011) was used for log-linear model analysis.

Results

Post-embryonic development time (post-EDT)

E. japonicus

Results for the effect of temperature on post-EDTs in *E. japonicus* are summarized in Table 1. Among all developmental stages, the first naupliar (N1) stage and the fifth copepodid (C5) stage always showed the shortest and

Table 1 Mean stage durations (D , days), standard deviations (SD), and stage specific survival rates (%) of *Eodiaptomus japonicus* from Lake Biwa reared at 10, 15, 20 and 25 °C. Sex ratio (females to males) and the survival rate of the adult stage are also indicated

Stage and sex	10 °C				15 °C				20 °C				25 °C			
	D	SD	%	n	D	SD	%	n	D	SD	%	n	D	SD	%	n
No. of eggs				86				36				36				36
N1	2.21	0.68	100	86	1.36	0.54	100	36	0.54	0.20	97	35	0.50	0.13	94	34
N2	4.40	1.39	81	70	2.16	0.72	81	29	1.66	0.38	69	24	1.11	0.31	85	29
N3	4.50	1.34	80	56	2.45	0.69	76	22	1.65	0.38	83	20	1.07	0.40	86	25
N4	5.19	2.35	91	51	2.01	0.66	95	21	1.60	0.64	75	15	1.12	0.41	84	21
N5	6.00	2.55	76	39	2.52	1.00	90	19	1.56	0.26	100	15	1.24	0.39	90	19
N6	6.57	1.65	74	29	2.44	0.49	95	18	1.91	0.37	87	13	1.24	0.31	79	15
C1	6.80	2.08	83	24	3.60	1.58	94	17	2.03	0.49	100	13	1.46	0.24	100	15
C2	7.58	1.26	75	18	4.36	1.34	94	16	2.48	0.66	100	13	1.63	0.25	100	15
C3	7.26	1.74	89	16	3.25	0.80	100	16	2.56	1.13	100	13	1.49	0.57	100	15
C4	7.50	0.85	100	15	3.68	0.66	100	16	2.96	1.03	100	13	1.63	0.43	100	15
C5 M	8.73	1.94	88	7	4.74	1.04	91	10	3.42	0.46	100	6	2.14	0.22	100	6
C5 F	10.50	4.14	86	6	4.80	0.96	80	4	3.62	0.63	100	7	2.38	0.68	100	9
N1-adult M	61.98	5.55		7	30.95	3.13		10	20.55	2.88		6	14.08	0.92		6
N1-adult F	67.88	7.36		6	33.06	3.80		4	23.79	3.08		7	15.09	2.83		9
Sex ratio	0.86				0.40				1.17				1.50			
Survival (adult)	15 %				39 %				36 %				42 %			

N1–N6 naupliar stages, C1–C5 copepodid stages, M male, F female, n number of individuals in the stage, N1-adult the post-embryonic development time from hatching to adulthood

longest durations, respectively. The mean stage duration of C5 females was longer than that of males for all four temperatures tested, though the differences were not significant (Kruskal–Wallis test, $p > 0.05$). Mean post-EDT from N1 to adult took 62–68 days at 10 °C, while it did not exceed 33 days at the higher temperatures tested. On average, males reached adulthood 6 days earlier than females at 10 °C, and 1–2 days earlier at higher temperatures, but the differences were not significant (Kruskal–Wallis test, $p > 0.05$). Male and female data were then combined to test the effect of temperature on post-EDT. Post-EDTs were significantly different among the temperatures tested (Kruskal–Wallis test, $p < 0.05$). The sex ratios, i.e., female to male ratios at adult stage, were <0.9 at lower temperatures (10 and 15 °C) and >1.1 at 20 and 25 °C.

At 20 and 25 °C, none of the individuals died during copepodid stages. Only 15 % of individuals survived until the adult stage at 10 °C, while around 40 % survived at higher temperatures. Our log-linear model (Table 2) showed that stage and temperature affected the frequency of dead and live individuals. The best model (number 8, Table 2) also included the interaction stage \times temperature. Such effect should not be considered since temperature is fixed by the researcher and does not determine the stage. This is nevertheless a common error for log-linear models associated with the fact that such models do not distinguish between response and predictor variables (as in Jimenez-Melero et al. 2007). Specific survival rates were lower for naupliar stages compared to copepodid stages (Kruskal–Wallis test, $p < 0.05$).

The relationship between temperature (T , °C) and median post-EDT (DT , days) exponentially decreased with increasing temperature from 10 to 25 °C (Fig. 1) and was well described by the Bělehrádek temperature functions:

$$DT = 12810(T + 3.064)^{-2.05} (n = 4, R^2 = 0.993, p < 0.05)$$

for females, and

$$DT = 12240(T + 3.336)^{-2.05} (n = 4, R^2 = 0.998, p < 0.05)$$

for males.

Bělehrádek’s functions fit the duration data well for each stage, with good coefficients of determination (Table 3).

Individual variability and moulting probabilities fitted by GDF

Variability of post-EDT at certain stage groups can be evaluated by the distribution of moulting rates from one stage group to the next. The fitted GDF showed the distribution of moulting rates depended on temperature and the individual variability of development time was highest at 10 °C (Fig. 2).

The values of the parameters of cumulative GDF $gamcdf [x/\alpha, \beta]$ are given in Table 4. The cumulative proportion for each group of individuals against development time was strongly fitted ($R^2 > 0.9$) to the gamma function at all experimental temperatures.

Somatic growth

The prosome length of adult *E. japonicus* decreased with increasing temperature (Fig. 3). Females were always larger than males at each temperature (Kruskal–Wallis test, $p < 0.05$). The mean adult prosome length was 0.868, 0.839, 0.817 and 0.816 mm for males, and 0.947, 0.922, 0.924 and 0.904 mm for females at 10, 15, 20 and 25 °C, respectively. The relationship between the mean prosome length of adults (PL , mm) and temperature (T , °C) was expressed as:

Table 2 Results of the log linear model for a three-way table: effect of temperature and stage on frequency of dead and live individuals of *Eodiaptomus japonicus*

Model		Goodness of fit tests		
		G^2	df	P value
1	Stage + temp + survival	155.470	73	<0.001
2	Stage \times temp	119.558	43	<0.001
3	Stage \times survival	101.820	63	<0.001
4	Temp \times survival	150.078	70	<0.001
5	Stage \times temp + stage \times survival	65.908	33	<0.001
6	Stage \times temp + temp \times survival	114.166	40	<0.001
7	Stage \times survival + temp \times survival	96.428	60	<0.002
8	Stage \times temp + stage \times survival + temp \times survival	60.428	30	<0.001
9	Saturated (full) model	0	0	

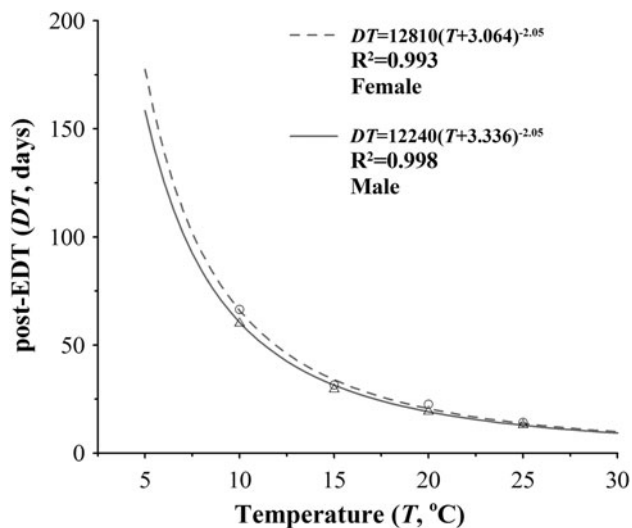


Fig. 1 Relationship between temperature and median post-embryonic development time (post-EDT, days) of *Eodiaptomus japonicus* males (open triangles, solid line) and females (open circles, dotted line) reared at four temperature conditions

Table 3 Parameters for Bělehrádek's temperature function of stage duration (days) in *Eodiaptomus japonicus*

Stage and sex	λ	a	R^2
Egg	1249	-2.004	0.999
N1	328.9	-1.427	0.980
N2	898.4	-3.758	0.979
N3	1073	-4.699	0.994
N4	715.5	-1.873	0.989
N5	676.2	-0.551	0.987
N6	620.8	0.600	0.975
C1	1029	-1.807	0.998
C2	1582	-3.773	0.999
C3	978.1	-1.104	0.993
C4	1414	-2.896	0.992
C5 M	2664	-7.096	0.989
C5 F	2144	-4.651	0.987

λ and a are constants of the function described in Eq. (1) in the text. M and F are male and female, respectively

$$PL = 1.077T^{-0.0547} (n = 4, R^2 = 0.854, p < 0.05)$$

for females, and

$$PL = 1.044T^{-0.0798} (n = 4, R^2 = 0.946, p < 0.05)$$

for males.

We calculated the instantaneous growth rate for *E. japonicus* at each of the four temperatures tested. The natural log-transformed body weight of copepodites linearly increased against the cumulative development

time at all tested temperatures (Fig. 4). The instantaneous growth rate (g , day⁻¹), i.e., the steepness of the slope, exponentially increased with increasing temperature (T , °C), being 0.06, 0.12, 0.18 and 0.29 day⁻¹ at 10, 15, 20 and 25 °C, respectively (Fig. 4). The temperature function was expressed as:

$$g = 0.0268e^{0.095T} (n = 4, R^2 = 0.994, p < 0.05).$$

Reproduction

Reproductive parameters of *E. japonicus* were significantly affected by temperature, with the exception of hatching success, which was high at all tested temperatures (i.e., 98–100 %, Table 5). CS exhibited the lowest and highest values at 10 and 15 °C, respectively. CS between 20 and 25 °C did not vary significantly (post hoc Tukey–Kramer test, $df = 3$, $p > 0.05$). EPR increased with increasing temperature, increasing 4.4-fold from 10 to 25 °C. Inversely, EDT, ICD, and LT decreased with increasing temperature; EDT, ICD and LT decreased from 10 to 25 °C by 4.7-fold, 3.3-fold and 5.8-fold, respectively. Mean adult longevity at 15 °C was the longest, being 69 days, with the next being 45 days at 20 °C (Table 5). A similar value of around 30 days was observed at 10 and 25 °C.

Cumulative egg production increased with increasing temperature (Fig. 5). At the end of life, the total number of eggs produced by a female ranged from 20 to 190, 60 to 210 and 20 to 230 eggs female⁻¹ at 15, 20 and 25 °C, respectively. At 10 °C few females were able to produce more than two clutches during their lifetime. The maximum number of clutches produced was observed at 25 °C, with 17 clutches produced through the reproductive life of a female. Individual variability of cumulative egg production was high and CV values were over 40 % at all temperatures.

Female PL and CS were not significantly correlated ($n = 260$, $R^2 = 0.028$, $p = 0.76$, Fig. 6). The largest CS of 28 eggs clutch⁻¹ was observed for a female whose PL was 1.0 mm at 15 °C. Despite large body sizes at 10 °C, the females produced small clutches—11–16 eggs clutch⁻¹.

Potential population growth

The population growth rate (r , day⁻¹) of *E. japonicus* calculated from the laboratory experiments increased linearly with increasing temperature (Fig. 7). The linear regression equation was expressed as:

$$r = 0.0112T - 0.096 (n = 4, R^2 = 0.956, p < 0.05).$$

This equation predicted that this copepod may cease population growth below 8.6 °C.

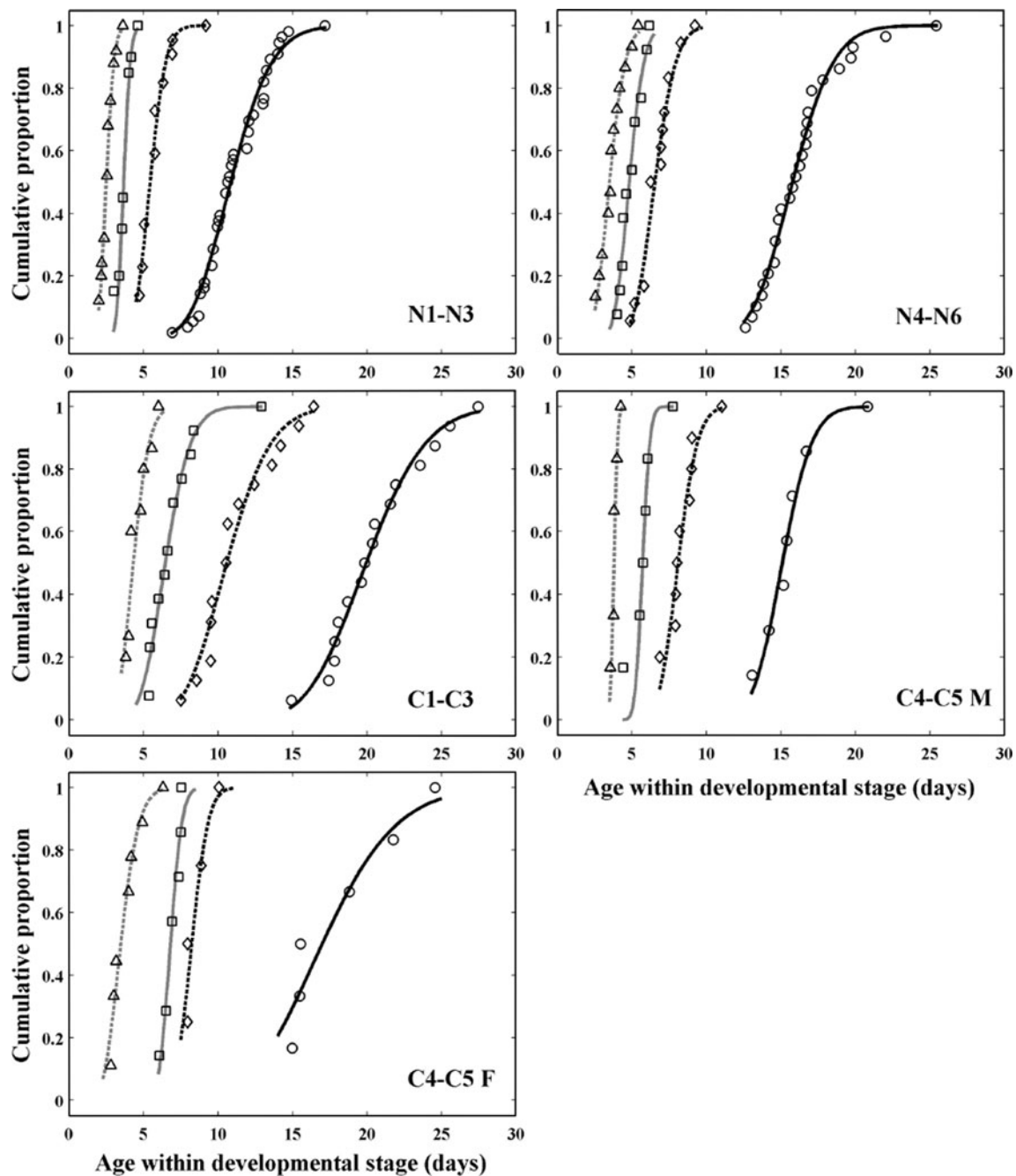


Fig. 2 Cumulative proportion of *Eodiaptomus japonicus* individuals moulting from one group of stages to the next as a function of age within developmental stages. Dots represent observed data at 10 °C (circles), 15 °C (diamonds), 20 °C (squares), and 25 °C (triangles). Naupliar stages were aggregated into two groups (N1–N3 and N4–

N6) as were copepodid stages (C1–C3 and C4–C5) while male (M) and females (F) were shown separately. The lines represent the expected data from the gamma density functions at 10 °C (solid black), 15 °C (dotted black), 20 °C (solid grey), and 25 °C (dotted grey)

Discussion

In the present study, embryonic and post-EDT of *Eodiaptomus japonicus* strongly depended on temperature, a common feature evident in other copepods (e.g., Landry 1983; Ban 1994; Devreker et al. 2007). Additionally, post-EDT was isochronous, except for the shortest N1 and the

longest female C5 stages, under sufficient food supply at all temperatures tested. This pattern of development was also identical to that observed in the same species by Kawabata (1989a) in the field and that observed in other calanoid copepod species, e.g., *Acartia clausi* (Landry 1983), *Eurytemora affinis* (Ban 1994; Devreker et al. 2007), *Calanus helgolandicus* (Bonnet et al. 2009), and *Pseudocalanus*

Table 4 Parameters (α , β and R^2) with confidence bounds at 95 % of the gamma density function ($gamcdf [x/\alpha, \beta]$) fit to the median development time for four groups of stages of *Eodiaptomus japonicus* at 10, 15, 20 and 25 °C

T (°C)	Stage group	GDF parameter (confidence bounds)		R ²
		α	β	
10	N1–N3	25.83 (21.79, 29.86)	0.426 (0.3587, 0.4933)	0.984
10	N4–N6	53 (44.04, 61.97)	0.2999 (0.2488, 0.351)	0.987
10	C1–C3	40.28 (30.48, 50.09)	0.4995 (0.3765, 0.6225)	0.984
10	C4–C5 M	90.89 (30.21, 151.6)	0.1668 (0.05548, 0.2781)	0.975
10	C4–C5 F	19.53 (–6.141, 45.21)	0.8852 (–0.3089, 2.079)	0.913
15	N1–N3	43.74 (24.6, 62.87)	0.1256 (0.07025, 0.1809)	0.980
15	N4–N6	35.62 (18.82, 52.43)	0.1858 (0.09867, 0.273)	0.972
15	C1–C3	21.49 (11.53, 31.45)	0.5007 (0.2636, 0.7377)	0.963
15	C4–C5M	62.67 (11.62, 113.7)	0.1302 (0.02441, 0.2361)	0.927
15	C4–C5 F	90.75 (–229.6, 411.1)	0.09117 (–0.2327, 0.415)	0.902
20	N1–N3	102.5 (25.26, 179.7)	0.03597 (0.00871, 0.06323)	0.973
20	N4–N6	38.91 (21.02, 56.79)	0.1253 (0.0668, 0.1838)	0.968
20	C1–C3	23.94 (14.91, 32.97)	0.2739 (0.1689, 0.3789)	0.975
20	C4–C5 M	208.4 (–100.1, 516.9)	0.02754 (–0.01309, 0.06816)	0.940
20	C4–C5 F	123.8 (9.036, 238.6)	0.05517 (0.004315, 0.106)	0.950
25	N1–N3	37.86 (26.35, 49.38)	0.06677 (0.0463, 0.08725)	0.988
25	N4–N6	18.63 (13.47, 23.79)	0.1917 (0.1382, 0.2451)	0.985
25	C1–C3	27.36 (–1.942, 56.67)	0.16 (–0.01266, 0.3326)	0.909
25	C4–C5 M	374.7 (–397.4, 1147)	0.01018 (–0.01078, 0.03113)	0.920
25	C4–C5 F	14.42 (3.909, 24.93)	0.2472 (0.06234, 0.4321)	0.960

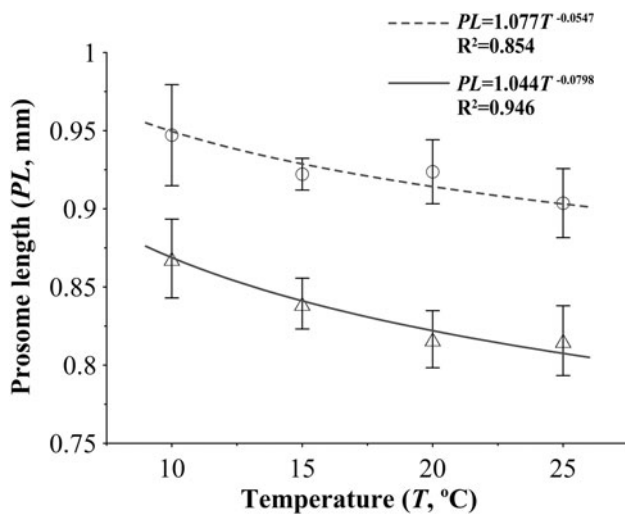


Fig. 3 Mean prosome length of adult males (*open triangles and solid line*) and females (*open circles and dotted line*) of *Eodiaptomus japonicus* reared at four temperature conditions under food satiation. Vertical bars indicate standard deviations. Regression equations and coefficients of determination are indicated

newmani (Lee et al. 2003), reared in the laboratory. The N1 stage of calanoid copepods is a non-feeding stage living on yolk (Mauchline 1998) and thus a rapid moult to the next feeding-stage, N2, is needed. The pre-adult C5 stage is usually longer than other developmental stages because

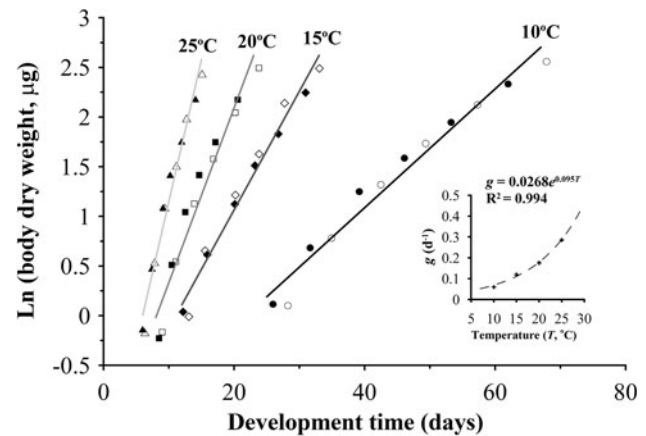


Fig. 4 Growth rates of male (*solid symbols*) and female (*open symbols*) copepodids of *Eodiaptomus japonicus* reared at four temperatures under food satiation. The regression lines were expressed as: $\ln W = 0.05982DT - 1.305$ ($R^2 = 0.969$) at 10 °C, $\ln W = 0.1195DT - 1.324$ ($R^2 = 0.977$) at 15 °C, $\ln W = 0.1758DT - 1.424$ ($R^2 = 0.947$) at 20 °C, and $\ln W = 0.286DT - 1.711$ ($R^2 = 0.971$) at 25 °C, with W the dry weight, and DT the cumulative development time of the copepod. The inset presents the relationship between instantaneous growth rates (g , day^{-1}) and tested temperatures (T , °C) with an exponential regression (*dotted line*). See details in the text

individuals need time to mature their reproductive organs (Ban 1994; Devreker et al. 2007).

It has been shown that physiological responses of copepods to temperature vary among species or local

Table 5 Mean values and standard deviations (SD) of reproductive parameters of *Eodiaptomus japonicus* from Lake Biwa reared at 10, 15, 20 and 25 °C

Parameters	10 °C			15 °C			20 °C			25 °C			P
	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n	
No. of pairs			20			10			14			15	
HS (%)	98.01			97.50			99.62			97.51			
CS	11.62	2.66	14	16.84	4.64	57	14.54 ^a	3.71	90	14.98 ^a	3.52	99	<0.05
EPR	1.31 ^a	0.32	3	3.20 ^a	1.70	8	4.09 ^{a,b}	0.95	10	5.75 ^b	1.89	13	<0.05
EDT	7.77 ^a	0.80	14	3.87 ^a	0.54	57	2.24	0.36	90	1.65	0.45	99	<0.05
ICD	9.38 ^a	1.61	6	5.91 ^a	2.50	48	3.51	1.18	80	2.85	1.81	84	<0.05
LT	8.05	6.28	14	2.52 ^a	2.43	57	1.74 ^{a,b}	2.58	90	1.39 ^b	1.64	99	<0.05
Longevity	37.53 ^{a,b}	12.33	8	68.83 ^a	21.43	9	44.97 ^{a,b}	8.79	10	30.48 ^b	18.85	15	<0.05

Values in the lines with the same superscript are not significantly different as determined with the Kruskal–Wallis and Tukey–Kramer post hoc tests; $p > 0.05$

HS hatching success (%), CS clutch size (eggs clutch⁻¹), EPR egg production rate (eggs female⁻¹ day⁻¹), EDT embryonic development time (days), ICD inter-clutch duration (days), LT latency time (days), Longevity longevity of females (days)

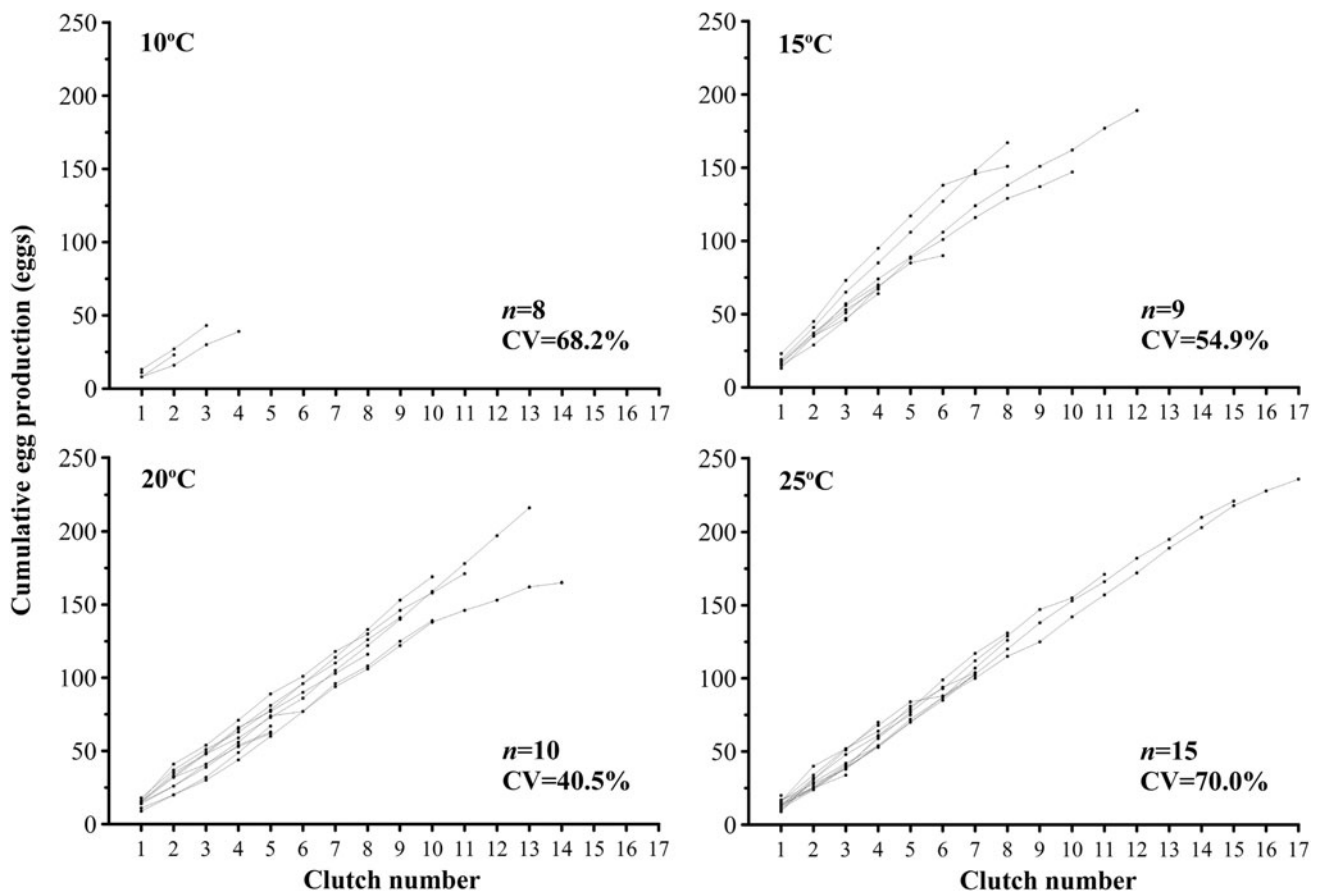


Fig. 5 Cumulative egg production for each *Eodiaptomus japonicus* female as a function of clutch number at each of the four temperatures tested. Each point represents a clutch of an individual female. n is the

number of reproductive females observed. CV is the coefficient of variation for cumulative number of eggs produced by a female during her entire lifetime (see details in the text)

populations of the same species living along different latitudes (McLaren et al. 1969; Landry 1975; Herzig 1983). In marine copepods, EDT of cold-adapted species is shorter

than that of warm-adapted ones, especially at low temperatures (McLaren et al. 1969; Landry 1975). From data obtained on several marine copepods, McLaren et al.

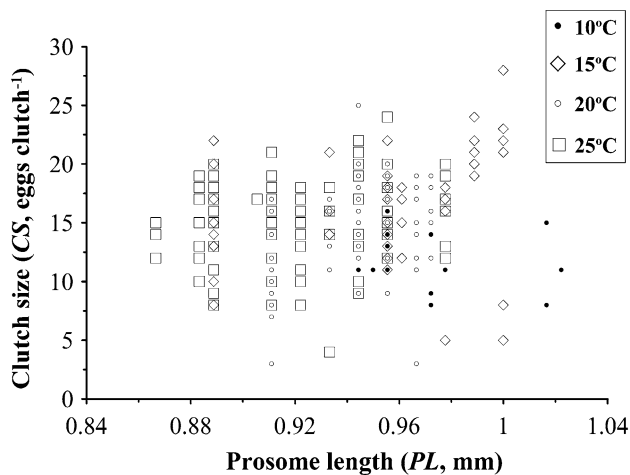


Fig. 6 Relationship between clutch size (CS, eggs clutch⁻¹) and prosome length (PL, mm) of *Eodiaptomus japonicus* females at four temperature conditions

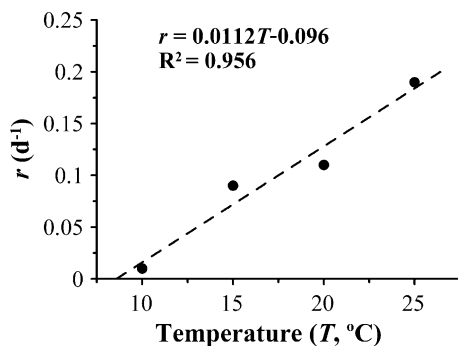


Fig. 7 Population growth rate (r , day⁻¹) of *Eodiaptomus japonicus* reared at four temperature conditions. The linear fit and its coefficient of determination are provided

(1969) found that biological zero indicated as a of Bělehrádek's temperature function for EDT was strongly related to the average temperature of their habitat. For *E. japonicus*, biological zero for EDT was -2.4 °C. Based on Fig. 3 of McLaren et al. (1969), an average habitat temperature of ca. 17 °C can be predicted, which is similar to the average temperature above 20 m in Lake Biwa during the growing season for *E. japonicus* from May to October (i.e., 18 °C, SPFES unpublished data). For freshwater copepods, Herzig (1983) showed that temperature-EDT curves for warm-water species could be separated from that for cold-water species. The temperature-EDT curve obtained in the present study of *E. japonicus* lies at the lower edge for warm-water copepods (Fig. 8).

In many previous studies, EPR increased with temperature up to a maximum level, but decreased or even ceased beyond the maximum (Dur et al. 2009; Holste and Peck 2005; Ianora 1998; Jiménez-Melero et al. 2012; Rodríguez et al. 1995; Uye 1981). Such maximum temperature levels

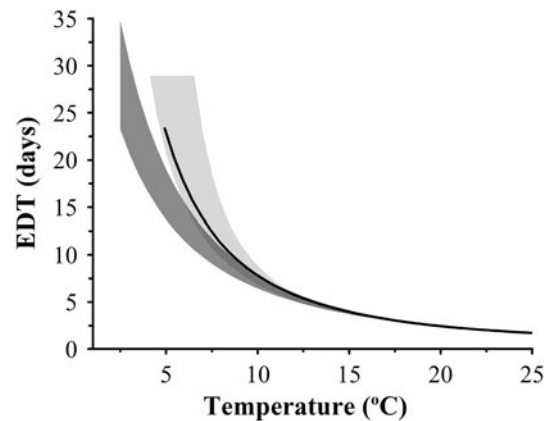


Fig. 8 Relationship between embryonic development time (EDT, days) and temperature for freshwater copepods. The black line represents the fitted function on the median EDT of *Eodiaptomus japonicus* obtained in the present study. Dark and light regions represent ranges of EDT against temperature for cold- and warm-water adapted species, respectively (Herzig 1983)

differ between species (Holste and Peck 2005) and depend on factors other than temperature, including female age (e.g., Parrish and Wilson 1978), food concentration and quality (e.g., Kiørboe et al. 1985; Broglio et al. 2003), and the difference between in situ and experimental temperatures (Kim 1995). The difference in egg production temperature optima is not only species-specific, but also population-specific (Holste and Peck 2005), and is likely due to adaptation to local conditions. In *E. japonicus*, EPR increased with temperature to the highest temperature tested, i.e., 25 °C. This may suggest that the threshold temperature for inhibiting EPR is over 25 °C and supports the idea that this copepod is warm-water adapted.

On the other hand, the fact that the smallest CS observed in this study was produced by larger females at 10 °C may be explained as a low-temperature stress. In general, CS is positively correlated with female body size in many temperate copepod species (cf., Ban 1994; Hirche 1992; Uye et al. 1983). However, no significant relationship between CS and body size was found in the present study. The largest individual variability of the post-EDT at 10 °C also supported this idea. Such individual development variability has been found to increase when the environment is non-optimal (Carlotti and Nival 1991).

Although high hatching success was obtained at all the temperatures tested, i.e., >98 %, survival to adulthood varied among the temperatures and showed the lowest value at 10 °C. Reproductive activity was also very low at 10 °C; only 40 % of pairs tested could reproduce successfully, while 70 % could at higher temperatures, and 63 % of them produced only a single clutch during their life. Finally, the temperature function of population growth rate (r) predicted that population growth of this copepod may cease below 8.6 °C. Somatic growth was also

predicted from the equation obtained in this study to be quite low at 10 °C. These results confirmed that 10 °C is not optimal for *E. japonicus* and suggests delayed growth and development during winter at ca. 8 °C.

The limited spatial distribution of *E. japonicus* in the epilimnion of Lake Biwa has been associated with poor food conditions (Okamoto 1984; Kawabata 1987). Nevertheless copepods, as ectotherms, exhibit a strong relation between water temperature and biogeographic range (Beaugrand et al. 2002, 2009). Even in more restricted areas such as a lake, adaptation to a specific spatial niche can be associated with temperature preferences (Lampert 1989). For instance, besides the food-limitation hypothesis, the residence of *E. japonicus* populations in the epilimnion can be satisfactorily explained by the temperature responses obtained in this study. *E. japonicus* is restricted to above 20 m throughout the growing season in the lake, where the average temperatures exceed 10 °C (Kawabata 1987). In this study, we found that *E. japonicus* populations could no longer increase at temperatures below 10 °C even with sufficient food supply. There are also strong interactions between these two environmental factors, as shown in *Daphnia* (Windler et al. 2004) that need thorough examination. Finally, organisms with short life cycles, such as copepods, may adapt through rapid evolution to fluctuating environments (Hairston and Dillon 1990). To clarify the spatial distribution of *E. japonicus* in Lake Biwa, further investigation of these aspects is required.

The cessation of growth below 10 °C, suggests that temperature is an important force limiting *E. japonicus* populations in winter. Over a 3-year investigation, Kawabata (1987) found that the abundance of *E. japonicus* was low in winter and increased in late spring or early summer when water temperature started to increase. According to the Bělehrádek's function calibrated on our data, it takes about 3 months for individuals to complete their development at winter temperatures in Lake Biwa. This corresponds to the overwintering period observed in the field (Kawabata 1987).

The long overwintering period may incur high risks for *E. japonicus* from fish and invertebrate predators. Few ovigerous females and mainly naupliar stages have been shown to occur in winter (Kawabata 1987). This can be associated with the fact that ovigerous females suffer high predation from visually oriented predators during winter because they are more easily perceived (Hairston 1987; Mahjoub et al. 2011). Nevertheless, there is no proof of predation risk during winter in Lake Biwa, the predatory stages of *Mesocyclops dissimilis* being infrequent in winter (Kawabata 1989b, 2006). The fact that *E. japonicus* overwintered in naupliar stages (Kawabata 1987) can be associated with growth cessation at low temperature suggested by our results.

The best estimate of different climate scenarios predicts that global average surface temperature will increase between 1.1 and 6.4 °C, with an average rise of 2.8 °C at the end of the 21st century (IPCC 2007). Our study showed that the population growth rate of *E. japonicus* was a positive linear function of temperature. In 2010, monthly average water temperature varied from 7.8 to 22.3 °C (SPFES, unpublished data), giving a population growth rate ranging between -0.009 and 0.15 day^{-1} from the function. The predicted increase in temperature of 2.8 °C will give water temperatures varying between 10.6 and 25.1 °C at the end of this century in Lake Biwa, resulting in a population growth rate ranging between 0.02 and 0.19 day^{-1} . Global warming may improve the environment for *E. japonicus*, which will be able to grow during winter. Additionally, we observed that the sex ratio is in favour of females at temperatures over 20 °C. IPCC scenarios result in a prediction for an extended period of water temperatures over 20 °C. In line with the present results, we predict that in the lake, under sufficient food supply, the population density of *E. japonicus* will be positively affected by the expected rise of temperature through a decrease of development times and an increase in both the survival rates and the reproduction frequency within a female-biased population. On the other hand, global warming may, in addition to raising water temperature, also change lake environments by altering thermocline depths and nutrient inputs, and by accelerating a decrease in dissolved oxygen (Magnuson et al. 1997). These physical changes in turn affect the primary production of a lake. For instance, an 80-year survey showed that climate change has contributed to diminishing Lake Tanganyika's primary productivity (O'Reilly et al. 2003; Verburg et al. 2003). A decrease in primary production associated with a decrease in food availability would negatively affect the total zooplankton abundance in Lake Biwa, considering its strong correlation with total phytoplankton biomass (Hsieh et al. 2011). Such complex interactions may occur in Lake Biwa and negatively affect the population of *E. japonicus*. Further studies on the effect of food on the life cycle traits, thus, would be a continuation of the present work. The crucial information obtained from such a study would provide the necessary foundation for calibrating a mathematical model to enable testing of several scenarios on the consequences of climate changes on this copepod: for example, the match/mismatch hypothesis (Durant et al. 2007).

In conclusion, the responses of life history traits in *E. japonicus* to temperature observed in this study help us understand the population dynamics observed in the field (Kawabata 1987). According to field observations (Kawabata 1987) and responses to temperature predicted from the experiments in the present study under sufficient food supply, this species may behave like a warm-water adapted

species despite inhabiting a temperate lake, such as Lake Biwa. Present data on life history traits will be used to calibrate the individual-based model developed for egg-carrying copepods by Dur et al. (2013), and consequently provide further insight into the population dynamics of this species in the lake. Besides temperature, food supply is another important environmental factor that affects life history traits and population dynamics of the copepod. Sometimes food availability can have even more impact than temperature (Ban 1994). Thus, it is necessary in the future to determine the food supply effect on *E. japonicus* and evaluate the interaction between temperature and food conditions to predict changes in population dynamics due to global warming and modern human impacts.

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