

Review [総説]

Effects of temperature and nutritional conditions on physiological responses of the freshwater copepod *Eodiaptomus japonicus* in Lake Biwa, (Japan)

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琵琶湖産カイアシ類 *Eodiaptomus japonicus* の生理的応答に対する
温度と餌条件の影響

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Abstract

The calanoid copepod *Eodiaptomus japonicus* is a key species in the zooplankton community and plays a vital role in the food chain of the Lake Biwa ecosystem. We summarize physiological responses of *E. japonicus* to different temperature and food conditions, providing an overview of potential impacts of global warming and eutrophication on its population dynamics in the lake. This warm-water adapted copepod was able to develop and reproduce in a wide range of temperatures above 10°C. The effects of food limitation were severely influenced at high temperatures. Both somatic and population growths were depressed under food-limited conditions at high temperatures due to a lowering of net growth efficiency. These results suggested that global warming would threaten *in situ* population growth of *E. japonicus* under food-limited conditions in this lake.

Keywords: anthropogenic impacts, life history traits, metabolic adaptation, zooplankton, freshwater ecosystems

摘 要

Eodiaptomus japonicus は、琵琶湖の動物プランクトンにおいて周年優占するカイアシ類であり、琵琶湖生態系において鍵となる種である。本研究では、水温と餌条件に対する本種の生理的応答を概説し、富栄養化と温暖化がそれらの個体群動態に与える潜在的な影響を検討した。温暖適応した本種は、10°C以上のとき広い温度範囲で成長と再生産が可能であり、餌不足の影響は高水温下で著しい。体成長も個体群成長も餌不足環境で低下したが、その影響は高温下において大きかった。これは高温条件での代謝コストの増大が純成長効率を低下させるためと考えられた。結局、中栄養湖である琵琶湖における本種個体群成長は、今後の温暖化によって餌不足環境では低下する可能性が示唆された。

キーワード：人為的影響、生活史特性、代謝適応、動物プランクトン、淡水生態系

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Introduction

Ambient temperature and food conditions are the main factors affecting the metabolism and nutritional intake of ectotherms, consequently influencing their life history traits and population dynamics (Mauchline, 1998; Dam, 2013). Copepods are one of the most widely distributed microcrustaceans in aquatic ecosystems. They are an important component of zooplankton populations and play a crucial role in the trophic dynamics of marine, brackish and freshwater ecosystems, serving as a link between phytoplankton and higher trophic levels (Hirst et al., 1999; Uye, 2000; Hsieh et al., 2011). Understanding processes that control copepod abundance and production is a major objective in aquatic ecology and limnology.

Although many studies have been conducted on calanoid copepods and other planktonic organisms, most have focused on marine and brackish water residents, not freshwater ones (Mauchline, 1998). Understanding responses of life history traits and metabolism to various temperature and nutritional conditions in freshwater copepods is essential when seeking to clarify effects of anthropogenic impacts, such as eutrophication and global warming, on copepod populations in freshwater lakes.

The freshwater copepod: *Eodiaptomus japonicus*

The small freshwater calanoid copepod *E. japonicus* (Burckhardt) is an endemic species in Japan, and widely distributed in temperate and subtropical regions. It is the dominant species in Lake Biwa (Kawabata, 1987) and Lake Ikeda (Baloch et al., 1998).

Population dynamics and distribution of *E. japonicus* have been well studied in Lake Biwa because of its high abundance and importance as a food resource for fishes (Kawabata, 1987; 1989). Several laboratory studies on life history traits (Liu et al., 2014; Liu et al., 2015) and metabolic rates (Liu and Ban, 2017) under different controlled conditions were conducted to understand more fully the inter-annual variations of this key species in the lake and its responses to eutrophication and warming due to global climate change.

Life cycle of *E. japonicus*

Whole life history traits of *E. japonicus* were first observed in a laboratory by Liu et al. (2014). Adult copepod size varied within ca. 1 mm. *E. japonicus* has a typical calanoid life cycle with six naupliar stages followed by five

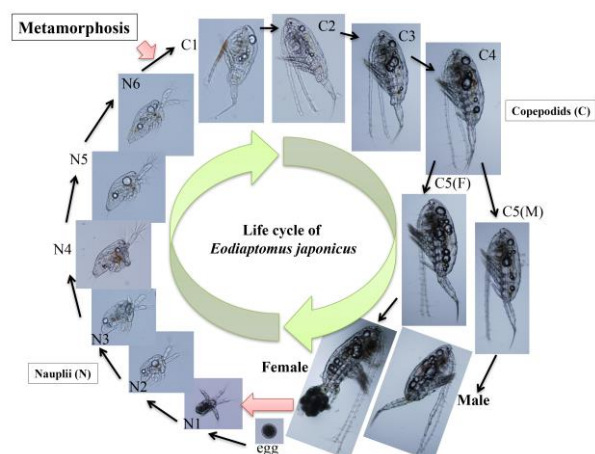


Fig. 1. Life cycle of the calanoid copepod *Eodiaptomus japonicus*. Successive six naupliar (N1–N6) and six copepodite (C1–adult) stages observed during their development are presented. M and F represent males and females, respectively. Pictures are not at the same scale.

図 1. カイアシ類カラヌス目 *Eodiaptomus japonicus* の生活環. 6 段階のノープリウス期 (N1–N6) と 6 段階のコペポダイト期 (C1–adult) を示す. M と F は、それぞれ雄と雌である. 写真の縮尺が異なることに注意.

copepodite and adult stages.

The first stage nauplius (N1) hatches from an egg and grows through six naupliar stages, after which the body shape metamorphoses into the copepodite stage (C1). Growth continues until the fifth stage (C5), in which sexual distinction can be easily discerned. The last copepodite stage is usually called the adult stage (Fig. 1). Adult females are usually larger than adult males.

After successful mating, the adult female spawns and carries an egg sac until hatching (Fig. 1). During the reproductive cycle, copepod reproductive parameters were commonly determined: for example, 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 CS/ICD in each clutch.

Population structure of *E. japonicus* in Lake Biwa

According to a 3-year field study of Kawabata (1987), *E. japonicus* was mainly distributed above the thermocline (5–20 m) in Lake Biwa. The horizontal distribution was almost uniform and vertical distribution was related to water column structure without diel vertical migration. However, more nauplii were distributed in shallow depth layers compared to copepodites. At the end of the stagnation period (May to September), adults were distributed in the same layer as that of nauplii. The maximum abundance of *E. japonicus* was observed in June, when water temperature ranged between 13 and 18°C, with population density reaching up to ca. 2×10^4 ind. m^{-3} (Liu et al., 2014).

Somatic growth and survivorship

Development time, body size, and survival rate are the basic life history traits in copepods. Information for these

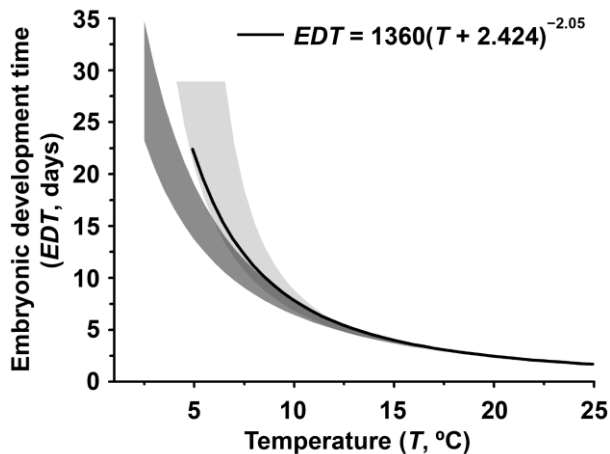


Fig. 2. Relationship between embryonic development time (EDT, days) and temperature (T , °C) for freshwater copepods. The black line represents the fitted Bělehrádek's function on the median EDT of *Eodiaptomus japonicus* with the equation given. Dark and light regions represent ranges of EDT against temperature for cold- and warm-water adapted species, respectively. Data based on Liu et al. (2014) and Herzig (1983).

図 2. 淡水産カイアシ類の胚発生時間 (EDT, days) と水温 (T , °C) の関係。黒の実線は *Eodiaptomus japonicus* の EDT 中央値で求めた Bělehrádek の温度関数を示す (Liu et al. 2014)。濃い影と薄い影の部分は、それぞれ寒冷および温暖適応種の発育時間の範囲を示す (Herzig 1983)。

traits is essential for understanding population dynamics in the field. Somatic growth is positively correlated to temperature and food supply, and has been recognized as a general rule for copepods (Ban, 1994; Lee et al., 2003; Jiménez-Melero et al., 2012). Under sufficient food supply, temperature is the main parameter controlling *in situ* copepod seasonal population dynamics (Uye, 2000; Halsband-Lenk et al., 2004).

To determine the relationship between development time (DT , days) and temperature (T , °C) in copepods, Bělehrádek's function is the most frequently used equation in the literature:

$$DT = l(T - a)^b,$$

where l , a and b are fitted constants. Exponential parameter b was mostly fixed at -2.05 (McLaren et al., 1969).

In Liu et al. (2015), body dry weight was plotted against adult median development time (MDT , days), and fitted with a von Bertalanffy's function (Fitzhugh, 1976), to calculate the growth coefficient (k , day^{-1}):

$$W_{Ber} = A(1 - Be^{-kMDT})^m,$$

where A is the asymptotic value for body weight at time $t \rightarrow \infty$, interpreted as the average value of body weight, B is a scaling parameter, and m is the inflection parameter for Richards function, three in Liu et al. (2015). *E. japonicus* body dry weight (W , μg) was calculated from the prosome length (PL , mm) using the exponential equation $W = e^{(2.59 \ln PL + 2.6995)}$ provided by Kawabata and Urabe (1998).

In *ad libitum* food conditions, both EDT (Fig. 2) and post-embryonic development time (post-EDT, Fig. 3) of *E. japonicus* strongly decreased with increasing temperature and were well described with the Bělehrádek's equation ($r^2 > 0.9$, Liu et al., 2014). EDT and stage duration of N1 were independent of food concentration (Liu et al., 2015), whereas they both depended on temperature, as shown in other copepods (Landry, 1975a; b). In general, early naupliar stages of copepods can survive on oil sacs or yolk until the mandible is sufficiently developed to start feeding (Mauchline, 1998). In *E. japonicus*, the N1 stage is a non-feeding stage (Kawabata, 1989; Liu et al., 2014); therefore, the EDT and the stage duration of N1 in this copepod can be described with a simple temperature function regardless of food concentration (Fig. 2).

Physiological responses of copepods to temperature vary among species or local populations of the same species

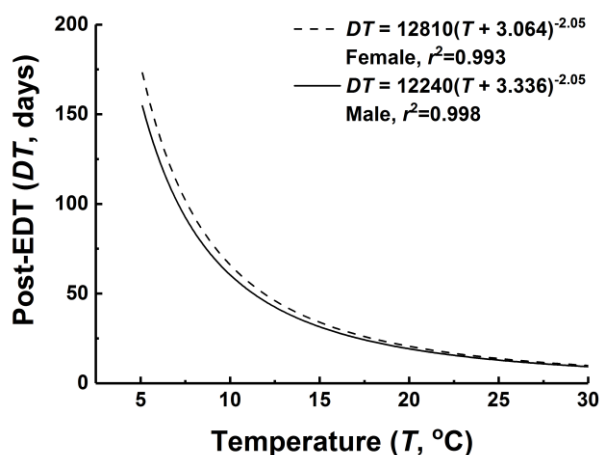


Fig. 3. Relationship between temperature and median post-embryonic development time (post-EDT, days) of adult *Eodiaptomus japonicus* males (solid line) and females (dotted line) reared under *ad libitum* food condition. The fitted Bělehrádek's equations are given. Data based on Liu et al. (2014).

図 3. 餌条件に制限がないときの *Eodiaptomus japonicus* における成体 (雄, 実線; 雌, 点線) までの後胚発生時間 (post-EDT, days) と水温 (T , °C) の関係. 性別ごとの Bělehrádek の温度関数を示した. データは Liu et al. (2014) を参照.

living along different latitudes (McLaren et al., 1969; Landry, 1975b; Herzig, 1983). Based on the evidence obtained from several marine copepods, McLaren et al. (1969) found that biological zero, indicated as a of Bělehrádek's temperature function for EDT, was related to the average temperature of their habitat. According to the Temperature-EDT equation for *E. japonicus*, biological zero for EDT was -2.4°C (Fig. 2). 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 (Liu et al., 2014). Herzig (1983) showed that Temperature-EDT curves for warm-water freshwater copepods could be separated from that for cold-water species (Fig. 2). The Temperature-EDT curve of *E. japonicus* lies at the lower edge for warm-water copepods.

Body size of *E. japonicus* increased with decreasing temperature in the presence of excess food (Liu et al., 2014) and increased with increasing food concentration (Liu et al., 2015). Ban (1994) showed that food condition was a more influential factor than temperature with respect to body size

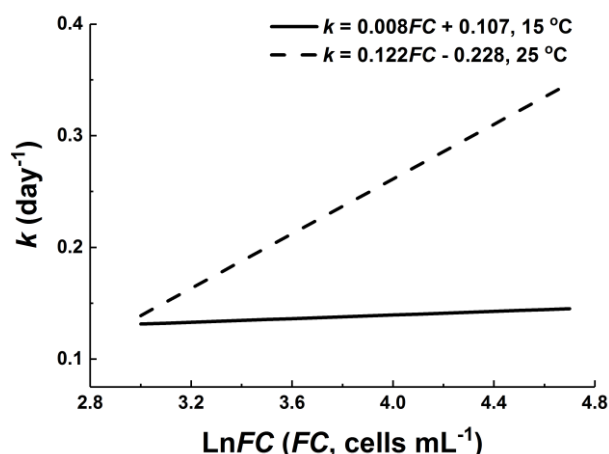


Fig. 4. Growth coefficient (k , day^{-1}) of *Eodiaptomus japonicus* showing a linear relationship with log-transformed food concentrations (LnFC , cells mL^{-1}) at 15°C (solid line) and 25°C (dashed line). Regression equations also provided. Data based on Liu et al. (2015).

図 4. 異なる温度 (15°C , 実線; 25°C , 点線) における *Eodiaptomus japonicus* の成長係数 (k , day^{-1}) と自然対数に変換した餌濃度 (LnFC , cells mL^{-1}) との関係, および, それぞれの回帰式. データは Liu et al. (2015) を参照.

in a freshwater copepod, *Eurytemora affinis*. In *E. japonicus*, a temperature increase from 10 to 25°C , which is typical of the range occurring in Lake Biwa, induced only a 5% decrease of adult prosome length under excess food supply (Liu et al., 2014), while food limitation induced a 4 and 16% reduction of body size under sufficient food supply at 15 and 25°C , respectively (Liu et al., 2015). This suggests a temperature-mediated food effect on body size of *E. japonicus*, implying that adult body size of this copepod is potentially more influenced by food shortage at temperatures $>15^{\circ}\text{C}$.

The growth coefficient, k , of *E. japonicus* estimated from the von Bertalanffy's function, linearly increased with log-transformed food concentration at 25°C but not at 15°C (Fig. 4), which may be attributed to temperature-mediated metabolic cost (Ikeda et al., 2001; Liu and Ban, 2017). As a result of physiological processes, temperature mediates food effects on carbon assimilation, and plays an important role in the efficiency of a diet supplied to animals (Lampert, 1977a). Net production efficiencies (NPEs) in *Daphnia pulex* were more influenced by food shortage at higher temperatures: for

Table 1. Survival rate (%) and reproduction parameters of *Eodiaptomus japonicus* under different temperatures (Temp., °C) and carbon concentrations (Carbon conc., mgC L⁻¹). Data from Liu et al. (2014) and Liu et al. (2015).

表 1. 異なる温度 (°C) と餌環境 (Carbon conc., mgC L⁻¹) における *Eodiaptomus japonicus* の生存率 (%) と各再生産パラメータ。データは Liu et al. (2014, 2015) を参照。

Temp. (°C)	Carbon conc. (mgC L ⁻¹)	Survival (%)	HS (%)	CS (eggs clutch ⁻¹)	EPR (eggs female ⁻¹ day ⁻¹)	ICD (days)	LT (days)	Longevity (days)
10	12.86	15	98.0	11.6	1.3	9.4	8.1	37.5
15	0.26	36	78.9	7.6	0.8	9.4	6.1	85.5
15	1.29	75	97.6	13.5	2.1	6.8	3.3	71.0
15	2.57	72	99.2	14.6	2.5	6.5	2.9	83.0
15	12.86	39	97.5	16.8	3.2	5.9	2.5	68.8
20	12.86	36	99.6	14.5	4.1	3.5	1.7	45.0
25	0.26	25	98.8	6.8	2.6	2.9	2.0	31.4
25	1.29	33	98.1	10.3	4.3	2.5	1.3	30.9
25	2.57	31	98.5	13.5	5.1	2.8	1.2	30.4
25	12.86	42	97.5	15.0	5.8	2.9	1.4	30.5

Survival, survival rate of adults; HS, hatching success; CS, clutch size; EPR, egg production rate; ICD, inter-clutch duration; LT, latency time.

example, when food supply decreased from 2.0 to 0.1 mgC L⁻¹, the NPE decreased from 85 to 60% and from 75 to 10% at 15 and 25°C, respectively (Lampert, 1977b). Therefore, food effects on individual growth in *E. japonicus* might only rarely be found in cold waters due to the low metabolic cost.

E. japonicus showed high mortality rates in the naupliar stages, especially at lower food concentrations, while mortality was quite low in copepodid stages (Liu et al., 2014; Liu et al., 2015). The highest survival rates observed during development until adulthood were observed at medium food supply, 1.29–2.57 mgC L⁻¹ at 15°C, while the range of food concentrations varied from 0.26–12.86 mgC L⁻¹ (Table 1). Previous studies have shown the highest survival rates exceeded 80% at medium food levels of 1.0 mg C L⁻¹ and for other freshwater copepods with food level ranges tested from 0.05 to 2.5 mgC L⁻¹ (Hart, 1996). An increase in mortality with temperature has often been observed in copepods (Jamieson, 1986; Zeller et al., 2004; Devreker et al., 2005). Williams and Jones (1994) showed that mortality of the copepod *Tisbe battagliai* increased with a reduction in food supply and was enhanced with a rise in temperature from 15 to 25°C. Similar results were obtained with *E. japonicus* (Table 1), suggesting that increases in water temperature might induce high mortality when *E. japonicus* faces severe food shortages in the field (Liu et al., 2015).

Natural populations of *E. japonicus* in Lake Biwa experience limited food conditions, as indicated by their smaller adult body size compared to that of *E. japonicus* reared in experiments where food supply was sufficient (Fig. 5). On the other hand, large zooplankton are known to be subject to high predation pressure by visual predators, e.g.,

planktivorous fish (Svensson, 1997). Copepods usually represent the principal prey for such small planktivorous fishes (Plounevez and Champalbert, 1999; Turner, 2004). Predation by fish might be another potential factor that influences the body size distribution of copepods *in situ*.

E. japonicus is known to be the main food resource for the dominant planktivorous fish, *Plecoglossus altivelis*, in Lake Biwa (Kawabata et al., 2002). Stomach content analysis of this fish showed ca. 90% occurrence of this copepod (Kawabata et al., 2002). Although the stomach contents were exclusively adult females, the body sizes of adult females have not been related to food selectivity by *P. altivelis* (authors' unpublished data).

Reproduction

Egg production of copepods is generally related to female body size due to the larger capacity of a larger body (Deevey, 1960; Klein Breteler and Gonzalez, 1988; Ban, 1994). However, no clear relationship between CS and body size was obtained for *E. japonicus* (Fig. 6). Small CS produced by larger *E. japonicus* females at 10°C can be explained as a low-temperature stress. The largest individual variability in somatic growth at 10°C (Liu et al., 2014) also supported this idea. Such individual variability for development has been found to increase under non-optimal environments (Carlotti and Nival, 1991).

In *E. japonicus*, high hatching ability (ca. 80–100%) of females seems to be independent of temperature and food conditions (Table 1) because such environmental factors do not influence yolk investment in copepod eggs (Jamieson, 1986). EPR of copepods increased with temperature up to a

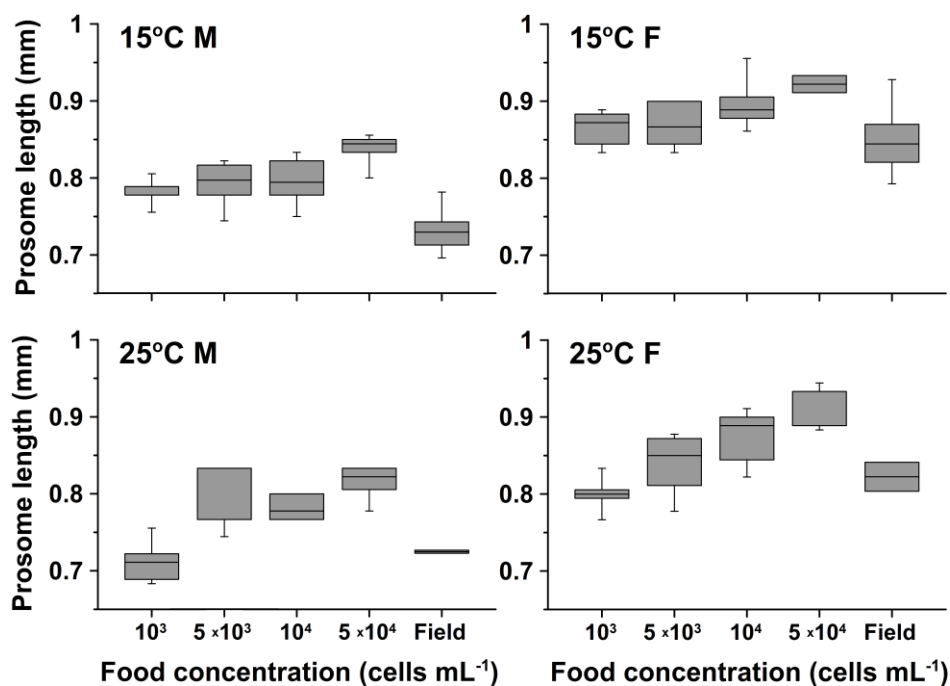


Fig. 5. Comparison of prosome length (mm) of adult *Eodiaptomus japonicus* reared in the laboratory (M in males and F in females) and sampled in Lake Biwa (field). Data based on Liu et al. (2015) and Liu (2016).

図5. 飼育実験と琵琶湖での *Eodiaptomus japonicus* 成体頭胸長 (mm) の比較 (M, 雄; F, 雌). データは Liu et al. (2015) と Liu (2016) を参照.

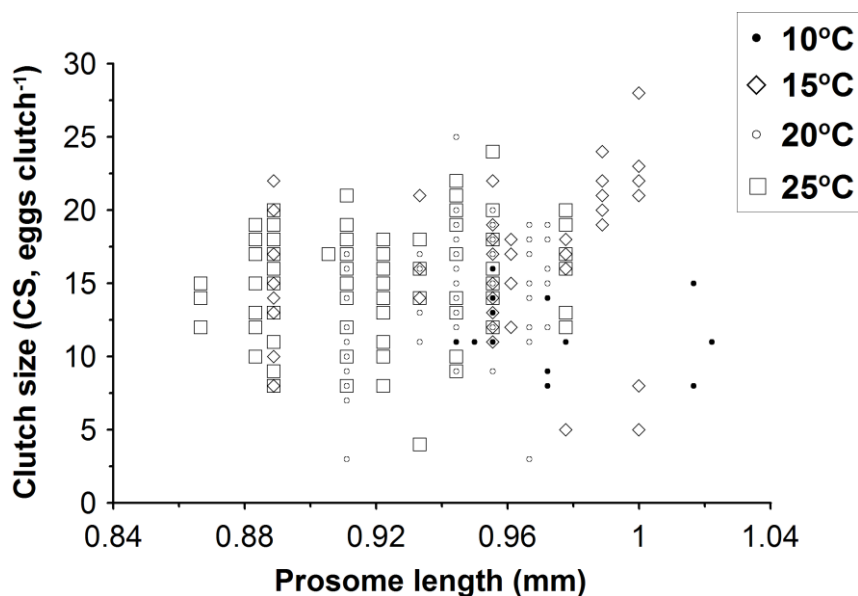


Fig. 6. Relationship between clutch size (CS, eggs clutch⁻¹) and adult prosome length (mm) of *Eodiaptomus japonicus* females at four temperature conditions. Data from Liu et al. (2014).

図6. 異なる4つの温度条件における *Eodiaptomus japonicus* のクラッチサイズ (CS, eggs clutch⁻¹) と雌の頭胸長 (mm) の関係. データは Liu et al. (2014) を参照.

maximum level, but decreased or even ceased beyond the maximum (Uye, 1981; Dur et al., 2009; Jiménez-Melero et al., 2012). Such maximum levels differ among species (Holste and Peck, 2005) and depend on factors that include female age (Parrish and Wilson, 1978), food quantity and quality (Kiørboe et al., 1985; Broglio et al., 2003), as well as temperature. In *ad libitum* food conditions, EPR of *E. japonicus* increased with temperature up to 25°C (Table 1). This suggests that the threshold temperature for inhibiting EPR is over 25°C and supports the idea that this copepod is warm-water adapted (Herzig, 1983; Liu et al., 2014). However, the CS of *E. japonicus* exhibited similar increasing trends against carbon supply at 15 and 25°C (Table 1), whereas ICD was obviously influenced by temperature and food supply with interaction effects (Liu et al., 2015). Consequently, EPR increased with increasing carbon supply at both temperatures, but always being higher at 25°C than at 15°C (Table 1). This difference may be attributed to prolonged ICDs at low temperature due to the longer LT: i.e., delayed spawning from the previous hatching (Liu et al., 2015).

Longevity of *E. japonicus* females always exceeded two months at 15°C and was about one month at 25°C in any food conditions (Table 1). Females in low temperature conditions have relatively long reproductive periods. According to Liu et al. (2014) reproductive activity was very low at 10°C; only 40% of pairs tested could reproduce successfully and 63% of them produced just a single clutch during their life-time at 10°C in spite of sufficient food supply, while 70% of the pairs successfully reproduced at higher temperatures.

Population growth

Knowing the relationship between population growth rate of zooplankton and environmental factors allows ecologists to clarify their population dynamics in the field. Population growth rate (r , day⁻¹) can be derived from Euler-Lotka's equation using parameters from a life table of target zooplankton and calculated iteratively (Liu et al., 2015):

$$\sum_{x=ia}^{\infty} l_x m_x e^{-rx} = 1,$$

where ia 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 \dot{E} is female longevity.

Population growth rate, r , of *E. japonicus* linearly increased with log-transformed food concentration at both 15

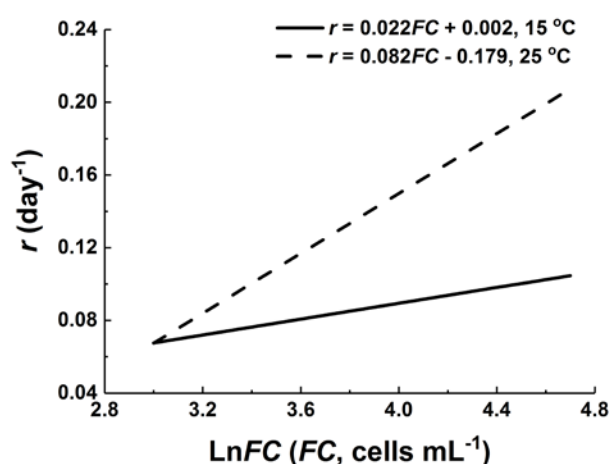


Fig. 7. Population growth rate (r , day⁻¹) of *Eodiaptomus japonicus* showed a linear relationship with log-transformed food concentrations (LnFC, cells mL⁻¹) at 15°C (solid line) and 25°C (dashed line). Regression equations are provided. Data based on Liu et al. (2015).

図 7. 異なる温度 (15°C, 実線 ; 25°C, 点線) における *Eodiaptomus japonicus* の個体群増加率 (r , day⁻¹) と自然対数に変換した餌濃度 (LnFC, cells mL⁻¹) との関係, および, それぞれの回帰式. データは Liu et al. (2015) を参照.

and 25°C but showed obvious increase at 25°C compared to 15°C (Fig. 7), implying that r is more influenced by food shortage at higher temperatures than that at lower temperatures, as observed for somatic growth (Fig. 4). Considering the potential food limitation of this copepod in Lake Biwa deduced from the comparison between body sizes of adults in laboratory studies and the field (Fig. 5), both somatic and population growths of this copepod might be affected by food shortage in Lake Biwa (Liu et al., 2015).

Metabolism

Metabolic physiology provides basic information for understanding the linkage between the biology of aquatic organisms and the ecology of populations and ecosystems (Brown et al., 2004). It is well known that temperature is one of the most important factors determining copepod life history traits (Lee et al., 2003; Jiménez-Melero et al., 2007; Beyrend-Dur et al., 2011), due to the strong influence of temperature on their metabolism (Brown et al., 2004).

In aquatic organisms, respiration as an index of metabolism is mainly determined from oxygen consumption. It is quite difficult to measure the respiration rates of

mesozooplankton such as copepods due to their small body mass and low oxygen demand, especially at low temperatures (Lee et al., 2001; Alcaraz et al., 2013; Cruz et al., 2013). Recently, a contactless optical spot-fiber oxygen sensor was developed to measure concentration of dissolved oxygen in water. Use of this sensor is becoming popular when measuring oxygen consumption by copepods (Bode et al., 2013; Kiko et al., 2015; Liu and Ban, 2017) because it is relatively precise and easier to measure, and fewer numbers of experimental animals are required than with traditional methods, e.g., the Winkler titration (Williams and Jenkinson, 1982) and oxygen electrode methods (Kjørboe et al., 1985).

A schematic diagram (Fig. 8) shows measurement of oxygen consumption of small aquatic animals using a fiber-optic oxygen meter (Firesting O₂, PyroScience, Germany), which was developed by Liu and Ban (2017). According to Liu and Ban (2017), respiration rates of *E. japonicus* increased exponentially from 8 to 28°C because temperature enhances metabolism in zooplankton (Brown et al., 2004). The respiration rates deviated from the exponential phase at 30°C for the copepods acclimatized at both 15 and 25°C with no significant differences (Kruskal-Wallis test, $p > 0.05$), indicating that the same metabolic plasticity might occur in the lake due to a lesser variation of *in situ* temperature, i.e., 8–25°C.

Generally, a negative correlation between respiration

rate and body weight has been reported in copepods where body weight varies ca. 2–3 orders between naupliar and adult stages (Comita, 1968; Fernández, 1978; Vidal, 1980). Respiration rates of *E. japonicus* copepodites did not show such a relationship due to the narrow range of body weights (Liu and Ban, 2017). This allows for the metabolic costs of wild populations to be evaluated using the respiration rate (R , $\mu\text{LO}_2 \text{ mg-dry-weight}^{-1} \text{ h}^{-1}$) and temperature (T , °C) equation obtained by Liu and Ban (2017):

$$R = 0.8072e^{0.0897T}.$$

Q_{10} is the most commonly used parameter to describe the relationship between metabolic rates and temperature among zooplankton, and is calculated from:

$$Q_{10} = \left(\frac{R_{T2}}{R_{T1}} \right)^{\frac{10}{T2-T1}},$$

where R_{T1} and R_{T2} are the rates of the studied process at temperature $T1$ and $T2$ (in °C), respectively.

In general, Q_{10} in a given species has been shown to vary with the habitat temperature to which it is adapted (Rao and Bullock, 1954), being 2–3.8 for boreal copepods (Comita, 1968; Nival et al., 1974; Lee et al., 2001; Isla and Perissinotto, 2004; Castellani et al., 2005). Q_{10} was 2.3 in *E. japonicus*, similar to values for temperate species, and 4.6 for arctic species of *Calanus glacialis* (Hirche, 1987). However, a Q_{10} of 1.4–2 was determined for three tropical species (Kiko et al.,

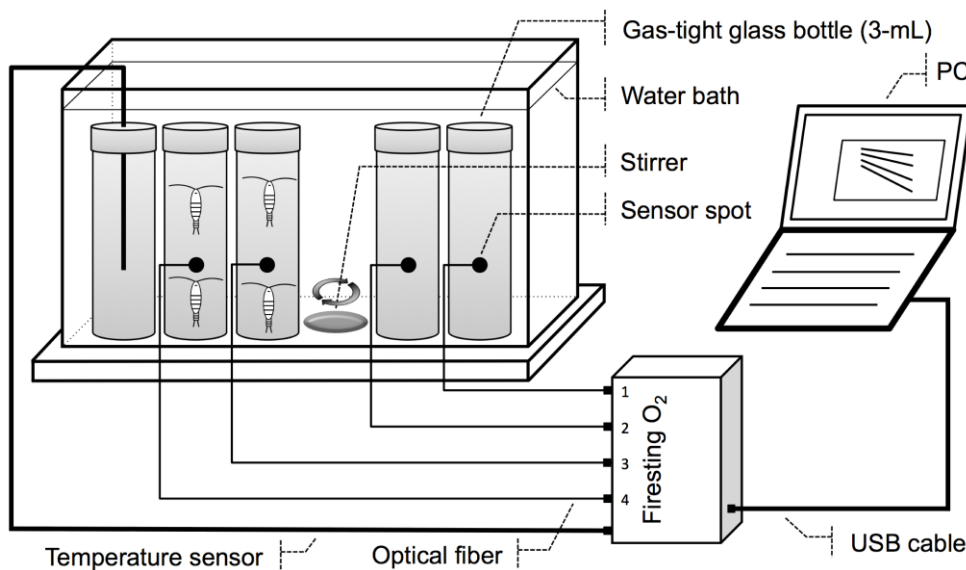


Fig. 8. Schematic diagram of a water-bath and closed-bottle unit for measuring oxygen consumption of small aquatic animals using a fiber-optic oxygen meter (Liu and Ban, 2017).

図 8. 非接触型酸素計を用いた微小水生生物の酸素消費量測定装置の模式図 (Liu and Ban, 2017) .

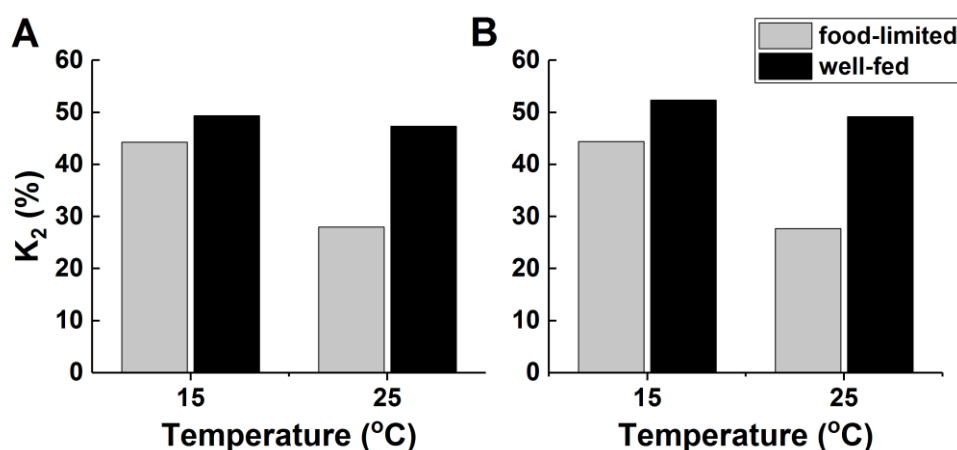


Fig. 9. Net growth efficiencies (K_2 , %) for food-limited (grey bars) and well-fed (black bars) *Eodiaptomus japonicus* males (A) and females (B) at 15 and 25°C. Data from Liu and Ban (2017).

図 9. 異なる温度 (15, 25°C), 餌条件 (餌制限, 灰; 餌潤沢, 黒) における *Eodiaptomus japonicus* 雄 (A) と雌 (B) の純成長効率 (K_2 , %) . データは Liu et al. (2017) を参照.

2015), while the median Q_{10} value for another 11 tropical species was 1.8 (Teuber et al., 2013), which was lower than for those of temperate and arctic species. These results imply that a Q_{10} of > 2 is typical for species inhabiting higher latitudes but not lower latitudes. This may be related to large seasonal temperature fluctuations at higher latitudes. Since high Q_{10} values in copepods indicate high sensitivity to temperature (Mauchline, 1998), copepods with a higher Q_{10} might adapt to a wide range of temperature fluctuations, while copepods having a lower Q_{10} might adapt to a narrower temperature range.

Temperature is the most influential factor in determining net growth efficiency (K_2) in zooplankton due to higher metabolic costs or carbon losses by respiration at higher temperatures (Ikeda et al., 2001; Lee et al., 2001). Food condition is another influential factor for K_2 in zooplankton (Lampert, 1977a) because metabolic costs are associated with food quantity (Kiørboe et al., 1985). In *E. japonicus*, K_2 was low in food-limited individuals at high temperatures for both males and females (Fig. 9), implying that high metabolic costs at higher temperatures induce decreasing somatic and population growth rates in food-limited environments (Fig. 4, 7).

Respiration rates of zooplankton also increased with increasing food concentration (Abou Debs, 1984; Urabe and Watanabe, 1990). This is considered to be associated with specific dynamic action (SDA): i.e., energetic costs required for biochemical processes with feeding (Kiørboe et al., 1985).

Feeding behavior itself potentially enhances the metabolic cost in aquatic organisms under food-limited conditions because of energy demanding processes such as maintaining metabolism and searching for scarce food (Kiørboe and Hirst, 2014). Therefore, the respiration rates measured by Liu and Ban (2017) might be conservative because all the laboratory experiments were conducted under non-feeding conditions. K_2 calculated by them could be the potential upper limit and it might be lower in mesotrophic Lake Biwa.

References

- Abou Debs, C. (1984): Carbon and nitrogen budget of the calanoid copepod *Temora stylifera*: effect of concentration and composition of food. *Marine Ecology Progress Series*, **15**, 213-223.
- Alcaraz, M., R. Almeda, E. Saiz, A. Calbet, C. M. Duarte, S. Agustí, R. Santiago and A. Alonso (2013): Effects of temperature on the metabolic stoichiometry of Arctic zooplankton. *Biogeosciences*, **10**, 689-697.
- Baloch, A. W., H. Maeta and T. Saisho (1998): Seasonal abundance and vertical distribution of zooplankton in Lake Ikeda. *Journal of Plankton Research*, **13**, 1-8.
- Ban, S. (1994): Effect of temperature and food concentration on post-embryonic development, egg production and adult body size of calanoid copepod *Eurytemora affinis*. *Journal of Plankton Research*, **16**, 721-735.
- Beyrend-Dur, D., R. Kumar, T. R. Rao, S. Souissi, S.-H. Cheng and J. S. Hwang (2011): Demographic

- parameters of adults of *Pseudodiaptomus annandalei* (Copepoda: Calanoida): Temperature–salinity and generation effects. *Journal of Experimental Marine Biology and Ecology*, **404**, 1-14.
- Bode, M., A. Schukat, W. Hagen and H. Auel (2013): Predicting metabolic rates of calanoid copepods. *Journal of Experimental Marine Biology and Ecology*, **444**, 1-7.
- Broglio, E., S. H. Jónasdóttir, A. Calbet, H. H. Jakobsen and E. Saiz (2003): Effect of heterotrophic versus autotrophic food on feeding and reproduction of the calanoid copepod *Acartia tonsa*: relationship with prey fatty acid composition. *Aquatic Microbial Ecology*, **31**, 267-278.
- Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage and G. B. West (2004): Toward a metabolic theory of ecology. *Ecology*, **85**, 1771-1789.
- Carlotti, F. and S. Nival (1991): Individual variability of development in laboratory-reared *Temora stylifera* copepodites: consequences for the population dynamics and interpretation in the scope of growth and development rules. *Journal of Plankton Research*, **13**, 801-813.
- Castellani, C., C. Robinson, T. Smith and R. S. Lampitt (2005): Temperature affects respiration rate of *Oithona similis*. *Marine Ecology Progress Series*, **285**, 129-135.
- Comita, G. W. (1968): Oxygen consumption in *Diaptomus*. *Limnology and Oceanography*, **13**, 51-57.
- Cruz, J., S. Garrido, M. S. Pimentel, R. Rosa, A. M. P. Santos and P. Ré (2013): Reproduction and respiration of a climate change indicator species: effect of temperature and variable food in the copepod *Centropages chierchiae*. *Journal of Plankton Research*, **35**, 1046-1058.
- Dam, H. G. (2013): Evolutionary adaptation of marine zooplankton to global change. *Annual Review of Marine Science*, **5**, 349-370.
- Deevey, G. B. (1960): Relative effects of temperature and food on seasonal variations in length of marine copepods in some eastern American and western European waters. *Bulletin of the Bingham Oceanographic Collection*, **17**, 54-84.
- Devreker, D., S. Souissi and L. Seuront (2005): Effects of chlorophyll concentration and temperature variation on the reproduction and survival of *Temora longicornis* (Copepoda, Calanoida) in the Eastern English Channel. *Journal of Experimental Marine Biology and Ecology*, **318**, 145-162.
- Dur, G., S. Souissi, D. Devreker, V. Ginot, F. G. Schmitt and J. S. Hwang (2009): An individual-based model to study the reproduction of egg bearing copepods: Application to *Eurytemora affinis* (Copepoda Calanoida) from the Seine estuary, France. *Ecological Modelling*, **220**, 1073-1089.
- Fernández, F. (1978): Metabolismo y alimentacion en copepodos planctonicos del Mediterraneo: respuesta a la temperatura. *Investigacion Pesquera*, **42**, 97-139.
- Fitzhugh, H. A. (1976): Analysis of growth curves and strategies for altering their shape. *Journal of animal Science*, **42**, 1036-1051.
- Halsband-Lenk, C., F. Carlotti and W. Greve (2004): Life-history strategies of calanoid congeners under two different climate regimes: a comparison. *Journal of Marine Science*, **61**, 709-720.
- Hart, R. C. (1996): Naupliar and copepodite growth and survival of two freshwater calanoids at various food levels: Demographic contrasts, similarities, and food needs. *Limnology and Oceanography*, **41**, 648-658.
- Herzig, A. (1983): The ecological significance of the relationship between temperature and duration of embryonic development in planktonic freshwater copepods. *Hydrobiologia*, **100**, 65-91.
- Hirche, H. J. (1987): Temperature and plankton. II. Effect on respiration and swimming activity in copepods from the Greenland Sea. *Marine Biology*, **94**, 347-356.
- Hirst, A. G., M. Shearer and J. A. Williams (1999): Annual pattern of calanoid copepod abundance, prosome length and minor role in pelagic carbon flux in the Solent, UK. *Marine Ecology Progress Series*, **177**, 133-146.
- Holste, L. and M. A. Peck (2005): The effects of temperature and salinity on egg production and hatching success of Baltic *Acartia tonsa* (Copepoda: Calanoida): a laboratory investigation. *Marine Biology*, **148**, 1061-1070.
- Hsieh, C. H., Y. Sakai, S. Ban, K. Ishikawa, T. Ishikawa, S. Ichise, N. Yamamura and M. Kumagai (2011): Eutrophication and warming effects on long-term variation of zooplankton in Lake Biwa. *Biogeosciences Discussions*, **8**, 593-629.
- Ikedo, T., Y. Kanno, K. Ozaki and A. Shinada (2001): Metabolic rates of epipelagic marine copepods as a function of body mass and temperature. *Marine Biology*,

- 139**, 587-596.
- Isla, J. A. and R. Perissinotto (2004): Effects of temperature, salinity and sex on the basal metabolic rate of the estuarine copepod *Pseudodiaptomus hessei*. *Journal of Plankton Research*, **26**, 579-583.
- Jamieson, C. D. (1986): The effects of temperature and food on naupliar development, growth and metamorphosis in three species of *Boeckella* (Copepoda: Calanoida). *Hydrobiologia*, **139**, 277-286.
- Jiménez-Melero, R., G. Parra and F. Guerrero (2012): Effect of temperature, food and individual variability on the embryonic development time and fecundity of *Arctodiaptomus salinus* (Copepoda: Calanoida) from a shallow saline pond. *Hydrobiologia*, **686**, 241-256.
- Jiménez-Melero, R., G. Parra, S. Souissi and F. Guerrero (2007): Post-embryonic developmental plasticity of *Arctodiaptomus salinus* (Copepoda: Calanoida) at different temperatures. *Journal of Plankton Research*, **29**, 553-567.
- Kawabata, K. (1987): Abundance and distribution of *Eodiaptomus japonicus* (Copepoda: Calanoida) in Lake Biwa. *Bulletin of the Plankton Society of Japan*, **34**, 173-183.
- Kawabata, K. (1989): Natural development time of *Eodiaptomus japonicus* (Copepoda: Calanoida) in Lake Biwa. *Journal of Plankton Research*, **11**, 1261-1272.
- Kawabata, K., T. Narita, M. Nagoshi and M. Nishino (2002): Stomach contents of the landlocked dwarf ayu in Lake Biwa, Japan. *Limnology*, **3**, 135-142.
- Kawabata, K. and J. Urabe (1998): Length-weight relationships of eight freshwater planktonic crustacean species in Japan. *Freshwater Biology*, **39**, 199-205.
- Kiko, R., H. Hauss, F. Buchholz and F. Melzner (2015): Ammonium excretion and oxygen respiration of tropical copepods and euphausiids exposed to oxygen minimum zone conditions. *Biogeosciences Discussions*, **12**, 17329-17366.
- Kjørboe, T. and A. G. Hirst (2014): Shifts in mass scaling of respiration, feeding, and growth rates across life-form transitions in marine pelagic organisms. *The American Naturalist*, **183**, E118-E130.
- Kjørboe, T., F. Møhlenberg and K. Hamburger (1985): Bioenergetics of the planktonic copepod *Acartia tonsa*: relation between feeding, egg production and respiration, and composition of specific dynamic action. *Marine Ecology Progress Series*, **26**, 85-97.
- Klein Breteler, W. C. M. and S. R. Gonzalez (1988): Influence of temperature and food concentration on body size, weight and lipid content of two calanoid copepod species. *Hydrobiologia*, **167**, 201-210.
- Lampert, W. (1977a): Studies on the carbon balance of *Daphnia pulex* DE GEER as related to environmental conditions. II. The dependence of carbon assimilation on animal size, temperature, food concentration and diet species. *Hydrobiologia*, **48**, 310-335.
- Lampert, W. (1977b): Studies on the carbon balance of *Daphnia pulex* DE GEER as related to environmental conditions. III. Production and production efficiency. *Hydrobiologia*, **48**, 336-360.
- Landry, M. R. (1975a): The relationship between temperature and the development of life stages of the marine copepod *Acartia clausi* Giesbr. *Limnology and Oceanography*, **20**, 854-857.
- Landry, M. R. (1975b): Seasonal temperature effects and predicting development rate of marine copepod eggs. *Limnology and Oceanography*, **20**, 434-440.
- Lee, H. W., S. Ban, T. Ikeda and T. Matsuishi (2003): Effect of temperature on development, growth and reproduction in the marine copepod *Pseudocalanus newmani* at satiating food condition. *Journal of Plankton Research*, **25**, 261-271.
- Lee, H. W., T. Ikeda and S. Ban (2001): Metabolism, body composition (C and N) and estimated net growth efficiency of a calanoid copepod *Pseudocalanus newmani* raised at different temperatures in the laboratory. *Plankton Biology and Ecology*, **48**, 114-120.
- Liu X. (2016): Physiological responses of a freshwater copepod *Eodiaptomus japonicus* on different temperature and food conditions, evaluating anthropogenic impacts in Lake Biwa. The University of Shiga Prefecture, Hikone, Japan, pp. 1-118.
- Liu, X. and S. Ban (2017): Effects of acclimatization on metabolic plasticity of *Eodiaptomus japonicus* (Copepoda: Calanoida) determined using an optical oxygen meter. *Journal of Plankton Research*, **39**, 111-121.
- Liu, X., D. Beyrend, G. Dur and S. Ban (2015): Combined effects of temperature and food concentration on growth and reproduction of *Eodiaptomus japonicus* (Copepoda: Calanoida) from Lake Biwa (Japan). *Freshwater Biology*, **60**, 2003-2018.
- Liu, X., D. Beyrend-Dur, G. Dur and S. Ban (2014): Effects

- of temperature on life history traits of *Eodiaptomus japonicus* (Copepoda: Calanoida) from Lake Biwa (Japan). *Limnology*, **15**, 85-97.
- Mauchline, J. (1998): The Biology of Calanoid Copepods. In *Advances in Marine Biology*. Vol. 33. Blaxter, J. H. S., A. J. Southward and P. A. Tyler (eds.), 1-710. Academic Press, London.
- McLaren, I. A., C. I. Corkett and E. J. Zillioux (1969): Temperature adaptations of copepod eggs from the arctic to the tropics. *The Biological Bulletin*, **137**, 486-493.
- Nival, P., G. Malara, R. Charra, I. Palazzoli and S. Nival (1974): Étude de la respiration et de l'excrétion de quelques copépodes planctoniques (crustacea) dans la zone de remontée d'eau profonde des côtes marocaines. *Journal of Experimental Marine Biology and Ecology*, **15**, 231-260.
- Parrish, K. K. and D. F. Wilson (1978): Fecundity studies on *Acartia tonsa* (Copepoda: Calanoida) in standardized culture. *Marine Biology*, **46**, 65-81.
- Plounevez, S. and G. Champalbert (1999): Feeding behaviour and trophic environment of *Engraulis encrasicolus* (L.) in the Bay of Biscay. *Estuarine, Coastal and Shelf Science*, **49**, 177-191.
- Rao, K. P. and T. H. Bullock (1954): Q10 as a function of size and habitat temperature in poikilotherms. *The American Society of Naturalists*, **88**, 33-44.
- Svensson, J. E. (1997): Fish predation on *Eudiaptomus gracilis* in relation to clutch size, body size, and sex: a field experiment. *Hydrobiologia*, **344**, 155-161.
- Teuber, L., R. Kiko, F. Séguin and H. Auel (2013): Respiration rates of tropical Atlantic copepods in relation to the oxygen minimum zone. *Journal of Experimental Marine Biology and Ecology*, **448**, 28-36.
- Turner, J. T. (2004): The Importance of Small Planktonic Copepods and Their Roles in Pelagic Marine Food Webs. *Zoological Studies*, **43**, 255-266.
- Urabe, J. and Y. Watanabe (1990): Influence of food density on respiration rate of two crustacean plankters, *Daphnia galeata* and *Bosmina longirostris*. *Oecologia*, **82**, 362-368.
- Uye, S. (1981): Fecundity studies of neritic calanoid copepods *Acartia clausi* Giesbrecht and *A. steueri* Smirnov: a simple empirical model of daily egg production. *Journal of Experimental Marine Biology and Ecology*, **50**, 255-271.
- Uye, S. (2000): Why does *Calanus sinicus* prosper in the shelf ecosystem of the Northwest Pacific Ocean? *ICES Journal of Marine Science*, **57**, 1850-1855.
- Vidal, J. (1980): Physioecology of zooplankton. III. Effects of phytoplankton concentration, temperature, and body size on the metabolic rate of *Calanus pacificus*. *Marine Biology*, **56**, 195-202.
- Williams, P. J. I. and N. W. Jenkinson (1982): A transportable microprocessor-controlled precise Winkler titration suitable for field station and shipboard use. *Limnology and Oceanography*, **27**, 567-584.
- Williams, T. D. and M. B. Jones (1994): Effects of temperature and food quantity on postembryonic development of *Tisbe battagliai* (Copepoda: Harpacticoida). *Journal of Experimental Marine Biology and Ecology*, **183**, 283-298.
- Zeller, M., R. Jiménez-Melero and B. Santer (2004): Diapause in the calanoid freshwater copepod *Eudiaptomus graciloides*. *Journal of Plankton Research*, **26**, 1379-1388.