

Metabolism, body composition (C and N) and estimated net growth efficiency of a calanoid copepod *Pseudocalanus newmani* raised at different temperatures in the laboratory

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Abstract: Metabolism (oxygen consumption) of laboratory-raised *Pseudocalanus newmani* copepodite stages 1 through 6 (C1–C6) at 10°C, and C6 at 3, 6, and 15°C was determined. Oxygen consumption rates (R : $\mu\text{l O}_2 \text{ indiv.}^{-1} \text{ h}^{-1}$) of males were found to be less than the rates of females for the C4–C6, largely because of lesser body mass of the former than the latter. From stepwise regression analysis, R of copepodites was expressed as a function of body dry weight (DW: μg) and temperature (T : °C) as $R=0.00172\text{DW}+0.00154T-0.00641$. While higher temperatures yielded smaller adults, the effect of temperature was not seen in their carbon and nitrogen compositions. Over the temperature range tested, males (mean: 52.7% of DW) were consistently richer in carbon than females (43.1% of DW). Based on these results, the carbon budget was established for males and females growing from C1 to C6 at 3 to 15°C, and the combined effects of temperatures on metabolism and growth were assessed in terms of the net growth efficiency or K_2 [$\text{growth} \times 100 / (\text{growth} + \text{metabolism})$]. The K_2 was highest at 3°C for both males (61.3%) and females (59.9%), decreasing gradually with rising temperatures. At a given temperature, the sexual differences in K_2 were not significant. The higher K_2 associated with lower temperature suggests higher production potential of this copepod at lower temperatures.

Key word: *Pseudocalanus*, metabolism, carbon, nitrogen, efficiency

Introduction

While the growth of marine planktonic copepods is considered to be governed primarily by temperature and food, temperature is more important than food for those copepods living in food-rich nearshore environments (Huntley & Boyd 1984; Huntley & Lopez 1992). Temperature is known to exert differential effects on the rates of ingestion, development, metabolism, molting and final adult size in *Rhincalanus nasutus* and *Calanus pacificus* (Mullin & Brooks 1970; Vidal 1980a, b, c, d), but such information is scarce for many other copepods.

The copepod genus *Pseudocalanus* is characterized by

small body size, feeding primarily on phytoplankton, and occurrence in large numbers in temperate–boreal, inshore waters of the Northern Hemisphere (Corkett & McLaren 1978). Frost (1989) revised the taxonomy of the genus and created *P. newmani* as a new species. In the Pacific coastal waters of Hokkaido, Japan, *P. newmani* is known to be an integral component of the zooplankton (Yamaguchi & Shiga 1997; Ban et al. 1998). According to Yamaguchi & Shiga (1997), the abundance of *P. newmani* reaches its annual maximum in late spring, following the phytoplankton spring bloom (20–30 $\mu\text{g chlorophyll } a \text{ l}^{-1}$). From late spring onward, *P. newmani* populations sink to deep layers (100–150-m depth) to avoid the lethal high temperatures in the surface layer, and population size is reduced. Nauplii and young copepodites of *P. newmani* are known to be the

main dietary component of the larvae of walleye pollock (*Theragra chalcogramma*) in this region, thereby seriously affecting the survival success rate of the larvae (Kamba 1977; Nakatani 1988). In spite of its importance as a secondary producer in this region, information about physiological responses to seasonally changing temperature in *P. newmani* is presently lacking.

As part of a study on pelagic ecosystem dynamics in the Oyashio region, Lee et al. (in press) successfully raised *Pseudocalanus newmani* from egg to adult in the laboratory under food-satiated conditions, and determined its development and growth rates and egg production rates at various temperatures. In this study, we report respiratory oxygen consumption rates and elemental carbon and nitrogen composition of this copepod reared in the laboratory at different temperatures. Combining the present results with those of Lee et al. (in press), the effect of temperature on the net growth efficiency of this copepod is discussed in the light of seasonal abundance of the copepod in the field.

Materials and Methods

Culture

Live *Pseudocalanus newmani* were collected with a plankton net (0.33 mm mesh) at a station (42°00'N, 141°01'E, 100 m deep) off southwestern Hokkaido on 19 March 1997. Seawater was collected with Van-Dorn water samplers from 10 m depth at the same station, filtered through GF/F filters and the thus obtained filtered seawater (FSW) was used for subsequent experiments. As food, a mixture of three kinds of microalgae including *Pavlova* sp. (10^4 cells ml⁻¹), *Heterocapsa triquetra* (5×10^2 cells ml⁻¹) and *Chaetoceros gracilis* (5×10^3 cells ml⁻¹) grown in f-2 medium (Guillard & Ryther 1962) was given throughout this experiment. In terms of carbon, the concentration of the mixed algae equated to 0.7 µg carbon ml⁻¹, which is evaluated to be well above the threshold concentration that would limit the growth of *Pseudocalanus* copepods (cf. Klein Breteler et al. 1995).

Batches of 20–30 ovigerous females were placed in 1-liter glass jars filled with FSW and the mixed algal diet, and incubated at temperatures of 3, 6, 10 and 15°C under 12L:12D light cycle for 14 d. The selection of temperatures reflected the annual range of habitat temperatures of *Pseudocalanus newmani* at the station (2–15°C, cf. Yamaguchi & Shiga 1997). Preliminary tests showed that *P. newmani* was unable to develop at 20°C. During this period, newly hatched nauplii (N1) appeared and were collected at 12-h intervals. Batches of 100–150 N1 were placed in 1-liter glass jars filled with FSW and the mixed algal diet. The nauplii were grown at the same temperature as the respective adults and under the same light conditions mentioned above. The specimens were transferred to new glass jars filled with fresh FSW and algal diet once every 2–4 d. After they reached copepodite stage 1 (C1), the number of

specimens was adjusted to 40–60 indiv. per glass jar. Development of one stage to the next was traced by collecting cast molts. Detailed analytical procedures are mentioned elsewhere (Lee et al. in press).

Oxygen consumption

Oxygen consumption rates of C6 males and females raised at 3, 6, 10 and 15°C were measured using specimens raised at those respective temperatures. Oxygen consumption rates of C1 through C6 were determined only for those raised at 10°C. For single measurements, 5 to 15 specimens were introduced into a glass bottle (capacity: 30 ml) filled with well-oxygenated FSW and incubated for 24 h. Concurrently, glass bottles without specimens were prepared as controls. At the end of incubation, water samples were siphoned out into two small oxygen bottles (capacity: 7 ml). Oxygen concentration was determined by the Winkler titration method. The precision of the Winkler procedure using 7-ml water samples expressed as the coefficient of variation (CV) is 0.46% (Ikeda & Hirakawa 1998). The limit of detection for water samples containing 6 mlO₂ l⁻¹ (10°C experiments) is estimated at: $6 \times 0.0046 \times 1.96 / \sqrt{2} = 0.038$ (mlO₂ l⁻¹), or 0.27 µlO₂ (0.038 × 7 × 1000/1000).

The specimens left in the experimental glass jars were removed, rinsed briefly with a small amount of distilled water to remove salts, blotted, and placed on a pre-weighed filter paper or aluminum pan. They were dried in an electric oven at 60°C for more than 6 h to obtain dry weight. An electrobalance (Mettler Tredo) was used for weighing to a precision of 1 µg. Dried specimens were used for the analysis of carbon and nitrogen composition with an elemental analyzer (Yanaco CHN Corder MT-5) using p-nitroaniline as a standard. General precision of the analysis was ca. 0.3%

Results

Oxygen consumption rates of C1–C6 at 10°C

Along with development from C1 through C6, oxygen consumption rates (R : µlO₂ indiv.⁻¹ h⁻¹) increased gradually, and the increase was much greater in females than in males (Table 1). Plots of R against DW revealed that the difference between females and males was largely due to dissimilar DWs (Fig. 1), and the regression equation of R on DW was calculated as

$$R = 0.00172DW + 0.0101 \quad (r = 0.976, n = 9, p < 0.001) \quad (1)$$

Oxygen consumption rates of C6 at different temperatures

While R of the C6 females and males decreased consistently with decreasing temperature from 15 to 3°C, their DWs increased greatly with decreasing temperature (Table 1). Prior to analysis of the effect of temperature on R , the effect of dissimilar DWs was removed by fitting R data for

both females and males at each temperature to the common slope (0.00172) of the R -DW relationship at 10°C mentioned above to obtain intercepts (R_0). The temperature-independence of the slope of the R -DW relationship has been verified in some planktonic copepods (cf. Comita 1968; Vidal 1980c). The relationship between R_0 and temperature (T °C) (Fig. 2) was expressed as;

$$R_0 = 0.00154T - 0.00641 \quad (r = 0.938, n = 8, p < 0.001) \quad (2)$$

From equations (1) and (2), R is expressed as a function of DW and T ;

$$R = 0.00172DW + 0.00154T - 0.00641 \quad (3)$$

Body size and C/N composition

DW of C6 males and females decreased progressively with increasing rearing temperatures (Table 1). The relationship was expressed as $DW = 0.86T + 19.68$ ($r = 0.999$, $p < 0.001$) for females, and $DW = 0.56T + 12.69$ ($r = 0.987$, $p < 0.05$) for males. The slope for the females was much steeper than that for the males (covariance test; $p < 0.05$).

Carbon (C) contents of adult specimens raised at temperatures 3–15°C ranged between 49.8–54.7% for males and 40.8–44.3% for females as a percentage of DW, and nitrogen (N) ranged between 8.0–9.4% for males and 10.6–11.3% for females (Table 2). Resultant C/N ratios (by weight) varied between 5.8–6.3 for males and 3.9–4.1 for females over the temperature range. Temperature effects on C, N and C/N ratios were not significant for either males or females (Kruskal-Wallis test, $p > 0.05$). However, within the same temperatures, males contained significantly higher C and lower N than females over the entire range of temperatures (U -test, $p < 0.001$). Reflecting these differences in C and N between males and females, C/N ratios of males were significantly higher than those of females (U -test, $p < 0.01$).

Table 1. Oxygen consumption rates (R) and dry weight (DW) of *Pseudocalanus newmani* copepodite 1 (C1) through C6 at 10°C and C6 at 3, 6 and 15°C all raised in the laboratory. n : number of replicates.

Temp. (°C)	Stage	n	DW ($\mu\text{g indiv}^{-1}$)	R ($\mu\text{l O}_2 \text{ indiv.}^{-1} \text{ h}^{-1}$)
10	C1	4	1.2±0.2	0.014±0.004
10	C2	4	2.2±0.1	0.015±0.005
10	C3	5	3.4±0.4	0.014±0.002
10	C4♀	6	5.0±0.7	0.017±0.003
10	C5♀	5	7.1±0.8	0.022±0.003
10	C6♀	4	10.8±1.9	0.030±0.007
10	C4♂	4	4.4±0.6	0.018±0.003
10	C5♂	4	5.3±0.2	0.019±0.002
10	C6♂	4	6.5±0.5	0.021±0.002
3	C6♀	6	17.2±1.7	0.023±0.004
3	C6♂	6	11.4±0.4	0.020±0.002
6	C6♀	4	14.5±0.7	0.026±0.002
6	C6♂	7	9.2±1.1	0.022±0.002
15	C6♀	8	6.9±0.7	0.027±0.002
15	C6♂	4	4.7±0.3	0.024±0.003

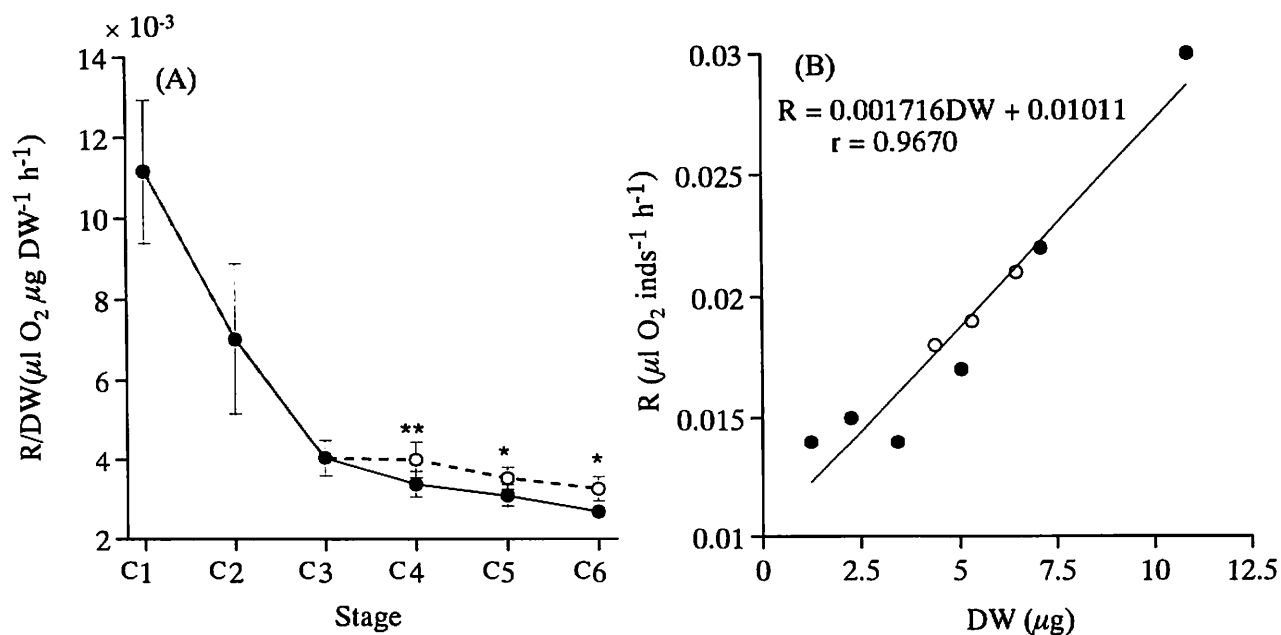


Fig. 1. A. Developmental changes in weight-specific oxygen consumption rates (R/DW) of *Pseudocalanus newmani* stage 1 (C1) through C6 raised at 10°C. Male (open circle) and female data (closed circle) are separated for C4–C6. Asterisks alongside the symbols denote significant difference level (t -test) at $p < 0.05$ (*) or $p < 0.01$ (**). B. The same data in (A) are re-plotted as the relationship between oxygen consumption rates (R) and dry weights (DW). The difference between males and females are not evident in this expression.

Table 2. Carbon (C) and nitrogen (N) composition of *Pseudocalanus newmani* C6 raised at 3, 6, 10 and 15°C in the laboratory. *n*: number of replicates.

Temp. (°C)	Stage	<i>n</i>	C (% of DW)	N (% of DW)	C/N
3	C6♀	3	43.3±1.0	10.6±0.2	4.1
3	C6♂	3	54.4±1.7	8.7±0.6	6.3
6	C6♀	2	44.3±6.3	11.1±0.5	4.0
6	C6♂	3	54.7±1.8	9.4±1.0	5.8
10	C6♀	2	43.8±3.1	11.3±1.0	3.9
10	C6♂	1	51.7	8.2	6.3
15	C6♀	4	40.8±2.4	10.6±0.7	3.8
15	C6♂	2	49.8±0.1	8.0±0.5	6.2
Grand \bar{X}	C6♀	4	43.1±1.6	10.9±0.4	4.0±0.1
	C6♂	4	52.7±2.3	8.6±0.6	6.2±0.2

Net growth efficiency

Net growth efficiency (K_2 , %) during copepodite development of *Pseudocalanus newmani* is defined as: $K_2 = 100G/(G+M)$, where G is growth achieved during the development of C1 to C6 and M is metabolism expended during that development. G and M were expressed as carbon in this study. In calculating G , carbon lost with molts was ignored since the amount is very small (e.g. 3.8% of body carbon at each molt in *Calanus pacificus*, Vidal 1980b).

Development and body mass data for each copepodite stage (males and females) of *Pseudocalanus newmani* at 3, 6, 10 and 15°C were fully reported by Lee et al. (in press). In calculating M , R was computed from mean (geometric) DW between stages, multiplied by developmental time, then the thus obtained data were integrated over all copepodite stages for both males and females. Integrated R data were converted to carbon units according to;

$$R \times 0.97 \times 24 \times 12/22.4 = 12.47R \quad (4)$$

where 0.97 is the respiratory quotient (RQ) for protein metabolism (Gnaiger 1983), 24 is hours in a day, and 12/22.4 is the carbon mass in 1 mol of CO₂.

G was obtained as the difference in body carbon of C1 and C6, assuming that the carbon content (% of DW) of C1 is similar to the mean content of C6 males and females in Table 2. Errors associated with the assumption would not be appreciable as the proportion of body mass of C1 was 12.9–24.8% that of C6 for males and 7.8–18.5% that of C6 for females.

K_2 ranges between 41.9–61.7% for males and 38.4–59.7% for females. For both sexes, the greatest K_2 was seen at 3°C, and decreased gradually with increasing temperature (Fig. 3). Sexual differences in K_2 were insignificant (paired *t*-tests, $p > 0.5$).

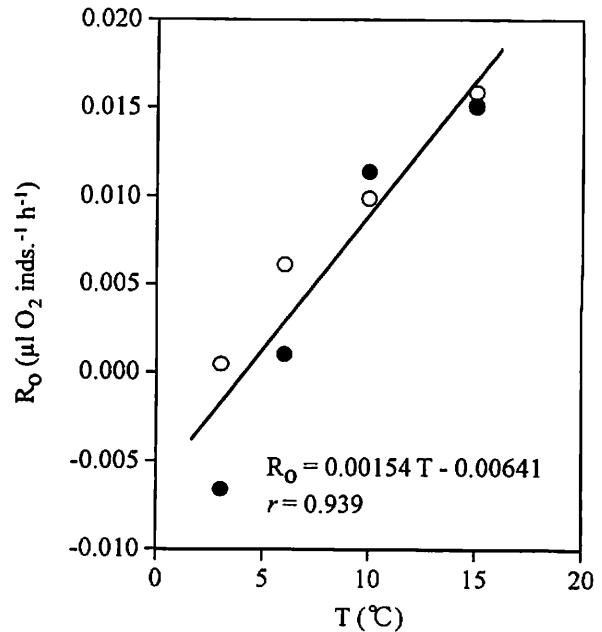


Fig. 2. Relationship between adjusted-oxygen consumption rate (R_0) and temperature (T °C) of C6 males (open circles) and females (closed circles) of *Pseudocalanus newmani* raised at 3, 6, 10 and 15°C in the laboratory. See text for details.

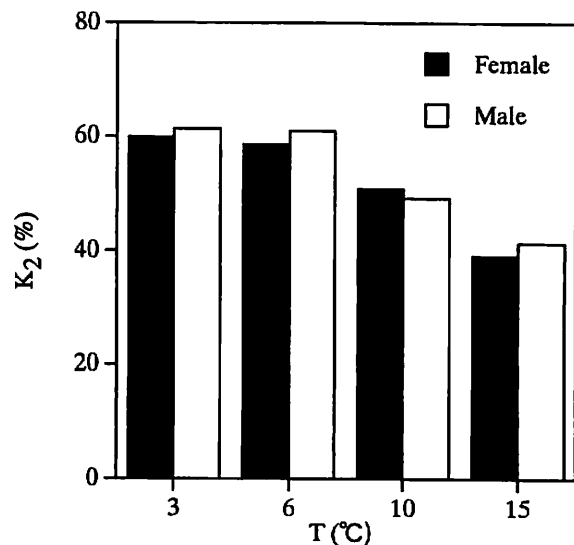


Fig. 3. Calculated net growth efficiency (K_2) for males and females of *Pseudocalanus newmani* growing from C1 to C6 at 3, 6, 10 and 15°C in the laboratory under the condition of sufficient food supply.

Discussion

Oxygen consumption rates (R) of various marine zooplankton are known to be a function of body weight (W) and are expressed as $R = aW^b$ (a , b : constants), with a typical body weight exponent (b) of 0.6 to 0.9 (Ivleva 1980; Vidal & Whitledge 1982; Ikeda 1985; and references therein). Within copepod species, mass exponents less than

unity have also been reported for oxygen consumption data in species, such as *Diaptomus* spp. ($b=0.76$, Comita 1968) and *Calanus pacificus* ($b=0.82$, Vidal 1980c). In the present study, the application of the power regression model for the R -DW relationship of *Pseudocalanus newmani* yielded $R=0.0108DW^{0.381}$ ($r=0.878$), showing an anomalously lower mass exponent (0.381) and lower correlation coefficient than that for the linear regression model shown above [cf. equation (1), $r=0.967$]. This feature seen in the R - W relationship of C1-C6 of *P. newmani*, which diverges from the general pattern, may be due to their narrower DW range (1.24 to 10.83 μg , cf. Table 1), as compared with the range of nearly two orders of magnitude for the other copepods mentioned above. Analyzing the R -DW relationship of small neritic copepods (DW range; 1-15 μg), Conover (1959) also noted better fitting to a linear regression than a power regression.

In marine copepods, R is known to increase with increases in temperature (T), but to decrease beyond their tolerance limits (Conover 1956; Anraku 1964). The maximum temperature copepods can tolerate is primarily species-specific, but varies to some extent among seasonal populations. In the present study, the R of *Pseudocalanus newmani* increased linearly with temperature increasing from 3 through 15°C. Within the range of physiological tolerance, Q_{10} values of biological processes are typically 2-3 (cf. Prosser 1961). Q_{10} values of *P. newmani* predicted from equation (3) are not constant over the 3-15°C temperature range, but vary with 2.41 for 3-6°C, 1.96 for 6-10°C, and 1.68 for 10-15°C. The temperature-dependent Q_{10} values of *P. newmani* are a reflection of the linear R - T relationship, which is deviation from the van't Hoff rule (i.e. exponential increase of R with T).

We examined literature data on the R - T relations of marine planktonic copepods, including *Acartia clausi* and *A. tonsa* (Conover 1956), *Calanus finmarchicus* (Marshall et al. 1935; Clarke & Bonnet 1939; Halcrow 1963), *C. hyperboreus* (Conover 1962), *Calanoides acutus* and *Euchaeta antarctica* (Hirche 1984), *Metridia lucens* and *M. longa* (Haq 1967), and several neritic copepods (Gauld & Raymond 1953; Anraku 1964). In fact, most R - T relations revealed by previous workers fitted well to the van't Hoff rule. However, exceptions were found in that R increased linearly with increasing T in *Centropages hamatus* (Gauld & Raymond 1953), *A. tonsa* (Conover 1956), and *C. hyperboreus* (Conover 1962). It is noted that direct comparison of these previous results with the present results on *Pseudocalanus newmani* may not be valid, since experimental designs between these previous studies and ours are different: acute exposure of field-collected copepods to new temperatures in the previous studies vs. rearing at graded temperatures in this study. As an interpretation for dissimilar responses of R to T , Conover (1956) considered that the linear R - T plots are indicative of a considerable degree of 'eurythermy' and the exponential R - T plots (=van't Hoff rule) are typical of 'stenothermy' in copepods.

Lee et al. (in press) determined body size of all developmental stages of *Pseudocalanus newmani* raised at 3 through 15°C, and noted that the effect of temperature emerged from C2 onward for both males and females. As a result, *P. newmani* adults raised at higher temperatures showed a reduction in DW (Table 1), and the reduction was more marked in females than in males. The correlation between reduced body size of copepods with increased temperatures has been well documented in both laboratory experiments (Corkett & McLaren 1978; Vidal 1980a; Escribano & McLaren 1992) and field observations (Deevey 1964, 1966; Viitasalo et al. 1995), although the sexual differences in the correlation have not been previously examined. Despite changes in DW, an effect of temperature on the C and N composition of *P. newmani* was not seen in this study (Table 2). Vidal (1980a) raised *Calanus pacificus* and *Pseudocalanus* sp. at 8, 12 and 15.5°C and found no temperature effects on the C content of each species. Higher C contents in males than in females, seen in *P. newmani* in this study, have also been reported for other copepods such as *Calanus helgolandicus* (Williams & Robins 1982) and *Calanopia thompsoni*, *Labidocera bipinnata* and *Microsetella norvegica* (Uye 1982). However, some copepods exhibited the reversed pattern or no differences between the sexes (Uye 1982).

The K_2 - T relationships of *Pseudocalanus newmani* (Fig. 3) indicate that this species attains highest K_2 (60-62%) at the lowest temperature (3°C), and K_2 decreases as temperature increases up to 15°C. Taking into account the lowest temperature that *P. newmani* encounters in the field (2°C; Yamaguchi & Shiga 1997), the temperature resulting in the maximum K_2 for *P. newmani* is considered to be close to 3°C. In marine zooplankters other than copepods, a euphausiid *Euphausia pacifica* has been reported to achieve its maximum K_2 of 36% at 11.4°C over a temperature range of 1-20°C (Iguchi & Ikeda 1995) and an amphipod *Themisto japonica* of 19% at 6.8°C over a temperature range of 1-29°C (Ikeda 1991). The differences in the maximum K_2 values and the temperatures resulting in the maximum K_2 reflect species-specific behavioral and physiological dissimilarities among these species. Lower K_2 values of *E. pacifica* and *T. japonica* compared with that of *P. newmani* may be due to higher locomotive activity (greater energy investment in metabolism) in the former two species. *E. pacifica* and *T. japonica* are active, continuous swimmers in contrast to *P. newmani*, which is largely suspended in the water.

In conclusion, the results of the present study indicate that *Pseudocalanus newmani* could cope with changes in habitat temperature over 3-15°C, by changing metabolic rates and adult sizes but maintaining similar C and N composition. Lee et al. (in press) noted that the significant reduction in adult size with increasing temperature resulted in smaller brood size of females and smaller offspring. Despite these adaptive modes for the wide temperature range, the K_2 - T relationship of *P. newmani* revealed higher alloca-

tion of assimilated food to growth at the lower end of its habitat temperature range.

Acknowledgments

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Literature Cited

- Anraku, M. 1964. Influence of the Cape Cod Canal on the hydrography and on the copepods in Buzzards Bay and Cape Cod Bay, Massachusetts. II. Respiration and feeding. *Limnol. Oceanogr.* **9**: 195–206.
- Ban, S., Y. Miyagawa, Y. Okuda and N. Shiga 1998. Succession of the calanoid copepod community in Funka Bay during spring phytoplankton bloom. *Mem. Fac. Fish., Hokkaido Univ.* **45**: 42–47.
- Clarke, G. L. & D. D. Bonnet 1939. The influence of temperature on the survival, growth and respiration of *Calanus finmarchicus*. *Biol. Bull. Woods Hole* **76**: 371–383.
- Comita, G. W. 1968. Oxygen consumption in *Diaptomus*. *Limnol. Oceanogr.* **13**: 51–57.
- Conover, R. J. 1956. Oceanography of Long Island Sound, 1952–1954. VI. Biology of *Acartia clausi* and *A. tonsa*. *Bull. Bingham Oceanogr. Coll.* **15**: 156–233.
- Conover, R. J. 1959. Regional and seasonal variation in the respiratory rate of marine copepods. *Limnol. Oceanogr.* **4**: 259–268.
- Conover, R. J. 1962. Metabolism and growth in *Calanus hyperboreus* in relation to its life cycle. *Rapp. Proc.-Verb. Cons. Int. Explor. Mer* **153**: 190–197.
- Corkett, C. J. and I. A. McLaren 1978. The biology of *Pseudocalanus*. *Adv. Mar. Biol.* **15**: 1–231.
- Deevey, G. B. 1964. Annual variations in length of copepods in the Sargasso Sea off Bermuda. *J. Mar. Biol. Ass. U.K.* **44**: 589–600.
- Deevey, G. B. 1966. Seasonal variations in length of copepods in South Pacific New Zealand waters. *Aust. J. Mar. Freshw. Res.* **17**: 155–168.
- Escribano, R. & I. A. McLaren 1992. Influence of food and temperature on lengths and weights of two marine copepods. *J. Exp. Mar. Biol. Ecol.* **159**: 77–88.
- Frost, B. W. 1989. A taxonomy of the marine calanoid copepod genus *Pseudocalanus*. *Can. J. Zool.* **67**: 525–551.
- Gauld, D. T. & J. E. G. Raymont 1953. The respiration of some planktonic copepods. II. The effect of temperature. *J. Mar. Biol. Ass. U.K.* **31**: 447–460.
- Gnaiger, E. 1983. Calculation of energetic and biochemical equivalents of respiratory oxygen consumption, p. 337–345. In *Polarographic Oxygen Sensors* (eds. Gnaiger, E. & H. Forstner), Springer-Verlag, Berlin.
- Guillard, R. R. & J. H. Ryther 1962. Studies on marine phytoplanktonic diatoms. I. *Cyclotella nana* Hustedt, and *Detonula confervacea* (Cleve) Gran. *Can. J. Microbiol.* **8**: 229–239.
- Haq, S.M. 1967. Nutritional physiology of *Metridia lucens* and *M. longa* from the Gulf of Maine. *Limnol. Oceanogr.* **12**: 40–51.
- Halcrow, K. 1963. Acclimation to temperature in the marine copepod, *Calanus finmarchicus* (Gunner.). *Limnol. Oceanogr.* **8**: 1–8.
- Hirche, H. J. 1984. Temperature and metabolism of plankton. I. Respiration of antarctic zooplankton at different temperatures with a comparison of antarctic and Nordic krill. *Comp. Biochem. Physiol.* **77A**: 361–368.
- Huntley, M. E. & C. M. Boyd 1984. Food-limited growth of marine zooplankton. *Am. Nat.* **124**: 455–478.
- Huntley, M. E. & M. D. G. Lopez 1992. Temperature-dependent production of marine copepods: a global synthesis. *Am. Nat.* **140**: 201–242.
- Iguchi, N. & T. Ikeda 1995. Growth, metabolism and growth efficiency of a euphausiid crustacean *Euphausia pacifica* in the southern Japan Sea, as influenced by temperature. *J. Plankton Res.* **17**: 1757–1769.
- Ikeda, T. 1985. Metabolic rates of epipelagic marine zooplankton as a function of body mass and temperature. *Mar. Biol.* **85**: 1–11.
- Ikeda, T. 1991. Assimilated carbon budget for the hyperiid amphipod *Themisto japonica* (Bovallius) from the Japan Sea as influenced by temperature. *J. Oceanogr. Soc. Jpn* **47**: 7–16.
- Ikeda, T. & K. Hirakawa 1998. Metabolism and body composition of zooplankton in the cold mesopelagic zone of the southern Japan Sea. *Plankton Biol. Ecol.* **45**: 31–44.
- Ivleva, I.V. 1980. The dependence of crustacean respiration rate on body mass and habitat temperature. *Int. Revue ges. Hydrobiol.* **65**: 1–47.
- Kamba, M. 1977. Feeding habits and vertical distribution of wall-eye pollock *Theragra chalcogramma* (Pallas), in early life stage in Uchiura Bay, Hokkaido. *Res. Inst. North Pacific Fish. Hokkaido Univ. Spec. Vol.* **175**–197.
- Klein-Breteler, W.C.M., S.R. Gonzalez & N. Schogt 1995. Development of *Pseudocalanus elongatus* (Copepoda, Calanoida) cultured at different temperature and food conditions. *Mar. Ecol. Prog. Ser.* **119**: 99–110.
- Lee, H.W., S. Ban, T. Ikeda & T. Matsuishi. Effect of temperature on post-embryonic development, egg production and adult body size in the marine copepod *Pseudocalanus newmani*. *J. Plankton Res.* (In press.).
- Marshall, S. M., A. G. Nicholls & A. P. Orr 1935. On the biology of *Calanus finmarchicus*. VI. Oxygen consumption in relation to environmental conditions. *J. Mar. Biol. Ass. U.K.* **20**: 1–27.
- Mullin, M. M. & E. R. Brooks 1970. Growth and metabolism of two planktonic copepods as influenced by temperature and type of food, p. 74–95. In *Marine Food Chains* (eds. Steele, J. H.). University of California Press, Berkeley.
- Nakatani, T. 1988. Studies on the early life history of walleye pollock *Theragra chalcogramma* in Funka Bay and its vicinity, Hokkaido. *Mem. Fac. Fish. Hokkaido Univ.* **35**: 1–57.
- Prosser, C. L. 1961. Oxygen: respiration and metabolism, p. 165–211. In *Comparative Animal Physiology* (eds. Prosser, C. L. & F. A. Brown), W. B. Saunders, Philadelphia.
- Uye, S. 1982. Length–weight relationships of important zooplankton from the Inland Sea of Japan. *J. Oceanogr. Soc. Jpn* **38**: 149–158.
- Vidal, J. 1980a. Physioecology of zooplankton. I. Effects of phytoplankton concentration, temperature, and body size on the growth rate of *Calanus pacificus*. *Mar. Biol.* **56**: 111–134.
- Vidal, J. 1980b. Physioecology of zooplankton. II. Effects of phy-

- toplankton concentration, temperature, and body size on the development and molting rates of *Calanus pacificus* and *Pseudocalanus* sp. *Mar. Biol.* **56**: 111–134.
- Vidal, J. 1980c. Physioecology of zooplankton. III. Effects of phytoplankton concentration, temperature, and body size on the metabolic rate of *Calanus pacificus*. *Mar. Biol.* **56**: 195–202.
- Vidal, J. 1980d. Physioecology of zooplankton. IV. Effects of phytoplankton concentration, temperature, and body size on the net production efficiency of *Calanus pacificus*. *Mar. Biol.* **56**: 203–211.
- Vidal, J. & T. E. Whitledge 1982. Rates of metabolism of planktonic crustaceans as related to body weight and temperature of habitat. *J. Plankton Res.* **4**: 77–84.
- Viitasalo, M. M., M. Koski, K. Pellikka & S. Johansson 1995. Seasonal and long-term variations in the body size of planktonic copepods in the northern Baltic Sea. *Mar. Biol.* **123**: 241–250.
- Williams, R. & D. B. Robins 1982. Effects of preservation on wet weight, dry weight, nitrogen and carbon contents of *Calanus helgolandicus* (Crustacea: Copepoda). *Mar. Biol.* **71**: 271–281.
- Yamaguchi, A. & N. Shiga 1997. Vertical distributions and life cycles of *Pseudocalanus minutus* and *Pseudocalanus newmani* (Copepoda; Calanoida) off Cape Esan, southwestern Hokkaido. *Bull. Plankton Soc. Jpn* **44**: 11–20. (In Japanese with English abstract.)