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Effect of temperature on growth and maturation pattern of *Caprella mutica* (Crustacea, Amphipoda): does the temperature–size rule function in caprellids?

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Abstract Many ectothermal marine animals mature at larger sizes in lower temperature environments and at smaller sizes in higher temperature environments. This phenomenon is called the temperature–size rule. To examine whether this rule controls the appearance of large adults in a winter population of caprellids, individuals of *Caprella mutica* were reared at different temperatures. Caprellids at 5°C died at instar III before they reached maturity. In contrast, the animals reared at 10, 15 and 20°C lived to higher instars and reached maturity within their lifetime. Somatic growth pattern did not change between 10 and 20°C. Maturation instar of males was not affected by temperature. This indicates that the appearance of large adults in winter is not a result of a change in somatic growth pattern with temperature change. However, female maturation size becomes larger due to a delay in maturation at lower temperature. This, in turn, indicates that the temperature–size rule plays a role in the mechanism controlling the appearance of large female adults in winter populations.

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Introduction

Seasonal temperature changes have a major influence on the pattern of growth and reproduction in ectothermic marine invertebrates (Olive 1995; Reitzel et al. 2004). The relationship between growth and temperature provides important information about the life history of marine invertebrates. Individuals experiencing higher temperature environments mature at smaller sizes than individuals experiencing lower temperature environments (Panov and McQueen 1998; Lee et al. 2003). For example, the total body size of adult female copepods *Pseudocalanus newmani* raised under laboratory conditions at 3, 6, 10 and 15°C was 1.33, 1.29, 1.24 and 1.13 mm, respectively (Lee et al. 2003). This phenomenon is called the temperature–size rule (reviewed by Atkinson 1995). This phenomenon is interpreted as a compensatory response to low reproductive rates at low temperatures from the aspect of adaptive plasticity (Angilletta et al. 2004), as fecundity is generally high in large females (Roff 2002).

Caprellids (Crustacea, Amphipoda) typically occur on algae and artificial substrates from the intertidal to the subtidal zone (Hirayama and Kikuchi 1980; Takeuchi et al. 1990; Sellheim et al. 2010). These habitats are influenced by diurnal and seasonal temperature fluctuations. In temperate and sub-boreal caprellid species, overwintering populations exposed to low temperatures have been found to comprise large adults, whereas summer populations were composed of small adults. For example, Bynum (1978) compared maturation patterns of female *Caprella penantis* between summer and winter populations in North Carolina and revealed that summer animals reached sexual maturity at a smaller size (3.7 mm) than winter animals (4.7 mm). Hosono and Sakurai (2006) also compared the size of mature females of *C. acanthogaster* in northern

Japan and found a significant negative relationship between maturation size and cumulative temperature. To date, however, it has not been clarified whether the temperature–size rule might control the appearance of large adults in winter. One way to solve this issue is to compare growth patterns between winter and summer generations using cohort analysis. However, because caprellids perform rapid growth rates and mature within about 1 month at 13–20°C (Takeuchi and Hirano 1991, 1992; Cook et al. 2007), a cohort may be composed of several generations hatched at different times and, therefore, discriminating the growth pattern in each generation may not be feasible. In this study, *Caprella mutica* were reared from juvenile to mature stages at different temperatures, and growth and maturation patterns were examined against temperature.

Materials and methods

Rearing system

The sampling site was located on the Pacific coast of northern Japan (41°56′ N, 140°57′ E); mean monthly water temperatures from 1999 to 2003 ranged from 2.8 to 19.2°C (data provided by Usujiri Fisheries Laboratory, Hokkaido University). Four rearing temperatures (5, 10, 15 and 20°C) reflecting the seasonal temperatures at the sampling site were used. Parent individuals were collected on October 4, 2002, for rearing at 15 and 20°C, on January 15, 2003, for rearing at 10 and 15°C, and on November 21, 2003, for rearing at 5°C. Individuals attached to Laminarian rearing ropes were collected by hand and transferred in pairs to 40-ml polystyrene containers (4 cm diameter and 7 cm height) with seawater and red algae (*Neorhodomela larix*; 5 cm) as substrate. Algae fragments were replaced every second day. Caprellids were daily fed commercial goldfish flakes (Tetrafin, Tetra Japan Inc.), which is composed of both vegetable and animal materials. This food was considered suitable for rearing *C. mutica* because of the omnivorous feeding habits of the species (Sano et al. 2003). Photoperiod was maintained at 12 h light: 12 h dark. To minimize the effect of field temperature on embryos, four or five pairs of parents were maintained through copulation, oviposition and hatching of embryos at each trial temperature. Embryos that emerged from the brood pouch were recorded as juveniles at instar I and 0 days, separated from the parent animals and subsequently reared together in groups of 10–20 juveniles until instar III. Molting of a juvenile reared within a group was confirmed by the number of the flagellar articles of antenna 1, in which the number of the articles increases by two segments with each molt. As soon as the sexes could be identified at the earliest at instar III, the juveniles were separated and reared individually. Daily

observations and water exchange were performed at fixed times under a binocular microscope (Olympus SZX 12). When an individual had molted, a digital photograph was taken through the microscope and the body length was measured with image analyzing software (NIH Image 1.56, National Institute of Health, USA). Body length was taken as the sum of the axial lengths of the head and the pereonites 1–7.

Identification of sex and maturity

Female caprellids can be identified by the presence of oostegites at pereonites 3 and 4, whereas males can be identified by the presence of abdominal appendages. Sexual maturation in females can be identified from the full formation of oostegites (Takeuchi and Hirano 1991). Although there is no morphological character to identify maturation in males, it is known that large males have elongated pereonites 1 and 2, an enlarged gnathopod 2 and dense setation on pereonite 2 and gnathopod 2, while females lack these characteristics (Hosono and Munehara 2001). The present study established a male maturation index using pereonite length. Male *C. mutica* ($n = 261$) were collected during monthly caprellid monitoring at a laminarian cultivation site in 1999–2000 and 2002–2003 (Hosono and Sakurai 2006). The relationship between body length, length of pereonite 2 (elongatable) and pereonite 3 (unelongatable) was analyzed with the R function applying two-piece linear regressions (http://www.aoki2.si.gunma-u.ac.jp/R/src/oresen.R. Accessed January 28, 2010):

$$P = a_1 L + b_1 \quad (L \le c);$$
$$P = a_2 L + b_2 \quad (L > c),$$

where $a_{1,2}$ and $b_{1,2}$ are parameters in the two regressions that switch at point c, P is the length of pereonite 2 or 3 and L is body length. These parameters were estimated for pereonites 2 and 3, respectively. Maturation criteria were defined as the pereonite ratio ($=P/L$) at the switching point c in pereonites 2 and 3.

Data analyses

Because *C. mutica* shows a distinct sexual dimorphism, somatic growth patterns were analyzed separately for each sex. To examine whether somatic growth patterns are different at the studied temperature levels, lengths at each instar were compared between temperatures using Kruskal–Wallis tests. Somatic growth patterns were also quantified from the following equations: $L = \alpha_1 x^{\beta_1} + \gamma_1$ in males and $L = \alpha_2 / \{1 + \beta_2 \exp(\gamma_2 x)\}$ in females, where L is body length, x is instar and $\alpha_{1,2}$, $\beta_{1,2}$ and $\gamma_{1,2}$ are parameters determined by sex (Takeuchi and Hirano 1991). Data for

juveniles from instars I–VI were shared between sexes in the parameter estimation for these equations.

The cumulative durations of instars were described through exponential growth curves: $D = \exp(\alpha_3 x + \beta_3) + \gamma_3$, where x is instar, D is cumulative duration of each instar and α_3, β_3 and γ_3 are parameters determined by temperature levels.

Statistical analyses were conducted with R, version 2.8 (R Development Core Team 2009), and the non-linear regressions were conducted with the statistical software STATISTICA 6.0.

Results

Sexual differentiation and maturity

At 5°C, juveniles died at instar III before sexual identification was possible (Table 1). At >10°C, in contrast, caprellids survived at least up to instar IX (Table 1). Male abdominal appendages could be confirmed at instar III at 20°C, and instar IV at 10 and 15°C. There was, however, no significant correlation between ratio of males appearing and temperature at instar IV (Cochran-Armitage test: $\chi^2 = 0.8$, $df = 1$, $P > 0.05$). After instar V, it was possible to identify the sex of all individuals reared at 10, 15 and 20°C.

Switching points c (L, P) were obtained by two-piece regressions: c_{p2} (8.38, 1.55 mm) and c_{p3} (9.36, 1.54 mm) (Fig. 1). Therefore, maturation was defined when the pereonite 2 ratio was >0.21 and the pereonite 3 ratio

was < 0.16 (Fig. 1). In the rearing experiment, the pereonite 2 ratio drastically changed at maturation (Fig. 2). When elongation of pereonite 2 was observed, other characteristics indicating maturation were observed as well, such as the development of gnathopod 2 and thickness of setation on pereonite 2 and gnathopod 2 (Fig. 2). Males started to mature at instar VIII, and all males matured by instar X (Fig. 3a). Maturation patterns in males were similar at 10, 15 and 20°C.

Maturation patterns in females were different at different temperatures. At 20°C, 88.9% of the females had matured at instar VIII, while at 15°C, all females had matured at instar IX (Fig. 3b). At 10°C, females started to mature at instar IX, but the maturation rate was only about 25%. All the females were confirmed to have produced eggs at their molting to maturity.

Somatic growth

At hatching, all juveniles measured between 1.27 and 1.31 mm and increased in size to between 2.26 and 2.50 mm at instar III. Despite this small size range, the analyses revealed significant differences in body length at different temperatures for instars I–IV among juveniles, for instars IV–V and VII–IX in males, and for instars VII–VIII in females (P each <0.05; Fig. 4). These differences in body size did not follow a pattern in which body length at each instar became larger with decreasing temperature. Estimated parameters in the equations were similar between temperatures (Table 2). Well-fitted regression curves were obtained for each sex (Table 2; males: $L = 0.11x^{1.96} + 1.27$,

Table 1 Number of individuals of surviving *Caprella mutica* examined at each instar and temperature

| Temperature	Sex	Instar													
		I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV
5°C	Juveniles (n)	357	234	32											
	Males (n)	–	–	–											
	Females (n)	–	–	–											
	Number of survivors (in total) in %	100	65.5	9.0											
10°C	Juveniles (n)	61	61	61	35										
	Males (n)	–	–	–	20	30	17	17	15	12	4	1			
	Females (n)	–	–	–	–	31	31	26	16	8					
	Number of survivors (in total) in %	100	100	100	90.2	100	78.7	70.5	54.1	27.9	6.6	1.6			
15°C	Juveniles (n)	37	37	37	25										
	Males (n)	–	–	–	12	17	16	15	15	15	7	2	1		
	Females (n)	–	–	–	–	10	12	10	9	9	4	4	1	1	1
	Number of survivors (in total) in %	100	100	100	100	73.0	75.7	67.6	64.9	64.9	29.7	16.2	5.4	2.7	2.7
20°C	Juveniles (n)	32	32	28	19										
	Males (n)	–	–	4	5	13	11	10	9	8	7	3			
	Females (n)	–	–	–	–	12	12	10	6	2	2	2	2	2	
	Number of survivors (in total) in %	100	100	100	78.1	75.0	71.9	62.5	46.9	31.3	28.1	15.6	6.3	6.3	
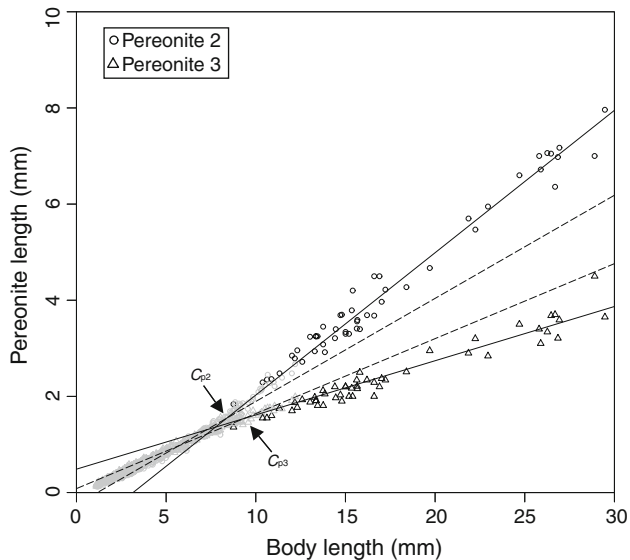
Fig. 1 Relationship between body length and length of pereonites 2 and 3 in male *Caprella mutica*. *Dashed* and *solid lines* indicate two-piece regression lines. Matured individuals (*black symbols*) and immatured individuals (*gray symbols*) were discriminated based on maturation criteria of *P/L* at switching points c_{p2} and c_{p3}

(a) Immature male, instar IX
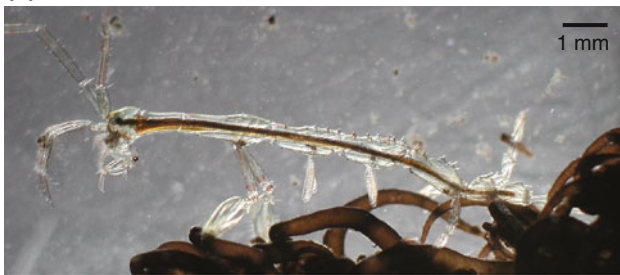
(b) Mature male, instar X

Fig. 2 Morphological change in male *Caprella mutica* at maturation. **a** Instar IX (immature individual), with a pereonite 2 ratio of 0.209 and a pereonite 3 ratio of 0.163; **b** Instar X (mature individual), with a pereonite 2 ratio of 0.248 and a pereonite 3 ratio of 0.136

Fig. 3 Percentages of matured individuals of (**a**) male and (**b**) female *Caprella mutica* at 10–20°C. Numbers of individuals examined at each instar are shown in Table 1. N.D., no data

Molting pattern

There were statistically significant differences in inter-molt duration between the sexes at instars V–VII at 10°C, at instar IX at 15°C and at instar VII at 20°C (*P* each < 0.05; Fig. 5). These differences, however, were only a few days. The data for both sexes were combined for later analysis. An exponential growth curve of the combined data from both sexes was well fitted to the cumulative duration of days from hatching to each instar at 10–20°C (r^2 each > 0.89; Fig. 5), while the estimated regression line at 5°C followed a linear model ($r^2 = 0.95$; Fig. 5). The number of days to maturity was inversely proportional to temperature. In females, mature individuals began to appear after 60 days (instar IX), 44 days (instar IX) and 28 days (instar VIII) at 10, 15 and 20°C, respectively. In males, mature individuals were confirmed after 57 days (instar IX), 32 days (instar VIII) and 30 days (instar IX) at 10, 15 and 20°C, respectively.

Discussion

Temperature–size rule in *C. mutica*

In this rearing experiment, the somatic growth pattern of *C. mutica* did not change with temperature within the range of 5–20°C. Boos (2009) also reared *C. mutica* from

$r^2 = 96.9$; females: $L = 11.47/(1 + 11.7e^{0.36x})$, $r^2 = 96.6$). The somatic growth pattern in males revealed a rapid size increase by which the body length reached between 13.8 and 14.5 mm at instar XI. In females, increment in body length was suppressed after instar VIII, having reached a size of about 10 mm.
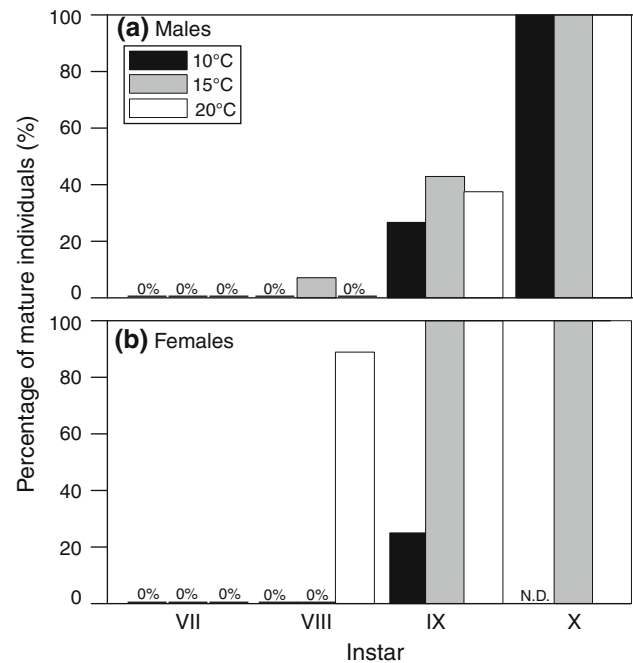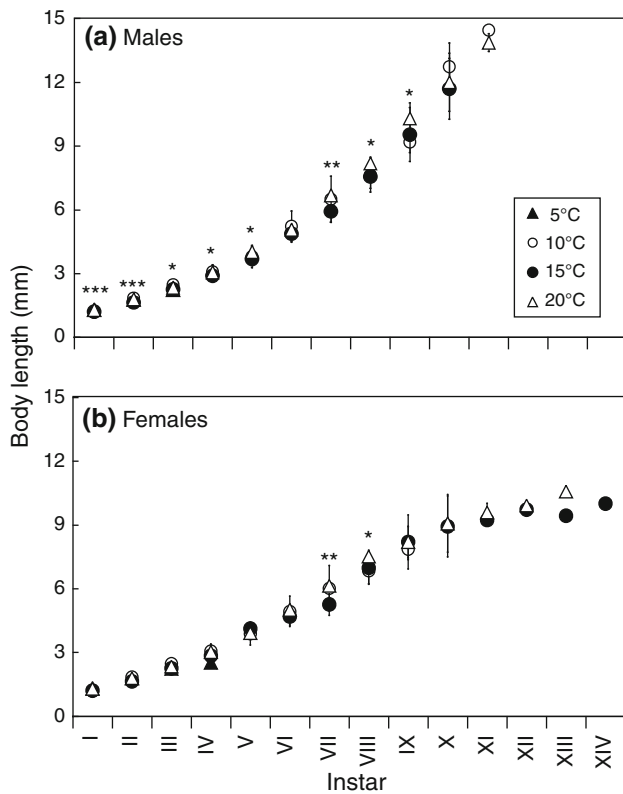
Fig. 4 Somatic growth patterns of (**a**) male and (**b**) female *Caprella mutica* at 5–20°C. * indicates significant differences between rearing temperature levels (***P < 0.001, **P < 0.01, *P < 0.05)

Table 2 Parameters of non-linear regressions between length and instar

Temperature	Male $y = \alpha_1 x^{\beta_1} + \gamma_1$				Female $y = \alpha_2/\{1 + \beta_2 \exp(\gamma_2 x)\}$			
	α_1	β_1	γ_1	r^2	α_2	β_2	γ_2	r^2
5°C	0.12	1.98	1.26	91.6	–	–	–	
10°C	0.10	2.03	1.40	92.9	11.34	10.98	0.36	96.0
15°C	0.11	1.94	1.19	96.4	11.22	12.39	0.37	95.4
20°C	0.13	1.92	1.23	98.6	11.57	12.37	0.38	97.7
All data	0.11	1.96	1.27	96.9	11.47	11.70	0.36	96.6

Juvenile data (instars I–IV) were used in both sexes

juvenile to immature stages at 4, 10 and 16°C and reported that the somatic growth at 10 and 16°C were similar, while growth at 4°C was only of little size increment. This somatic growth pattern reported for *C. mutica* differs from the results of many other rearing experiments in ectothermic animals. In fact, Atkinson (1995) estimated that more than 80% of ectothermic species studied in laboratories exhibited faster growth but were of smaller adult body size at higher rearing temperatures compared to lower temperatures. Why did the somatic growth pattern of *C. mutica*
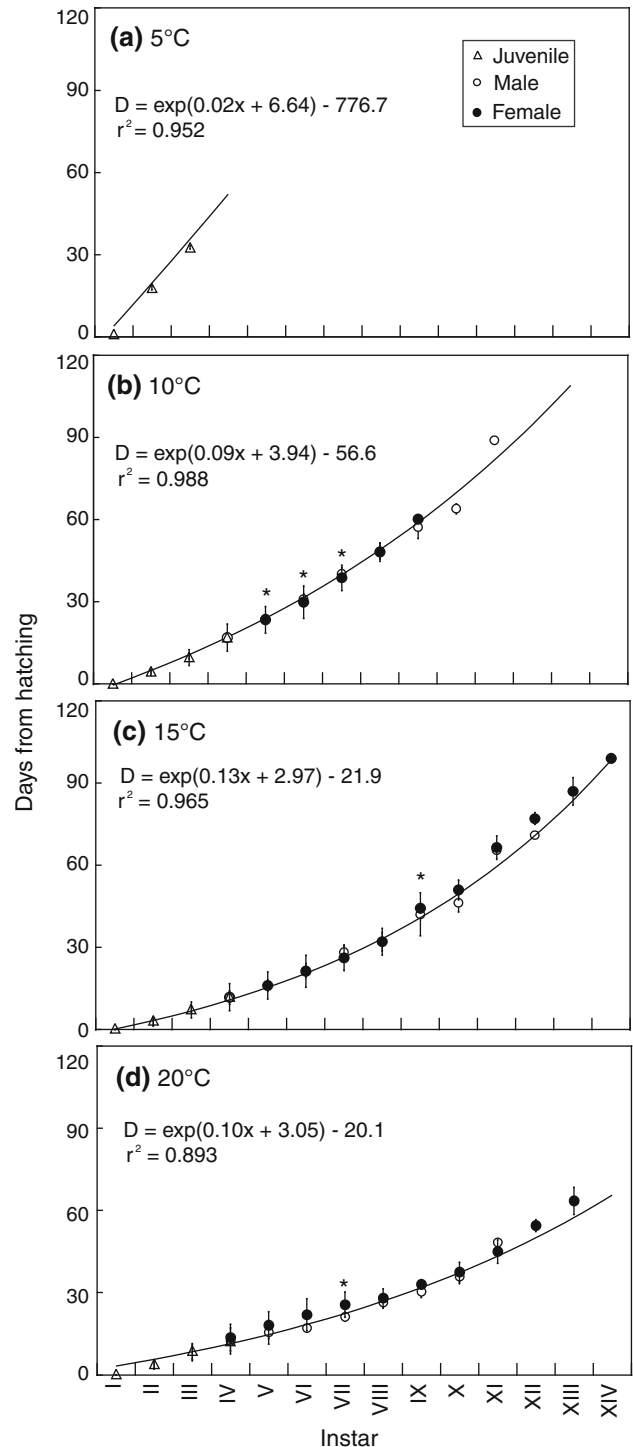

Fig. 5 Durations of molt cycles in *Caprella mutica* at 5–20°C (**a–d**). Non-linear regression curves are shown. * indicates significant difference between sexes (*P* < 0.05)

not change with temperature? The physiological basis of the temperature–size rule is explained by Bertalanffy's growth function (Bertalanffy 1960), in which growth rate is the difference between rates of anabolism and catabolism:

$$dW/dt = aW^c - bW^d,$$

where W is body mass, a and b are coefficients of anabolism and catabolism, and c and d are exponents that define the allometry of anabolism and catabolism. Temperature change can influence the largest attainable body size, because generally coefficients and the exponents related to the catabolism in the function (i.e., b and d) have greater sensitivity for temperature change than those related to the anabolism (see discussion in Angilletta et al. 2004). Vassilenko (1986) measured the metabolic rates of several caprellid species, including *C. mutica*, and found that the rates were only about 2/3 of those found in gammarid amphipods. The reason that the temperature–size rule was not observed in *C. mutica* at 10–20°C is considered to be the result of a regulation in the increase in catabolism with increased temperature due to caprellid-specific low metabolic rates observed between 10 and 20°C.

Field studies of caprellid populations report that larger adults tend to appear in winter. Bynum (1978), for example, compared maturation patterns of female *C. penantis* between summer and winter populations using the size at which 50% of the females were sexually mature and found that summer animals reached sexual maturity at a smaller size (3.7 mm) than winter animals (4.7 mm). Hosono and Sakurai (2006) also compared the size of mature females in *C. acanthogaster* and found a significant negative relationship between maturation size and temperature. Similarly, Fedotov (1992) reported that the premature females in March matured in May at sizes between 7 and 15 mm, whereas females that matured in June were 6 mm in size (cf. Table 3 and Fig. 1 in Fedotov 1992). This temperature-related size shift in matured females can most likely be explained by the completion of maturation at different instars observed in the present rearing experiments. The maturation instar of female *C. mutica* changed with decreased temperature, with 100% reaching maturity at instar VIII at 20°C, instar IX at 15°C, and only 25% reaching maturity at instar IX at 10°C. The somatic growth pattern, in contrast, did not change with temperature. As a result, mature females were larger at lower temperatures (estimated mean sizes are 6.92, 7.87 and 8.69 mm at instar VIII (20°C), instar IX (15°C) and instar X (10°C), respectively). This indicates that the phenomenon reported in previous field studies is a consequence of plasticity in female maturation timing based on the temperature–size rule.

Cook et al. (2007) reared *C. mutica* at 13°C and reported that females mature at instar VII, which is even earlier than the lowest instar at which maturation was observed in the present study (instar VIII at 20°C). This difference may be explained by differences in rearing conditions: for example, food (diatoms in Cook et al. (2007) and commercial goldfish flakes in the present study) and light condition

(14L: 10D in Cook et al. (2007) and 12L: 12D in the present study). These contrasting results reflect the high variability in maturation timing of female *C. mutica*.

Male maturation patterns, assessed by morphological maturation indices, were similar at the different temperatures assessed in the present study. Takeuchi and Hirano (1991) reported that male *C. danilevskii* can successfully copulate before considerable morphological development of the gnathopod 2, which implies that functional maturation precedes morphological maturation. It is possible that morphological maturation does not correspond to functional maturation in *C. mutica* as it does in *C. danilevskii*. However, morphological immaturity in males would be a considerable disadvantage for reproductive success in nature. In the presence of male–male competition, for example, larger males of gammarid (*Eogammarus oclairi*) have a smaller risk of losing the female during pre-copulatory pair formation than smaller males (Iribarne et al. 1995). Male caprellids show pre-copulatory guarding behavior toward females, defending them from non-guarding males (Lewbel 1978; Aoki 1996). Little is known of the intensity of male–male competition in *C. mutica*, but pre-copulatory guarding was observed in all parents in the present study. Therefore, morphological maturation in male *C. mutica* can be also considered to be directly reflected in their reproductive success. Size- or morphology-dependent reproductive success in males would prevent the occurrence of small maturation size in males and is suggested to be one of the reasons why male maturation timing did not change as observed for females in the present study.

Seasonal population fluctuation in the field

Hosono (2009) described reproductive patterns of *C. mutica* at 5–20°C. This information and the present study explain how seasonal changes in growth and reproduction influence fluctuations in the dynamics of field populations. At 5°C, juveniles of *C. mutica* only survived up to 1.5 months, but mature females were able to oviposit within an interval of about 1 month at this temperature (Hosono 2009). Between 10 and 20°C, caprellids developed to maturity in 1–2 months, and adults of the species reproduced at intervals of 10–20 days (Hosono 2009). Therefore, when low temperature conditions (<5°C) persist for long periods, newly hatched juveniles cannot develop to mature stage and the population will show a bimodal structure with mostly large adults and small juveniles. When temperature exceeds 10°C, juveniles develop normally, molting and reproductive rates increase exponentially, recruitment occurs continuously and the population will be evenly composed of mixed generations with short generation times at higher temperatures.

Fedotov (1992) investigated population dynamics of *C. mutica* in a sea grass meadow (*Zostera marina*) in Posyet Bay, Russia, and reported that there were two generations in the population: a spring generation with rapid growth rates and a summer generation with moderate growth rates that overwintered into the next season. That growth rates of the two generations depend on the prevailing temperatures experienced in each season is consistent with the predictions stated in the present study.

Fedotov (1992) also considered juveniles (<4 mm) and mature females with empty brood pouches found from August to October belong to a summer generation that did not reproduce in that season. However, the mean sea surface temperature at Posyet Bay measured from August to October was between 13 and 23°C (estimated from Fig. 3 in Gayko 2000). In this temperature range, *C. mutica* can mature within 2 months and can repeatedly oviposit at intervals of about 10 days. Therefore, the presence of mature females and juveniles from August to October reported by Fedotov (1992) is more likely to indicate the active reproduction of *C. mutica* during this period.

This paper is the first to show changes in growth and maturation patterns at different temperatures in *C. mutica*. Although the somatic growth pattern did not change with temperature, the maturation pattern of females followed the temperature–size rule. The present results could help to further understanding of population dynamics of *C. mutica* inhabiting areas with different thermal ranges.

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