

Temperature explains reproductive dynamics in caprellids at different latitudes

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ABSTRACT: Due to growing concerns regarding ocean warming, it has become important to precisely understand the influence of temperature on the reproduction of marine organisms. This study investigated the population dynamics of the small temperate epifaunal crustaceans *Caprella danilevskii* and *C. scaura* and the boreal species *C. cristibrachium*, which occur sympatrically in a boreal area, and examined whether reproductive dynamics within a location and along a latitudinal gradient can be explained by seasonal temperature fluctuations. Although the 2 temperate species are known to reproduce throughout the year in their temperate habitat, the population dynamics of all 3 caprellids showed the same pattern in that active reproduction was limited to June–October. A simple simulation using a temperature–maturation function in caprellids could explain the occurrence of mature females and the timing of active reproduction in the study area. While the simulation predicted continuous reproduction at temperatures above 12°C, the caprellid densities decreased immediately after the peak temperature in the field. These results suggest that the reproductive patterns and population dynamics in caprellids within/between locations can be simply explained by maturation time, which is controlled by local temperature fluctuations, but the results also highlighted the existence of other ecological factors (e.g. food availability or predation pressure) that can cause drastic population decreases in the summer.

KEY WORDS: Epifauna · *Caprella* · Reproductive dynamics · Life history

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INTRODUCTION

The influence of temperature on reproductive timing has been a central theme in phenological studies of marine organisms. Recently, because of growing concerns regarding ocean warming, it has become important to precisely understand the influence of temperature on the reproduction and population processes of marine organisms, especially for the purpose of predicting future species distribution (e.g. Lima et al. 2007, Mieszkowska et al. 2013) or potential competition between native and invasive species (Stachowicz et al. 2002, Reinhardt et al. 2013).

In marine macro-plant communities, temperature also has a strong influence on the timing of life-history events of associated epifaunal species. Because of

the importance of small mobile epifauna as a secondary producer in the community (Duffy 1990, Norderhaug & Christie 2011, Best & Stachowicz 2012) and the conspicuous seasonal fluctuation in animal density (e.g. Mukai 1971, Zakhama-Sraieb et al. 2011), many studies of factors controlling epifaunal species population dynamics have been performed. Epifaunal densities are controlled by or correlated with various ecological processes, such as seasonal changes in algal biomass (Mukai 1971, Guerra-García et al. 2011a), fluctuation in food availability (Duffy 1990, Edgar 1990), predation pressure (Duffy & Hay 1990), seasonal changes in habitat character as a refuge (Martin-Smith 1993, Norderhaug 2004) and changes in the habitable space in the algal community (Christie & Kraufvelin 2004). However, because tem-

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perature and other ecological processes have simultaneous effects, the combined influences of the processes make it difficult to identify their individual effects on population dynamics.

Caprellids (Amphipoda, Crustacea) are typical epifauna and are suitable organisms to quantify the effects of temperature and other ecological processes that control the seasonal fluctuations of epifaunal densities in algal communities. Since Takeuchi & Hirano (1991) succeeded in rearing *Caprella danilevskii*, knowledge of their life-history parameters, such as growth rate and reproductive traits, has been obtained from laboratory experiments (e.g. Takeuchi & Hirano 1992a,b, Cook et al. 2007, Baeza-Rojano et al. 2011, Hosono 2011). Caprellid population dynamics in the field have also been studied from various perspectives, including relations with the habitable substrate (Harrison 1940, Aoki 1988, Guerra-García et al. 2011a), influence of environmental conditions (Sconfiatti & Luparia 1995), and invasive species biology (Ashton et al. 2010, Prato et al. 2013). This information on caprellids enables the separate evaluation of the effect of temperature and other ecological processes.

With respect to reproductive dynamics, various patterns occur in caprellids. Many temperate-zone species reproduce continuously throughout the year (e.g. Imada & Kikuchi 1984), and boreal and arctic species reproduce in a limited season (Hughes 1978, Węśławski & Legeżyńska 2002). Because these reproductive periods gradually decrease with increasing latitude, the reproductive pattern in caprellids is bound to the local temperature range (Sconfiatti & Luparia 1995). Differences in reproductive patterns among locations (latitudes) and seasonal changes in reproductive potential within a location could be investigated by evaluating how local temperature influences maturation time. A simple approach is to investigate the population dynamics of a species with a wide latitudinal range to determine whether the species population dynamics can be explained by local temperature fluctuations, and to examine whether differences in reproductive dynamics can be explained using the same logic between latitudes.

In northern Japan, 3 caprellids (*Caprella cristibrachium*, *C. danilevskii* and *C. scaura*) occur sympatrically on the perennial red algae *Gelidium amansii* (Hosono 2006). Of these 3 species, *C. danilevskii* and *C. scaura* are mainly distributed in a temperate area: occurrences of *C. danilevskii* in the northern hemisphere are reported from Trinidad (10°N) to South Sakhalin (48°N), and *C. scaura* from the Virgin

Islands (18°N) to Vladivostok (43°N) (McCain & Steinberg 1970). These 2 temperate species reproduce continuously throughout the year (Imada & Kikuchi 1984, Prato et al. 2013). In contrast, *C. cristibrachium* is distributed in boreal regions, such as Alaska, the Bering Sea, and Possjet Bay of the northern coast of the Sea of Japan (Vassilenko 1974).

The present study includes the following: (1) an investigation of the population dynamics of the 3 caprellid species in terms of the seasonal change in population structure, (2) estimation of a relationship between temperature and maturation time in caprellids based on published data, (3) determination of whether the relationship can explain the observed reproductive dynamics in the study area, and (4) evaluation of whether the relationship can predict different patterns of reproductive dynamics in higher and lower latitude areas.

MATERIALS AND METHODS

Population dynamics in the field

Monthly sampling of the caprellid populations were conducted at Usujiri (41° 57' N, 141° 58' E; Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m511p129_supp.pdf), Hokkaido Island, Japan, during July 1999–June 2000 and August 2002–August 2003. Four areas (25 × 25 cm) of a bed of the perennial red alga *Gelidium elegans* (<4 m depth) were selected randomly, and the algae within the areas were collected. The collected algae were brought back to the laboratory and rinsed in fresh water to separate the epifauna. Epifaunal species were retrieved with a 100 µm mesh sieve, and the caprellids were collected, fixed with 90 % ethanol, and identified under a stereomicroscope. Algal dry weights were measured to calculate the caprellid density. For population structure analysis, approximately 200 individuals of each caprellid species were randomly selected from the monthly samples, and the sex, maturity and body lengths of the specimens were measured. The body length was taken as the sum of the axial lengths of the head and pereonites 1–7. Female caprellids could be identified by the presence of oostegites at pereonites 3–4, and males could be identified by their abdominal appendages. Individuals that expressed no sexual characteristics were categorized as juveniles. Sexual maturity in the females was identified by a complete brood pouch with setae on the edge of oostegites. Illustrations of the target species can be found in Fig. S2 in the Supplement. The number of *C. scaura*

specimens from the original sampling site was insufficient to make a size histogram, so additional samplings were conducted from the caprellid population on another red alga species (*Neorhodomela aculeate*) near the main sampling area in October 2002 and April–May 2003. Daily water temperature data were provided by the Usujiri fisheries laboratory of Hokkaido University.

The relationship between the experienced temperature and size of the mature females was described by a generalized additive model (GAM) in which the size of the mature females is the response variable and the mean temperature for 30 d before each sampling date is the explanatory variable, using Gaussian distribution (i.e. normal distribution) for a response variable and identity link function (i.e. prediction is directly of the values of the response). To test the linearity/non-linearity of the relationship, the GAM was compared with a simple linear model using the Akaike information criterion (AIC). These analyses were performed with the mgcv package in the software R 2.14 (R Development Core Team 2011).

Simulation of reproductive dynamics

The relationship between temperature and maturation time in caprellids was estimated based on previously published data (see Table 1) by fitting the following Belehradek equation:

$$D = a(T - b)^c \quad (1)$$

where D is the days to maturation, T is the temperature, and a, b, c are constants to be fitted (Takeuchi & Hirano 1992b). The parameter a determines the rate scale, b represents the temperature for biological zero (the theoretical limit of no growth), and c describes the effect of temperature on the reaction duration. Generally, this equation represents a species-specific response to temperature change. However, the parameters in the Belehradek equation for the 3 species are unknown, except for the incubation period parameters of the temperate *C. danilevskii* (Takeuchi & Hirano 1992b). In the present study, 2 Belehradek equations were examined: (1) parameters a – c were estimated using all the data on caprellids that was previously published, or (2) the values of parameters b and c were fixed to the values known for *C. danilevskii* ($b = 5.5$ and $c = 0.90$), and parameter a was estimated from the maturation time of temperate *C. danilevskii* and *C. scaura* (Takeuchi & Hirano 1991, Sakaguchi 1989).

These parameters were estimated by the non-linear least-squares methods using the 'nls' function in R. The 2 estimated Belehradek equations were applied to a simple simulation of reproductive dynamics (as described below), and the equation that could explain the reproductive dynamics observed in the study area was determined.

The Belehradek equation expresses the maturation time as a function of temperature. Thus, the days to maturation can be solved as a minimum n_1 satisfied by the following inequality:

$$a < \sum_{i=1}^{n_1} (T_i - b)^{\frac{1}{c}} \quad (2)$$

where i is days from birth, and T_i is the observed temperature at i . Because caprellids usually reproduce several times after maturation, the days to the second and third reproduction were also solved as n_2 and n_3 with the assumption that $a_2 = a + 5(20 - b)^c$ and $a_3 = a + 10(20 - b)^c$ based on the reproductive interval of 5 d at 20°C observed in *C. danilevskii* in this study area (Takeuchi & Hirano 1992a). In this simulation, I assumed one female caprellid birth every day from June 1, 1999 to October 1, 2001 and calculated the days to reproduction (n_1 , n_2 , n_3) for every female; I then counted the number of reproductions each day during the simulated period. Note that this calculation only considers the timing of reproductions and does not consider the recruitments of the individuals that are produced by the reproductions. More realistically, active reproduction and a fast maturation time in the high-temperature season may increase the numbers of births and maturations per day. Conversely, reproduction may cease in the low-temperature season. However, to make it easier to evaluate the influence of temperature on reproductive dynamics, I assumed that only one female per day would be generated continuously through the examined period.

The reproductive patterns in latitudinally different areas were also simulated. Amakusa facing the East China Sea (32° 43' N, 130° 32' E) and Rugozero in the White Sea (66° 34' N, 33° 08' E) were selected as reference areas because detailed reproductive traits of caprellids in these areas have been reported by Imada & Kikuchi (1984) and Heptner (1963). Annual temperature data for Amakusa, archived at www.jodc.go.jp/data/coastal/obs_detail_data.htm (accessed 15 Oct 2013), were used. Temperature data for Rugozero was estimated from Heptner (1963; his Fig. 7). Using the same simulation method in the boreal area and the temperature observed in each referenced area, the number of reproductions per day was counted for 2 years.

RESULTS

Fluctuation of algal biomass and caprellid densities

In the study area, the sea surface temperature was the lowest in February–March (min: 0.7°C in February 2000 and March 2003), and it was highest in August–September (max: 25°C in August 1999, 21.5°C in August 2002; Fig. 1A). The biomass of *Gelidium elegans* was low in the high-temperature season (131.1 and 410 g m⁻² in August 1999 and August 2002) and increased in the low-temperature season (450.9 g m⁻² and 949.5 g m⁻² in March 2000 and 2003; Fig. 1A).

Dynamics of caprellid densities per algal biomass and per area were similar to each other, except for that of *C. danilevskii* in 1999–2000. Caprellid densities peaked in the high-temperature season (July and August; Fig. 1B–D), which did not correspond to the peak of *Gelidium* biomass (Fig. 1A). The densities of the 3 caprellid species showed similar temporal patterns; they were highest in the high-temperature season (around August) and then drastically decreased from September to October.

Seasonal change in population structure

In *Caprella cristibrachium*, the smallest size juveniles were found from June to August with high frequency, but the number of these juveniles decreased from September to December, and few juveniles were found from January to April. An overwintering generation could be identified by the mode change from 7 mm in January to 10 mm in May. However, the abundance of these large individuals decreased in June, and the population was mainly composed of smaller individuals (<7 mm). The maturation patterns in females were different in the overwintering generation and in the following generations. From the pattern of occurrence of mature females, many females matured at 7–8 mm in April, while approximately 50% of the females matured at a smaller size of 5–6 mm in July (Fig. 2A).

In the *Caprella danilevskii* population, the smallest juveniles were found at a high frequency in June–October (Fig. 2B). However, the occurrence of juveniles drastically decreased in December and was nearly zero in March–May. Based on the size structure of the population, an overwintering generation could be identified from a change in the

modal size (4 mm in December to 8 mm in May). However, the number of large individuals decreased in July, and the population was mainly composed of smaller individuals (<5 mm). Most of the females in the 4–5 mm size group in August–September were already mature; conversely, most of females in the 4–5 mm size group in October–May belonged to an immature stage, and matured at 6–9 mm the following May–June (Fig. 2B), although a few females did mature at 4–6 mm in March. These maturation patterns indicate that the females mature at different sizes in an overwintering generation compared to the following generation.

In the population of *Caprella scaura*, the smallest juveniles were found at a high frequency in May–August (Fig. 2C). However, the occurrence of juveniles drastically decreased in September and was nearly zero from January to April. Because of the low population density of the species during September–January, we could only analyze the population structure from February onwards. Similar to the other 2 species, an overwintering generation could be identified due to a successive change in modal size from February to May. After June, the population gradually changed to a size structure mainly composed of small individuals. The size of females at maturation varied between the high and low-temperature seasons. For example, most females in the 6–7 mm size group were mature in October, while most females in the same size class from February–March were not yet mature, instead maturing at 8–9 mm in April–May.

Including the data from 1999–2000 (Figs. S3 & S4 in the Supplement), the mean size of the mature females in each month decreased with the mean temperature in the 30 d before each sampling date. Using model selection to examine the linearity of the relationship, non-linear models were selected for all 3 caprellids (Table 1). However, the estimated curve in boreal *C. cristibrachium* showed a linear form, and the mature size significantly decreased with increasing temperature (Fig. 3A). In contrast, the estimated curves in the females of temperate *C. danilevskii* and *C. scaura* showed that the mean size of the mature female increased with decreasing temperature in the range of 5–20°C, but the mean size did not increase in the lower temperature range of 2–5°C (Fig. 3B,C). Those data that deviated from a linear relationship in the low temperature range corresponded to individuals that matured in March and April, unlike many other females in the overwintering generation (Fig. 2B,C).

Reproductive dynamics

The relationship between days to maturation (D) and temperature (T) was estimated based on fifteen experiments with 10 *Caprella* species (Table 2,

Fig. 4). The biological zero (parameter b) in the 'all species' equation was estimated to be 2.0°C rather than the 5.5°C used in the 'temperate species' equation, i.e. $D = 335.2(T - 2.0)^{-0.84}$ rather than $D = 252.4(T - 5.5)^{-0.90}$. Both simulations using the 2 estimated

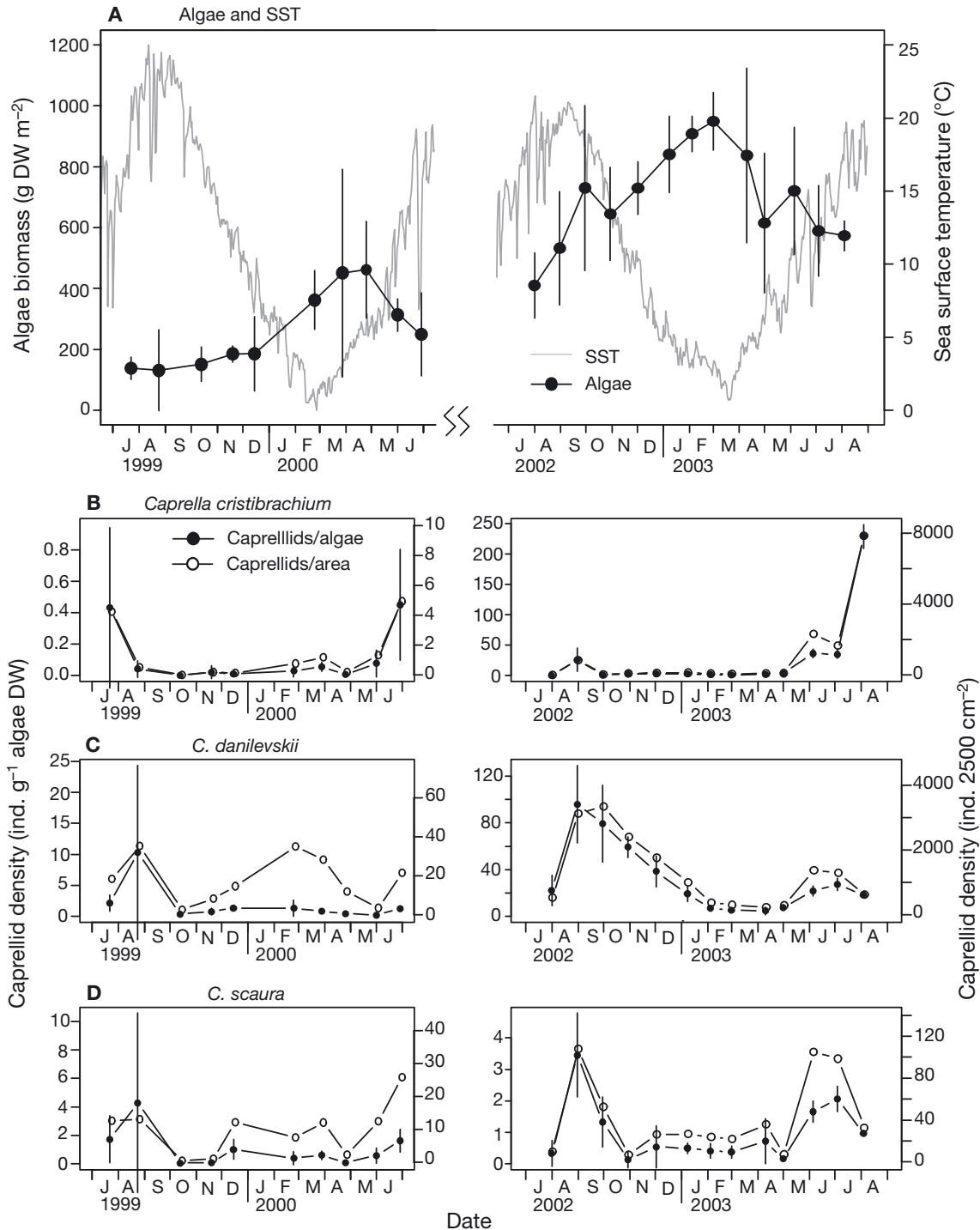


Fig. 1. (A) Seasonal fluctuation of the sea surface temperature (gray line) and mean (\pm SD) algae biomass (\bullet) and (B–D) mean (\pm SD) caprellid densities relative to algal biomass (\bullet) and area (\circ) during 2 research periods (Jul 1999–Aug 2000 and Jul 2002–Aug 2003). Note differing y-axis scales for each of the two parts of (B–D)

Table 1. Comparison of the results of the linear model and the generalized additive model (GAM) for the relationship between female body length and temperature. df: degrees of freedom for the linear model; edf: estimated df for the GAM; AIC: Akaike's information criterion. The p-value for the non-linear model is approximate

Model and terms	— <i>Caprella cristibrachium</i> —				— <i>C. danilevskii</i> —				— <i>C. scaura</i> —			
	df / edf	F	p	AIC	df / edf	F	p	AIC	df / edf	F	p	AIC
Linear model				582.5				963.2				393.4
Temperature	1	289.5	<0.001		1	337.5	<0.001		1	7.083	0.009	
GAM				579.4				927.4				380.5
Temperature	4.076	62.53	<0.001		4.819	72.08	<0.001		4.099	4.990	<0.001	

equations predicted that caprellids born at a temperature above 12°C could mature within 1–2 mo, and that the maturation was carried over to the next year when the caprellids were born below 12°C (after October) (Fig. 5). However, the equation for the temperate species predicted that no female could mature in January–May (Fig. 5A), while the equation for all

species predicted that several females could mature starting in March (Fig. 5B). The overlap of reproduction by the overwintering generation and the following generation was predicted to be from mid-June to early July by the equation for temperate species (Fig. 5A), while the overlap was predicted to be from late May to early June by the equation for all species

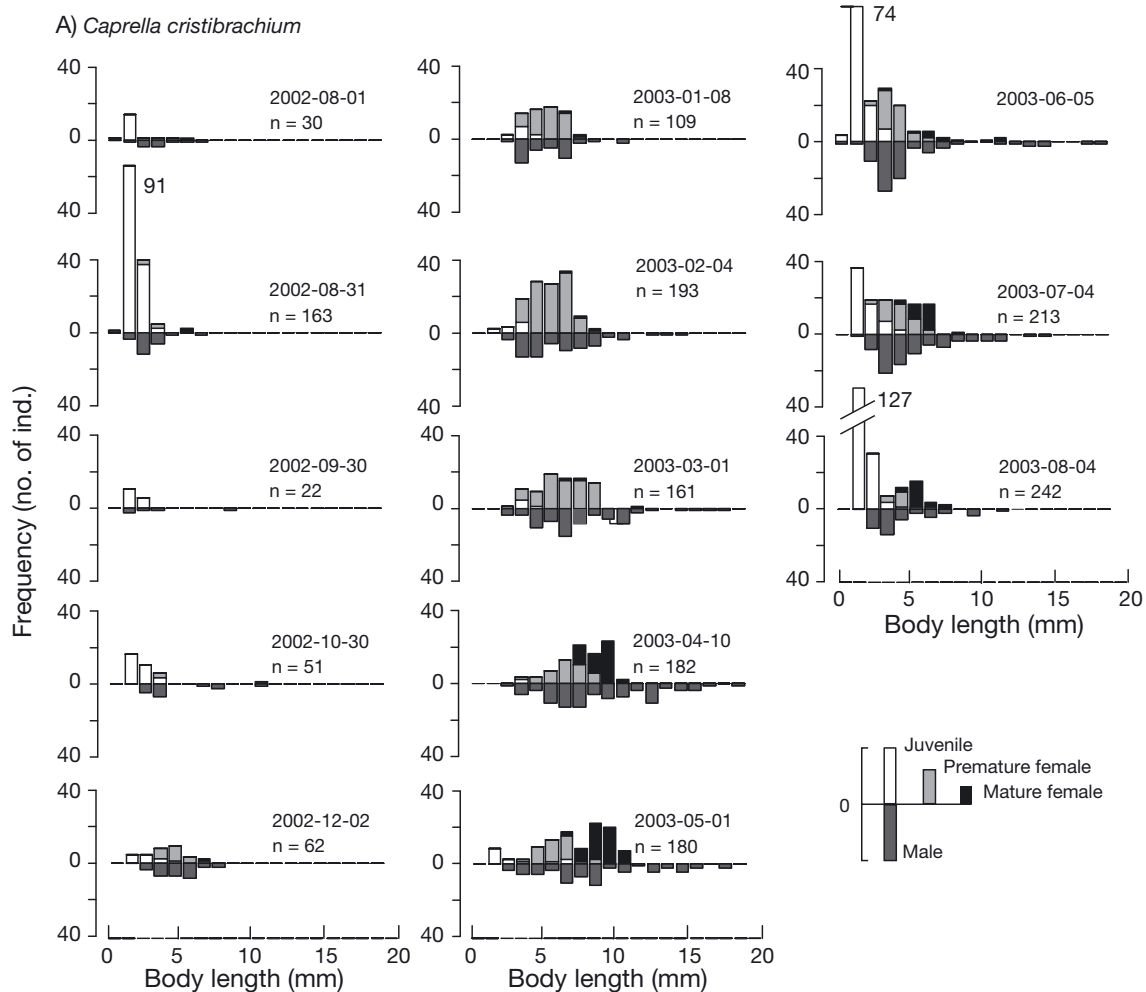


Fig. 2. (Above and next page.) Population structure of the 3 caprellid species studied: (A) *Caprella cristibrachium* in Aug 2002–Aug 2003; (B) *C. danilevskii* in Aug 2002–Jul 2003; (C) *C. scaura* by month without distinguishing the sampling year

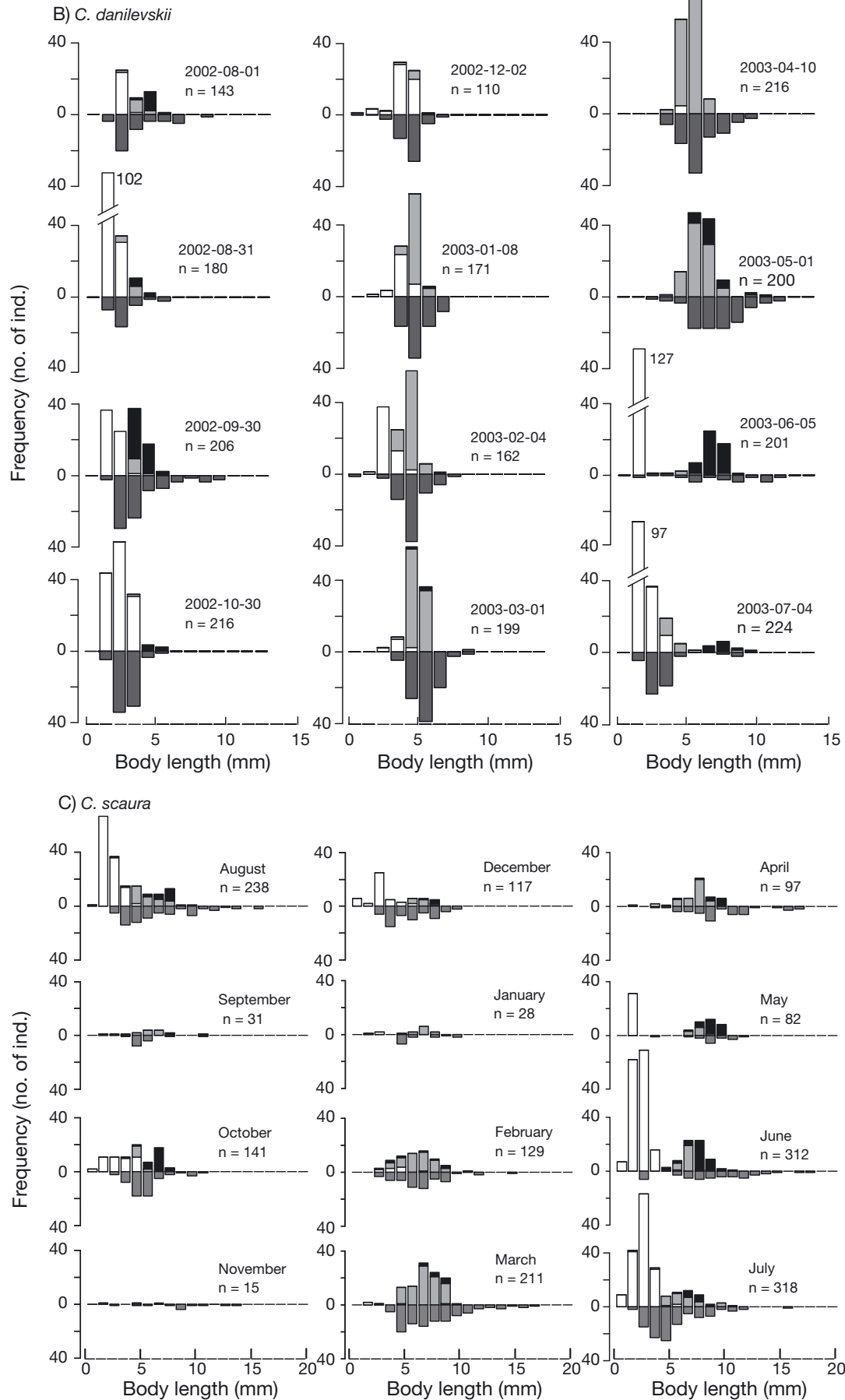


Fig. 2. (continued)

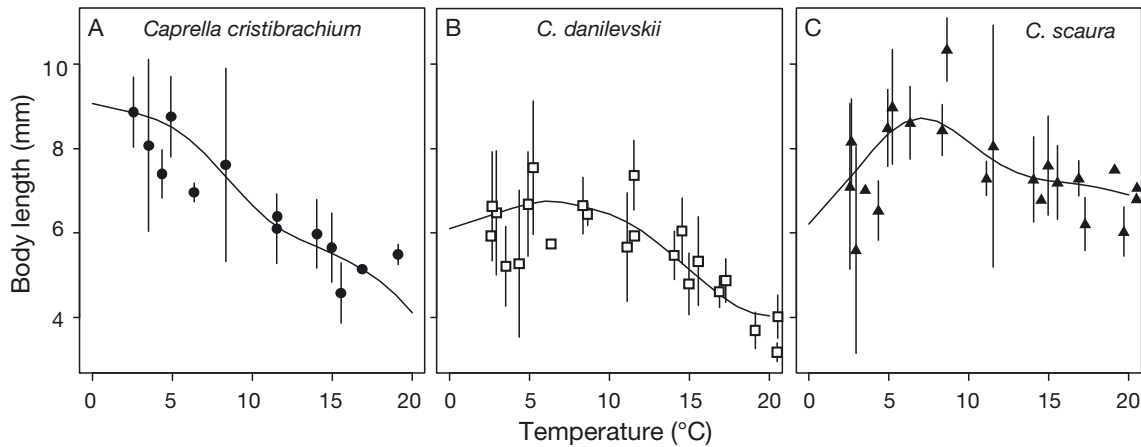


Fig. 3. Mean (\pm SD) body size of mature female caprellids against the mean sea surface temperature for 30 d before the sampling day

(Fig. 5B). In the actual populations in the study area, a small but steady number of females in all 3 caprellid species matured in March–May (Fig. 2), and a mass occurrence of the smallest juveniles was observed in May–June. This result indicates that the equation for all species has a better ability to describe the reproductive dynamics in the boreal study area than the equation for temperate species. Therefore, the equation for all species was applied in further simulations.

Considering that there are several reproductions after maturation, the simulation predicted that active

reproduction would occur from late May to mid-July, while reproduction ceased from January to February (Fig. 6B). The simulation also predicted that active reproductions continued from the high-temperature season (August) to the low-temperature season (December). However, the actual population densities were highest in August, and then they drastically decreased in September–October (Fig. 1B–D).

Given another temperature range for the estimated Belehradek equation, the reproductive dynamics were simulated in temperate and arctic areas (Fig. 6). The simulation predicted continuous reproduction throughout the year in a temperate area (Fig. 6A) and a limited reproductive period of July–September in an arctic area (Fig. 6B).

DISCUSSION

Population dynamics in a boreal zone

In caprellids, continuous reproduction through the year has been reported for many temperate species (Bynum 1978, Lewbel 1978, Caine 1979, Imada & Kikuchi 1984, Aoki 1988, Sconfiotti & Luparia 1995, Guerra-García et al. 2009, 2011b, Prato et al. 2013). In contrast, *C. septentrionalis* reproduces as a single brood per year, with juveniles hatching in June in an arctic area of the White Sea (Heptner 1963). The reproductive dynamics investigated in the boreal area showed intermediate characteristics between these areas. All 3 caprellid species in the present study had a limited reproductive period, mainly June–October. The early summer reproduction was performed by an overwintering generation charac-

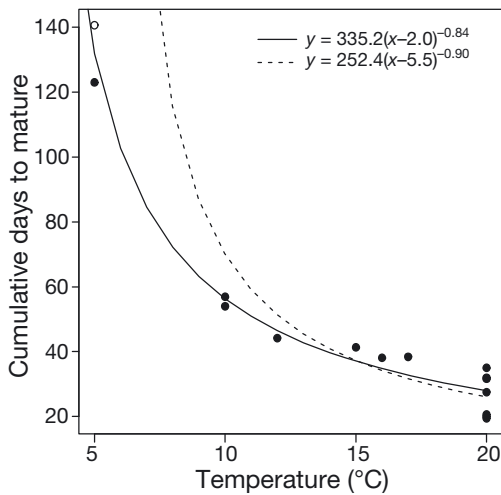


Fig. 4. Relationship between the temperature and the number of days to maturation in caprellids. Filled symbols: observed values (Table 2 lists references for all data points); open symbol: estimated value based on Hosono (2011); solid line: estimated Belehradek equation based on all species data; dashed line: Belehradek equation for temperate species with fixed parameters $b = 5.5$ and $c = -0.90$

Table 2. Maturation time of caprellids

<i>Caprella</i> species	Temp. (°C)	Days to maturation	Reference
<i>C. acanthogaster</i>	5	123.0	Hosono (in press)
<i>C. brebiostris</i>	20	27.5	Takeuchi & Hirano (1991)
<i>C. cristibrachium</i>	20	35.0	Hosono (2006)
<i>C. danilevskii</i>	20	20.0	Takeuchi & Hirano (1991)
<i>C. generosa</i>	20	19.5	Takeuchi & Hirano (1991)
<i>C. grandimana</i>	17	38.4	Baeza-Rojano et al. (2011)
<i>C. laeviuscula</i>	12	44.2	Gardella (1962)
<i>C. mutica</i>	5	140.7	Instar IX estimated from growth curve at 5°C in Hosono (2011)
<i>C. mutica</i>	10	54.0	Instar VII in Boos (2009)
<i>C. mutica</i>	10	56.9	Instar X in Hosono (2011)
<i>C. mutica</i>	15	41.3	Instar VIII in Hosono (2011)
<i>C. mutica</i>	16	38.1	Instar VII in Boos (2009)
<i>C. mutica</i>	20	31.6	Instar X in Hosono (2011)
<i>C. okadai</i>	20	20.6	Takeuchi & Hirano (1992b)
<i>C. scaura</i>	20	32.0	Sakaguchi (1989)

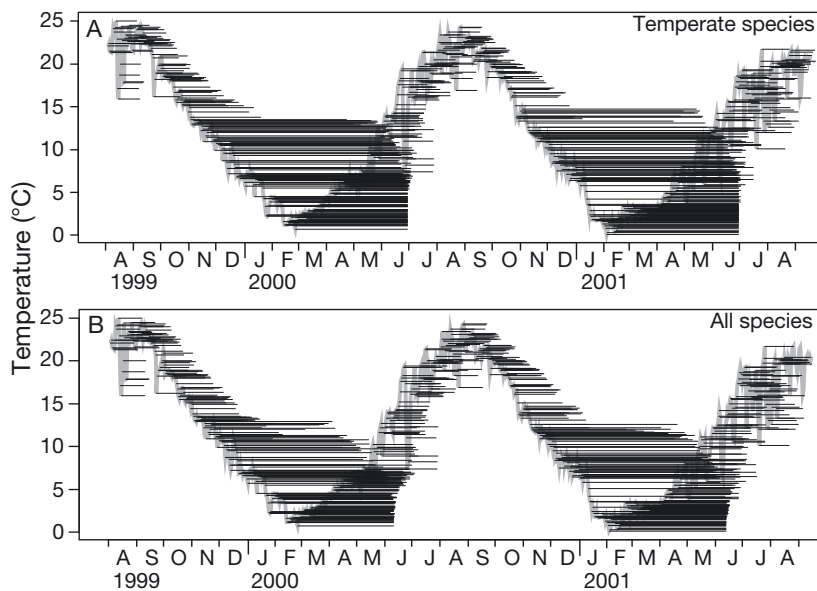


Fig. 5. Simulation of the reproductive dynamics in the study area. Development time estimated by (A) Belehradek equation for temperate species (dashed line in Fig. 4) and (B) Belehradek equation for all species data (solid line in Fig. 4). Gray line: observed temperature; horizontal lines: estimated development time from birth to maturation (left to right) — line length = n_1 calculated in the simulation (see 'Materials and methods')

terized by larger females, and subsequent reproductions were performed by generation(s) characterized by smaller females. Because these 3 caprellids can mature in a short time of 20–35 d and reproduce in a short interval of 3.0–10.4 d at 20°C (Sakaguchi 1989, Takeuchi & Hirano 1991, Hosono 2006), the 3 caprellid populations, after an overwintering generation, are considered to be comprised of multiple genera-

tions characterized by a fast growth rate and a smaller maturation size in the high temperature season. This generational exchange pattern is consistent with the simulated result using a temperature–maturation time relationship. These results also show that the 3 caprellids in the study area have similar reproductive patterns corresponding to the local temperature fluctuation, regardless of whether they are temperate or boreal species.

The validity of applying the Belehradek equation needs to be confirmed, because the parameters for the equation were estimated using a temperature range of 5–20°C, whereas the simulations had to extrapolate within the range of 0.7–25°C. The equation represents developmental inhibition at low temperature as a biological zero (parameter b). The developmental time is also delayed at high temperatures depending on physiological tolerance. Because such a condition is not assumed in the equation, the estimated developmental time may be excessively short at high temperatures. However, Takeuchi & Hirano (1992b) reported that the incubation periods of *C. danilevskii* in the range of 10–26°C can be expressed by Belehradek equations. Therefore, it would be appropriate to assume that the equation holds in the temperature range in the present study, and in fact, the short maturation time predicted by the equation in the high temperature season is consistent with the active reproductions observed in the field. The minimum temperature of 0.7 in the simulation is also out of the actual range. The agreement between the simulation results and the traits of the natural population in the low-temperature season indicates that the estimated equation can partly explain the reproductive dynamics in the boreal study area. However, there is little doubt that the accuracy of the simulation is low due to the lack of information on the maturation pattern at temperatures <0.5°C.

The reproductive pattern of caprellids at low temperatures could not be simply interpreted as an

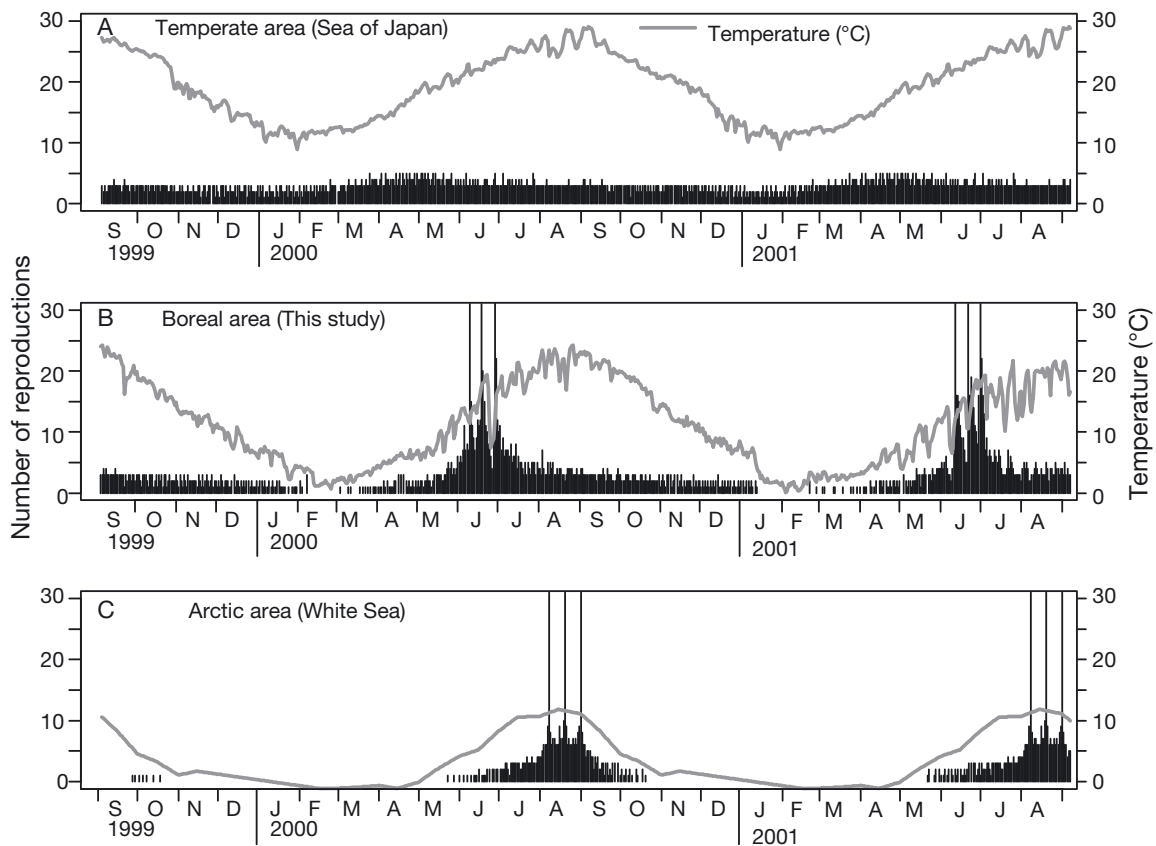


Fig. 6. Simulations of the reproductive dynamics in temperate areas in (A) the Sea of Japan, (B) the boreal area used in this study, and (C) the Arctic area in the White Sea. Gray line: temperature at each site; vertical bars: number of reproductions per day predicted by the simulations

extrapolation of that in the temperate area. This was verified by the fact that the maturation time of temperate species in the boreal area could be expressed by the same equation as used for boreal species. The equation with $b = 5.5^{\circ}\text{C}$ reported in the temperate area (dashed line in Fig. 4) cannot explain fully—and apparently contradicts—what is observed in the field. In contrast, the equation estimated from the ‘all species’ data ($b = 2.0$; solid line in Fig. 4) represented the reproductive dynamics in the field well. This indicates that development and maturation does not cease at temperatures less than 5.5°C even in temperate species and that temperate species have the same maturation time as a boreal species in the study area.

Non-linear responses to temperatures of female maturation size in temperate species could explain their similar maturation times to the boreal species. In caprellids, female maturation size is negatively correlated with the experienced temperature (Bynum 1978, Hosono & Sakurai 2006). However, the temperate species showed non-linear responses at

temperatures below 5°C , and the mature females at that temperature were smaller than the size expected from a linear relationship, in contrast to the size of mature females in the boreal species. Hosono (2011) showed that a larger maturation size at a low temperature was caused by a delay in the maturation instar, and inversely, maturation at a younger instar at a high temperature led to a smaller maturation size. Thus, maturation at a smaller size at a low temperature, as observed in the 2 temperate species, may allow these species to mature faster than the expected timing based on a linear relationship with temperature. However, because a large female with high fecundity at lower temperature is generally interpreted as a compensatory response to low reproductive rates at low temperatures related to adaptive plasticity (Angilletta et al. 2004), the presence of smaller females at lower temperatures appears to be unreasonable from the view point of adaptive significance. Further studies on the adaptive significance and physiological mechanism of the non-linear responses at a low temperature are needed.

Reproductive dynamics in caprellids

Given another temperature range for the estimated Belehradek equation, it is possible to examine whether the caprellid reproductive pattern is simply controlled by local temperature fluctuations. The simulation for a temperate area (8.9–29.2°C) predicted continuous reproduction through the year, which is same as the reproductive dynamics of *C. danilevskii* reported in Imada & Kikuchi (1984). However, the simulation for a high-latitude area predicted a short reproductive period of July–September. Heptner (1963) reported a limited reproductive period for *C. septentrionalis* of only May–July in the White Sea, and Węślawski & Legeżyńska (2002) also reported the emergence of juveniles in July in Hornsund (77°N). The prediction for high-latitude area is consistent with these observations in terms of the fact that these periods are shorter than the period in the boreal area (June–October). However, the estimated period is longer and later compared with the observations by Heptner (1963) and Węślawski & Legeżyńska (2002). These deviations in length and timing are considered to be due to the lack of information on the maturation time at temperatures lower than 5°C (Table 2). Experimental studies or observations of the developmental pattern of caprellids at low temperatures (<5°C) are required to allow precise prediction of their reproductive dynamics.

To some extent, using the temperature–maturation function enabled prediction of reproductive dynamics in various locations. It should be noted, however, that this function was estimated based only on the data obtained under suitable rearing conditions for each species, i.e. those data did not include the response near or beyond the physiological limits of each species. In other words, the function cannot yet be relied upon to predict responses of a caprellid beyond each habitable temperature range.

Factors regulating caprellid densities in algae beds

Clarification of the relationship between temperature and reproductive dynamics raises a new question regarding the population dynamics of epifaunal species. Caprellid population densities were the highest during the high-temperature season when the biomass of their habitat *G. elegans* was low, but densities drastically decreased in September, in spite of their high reproductive potential. As an external factor affecting caprellid densities, extreme high temperature and low dissolved oxygen were

reported to disperse the *C. equilibra* population (Sconfiatti & Luparia 1995). However, because this study area is situated on the open coast facing the Pacific Ocean, the temperature and dissolved oxygen are considered to be stable through the year. With regard to the temporal coincidence between the caprellid population and the habitat substrate, Mukai (1971) reported that the population densities of amphipods, including caprellids, corresponded to the *Sargassum* biomass. Similarly, Guerra-García et al. (2009, 2011a) reported that the density of caprellids on macroalgae was highest with the highest development of the seaweeds. Aoki (1988) investigated the population dynamics of *C. verrucosa* in *Sargassum patens* beds with short monitoring intervals and reported that the caprellid density drastically decreased ahead of the decline of the *Sargassum* seaweed. That author noted that a sudden increase in predation pressure or the seasonal change in epiphytic diatoms, caprellid prey, were important factors in the drastic decrease in the caprellids. Duffy (1990) revealed that *C. penantis* significantly reduced the biomass of epiphytes on the macroalgae, not that of the macroalgae itself, in a study on the function of epifauna as grazers. More generally, the dynamics of epiphytic animals are affected by the dynamics of the macroalgae that serve as their habitat and by the fluctuation of epiphytes that provide food (Edgar 1990). Furthermore, the additional complexity of the habitats provided by epiphytes has an important effect in determining seasonal patterns of epifaunal abundance (Martin-Smith 1993). In the present study, caprellid densities changed inversely with the biomass of *G. amansii*, suggesting that the change in *G. amansii* biomass did not alter its function as a refuge or habitable space for caprellids. Therefore, drastic decreases in the caprellid population in the summer may be caused by seasonal changes in the availability of epiphytes as food or changes in predation pressure.

CONCLUSIONS

This study revealed that both reproductive dynamics within a location and the reproductive patterns between locations in caprellids can be explained simply by the idea that maturation time is controlled by local temperature fluctuation. However, the timing of the decreases in the population densities in the summer could not be explained by the reproductive dynamics, indicating the importance of other ecological mechanisms, such as preda-

tion or food availability. This study also found a non-linear relationship between the maturation sizes of female caprellids at a low temperature. This non-linear response of temperate species in a boreal zone may allow them to exhibit reproductive dynamics similar to those of boreal species.

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