Estimation of optimum temperatures for terrestrial hermit crabs in the zoeal stage using the thermodynamic Sharpe–Schoolfield–Ikemoto model

Takeo Yamamoto[1]*, Katsuyuki Hamasaki[2]

[1]Miyazu Field Station, Japan Fisheries Research and Education Agency, 1721 Odasyukuno, Miyazu, Kyoto 626-0052, Japan. [2]Department of Marine Biosciences, Tokyo University of Marine Science and Technology, Konan, Minato, Tokyo 108–8477, Japan.

*Corresponding author, e-mail: yamamoto_takeo58@fra.go.jp, Tel: +81-772-1306.

Abstract

The intrinsic optimum temperatures (T_Φ) for the zoeal stages of five species of the terrestrial hermit crab genera *Birgus* and *Coenobita*, namely *B. latro*, *C. brevimanus*, *C. purpureus*, *C. rugosus*, and *C. violascens*, were estimated based on the relationship between temperature and the number of developmental days using the nonlinear thermodynamic Sharpe–Schoolfield–Ikemoto model. The results showed that the T_Φ estimates (approximately 26 °C) corresponded to the temperatures at which high survival rates were observed for the zoeae, except for *C. rugosus*, whose T_Φ was approximately 24 °C. The low T_Φ of *C. rugosus* when compared to the other species may have been due to the relatively high northern latitude of its distribution and its late breeding season. The optimum temperatures determined for these terrestrial hermit crabs would be useful in understanding and predicting the changes in and northward expansion of their distributions.

Key words: development rate; intrinsic optimum temperature; SSI model; thermal biology

Introduction

The physiological processes of ectotherms, such as metabolism, growth, and reproduction, are temperature dependent (e.g. Anger 2001; Rebaudo and Rabhi 2018). The fitness levels of ectotherms are generally enhanced when these processes are facilitated under optimum temperatures (e.g. Amarasekare and Savage 2012; Shi et al. 2013), whereas extreme temperature conditions have detrimental effects such as decreased survival rate, retarded growth, and reduced reproductive capacity. Therefore, information on the optimal temperatures for ectotherms is crucial for maintaining and increasing the production of wild populations and aquaculture.

The optimum temperature for ectotherms has generally been selected based on the temperature-survival rate relationship, where the temperature yielding the peak survival rate is chosen. It also be considered as the temperature at which the development rate is maximum (Rebaudo and Rabhi 2018). On the other hand, the Sharpe–Schoolfield–Ikemoto model (SSI model; Ikemoto 2005, 2011a, b) is an S-curve model applied to determine the relationship between mean incubation temperature and developmental rate, which is based on the laws of thermodynamics. Ectotherms have various enzymes in their bodies, each with a relationship between temperature and rate of reaction. The SSI model assumed that the development is regulated by a single control enzyme whose reaction rate determines the development rate of the organism. The intrinsic optimum temperature (T_Φ) parameter in the SSI model represents the temperature associated with the highest probability of an enzyme being active. This parameter is valuable not only for ectotherms like insects and mites (e.g., Ikemoto 2005; Shi et al. 2012, 2013, 2019; Sreedevi et al. 2013) but also for land plants (Shi et al. 2019).

Four studies have applied the SSI model to decapod

crustacean larvae (Yamamoto et al. 2017, 2021; Quinn 2019, 2021). We have previously demonstrated that T_Φ estimates correspond to the temperatures at which high survival and growth rates can be observed (Yamamoto et al. 2017, 2021). Quinn (2019, 2021) confirmed the good fit of the SSI model with the relationship between temperature and developmental rate but did not assess the validity of T_Φ estimates. The paucity of existing studies may be because the optimal application of the SSI model requires datasets with many temperature treatments over a wide thermal range, a condition rarely satisfied by crustacean datasets (Yamamoto et al. 2017; Quinn 2021).

Zoeae of terrestrial hermit crabs inhabit estuarine and coastal waters with unstable temperature fluctuations. They transition to land during the megalopal stage. Therefore, understanding the optimum temperatures in the zoeal stage is crucial for gaining knowledge about larval survival and dispersal, population connectivity, neonatal dynamics, and geographical distribution. In their study, Hamasaki et al. (2020) reared larvae of terrestrial hermit crabs at five temperature levels and found that the survival rate of the zoeal stage was high (>75 %) at approximately 25–31 °C. In this study, we aimed to re-evaluate the data presented in Hamasaki et al. (2020) to estimate the T_Φ using the SSI model.

Materials and Methods

Data source

We applied the SSI model to the total zoeal stage, from hatching to metamorphosis into the megalopal stage, for five species of the terrestrial hermit crab genera *Birgus* and *Coenobita*: *B. latro*, *C. brevimanus*, *C. purpureus*, *C. rugosus*, and *C. violascens* (Hamasaki et al. 2020). The temperature (T)-dependent development day (D) datasets used in the present study are shown in Table S1.

Data analysis

Two programs, OptimSSI-program (Ikemoto et al. 2013) and DEoptim.sqrt.SSI-program (Shi et al. 2017; named by Ikemoto and Kurahashi 2023), have been developed to estimate the parameters of the SSI model. We used the former because the latter sometimes yields biologically unacceptable parameter values (Ikemoto and Kurahashi 2023). The confidence intervals for T_Φ were estimated using the mABCSSI-program (Ikemoto et al. 2013).

The equation for the SSI model is as follows:

$$r(T_k) = \frac{\rho_\Phi \frac{T_k}{T_\Phi} \exp\left[\frac{\Delta H_A}{R}\left(\frac{1}{T_\Phi} - \frac{1}{T_k}\right)\right]}{1 + \exp\left[\frac{\Delta H_L}{R}\left(\frac{1}{T_L} - \frac{1}{T_k}\right)\right] + \exp\left[\frac{\Delta H_H}{R}\left(\frac{1}{T_H} - \frac{1}{T_k}\right)\right]}$$

Here, $r(T_k)$ is the development rate (1/D; dependent variable) at absolute temperature T_k (K) (273.15 K = 0 °C; independent variable), and all other parameters are constants (Ikemoto 2005). T_Φ is the intrinsic optimum temperature at which the probability of an enzyme being active is maximised; T_L and T_H are temperatures at which the enzyme is half active and half inactive; T_Φ, T_L, and T_H represent absolute temperatures; ΔH_A, ΔH_L, and ΔH_H represent enthalpy changes; R is the universal gas constant (1.987 cal/deg/mol); and ρ_Φ is the approximate development rate at T_Φ. T_Φ is related to the other parameters in the model as follows:

$$T_\Phi = \frac{\Delta H_L - \Delta H_H}{R \ln\left(-\frac{\Delta H_L}{\Delta H_H}\right) + \left(\frac{\Delta H_L}{T_L}\right) - \left(\frac{\Delta H_H}{T_H}\right)}$$

The data ranges used for linear fitting ($D\,T = a + b\,D$; derived from the heat summation theory equation) were visually chosen for this calculation (Ikemoto et al. 2013). In the OptimSSI program's calculation process, optTL was designated "0" because the data points did not clearly show an S-shaped curve in the low temperature range (Ikemoto et al. 2013; Yamamoto et al. 2017).

Results

Table 1 presents the results of fitting the development rate data of the zoeal stage terrestrial hermit crabs with the SSI model. The relationship between temperature and larval development rate is shown in Fig. 1. The SSI model exhibited a good fit with the temperature-dependent development data. The estimated T_Φ values for *B. latro*, *C. brevimanus*, *C. purpureus*, and *C. violascens* in the zoeal stage were all approximately 26 °C, whereas the value for *C. rugosus* was relatively lower at approximately 24 °C.

decapod crustacean larvae were within the temperature ranges of their natural habitats and aligned with the optimal temperatures for larval survival and growth (Yamamoto et al. 2017, 2021).

Hamasaki et al. (2020) reported that the survival rate of *C. rugosus* zoeae was low (25 %) at 22 °C and high (92–94 %) at 25–30 °C. Thus, there is no experimental data that *C. rugosus* zoeae have a high survival rate at T_Φ (approximately 24 °C). Is it reasonable, then, that *C. rugosus* had a lower T_Φ estimate than the other species? Among the terrestrial

Table 1. Parameter estimates of the Sharpe–Schoolfield–Ikemoto (SSI) model for the rate of development from hatching to metamorphosis into the megalopal stage for five terrestrial hermit crab species of the genera *Birgus* and *Coenobita* using the OptimSSI program, with confidence intervals (CIs) for T_Φ assessed using the mABC program.

Parameter (unit)	*Birgus latro*	*Coenobita brevimanus*	*Coenobita purpureus*	*Coenobita rugosus*	*Coenobita violascens*
T_Φ (°C)	26.46	26.12	26.04	23.97	26.00
ρ_Φ	0.0457	0.0412	0.0445	0.0310	0.0431
ΔH_A	18718	32575	25851	30766	24904
ΔH_L	−125730	−164075	−148214	−140486	−149211
ΔH_H	142387	83549	116263	69930	123177
T_L (°C)	18.39	21.89	20.11	18.96	19.85
T_H (°C)	34.13	33.29	33.58	32.70	33.51
χ^2	0.055	0.093	0.105	0.105	0.050
R^2	0.823	0.771	0.803	0.815	0.901
95 % lower CI (°C)	26.44	26.11	26.00	23.96	25.91
95 % upper CI (°C)	26.49	26.14	26.11	23.98	26.15

Discussion

We estimated the T_Φ values for five species of terrestrial hermit crabs in the zoeal stage: *B. latro*, *C. brevimanus*, *C. purpureus*, *C. rugosus*, and *C. violascens*. The T_Φ estimates for four species, namely *B. latro*, *C. brevimanus*, *C. purpureus*, and *C. violascens*, were approximately 26 °C, falling within the high survival range (25–31 °C; Hamasaki et al. 2020) as well as the sea water temperature range during the main larval release seasons in the main distribution area in Japan (25–31 °C; Hamasaki et al. 2020). This result corresponds with those of our previous studies, wherein the T_Φ estimates for

hermit crabs used in this study, species with higher northern latitudes of distribution are more cold tolerant in the juvenile stage (Sanda et al. 2019). The northern limit latitude of the distribution of *C. rugosus* (31 °N) is second only to that of *C. purpureus* (35 °N), and the low lethal temperature for juvenile *C. rugosus* (10.19 °C) is second only to that of *C. purpureus* (7.91 °C) (Sanda et al. 2019). In other words, *C. rugosus* is distributed at relatively high latitudes and with low temperature tolerance but is not comparable to *C. purpureus*. In Okinawa Island, Japan, where *C. purpureus* and *C. rugosus* occur sympatrically, the breeding season is from late May
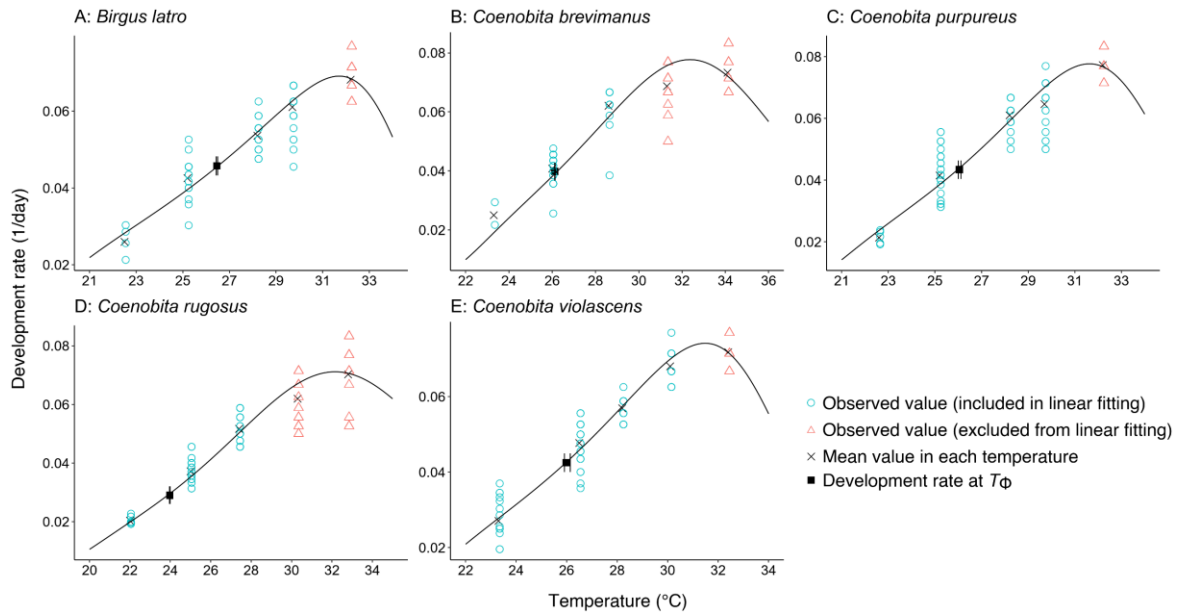
Fig. 1. Effects of temperature on the rate of development from hatching to metamorphosis into the megalopal stage for five terrestrial hermit crab species of the genera *Birgus* and *Coenobita*. Horizontal bars denote the T_Φ confidence intervals.

to November for *C. rugosus* and from late May to mid-September for *C. purpureus* (Nakasone 2001). This means that *C. rugosus* zoeae are exposed to lower temperatures than *C. purpureus* zoeae. Therefore, cold tolerance would be stronger for *C. rugosus* in zoeae and *C. purpureus* in juveniles. Previous studies have found that *C. purpureus* is more abundant than *C. rugosus* at the northern limit of their distribution range; however, the northern limit of the distribution of *C. rugosus* continues to move northward (Sanda et al. 2018; Hamasaki et al. 2019). The ongoing northward expansion of *C. rugosus* may be due to its high tolerance to low temperatures in the zoeal stage.

In conclusion, the T_Φ estimates for the terrestrial hermit crabs zoeae were found to correspond to the optimal temperatures for larval survival, as in other decapod crustacean larvae (Yamamoto et al. 2017, 2021). This information on the optimum temperature for terrestrial hermit crabs, which are widely distributed from tropical to subtropical regions and serve as good indicators of global warming, will be useful in understanding and predicting the changes in and northward expansion of their distributions.

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