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Thermal preference of the common brown shrimp (*Crangon crangon*, L.) determined by the acute and gravitational method

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ABSTRACT

Temperature is of critical importance for ectotherms, having vast impacts on physiology, behavior and distribution. In many species, however, the behavioral component of temperature selection is not well understood. This study addresses the thermoregulatory behavior of the common brown shrimp (*Crangon crangon*, L.), which is a central component of the Wadden Sea ecosystem and an important fishery resource of high commercial value. To investigate whether brown shrimp are thermosensitive and perform behavioral thermoregulation, we examined the short- and long-term thermoregulatory behavior by using the acute and gravitational method for temperature preference testing. For the acute method, female adult brown shrimp were acclimated to 5 temperatures between 9 °C and 19 °C for two weeks. For the gravitational method, the shrimp were acclimated to 3 temperatures within the same range. Hereafter, thermal preferenda were determined in an annular shaped preference chamber. Acute and gravitational thermal preference experiments revealed brown shrimp to be thermosensitive and perform behavioral thermoregulation. Using the acute method, a positive correlation of acclimation and preferred temperature was observed, resulting in a final thermal preferendum of 15.9 °C. In experiments using the gravitational method, preference temperature was heavily modulated by the photoperiod, with brown shrimp selecting temperatures more precisely during the scotophase than the photophase. Determined at dark exclusively, however, no effect of acclimation temperature on gravitational preference after 24 and 48 h was observed. Preferenda ranged between 13.5-15.0 °C after 24 h and 12.0-14.9 °C after 48 h, respectively, and no significant differences between both methods were detected. Based on these findings, 20-24 h of gradient exposure can be considered sufficient to obtain thermal preferenda that are unaffected by the animal's prior thermal history. Thermal preferenda determined in the present study were higher than the average temperature experienced by brown shrimp in the field. Still, thermal preferenda were considerably lower than previously reported optimum temperatures for brown shrimp.

1. Introduction

Temperature is considered as a central abiotic environmental factor, profoundly affecting and driving aquatic ecosystems. Environmental temperature is of critical importance for aquatic ectothermic organisms, as ectotherms do not possess the ability of endogenous thermoregulation (Bicego et al., 2007; Fry, 1947). Thus, the temperature in the surrounding directly operates on body temperature, affecting almost all aspects of an ectotherm's physiology, ecology and behavior (Angilletta, 2009; Bicego et al., 2007; Fry, 1947; Huey and Stevenson, 1979). Supposing the ability of thermoreception, however, ectotherms can use behavior to respond towards environmental temperature by avoiding suboptimal and selection for optimal thermal conditions (Angilletta, 2009; Lagerspetz and Vainio, 2006; Neill and Magnuson, 1974). This thermoregulatory behavior allows ectotherms to actively modulate body temperature in a heterogeneous thermal environment, optimizing physiological processes and minimizing disadvantageous temperature effects through external means (Angilletta, 2009; Beitinger and Fitzpatrick, 1979; Neill, 1979).

Based on Fry's bipartite definition of the final thermal preferendum (Fry, 1947), thermoregulatory behavior and thermal preferenda of aquatic ectotherms can be revealed by means of two experimental methodologies. Both methodologies rely on laboratory based temperature gradient experiments. As the final thermal preferendum was defined as the (1) "*…temperature at which the preferred temperature is equal to the acclimation temperature*" and (2) "*…temperature at which all individuals will ultimately congregate, regardless of their thermal experience…*" (Fry, 1947), short and long-term experiments can be conducted to elucidate behavioral thermoregulation (Jobling, 1981; Reynolds and Casterlin, 1979a; Richards et al., 1977). Short-term approaches, i.e. acute thermal preference tests, use pre-acclimated test animals that are

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exposed to a thermal gradient for a reduced period of time. The thermal preference for each acclimation temperature is determined within the first two hours the animals have been introduced into the test apparatus (Reynolds and Casterlin, 1979a; Richards et al., 1977). Subsequently, the final thermal preferendum using the acute method is determined graphically, assigning the temperature where preference equals acclimation temperature among the different acclimation groups (Fry, 1947; Reynolds and Casterlin, 1979a; Richards et al., 1977). For long-term tests, i.e. gravitational thermal preference tests, the experimental organisms are subjected to a thermal gradient until a stable thermal preferendum is reached. Gravitational thermal preference is usually obtained 24-96 hours after the animals were introduced into a thermal gradient (Reynolds and Casterlin, 1979a; Richards et al., 1977). In contrast to the acute method, temperature selection in gravitational preference tests should be unaffected by previous thermal acclimation as well as the individual thermal history of the test organisms. In the gravitational approach, sufficient time for reacclimation is provided enabling the tested animals to gravitate to their final or ultimate thermal preferendum (Reynolds and Casterlin, 1979a). So far, both methodologies have been widely used to investigate thermal requirements as well as thermal preferenda of a variety of molluscs, crustaceans and fishes (e.g., Badenhuizen, 1967; Diaz et al., 2000; Lewis and Ayers, 2014; Mathur et al., 1982; Reynolds and Casterlin, 1979b).

The outcomes of the acute and gravitational approach, however, differ to some extent. Acute preference tests reveal a single, so called crossover-preferendum, i.e. where preference equals acclimation temperature (Reynolds, 1978). In contrast, gravitational preference tests reveal a zone of preferred temperatures representing thermal selection under natural conditions more realistically. This temperature preference zone typically spans 2-4 °C (Golovanov, 2006; Magnuson et al., 1979). As gravitational preference is not affected by the prior thermal history, the gravitational method is a suitable tool to study the effects of a variety of factors potentially affecting temperature preference, e.g. seasonal and gender related differences, effects of scoto- and photophase or physiological state (Golovanov, 2006). The time the final or ultimate preferendum is attained, however, might differ between species and has therefore to be evaluated individually.

The common brown shrimp is a demersal, decapod crustacean species and widely distributed along European coasts (Campos and van der Veer, 2008; Tiews, 1970). Within the Wadden Sea, which is considered as its main area of distribution, the common brown shrimp occurs at high densities and represents a key species for the ecosystem, being an important prey for crustacean species, fish and birds as well as an epibenthic predator of epi- and infaunal species (del Norte-Campos and Temming, 1994; Oh et al., 2001; van der Veer and Bergman, 1987). Brown shrimp also support a well established and commercially important fishery with annual landings of ~30000 t during the last decade (ICES, 2011). Brown shrimp are highly adaptable to several environmental factors and are able to persist in a wide range of environmental temperatures (Campos and van der Veer, 2008; Madeira et al., 2012; Reiser et al., 2014). Still, the thermal biology of the common brown shrimp is poorly understood and information on thermal requirements as well as the behavioral component of thermal selection are very limited.

To obtain a better understanding of the biology of the common brown shrimp and to evaluate the potential effects of climatic driven changes on this species as the recently observed northward shift (ICES, 2005), basic knowledge concerning its thermal biology as well as the ability of thermoreception and behavioral thermoregulation is essential. The objective of the present study was therefore to determine whether adult female brown shrimp are thermosensitive and perform behavioral thermoregulation. We determined thermal preferenda using an annular chamber system (Myrick et al., 2004; Reiser et al., 2013) intending to set a methodological framework for future thermal preference studies on the common brown shrimp.

2. Materials and Methods

2.1. Animal sampling, maintenance and acclimation

Brown shrimp were sampled at the coast off Büsum (54°07’09”N, 8°51’43”E) at low tide using a push net (2 mm mesh size) in approximately 1 m water depth. Post catch, the animals were transferred to a well aerated water tank with 1:1 artificial sea water (30 PSU) and natural sea water of the sampling location to promote acclimation to husbandry conditions during transport (approximately 2 h) to the laboratory facilities of the Institute of Hydrobiology and Fisheries Science, University of Hamburg. Here, brown shrimp were transferred to a 1 m^3 circular tank with aerated artificial seawater of 30 PSU connected to an in-house temperature controlled recirculating water system equipped with a foam fractionator and a moving bed biofilter. Upon 1 day of acclimation, animals were sorted to the nearest 5 mm total length (TL) and sex was determined based on the appendices of the first and second endopodite (Tiews, 1954). Female brown shrimp of 5 cm TL were transferred to separate circular holding units connected to the recirculating water system. Subsequently, water temperature was slowly adjusted to obtain the final acclimation temperatures of 9.0 ± 0.1, 11.5 ± 0.1, 14.0 ± 0.05, 16.5 ± 0.1, 19.0 ± 0.1, 21.5 ± 0.2 and 24.0 ± 0.2 °C in each respective tank. During thermal acclimation for 14 days, shrimp were fed dry feed (Marico Advance, Coppens International, Netherlands), live Artemia nauplii (SEPArt, Inve Aquaculture, Belgium) and chopped herring and sprat pieces to apparent satiation every day. Animals were maintained at 10:14 L:D photoperiod (Meixner, 1969).

2.2. Annular chamber system

Acute and gravitational thermal preference tests were conducted in an annular shaped thermal preference chamber (Reiser et al., 2013). In brief, the annular chamber used for the present study had a total diameter of 145 cm, holding a 15 cm wide swimming channel of 5.5 cm water depth (Fig. 1). Water was distributed at 3.5 l min^{-1} to each of the 8 outermost compartments of the annular chamber, i.e. reservoir channels, resulting in ~100% water exchange of the swimming channel min^{-1}. Warm water (14, 19 and 25 °C) was obtained by 3 kW immersion heaters (RY330, Redring Electric LTD, Peterborough, UK) and electrical titanium heating rods (600 W, Schego, Offenbach am Main, Germany). Cold water (3 °C and 9 °C) was obtained via the central in-house cooling unit (EUWAB24KAZW1, DAIKIN Airconditioning Germany GmbH) charging two titanium heat exchangers (VT04 CD16, GEA Ecoflex, Sarstedt, Germany). All temperatures were kept at their respective set value ± 0.2 °C.

Thirty-two equally spaced temperature sensors (DS1820-LC, B + B Thermo-Technik GmbH, Donaueschingen, Germany) were mounted on the outer wall of the swimming channel at mid-water depth and connected to a digital USB-thermometer (TLOG64-USB, B + B Thermo-Technik GmbH, Donaueschingen, Germany). Temperature was recorded every 15 sec and visualized in real-time using the PC-Datalogger Software (PC-Datalogger, B + B Thermo-Technik GmbH, Donaueschingen, Germany). Within the swimming channel, a stable thermal gradient of 3-25 °C was established (Fig. 2). Eight cold cathode tube lights (350 V, 2.4 W, 6 mA, Conrad Electronics, Hirschau, Germany) for even and diffuse illumination were mounted in equal distances on a circular PVC frame suspended 1.5 m above the experimental chamber. To allow for observation during day and night, the area below the swimming channel was illuminated by equally spaced infrared LEDs (SFH 485 P, 880 nm, OSRAM). Perpendicular to the center of the preference chamber, a mirror was mounted at 45°, deflecting the swimming channel to a camera (EcoLine TV7002, ABUS Security-Center GmbH & Co. KG, Germany) equipped with a daylight filter (SKR FIL 093, Joseph Schneider Optische Werke GmbH, Bad Kreuznach, Germany) and the CAT-filter removed. To allow for continuous surveillance of the test