Temperature selection and the final thermal preferendum of snow crab (*Chionoecetes opilio*, Decapoda) from the Barents Sea

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Abstract

The snow crab (*Chionoecetes opilio*) is an invasive species new to the Barents Sea that expands its geographic range by larval drift and adult migration. To evaluate the potential spreading of the species in the Barents Sea, we investigated temperature selection and the final thermal preferendum (FTP) of 9 adult males in a free choice horizontal temperature gradient (~1.0–5.5 °C) for 24 hours. The crabs displayed clear behavioral thermoregulation – at test start they explored the entire temperature range but eventually gravitated towards a FTP zone of 1.0–1.6 °C (mean 1.4 °C) after 6 h in the gradient. Our tests show that adult male snow crab is limited to cold waters, and suggest a spreading further into the Euro-Arctic shelf seas.

Introduction

Commercial fishing for snow crab (*Chionoecetes opilio*) in the Barents Sea only started in the last few years. The invasion of snow crab as a non-native species in the Barents Sea has prompted the rapid growth of the snow crab fishery in Norway with 3061 t landed in 2017 (Kuzmin et al. 1999, Lorentzen et al. 2018). The potential of the snow crab fishery in the Barents Sea depends on the growth of the population and the future spread of the species. Today snow crab occurs mainly in the eastern part of the Barents Sea, where it inhabits muddy and sand grounds at depths around 200 to 400 m (Alsvåg et al. 2009; Pavlov and Sundet 2011). Since first observed in 1996 it has gradually spread westwards into Norwegian waters and the distribution is expected to expand rapidly (Pavlov and Sundet 2011). Snow crab is considered a coldwater stenothermic species, which is particularly susceptible to warming events (Hardy et al. 2000). In the Bering Sea, snow crab occurs across ambient temperatures between -1.0 ºC and 6 ºC year round (Tremblay 1997; Hardy et al. 2000; Dawe and Colbourne, 2002; Zisserson and Cook, 2017). In the Barents Sea, on the other hand, the thermal habitat of snow crab is little known. Bottom temperatures of the Barents Sea are sub-zero to zero in the east and north influenced by sinking Arctic surface water (Knipowitsch 1905; Midttun 1985; Boitsov et al. 2012). To the west and south-west and along the northern coast of Norway bottom temperatures are >6 °C due to the inflow of the warm North Atlantic Current (Loeng 1991) but are gradually cooled to the east where Atlantic and Arctic waters meet and mixes. Through laboratory tests, we aim to better understand the spread potential for adult benthic dwelling snow crab in the Barents Sea. In a hetero-therm environment, ectotherms eventually gravitate toward a stable and narrow thermal zone, the final thermal preferendum (FTP), which is considered to be a species-specific trait unaffected by thermal history (e.g. acclimation temperature in the laboratory) (Fry 1947; Jobling 1981; Elliot and Elliott 2010; Christiansen et al. 2015). Final thermal preferenda are usually obtained after 24 h in a laboratory gradient (Jobling 1981). Here we tested temperature selection and the FTP by adult male snow crab, and provide the first circumstantial evidence for a potential poleward and a north-west spread (i.e., towards the eastern part of Svalbard Archipelago) for this invasive species in the Barents Sea.

Methods

Male snow crabs (*Chionoecetes opilio*) were caught by commercial conical pots in the area of the North East Atlantic Fisheries Commission (NEAFC) known as "Smutthullet" (latitude: 74.58 °N, longitude: 38.49 °E) at 250 m depth (1.5 °C). Intact crabs (N=400) were transported live to the Aquaculture Research Station in Tromsø, Norway (latitude ~70°N), where they were kept in a 3000 L holding tank supplied with running seawater and acclimated for 14 days at ~ 5.0 °C, salinity ~ 32 and natural light regime before the start of the experiment. Altogether 9 adult males (mean body weight = 780 g (± 40 g SD.), were chosen randomly and tested in a horizontal temperature gradient (dimension: 2.6 x 0.9 x 0.3 m; temperature range: ~ 1.0–5.5 °C) as described by Christiansen et al. (2015). At the start of each test, a single animal was removed from the holding tank and a temperature data storage tag (TidbiT, V2, UTBI-001, Temperature logger) was attached dorsally to the carapace, and the animal was released into the gradient at holding temperature. The logger was programmed to monitor ambient temperature every minute, i.e. a 24 h test period would render 1440 temperature recordings per animal. In effect, an animal was left undisturbed during tests while it freely monitored the ambient temperature across the gradient (see also Christiansen et al., 2015). From February 2016 to March 2016, single fed animals were tested in the gradient. The corresponding temperature data were downloaded to a PC, and tested animals were returned to the holding tank. The data obtained from each individual were recalculated to median values per hour, and the trend in selected temperature during the trial for all 9 animals was analysed using linear regressions. This to identify periods when selected temperature either changed or leveled out with time. Selected temperatures are presented in boxplots showing the minimum and maximum range values, the upper and lower quartiles and the median. Statistical analyses were performed using SYSTAT v. 12 (Systat Software, Inc. USA).

Results

Male snow crabs explored the entire temperature range of the gradient at test start and for about 6 h. Thereafter, animals displayed clear behavioral thermoregulation, and consistently sought the coldest end of the gradient for the remaining 18 h although with occasional excursions into warmer waters (Fig. 1). Selected median temperatures (SMT) during the 24 h test time are shown in Fig. 1. The SMT decreased significantly with time (t) within the first 6 h according to the linear equation: SMT =-0.549$t_{(0\text{-}6h)}$ +4.449 ($R^2 = 0.891$; $F_{1,5} = 40.7$; $p=0.001$; *slope* $t=-6.384$; $p= 0.001$)). For the remaining test period (i.e., 6–24 h), SMTs leveled out and stabilised within a temperature zone of ~1.0–1.6 °C (mean ~1.4 °C) ($F_{1,16} = 0.874$; $p= 0.364$), which we designate as the final thermal preferendum (FTP) (Fig. 1).

Discussion

During the tests single male snow crabs were able to freely and undisturbed explore the entire temperature gradient, regulate body temperature by behavioral means and record ambient temperatures *in situ*. A high level of precision was obtained and the accuracy is deemed credible, suggesting that the animals actually displayed a FTP of ~1.0–1.6 °C already after 6 h in the gradient. Overall, the free choice selection of temperatures in the gradient were significantly below the imposed acclimation temperature of the holding tank (~ 5.0 °C). Thus, snow crab from the Barents Sea seems to share the same physiological capacity as its conspecifics in the northern Pacific and western Atlantic (Tremblay 1997; Hardy et al. 2000; Dawe and Colbourne 2002). Due to technical limitations, our tests precluded access to sub-zero temperatures. Therefore, the actual temperatures selected by adult snow crab in the Barents Sea may be even lower than those reported in our study. This is supported by a recent study from the Kara Sea showing that juvenile snow crab may enter also sub-zero waters (Zalota et al. 2018). Snow crab, on the other hand, clearly avoided temperatures >2 °C after 6 h in a gradient. Bottom temperatures between sub-zero and 3°C cover ~70–95% of the Barents Sea (Jakobsen and Ozhigin, 2011; Boitsov et al. 2012). So the FTP of adult snow crab matches present day shelf temperatures east and northeast of Svalbard Archipelago at latitudes ~ 74–80 °N, large parts of the northern and central Barents Sea and to the northeast of Kola Peninsula (Christiansen et al. 2015). Our tests and the recent observation of snow crab in the Kara Sea (Hjelset 2014; Zalota et al. 2018) provide strong circumstantial evidence that this benthic top-predator is indeed well suited to the temperature conditions on the Euro-Arctic shelves. Adult snow crab and the introduced red king crab (*Paralithodes camtschaticus*) have few natural enemies in the Northeast Atlantic. Adult crabs actively explore new territory and may freely seek optimum conditions and avoid pejus temperatures. By contrast, the mero-planktonic larvae have no free choice option and are subjected to and dispersed by the prevailing currents of the Barents Sea. The upper thermal limits for adult snow crab are little known but crabs were most active at 0 °C and metabolic costs exceed energy intake at 6-7 °C (Foyle et al. 1989). The spreading of adult snow crab in the Barents Sea depends inter alia on the ongoing ocean warming and the concomitant effect on bottom temperatures. Previous studies (Hansen 2016; Lorentzen et al. 2018) and our results suggest that there is a strong potential for snow crab to become a highly valuable fisheries resource in the northern Barents Sea. The economic benefits of snow crab fisheries and other fisheries must however be weighed against the ecological costs (Christiansen 2017). The snow crab of the Barents Sea is omnivorous and studies unequivocally show that this benthic top-predator, as does red king crab, impoverishes biodiversity and exhausts the Barents Sea bottom fauna (Pavlov and Sundet, 2011, Christiansen et al. 2015). Besides being a voracious predator, snow crab is an important vector for parasites and epifaunal organisms and may facilitate their spread into new areas in the Barents Sea (Jakobsen and Ozhigin, 2011). In conclusion, adult male snow crab displays clear behavioral thermoregulation in a hetero-thermal environment, consistently selects temperatures in the coldest end of a thermal gradient (1.0–1.6 °C) and avoid higher temperatures. Based on the existing environmental conditions in the Barents Sea one may expect that snow crab will spread towards the colder north and Svalbard Archipelago as was suggested for the red king crab (Christiansen et al. 2015). Experimental tests do have their limitations, but physiological thresholds and responses to single environmental conditions may be identified with a high degree of precision. To further explore the thermal behavior of snow crab, the use of data storage tags on animals released into the wild is a warranted complement to experiments.

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Compliance with ethical standards

Conflict of interest

The authors declare that they have no conflicts of interest.

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Figure 1. Boxplot of temperatures selected by 9 adult male snow crabs (*Chionoecetes opilio*) tested individually for 24 h in a thermal gradient (~ 1.0–5.5 °C). The boxplot consists of the minimum and maximum range values, the upper and lower quartiles and the median.