

# Thermal behaviour of edible crab *Cancer pagurus* Linnaeus, 1758 in coastal Norway

Snorre Bakke<sup>1,3</sup>, Sten I. Siikavuopio<sup>2</sup> and Jørgen S. Christiansen<sup>3,4</sup>

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Ocean warming drives latitudinal shifts in the distribution of ectotherm species. The rate and magnitude of such shifts are constrained by physiology and behavioural thermoregulation. Here, we investigated the thermal preference and lower critical temperature (CT<sub>min</sub>) in female edible crab *Cancer pagurus*, a decapod crustacean with an ongoing northward dispersal along the Norwegian coast. The temperature selected by individual crabs from a northern (latitude ~69°N) and southern (latitude ~62°N) location was examined in a horizontal gradient (5.5–14.5°C) under a simulated day and night light regime. Irrespective of origin, crabs showed pronounced responses to the light cycle – during the day crabs stayed inactive in the warm end of the gradient but during night they actively explored the entire gradient. A preferred temperature of ~13 °C (measured as mode of loggings) was identified for crabs from both locations. Righting reflex experiments of crabs exposed to a rapid temperature drop (7 - 1 °C at -0.1 °C/min) identified a CT<sub>min</sub> of ~1.3 °C (i.e., the temperature at which 50% of crabs failed to right from an up-side-down position), and with no significant difference between locations ( $p > 0.05$ ). Our results provide important information about the functional characteristics of edible crab, and are discussed in context of the biology and ongoing northward dispersal of the species.

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1. Møreforskning Ålesund AS, NO-6021 Ålesund, Norway

2. NOFIMA – The Norwegian Institute of Food, Fisheries and Aquaculture Research, NO-9291 Tromsø, Norway

3. Department of Arctic and Marine Biology, UiT - The Arctic University of Norway, NO-9037 Tromsø, Norway

4. Environmental and Marine Biology, Åbo Akademi University, Turku, Finland

Corresponding author: Snorre Bakke

E-mail: [snorre.bakke@moreforsk.no](mailto:snorre.bakke@moreforsk.no)

## INTRODUCTION

The edible crab (*Cancer pagurus* Linnaeus, 1758) is a subtidal decapod crustacean and an important fisheries resource across most of its distribution in the north-eastern Atlantic. Around 50 thousand metric tons are landed in Europe annually (FAO 2015), of which ~5 thousand are harvested by Norwegian fishers (Søvik *et al.* 2017). In the late 1970's Torheim (1977; 1979) suggested that the northern distribution border of the edible crab was just north of 68°N, and reported that he only found a high enough density of crabs to sustain a fishery south of ~67°N.

Currently, the edible crab is harvested as far north as 69°N (Woll *et al.* 2006; Bakke *et al.* 2016), and have been observed in waters close to 71°N (Brattgard 2011). Due to rising ocean temperatures, such displacement and shifts in distribution are evident for much of the worlds marine biota (Perry *et al.* 2005; Poloczanska *et al.* 2013), and worries are raised regarding both the potential ecological and socio-economical consequences of these changes (Allison *et al.* 2009; Cheung *et al.* 2009; Cheung *et al.* 2010). To better understand how species respond to these environmental changes it is important to know their preference,

tolerance, and ability to adapt to temperature.

The effect of ocean warming on physiological performance and thresholds has been studied extensively in marine ectotherms (see for instance Somero 2012; Pörtner and Gutt 2016; Pörtner *et al.* 2017). For benthic crustaceans, warming is especially considered critical for stenotherm animals, isolated intertidal populations, and for individuals residing at the warmer low latitude boundary of their realized habitat, where seasonal temperatures approach upper thermal performance limits (Stillman and Somero 2000; Kelly *et al.* 2012). Motivated by concern for the displacement or extinction of crustaceans from warming habitats, many studies have focused on the upper critical or Pejus (from good to bad) temperatures (see below). Several marine crustaceans however show a certain degree of eurythermy, and usually have a corresponding wider biogeographical distribution. For instance, the edible crab is exposed to a range of ambient temperatures across its geographic distribution, which stretches from northern Africa to beyond the Arctic Circle (FAO 2015). For individuals living at the highest latitudes, where low temperatures impose restrictions on metabolic processes, ocean warming and shifting isotherms might create a potential for better physiological performance and expansion of distribution boundaries.

This “border-of-opportunity” hypothesis however assumes that high latitude residents do not constitute a cold-adapted ecotype. The effect of temperature on geographically separated crustaceans has been investigated in several studies (Fox 1936; Fox and Wingfield 1937; Tashian 1956; Roberts 1957; Vernbergs and Vernberg 1966; Stillman and Somero 2000; Stillman 2003; Stillman 2004; Faulkner *et al.* 2014; Gaitán-Espitia *et al.* 2014; Cumillaf *et al.* 2016), and shows that both origin and local thermal conditions indeed affect physiological performance and tolerance. Most of these studies have however examined intertidal crustacean species (with highly variable thermal environments) or made comparison between closely related crustaceans (from the same genus or family), with a strong emphasis on upper thermal limits. Cuculescu *et al.* (1998) identified the upper thermal tolerance limits for the edible crab, and also found it to vary with season and acclimation temperature. However, whether thermal acclimatization exists across latitudes for the edible crab is not known, and we lack information regarding the species preference and tolerance to lower temperatures, i.e., similar to those experienced during winter and at the northern margin of its distribution.

As opposed to thermal limits, which are largely affected by acclimation temperature, it has been suggested that there is a species specific *thermal preferendum*, which Fry (1947) defined to be the “temperature around which all individuals will ultimately congregate, regardless of their thermal experience” (if allowed to move freely in a heterothermic environment). The thermal preferendum is usually determined either by the “gravitational method”, identified as the prevailing temperature selected by an animal held in a thermal gradient over time (typically 24–48 hours), or through the “acute method”, identifying the

more immediate thermal preference of individuals acclimated to different temperatures (Reynolds and Casterlin 1979), and where the thermal preferendum is considered the temperature where the acclimation temperature and the acute temperature preference of a species is the same (Fry 1947; Reynolds and Casterlin 1979). Some studies on fishes and crustaceans have however suggested that the thermal preferendum might not be as stringent as previously believed, and that it for a given species may vary with ontogeny (McCauley and Huggins 1979; Lafrance *et al.* 2005), season (McCauley and Huggins 1979; Clark and Green 1991; Despatie *et al.* 2001; Reiser *et al.* 2016) and even personality traits (Sonia *et al.* 2015; Cerqueira *et al.* 2016). Thermal preferendum has also been found to vary between populations of coho salmon (*Oncorhynchus kisutch*) raised in the same environment (Konecki *et al.* 1995), however, studies on other juvenile fish have identified the same thermal preferendum for geographically separated populations (Wagner and Wahl 2007; Siikavuopio *et al.* 2014). On the other hand, the thermal preferendum within crustacean species originating from different thermal habitats remains to be investigated.

In this study we investigate the thermal behaviour and identify the thermal preference and the critical thermal minimum (CT<sub>min</sub>) in female edible crab from two latitudes in coastal Norway.

## MATERIALS AND METHODS

### Origin of animals and thermal history

Live intact females of edible crab *Cancer pagurus* were sampled from the northern margin of the species distribution (i.e., Senja Island, Troms County, location: 69°09.200N/16°50.590E), depth: ~20m and from a location about 900 km further south (i.e., Ålesund, Møre og Romsdal County, location: 62°28.556N/5°56.324E, depth: ~20m (Figure 1).

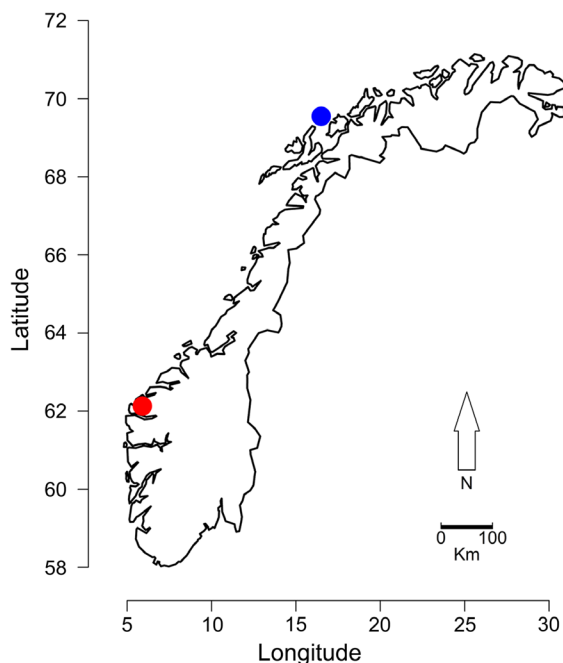
To ensure a sufficient number of intact specimens when starting our winter experiments, about 30 crabs were sampled from each area at the end of the commercial fishing season (mid-November) in 2015, using baited pots in cooperation with local fishermen. Details on crabs and origin of catch are presented in Table 1. Only female crabs were tested because they are likely more affected by environmental temperature due to their complex reproductive cycle (Bennett 1995).

Corresponding temperature data (mean for years 2000–2015, depth: 0–200 m) in proximity to the respective catch sites were provided by the Institute of Marine Research ([www.imr.no](http://www.imr.no)) (Table 2).

Crabs were transported to the laboratory in Ålesund (5 days refrigerated transport by boat and car for crabs from the north), where they were kept under a 12h/12h light/dark cycle (one hour ramp) in six 400 l fiberglass tanks containing rocks and artificial (plastic) kelp as shelter (OK Marine AS, Kristiansand, Norway). As the main aim of our study was to examine the thermal behaviour and tolerance in cold water,

Table 1. Female edible crab *Cancer pagurus* used in experiments. CW=Carapace width.

Group	Location of catch	Date of catch	Mean size (mm CW $\pm$ s.d.)	N Experiment 1	N Experiment 2
North	69°09.200N/16°50.590E	20.11.2015	144 $\pm$ 9	6	8
South	62°28.556N/5°56.324E	22.11.2015	143 $\pm$ 8	6	8

Figure 1. Map of Norway showing origin of edible crab *Cancer pagurus* used in experiments; blue = north and red = south. Details presented in Table 1.

the crabs were held from mid November 2015 till end of March 2016, when seasonal water temperatures were expected to be at their annual low. Tanks were supplied with unfiltered seawater from 40 meters depth, and temperature declined gradually from  $\sim 11^{\circ}\text{C}$  (November) to  $\sim 8^{\circ}\text{C}$  (March), which was the holding temperature at the onset of experiments. During the holding period the crabs were fed in excess with pieces of fishes (saithe and herring) at least once a week.

### Experiment 1 – Thermal preference

To study the thermal preference of crabs we employed the “gravitational method” (see Reynolds and Casterlin 1979) using the same approach as used for red king crab (*Paralithodes camtschaticus*) by Christiansen *et al.* (2015). A fiberglass tank consisting of two separate and parallel channels (260x90x30 cm), each with water volume of  $\sim 500$  l, was used (Figure 2). Water inlets at four cells along the channels were connected to a cold and warm circuit, allowing mixing of water and reversing the temperature gradient. The gradient in each channel spanned  $9^{\circ}\text{C}$  from  $\sim 5.5$  to  $\sim 14.5^{\circ}\text{C}$ . There was a temperature difference of about  $2^{\circ}\text{C}$  between cells. To ensure that the observed behaviour was solely driven by ambient temperature, no shelter or sediments were used, and the gradient in the two channels

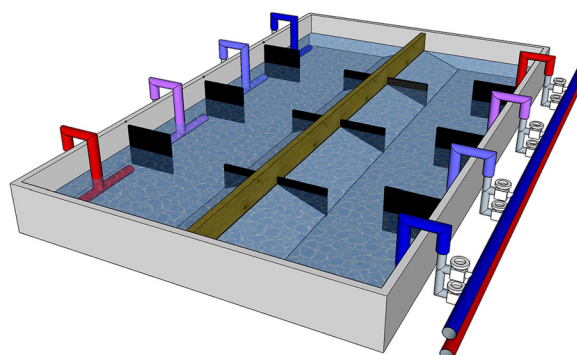


Figure 2. Raceway system with two thermal gradients. Temperature gradients were obtained by mixing cold (blue) and warm (red) water on four inlets along the channel. Ball plug valve at each point and temperature allowed fine tuning of temperature and reversal of the thermal gradient. Flow-meters attached to each inlet point allowed accurate mixing of volumes of water (not shown in figure).

was run in opposite direction which was reversed after every second test.

As juvenile and mature crabs occupy different habitats and show different seasonal behaviour (Bennett 1995; Robinson and Tully 2000) only crabs of about 140 mm carapace width (CW) were used, i.e., well above body size at physiological maturity (Haig *et al.* 2016; Bakke *et al.* 2018). Two days prior to tests, a single crab from each location was taken from the holding tank and fitted with a temperature logger dorsally on the carapace (IBcod type Z, Alpha Mach, Quebec, Canada) before being left undisturbed and unfed in a separate tank at the holding temperature  $8^{\circ}\text{C}$ . The temperature logger was set to register temperature every second minute. During the two-week experimental period (March), a total of twelve unfed crabs were tested once ( $n=6$  from each location) and single individuals were allowed to move undisturbed in the thermal gradient for a period of  $\sim 40$  hours, maintaining the same light/dark cycle as during holding (onset of light at 06.00 h and onset of darkness at 18.00 h (one hour ramp)). Single crabs were exposed to the gradient between 12:00 h and 16:00 h (light hours). The behaviour may be affected by the temperature of release (Lewis and Ayers 2014), therefore, crabs were released into a gradient temperature similar to that of the holding tank ( $\sim 8^{\circ}\text{C}$ ). To simplify comparisons and to reduce putative effects of handling, the onset of first night (18:00 h) was used as a starting point for data analyses. Onset of daylight on the second day (08:00 h) was set as endpoint of data analyses, yielding 1140 data loggings for each individual. For each crab, the mode of all temperature loggings (nearest  $0.5^{\circ}\text{C}$ ) was used as a measure of

preferred temperature (Haro 1991), i.e., the 0.5°C temperature interval with most temperature loggings. Modes rather than means were used because individual variability in activity within the thermal gradient would strongly influence the standard deviation of mean values. The modes were averaged among crabs from the two locations, and the difference in preferred temperature between groups was tested with a Welch's T-test.

It appeared that northern crabs spent more time at lower temperatures during night. To test this, the mean proportion of temperature loggings ( $n = 5$  crabs per location) being below the median temperature of the gradient (10°C) was compared between the two groups using a Student's T-test. A Shapiro-Wilks test was used for test of normality, and equality of variances tested by an F-test

To investigate the crabs' ability to move across gradient temperatures the five largest temperature changes between two consecutive temperature loggings were extracted for each individual (five changes towards a higher and five changes towards a lower temperature). Care was taken not to include data from the same run/thermal movement, i.e., loggings that were closer than one hour in time were excluded. The rate of temperature change registered by single crabs in the gradient (proxy for movement) was modelled as a function of the interaction between origin (north or south) and direction of movement (towards high or towards low temperatures), and as a function of carapace width. A generalized linear mixed-effects model was used, with Crab ID included as a random effect. Except for one value from a northern crab (migration during early morning), all the largest changes between two consecutive loggings were found during night-time. Time of day was therefore not included as a factor in the model.

### Experiment 2 – Righting reflexes at decreasing temperature

In April 2016, eight additional crabs from each location were transferred from the holding tank to a separate tank at ~7°C for two days without food. During tests, the crabs were held individually in 30x30 cm chambers in a tank provided with recycled refrigerated seawater (Adriatic Sea International, Rome, Italy) and with a perforated grid on the bottom to give foothold. The critical minimum temperature (CT<sub>min</sub>) was inferred from the ability of crabs to turn from an up-side-down position back into an upright position (i.e., the righting reflex) at given temperatures (Lagerspetz and Bowler 1993). Before onset of tests, the crabs were kept in darkness at 7.0°C for 15 minutes in an up-right position. The temperature was lowered from 7.0 to 1.0°C at a constant rate of ~-0.1°C/min. At every temperature reduction of 0.5°C, i.e., at 5 min intervals, the crabs were turned up-side-down and left undisturbed for two minutes and then inspected. If crabs did not return to the upright position, the observation was registered as a failed righting reflex. Crabs were then manually turned upright before next inspection 3 minutes later. The probability of righting reflexes was modelled with a generalized linear model (GLM) with

the binary response (1 = up-side-down position maintained, 0 = upright position achieved) as a function of the interaction between temperature and location (north or south). The CT<sub>min</sub> was considered the modelled temperature at which 50% of the crabs failed to show righting reflex. After the experiment, crabs were returned to the holding tanks (i.e., from 1.0 to 7°C).

Statistical analyses and graphical illustrations were made in R Version 3.3.1 (R Core Team 2016), except for Figure 2 which was made in SketchUp (Trimble, CA, USA).

## RESULTS

The seasonal temperatures at the two sampling sites are shown in Table 2. Overall the southern location was around 1°C warmer than the northern, but with more pronounced differences during late summer and autumn (shallow water (<50 m) was on average 2-3°C warmer in the south). Assumptions are made that bottom temperatures at sampling sites were similar to the temperatures measured at the corresponding depth of the water column.

### Experiment 1 – Thermal preference

The temperature loggings by 10 individual crabs are shown in Figure 3. (Data from two crabs were omitted - one animal (North) lost the logger and one immotile animal (South) had started to spawn.) The estimated mean preference temperature (mode of loggings) was similar for crabs at both locations i.e., 12.9 (± 0.4)°C (North) and 13.0 (± 1.6)°C (South) (Table 3).

The proportion of individual crab loggings at different temperature intervals was plotted for the three consecutive periods: first night, daytime and second night (Figure 4). During both nights the temperature loggings showed that the crabs utilized the entire thermal gradient. During daytime, on the other hand, little movement was registered, with crabs from both locations consistently lying quiescent in the warmer end of the gradient. When comparing crabs from the two locations in terms of proportion of loggings made below or above the median temperature of the gradient (i.e., 10°C), separate tests for first and second night showed no significant difference. However, night-time data overall showed a significantly higher proportion of cold water loggings by crabs from the north (~30% of nightly observations <10°C) compared to crabs from the south (~10% of nightly observations <10°C) ( $p = 0.04$ ,  $df = 8$ ).

Analysis of the rate of movement and subsequent temperature shifts within the gradient showed no effect of origin, direction of movement, or carapace width. The interaction term (origin x direction of movement) was however significant ( $p = 0.04$ ,  $df = 88$ ), with Tukey's simultaneous tests indicating a higher rate of movement towards warmer waters for southern crabs compared to crabs from the north (Table 3).

### Experiment 2 – Righting reflexes at decreasing temperature

Results from the righting reflex experiment showed a tendency



Table 2. Temperature at depths in proximity to sampling sites of female edible crab *Cancer pagurus*.

Location/Depth	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
North*												
5-10 m	5.9	5.0	4.6	5.0	6.5	8.7	10.9	11.5	11.0	10.0	8.7	7.3
10-50 m	6.1	5.3	4.9	5.1	6.2	7.6	8.8	9.4	10.2	10.1	8.8	7.4
50-100 m	6.7	5.9	5.5	5.5	6.1	6.8	7.3	7.6	8.3	9.6	9.0	7.9
100-200 m	7.7	7.1	6.6	6.5	6.7	7.1	7.3	7.5	7.6	8.0	8.4	8.4
South*												
5-10 m	6.5	5.7	5.5	5.9	7.7	10.0	12.3	14.1	14.2	11.8	9.7	7.9
10-50 m	6.9	6.2	5.7	5.8	7.0	8.3	9.3	11.5	12.9	12.1	10.2	8.5
50-100 m	8.0	7.0	6.5	6.6	7.1	7.7	7.9	8.2	8.7	10.2	10.1	9.4
100-200 m	9.0	8.0	7.6	7.6	7.8	8.1	8.1	8.0	8.2	8.6	9.2	9.3
Difference South-North												
5-10 m	0.6	0.7	0.8	0.9	1.3	1.3	1.4	2.6	3.2	1.8	1.0	0.6
10-50 m	0.7	0.9	0.8	0.7	0.8	0.7	0.5	2.1	2.7	2.0	1.4	1.0
50-100 m	1.3	1.0	1.1	1.1	1.0	1.0	0.6	0.6	0.4	0.6	1.1	1.5
100-200 m	1.3	0.9	1.0	1.1	1.1	1.0	0.8	0.5	0.6	0.6	0.8	0.9

\* Temperature data were obtained from the hydrographical stations Eggum (North) and Bud (South), both operated by the Institute of Marine Research. (Data are available online <http://www.imr.no/forskning/forskningsdata/stasjoner/>). Cells with light grey shading denote temperatures in proximity to preferred temperatures (see Results/Discussion). Cells with dark grey shading denote temperatures likely to be below lower Pejus (see Discussion). Depths with highest temperature are shown in bold.

Table 3. Summary results on thermal preference and movement for female edible crab *Cancer pagurus*.

Group	MTP <sup>1</sup> (°C ± s.d.)	max Thermal movement <sup>2</sup> ( Δ°C /min ± s.d.)	
		Towards warm	Towards cold
North	12.9 ± 0.4	1.09 ± 0.35 <sup>a</sup>	1.13 ± 0.35 <sup>a</sup>
South	13.0 ± 1.6	1.49 ± 0.27 <sup>b</sup>	1.31 ± 0.29 <sup>ab</sup>
Overall	13.0 ± 1.1	1.22 ± 0.33	1.29 ± 0.35

<sup>1</sup>. Mean Temperature Preference. Averaged from the mode of temperature loggings for each crab. <sup>2</sup>. Rate of movement in the thermal gradient. Different superscript letters denote significant differences at the 5% level.

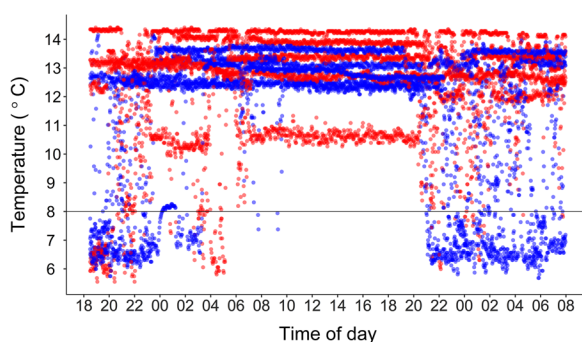


Figure 3. Movement of individual edible crab *Cancer pagurus* in a thermal horizontal gradient. Blue dots show crabs originating from north (n=5) and red dots crabs from south (n=5). Horizontal line denotes acclimation (and introduction) temperature at onset of tests.

towards a lower CT<sub>min</sub> for northern crabs. However, when modelled, the effect of origin was not statistically significant ( $p = 0.08$ ). Overall, 50% of the crabs lost their righting reflex at  $1.28 (\pm 0.68 \text{ SE})^\circ\text{C}$ . All crabs survived the experiment and the subsequent one-week holding period at  $7^\circ\text{C}$ .

## DISCUSSION

Reptant decapod crustaceans are well suited for thermo-behavioural studies, as they can readily move and maintain preferred positions within thermal gradients (Crossin *et al.* 1998; Lewis and Ayers 2014; Christiansen *et al.* 2015; Padilla-Ramírez *et al.* 2015; Nielsen and McGaw 2016). This has also been demonstrated in our study where a clear thermal behaviour

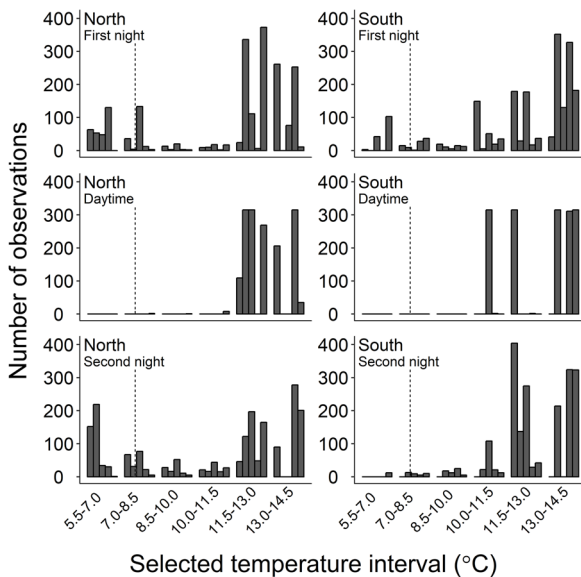


Figure 4. Number of observations at different temperature intervals selected by individual edible crab *Cancer pagurus* during the ~40 hour period within the thermal gradient. One observation equals 2 minutes. Figure shows observations for first night (top), daytime (middle) and second night (bottom) for crabs from North (left) and South (right). For each location, the position of a bar within temperature intervals corresponds to the same individual. Vertical dotted line denotes acclimation (and introduction) temperature at the onset of tests.

is observed for female edible crab. When conducting gradient experiments it is important to reduce contact- or corner-seeking behaviour (Lagerspetz and Vainio 2006). Studies on the behaviour of edible crab have shown that it readily seeks shelter or burrows into the sediment (Bennett and Brown 1983; Lawton 1989; Skajaa *et al.* 1998). Our own observations, both in the holding tanks and in the thermal gradient, revealed that some crabs were attracted to the walls of the tank. Although the position of single crabs might result from positive thigmotaxis, the consistent selection of the high temperature areas strongly suggests that temperature was the main driving force in behaviour.

Under aerobic conditions, physiological processes in ectotherms are adapted to the “thermal window” between the upper and lower Pejus temperature (Lagerspetz and Vainio 2006; Pörtner *et al.* 2017), with preferred temperatures often corresponding to optimal performance for growth (Jobling 1981). But thermal preference does not necessarily match temperatures at optimal physiological performance for all life history processes (Angilletta *et al.* 2002). Studies on elasmobranchs, bony fishes and reptiles have for instance shown that gravid animals select higher temperatures during gestation (Christiansen *et al.* 1997; Angilletta 2009; Schlaff *et al.* 2014). Whether such optimization strategies exist for crustaceans are unclear and studies on (intertidal) crab species are inconsistent

(Kerr *et al.* 2012; Clark and Backwell 2016). March and April (the period of our experiments) is the season when ovigerous female edible crabs incubate their eggs (Williamson 1904; Meek 1914; Bennett and Brown 1983; Le Foll 1986; Woll 2003; Ungfors *et al.* 2007; Hunter *et al.* 2013). In the North Atlantic, edible crab do not necessarily spawn every year, but spawning success depends on time of mating, body size and nutritional gain after moulting and mating (Pearson 1908; Edwards 1979; Latrouite and Noël 1993; Ungfors 2007). Except for one spawning crab (not used in data analysis), none of the other test crabs were berried even by the end of May. Thus, crabs used in our experiments had either skipped spawning or had yet to build up energy reserves to spawn.

The mean preferred temperature did not differ across latitudes for adult female edible crab and revealed a final thermal preferendum of  $13 \pm 1^\circ\text{C}$  (Table 3). Our results are in line with studies on fishes (Wagner and Wahl 2007; Siikavuopio *et al.* 2014), and conform to the theory of a final thermal preferendum (Fry, 1947; Reynolds and Casterlin, 1979; Jobling, 1981).

On the other hand, whether variations in thermal preferendum exist throughout development or between seasons, such as demonstrated in brown shrimp (*Crangon crangon*) (Reiser *et al.* 2016), remains to be investigated. Further, physiological performance and life history traits may vary among geographically separated populations, and differences in some of these traits, including thermal tolerance, can be evident even after long periods at the same environmental condition (see Sanford and Kelly 2011). But the similar CTmin for edible crab from both locations suggests that putative differences in thermal behaviour had been eliminated during the 20-week holding period. However, the tendency for northern crabs to spend more time in the low temperature range of the gradient (Figure 3 and Figure 4) warrants further investigations into potential physiological differences.

Irrespective of origin, our study shows that edible crab displays a high degree of eurythermy because it readily moves within the entire gradient ranging from ~5.5 to ~14.5°C (Figure 3 and Figure 4). In nature, such flexibility is clearly most advantageous during spring and autumn when temperature gradients in the water column peak (see Table 2, and Karlsson and Christiansen 1996). It is well known that edible crab migrates to shallow inter-tidal water during summer where they feed on molluscs and barnacles, and sharp temperature changes may occur during foraging as shown from studies in southern Norway (Karlsson and Christiansen 1996). It is thus tempting to speculate that the observed tendency for southern crabs to move at a higher speed between temperatures (Table 3) is an adaptation to a more varying thermal environment. Our observation alone is however insufficient to make such conclusions, as the differences also could be related to subtle unidentified physiological differences between crabs at the two locations.

The edible crab is a nocturnal forager, with movements and

metabolic activity being very much reduced during daytime (Ansell 1973; Aldrich 1975; Karlsson and Christiansen 1996; Skajaa *et al.* 1998; Scott *et al.* 2018). This is also supported by our results (Figure 3 and Figure 4) – at the onset of light, crabs consistently moved toward the warm end of the gradient where they stayed largely inactive during daytime. Field and laboratory investigations on fishes and crustaceans have shown that animals may leave the preferred temperature and salinity zones to forage under sub-optimal conditions (Sims *et al.* 2006; Curtis and McGaw 2012). Our findings may suggest a similar strategy for edible crab where starved crabs explored the entire temperature gradient during night (likely in search of food), but returned to the preferred temperature zone to reduce physiological stress during daytime. To confirm this, future work should investigate whether this nocturnal exploration of the gradient is reduced in fed crabs, or if thermal behaviour is unaffected by nutritional status, such as shown with red king crab (Christiansen *et al.* 2015).

The upper critical temperature (CT<sub>max</sub>) in edible crab acclimated to winter temperature (8°C) is about 22°C (Cuculescu *et al.*, 1998). Given a lower critical temperature (CT<sub>min</sub>) of about ~1.3°C (our study), this suggest a thermal tolerance range of about 21°C (~30 Δ °C if considering CT<sub>max</sub> of warm-acclimated crabs (~31°C), Cuculescu *et al.* 1998). In Norwegian waters, the edible crab seldom meets CT<sub>max</sub> and CT<sub>min</sub> (Table 2). In a recent review, Pörtner (2017) emphasized the need to consider non-critical thresholds, like Pejus temperatures, when determining the thermal performance of a species. For edible crab the upper Pejus temperature was ~15–16°C for animals acclimated in the laboratory at 10°C (Metzger *et al.* 2007). Further support is found in studies on the temperature effect on neural responses in limbs of edible crab. Both Pearson *et al.* (1999) (working on edible crabs acclimated to 8°C in the lab) and Hyde *et al.* (2015) (using edible crabs collected during the winter), found the highest excitatory junction potential (EJP) between 6 and 15°C, with a rapid decline in EJP above 15°C. In the experiment by Pearson *et al.* (1999) there was also a drop in EJP from 6 to 5°C, indicating that a lower Pejus temperature for winter acclimated edible crabs might be in this range. This is further supported in field studies by Karlsson and Christiansen (1996) who observed that temperatures below 5 °C appeared to limit the vertical migration of edible crab in the intertidal zone. Thus, a functional thermal range for female edible crab appears to be in the range 5–16°C, likely with an optimum around 13°C (Table 3). In context of the species natural thermal environment, it is apparent that, even though the temperatures experienced are far from critical, the thermal window matching preferred temperatures shrinks rapidly at higher latitude (Table 2). It is thus clear that northern crabs spend most the time in suboptimal conditions and that low temperatures, especially during the winter months, are likely to impede physiological performance and limit northward dispersal. The distribution of marine crustaceans is also shaped by the seasonal temperatures required to sustain basic life

history processes (Hall and Thatje 2009; Levinton and Mackie 2013). The narrow thermal window of warmer seawater during summer and autumn months is critical for edible crab, as this is the main period for moulting, mating and subsequent energy acquisition (Williamson 1900; Edwards 1967; Edwards 1979; Bennett 1995; Tallack 2007; Bakke *et al.* 2018). Given the temperature effect on these processes (Cossins and Bowler 1987), and the positive relationship between thermal preference and optimal growth (Jobling 1981), it is likely that any further expansion of the realized habitat of edible crab will highly depend on the rate and magnitude of ocean warming and the concomitant temperature rise in shallow water in summer.

Large crustaceans are often key species in benthic communities, and their abundance can be important in regulating trophic structures of marine ecosystems (Boudreau and Worm 2012). The edible crab is an opportunistic forager, feeding on both soft and hard bottom fauna (Shelton *et al.* 1979; Lawton 1989; Hall *et al.* 1991). It is therefore likely that the species will have a significant impact on the ecosystem as it expands its distribution northward. For instance, Fagerli *et al.* (2014) suggested that the return of kelp forests in central Norway might be due to the increased abundance of edible crab in these areas, in that the crab prey on and reduce the number of grazing sea urchins. Future studies should therefore monitor the ecological impact of this northward migrating species.

It should be emphasized that our study was conducted on adult female crabs only, and that flexibility in thermal performance and tolerance can vary across ontogeny (Pörtner and Peck 2011). In an ecological context it is therefore important to consider the effects of temperature change on all life stages (Sinclair *et al.* 2016). Whether thermal adjustments occur during different life stages of edible crab should therefore be investigated, especially considering that juvenile crabs occupy the shallow sub-tidal to intertidal zone (Williamson 1900; Bennett 1995), where they are exposed to larger seasonal and diurnal fluctuations in ambient temperature. Thermal preference and tolerance should also be investigated in male crabs, which are less motile (Bennett and Brown 1983; Karlsson and Christiansen 1996) and which possibly form local populations in some areas (McKeown *et al.* 2017). Finally, the effect of temperature on the earliest life stages of this species should be investigated. Given the relatively high optimal developmental temperatures for laboratory reared larva (around 14°C, Weiss *et al.* 2009), and the relatively low surface water temperatures in northern Norway (Table 2), it is likely that larval development is strongly impeded in the northern part of the crabs' distribution. Temperature studies on the offspring of northern crabs might help to determine if the increased abundance in the north is due to a higher survival of larvae in warmer waters (Lindley and Kirby 2010), or if larvae are adapted to lower temperatures, such as suggested for American lobster (*Homarus americanus*) (Quinn *et al.* 2013).

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