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THE ARCTIC  
UNIVERSITY  
OF NORWAY

Department of Arctic and Marine Biology, Faculty of Biosciences, Fisheries  
and Economics

# Life history and distribution of the edible crab (*Cancer pagurus*) in Norway

*Effect of temperature and other environmental parameters at  
high latitudes*

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**Snorre Bakke**

*A dissertation for the degree of Philosophiae Doctor – May 2019*





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**Effect of temperature and other environmental parameters at high latitudes**

**Snorre Bakke**

Thesis submitted in partial fulfilment of the requirements for the degree of Philosophiae Doctor in  
Natural Science

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Graduating institute:

**Department of Arctic and Marine Biology**

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**Møreforskning Ålesund AS**





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## Supervisors

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## Preface and acknowledgements

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This PhD have been a cooperation between Møreforsking Ålesund AS (my employer) and the Arctic University of Norway – UiT (the graduating institute).

Since the early 1990s, Møreforsking has conducted several research projects on the edible crab. This includes both applied projects (together with fishers and the crab industry), and more basic research on the species biology and physiology. Most of this work has been led by Astrid K. Woll, who also established the reference fleet of crab fishers in 2001. As Astrid was retiring in 2014, internal funds were set aside by Møreforsking to finance my PhD, with the goal to maintain the position of the institute with regards to research on the edible crab in Norway. Financial support was also provided by Møre and Romsdal county (“Kompetanseløft i Møre og Romsdal”).

The PhD was initially planned as a 3-year full time study, but as I also have been involved in other research projects and some additional administrative work as a research manager, it was extended by one year. Although it sometimes has been difficult focusing both on the job as PhD student and as a researcher involved in other projects, the last four years have been very educational in that I have had to balance the work between my research, research proposals and administrative work in projects. As I see it, this is important part of being a scientist. My completion of this PhD would, however, not have been possible without the help of several people, to whom I wish to express my gratitude.

I would like to thank my supervisors in Tromsø, Einar Magnus Nilssen, Jørgen Schou Christiansen, Sten I. Siikavuopio and Carsten Hvingel, all mainly working with arctic species, that dared to take on the supervision of a student wanting to study a boreal marine crustacean. Also thank you to my “local” supervisor Agnes C. Gundersen at Møreforsking, for giving me the opportunity to do this PhD and for helping me balancing the work as a PhD student, researcher, and, during the last couple of years, a research manager.

A special thank you to Astrid Woll who as my supervisor during my Bachelor studies introduced me to the physiology and biology of the edible crab, and whom together with Wenche E. Larssen became my “mentors” when I started working at Møreforsking. Thank you both for all the fruitful discussions, for sharing of your insight, and for laying much of the foundation for me to conduct this PhD.

I would also like to thank my fellow co-workers at Møreforsking for the support during the last four years, and my fellow research managers, Margareth Kjerstad and Liv Guri Velle, for helping me with some of the administrative work when I needed time to focus on this PhD.

Thanks also to Martin Wiech, for mutual support during the ups and downs in our PhD journeys, the cooperation during fieldwork and for the good discussions together with the rest of the “cadmium team” at the Institute of Marine Research: Arne Duinker, Amund Maage and Sylvia Frantzen.

Thanks to all my co-authors for giving me the opportunity to work together with so many knowledgeable and inspirable people. I really hope that I will be able to cooperate with you all in future research projects.

This work would neither have been possible without the assistant from several fishermen. From south to north, a special thank you to Helge Susort, Roger Geitung, Leif Nidar Bakeng, Ronny Støen, Ketil Martinsen, Willy Olsen and Håvard Pettersen. Thanks also to HitraMat AS, and especially Kolbjørn Ulvan, for the discussions and information on crab fishery, processing and quality of crabs.

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Finally, and most importantly, I would like to thank my family. Mariann, and my children Jonatan and Oline, for the patience and moral support, and for tolerating my physical and mental absence from time to time, and my mom and dad, who have always allowed me to follow my interests.

**Contribution to other scientific work during the PhD study period:**

Larssen, W. E., **Bakke, S.** and Woll, A. K. (2015). Microscopic and macroscopic (visual) determination of gonad development in female *Cancer pagurus*. In: Blue Bio-resources. A. C. Gundersen and L. G. Velle, Orkana Akademisk: 19-37.

Søvik, G., Furevik, D., Jørgensen, T., **Bakke, S.**, Larssen, W. E., Thangstad, T. H. and Woll, A. K. (2016). The Norwegian Nephrops fishery – history, exploitation and management. Sustainable bio-resources. B. J. Thu and A. C. Gundersen, Orkana Akademisk: 95-118.

**Bakke, S.**, Wiech, M., Pan, M. and Søvik, G. (2016). *The edible crab in Troms county. Harvest potential, catch composition and quality of crabs.* (In Norwegian: Taskekrabbe i Troms. Fangstpotensiale, fangstsammensetning og kvalitet). Ålesund, Møreforsking (Report MA 16-06): 29 p.

Wiech, M., Vik, E., Duinker, A., Frantzen, S., **Bakke, S.** and Maage, A. (2017). "Effects of cooking and freezing practices on the distribution of cadmium in different tissues of the brown crab (*Cancer pagurus*)." *Food Control* 75: 14-20.



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## Summary

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The edible crab (*Cancer pagurus*, Linnaeus 1758) is a large decapod crustacean distributed across the north-east Atlantic Ocean, from the Canary Islands in the south to Finnmark county in northern Norway. The species sustains the second largest crustacean fishery in Europe, with about 50 thousand tonnes landed annually. In Norway, the annual landings during the last 10 years have been around 5 thousand tonnes.

Different regulatory measures are in effect across European waters to protect the crab population from over-exploitation. In Norway, the fishery is only regulated through a minimum legal landing size (MLS), which is 110 mm and 130 mm carapace width (CW), respectively south and north of 59°30'N. At the time of their implementation, these MLS values were based on knowledge transferred from other countries, limited investigations in Norway during the 1920s, and requests by the fisheries industry. More thorough biological studies of the edible crab in Norway are, however, lacking, and prevent fisheries authorities from deriving well-informed management decisions. The aim of this study has been to provide a better understanding of how the environmental conditions at higher latitudes might affect the biology, life history, and distribution of *Cancer pagurus* in Norwegian waters.

In a trans-national collaboration, the size at onset of physiological maturity was compared between female crabs collected from different areas in northern Europe (**Paper I**). The results from this study show that the size at which female crabs from central Norway become mature is similar to that of crabs from waters around the UK and Ireland. Neither was any difference in size at maturity found when comparing female crabs collected from latitudinally separated areas off Norway (**Paper II**), with maturity estimates comparable to results obtained from studies in the same areas 10 years earlier. Analysis of data gathered by fishers on the occurrence of soft crabs show that moulting frequency in female crabs decline with increasing latitude, demonstrating slower growth and a higher age at maturity for crabs at more northern latitudes. The data also show that peak periods of moulting occur later at higher latitudes, indicating that the reproductive cycle of crabs in the north is delayed compared to that of crabs further south. It is believed that these spatial differences in frequency and timing of the onset of moulting are due to geographical differences in temperature.

No difference in lower thermal tolerance limit was found in laboratory experiments when comparing female crabs collected off the coast of northern Norway with crabs collected 900 km further south (off the coast of central Norway) (**Paper III**). A common and rather warm preference temperature (~13 °C) was identified in thermal behaviour experiments in which individuals could move freely within a temperature gradient. A clear diurnal pattern in crabs' behaviour was also observed, with crabs exploring the whole thermal gradient during the night but remaining inactive in the warm end of the gradient during daylight hours.

Video transects conducted in Sognesjøen on the west coast of Norway in March 2014 reveal a high abundance of crabs at ~400 meters depth (**Paper IV**). These observations show that the topography of Norway, with its deep fjords, forces crabs in some areas to move to depths greater than the bathymetric numbers given in popular species information fact sheets. Analysis of the video material also reveal high concentrations of shell remnants scattered across the seabed, indicating that natural mortality might be high when crabs spend the winter months at these depths.

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## List of papers

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- Paper I** Haig, J. A., **Bakke, S.**, Bell, M. C., Bloor, I. S. M., Cohen, M., Coleman, M., Dignan, S., Kaiser, M. J., Pantin, J. R., Roach, M., Salomonsen, H. and Tully, O. (2016). Reproductive traits and factors affecting the size at maturity of *Cancer pagurus* across Northern Europe. *ICES Journal of Marine Science*, 73 (10): 2572–2585.
- Paper II** **Bakke S.**, Larssen W.E., Woll A.K., Søvik G., Gundersen A.C., Hvingel C., Nilssen E.M., (2018). Size at maturity and molting probability across latitude in female *Cancer pagurus*. *Fisheries Research*, 205, 43-51.
- Paper III** **Bakke S.**, Siikavuopio S., Christiansen, J.S. (2019) Thermal behaviour of edible crab *Cancer pagurus* in coastal Norway. *Fauna norvegica*, 39, 1-11.
- Paper IV** **Bakke S.**, Buhl-Mortensen L., Buhl-Mortensen P. Some observations of *Cancer pagurus* in deep water. *Crustaceana*, 92 (1), 95-105.

## Introduction

### Distribution, habitat, and ecology of *Cancer pagurus*

The edible crab (*Cancer pagurus*, Linnaeus 1758), also known as the brown crab, is a large reptant decapod crustacean occupying waters in the north-east Atlantic Ocean. Its distribution stretches from the Canary Islands in the south (~30 °N, González, 2016) to Finnmark county in northern Norway (~70 °N, Brattegard, 2011), covering a latitudinal range of more than 5000 km. The species is also found in the Mediterranean, but its sporadic occurrence in checklists indicate that it is rare there (Koukouras et al., 1992; Udekem d'Acoz, 1999; Frogia, 2010; Marco-Herrero et al., 2015). Few individuals are also found at the species poleward and equatorward latitudinal boundaries, where their further spread is likely restricted by the respective cold and warm water conditions. The highest abundance of crabs is found in the more temperate waters along the western French coast, in the English Channel, around the British Isles, in the North Sea, off the western coast of Sweden, and along the Norwegian coast (Figure 1).



Figure 1 - Map of distribution of *Cancer pagurus*. From FAO.

Relative to, for instance, the intertidal shore crab (*Carcinus maenas*), *Cancer pagurus* is considered a stenotherm species (Cuculescu & Bowler, 1993; Cuculescu, 1996; Hyde et al., 2015) and is most common in the subtidal zone down to depths of 100 meters (Neal & Wilson, 2008), although individuals have been registered as deep as 520 meters (Udekem d'Acoz, 1999 citing Clark 1986). Juvenile crabs, which are more tolerant to fluctuations in salinity (Wanson et al., 1983), occupy the intertidal zone (Williamson, 1900; Pearson, 1908), where they shelter under boulders of rock or in the holdfast of kelp (Moore, 1973; Eriksen & Moen, 1993; Robinson & Tully, 2000a; Heraghty, 2013), feeding on other small crustaceans, gastropods, and epifaunic polychaetes (Lawton, 1989; Eriksen & Moen, 1993). When approaching sexual maturity crabs migrate to deeper waters where they occupy both hard and soft substrate, foraging mainly for bivalve molluscs, crustaceans, gastropods, and sea urchins (Shelton et al., 1979; Woll, 1995; Hallbäck, 1998; Fagerli et al., 2014). Foraging occurs at night

(Williamson, 1900; Lawton, 1989; Skajaa et al., 1998). Some crabs (often recently moulted individuals) then migrate to shallow water during high tide to feed on molluscs and barnacles (Seed, 1969; Karlsson & Christiansen, 1996; Silva et al., 2010). When in shallow water, the crabs are exposed to predation from seagulls (Sibly & McCleery, 1983; Tallack, 2002). In depths beyond the reach of avian predators, juveniles are preyed upon by octopus (Boyle et al., 2009), a range of fish (Hallbäck, 1998) and possibly larger conspecifics (Amaral et al., 2009). In general, adult *Cancer pagurus* have few known natural predators, but they have occasionally been found in the stomach of large fish (Nordgaard, 1912; Rae & Shelton, 1982) and are probably vulnerable to cannibalistic attacks from other crabs immediately after moulting (Edwards, 1979; Le Foll, 1982). Crabs are also susceptible to various viruses, bacteria, and parasites, but there is limited knowledge on the prevalence within populations and the extent of mortality caused by these pathogens (Stentiford, 2008).

### Life history of female *Cancer pagurus*

Likely inspired by Pearson (1908, p.180), Bjerkan (1927a, p.12) constructed a diagram to illustrate the probable reproductive cycle of female *Cancer pagurus* (Figure 2). He emphasized that, apart from limited investigations of his own, most of the knowledge he presented on *Cancer pagurus* biology came from studies initiated in England and Scotland 20 to 30 years earlier. Bjerkan was likely referring to comprehensive studies by Cunningham (1898), Williamson (1900, 1904), Pearson (1908) and Meek (1904, 1912, 1914, 1916), all pioneers in study of the life history of *Cancer pagurus*. Although simplified, the figure gives a good overview of the seasonality of important reproductive events in female crabs and is a useful reference point when presenting details about the species life history processes.

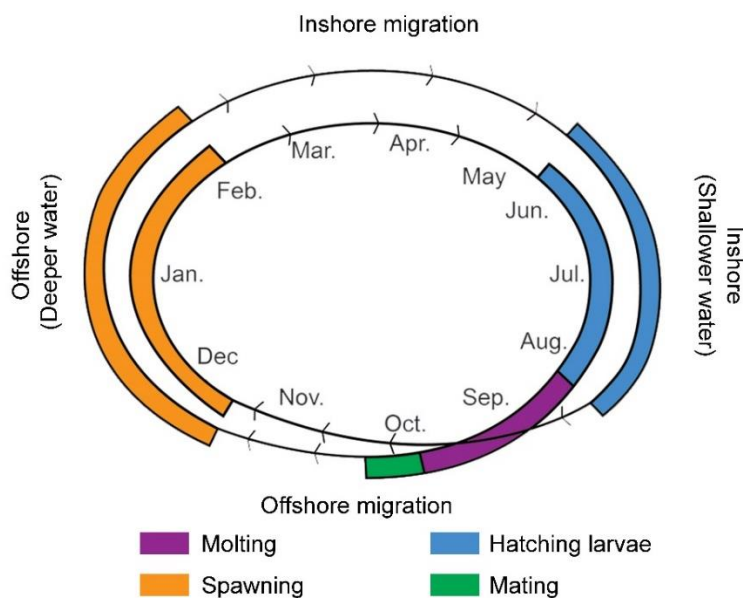


Figure 2 – Biannual reproductive cycle for female *Cancer pagurus*. Redrawn from Bjerkan (1927a, p.12). Starting from moulting (purple) and mating (green), the crab spawn during winter (orange, outer circle) and release larvae in spring/summer (blue, outer circle). After hatching, the crab has stored sperm for an additional spawning the following winter (orange, inner circle) before hatching again occurs (blue inner circle). The crab can then moult and mate again (purple), and the cycle repeats.

The life of *Cancer pagurus* starts in the form of pelagic larvae, hatching first as a protozoa, and developing through five zoeal stages and a megalopa stage (Ingle, 1981). Hatching typically occurs between late spring and early autumn (Edwards, 1979), with some variation between areas. In the English Channel hatching occurs between February and July (Lebour, 1947; Lindley, 1987; Thompson et al., 1995), while in the North Sea and around Orkney and the Shetland Islands hatching occurs between June and November (Meek, 1904; Rees, 1952; van der Baan et al., 1972; Lindley, 1987; Eaton et al., 2003; Hazlehurst, 2007; Tallack, 2007b). Diving investigations and observations of laboratory held berried crabs indicate that hatching along the west coast of Norway occurs between June and October (Nordgaard, 1912; Woll, 2003). The spatial (and seasonal) variation in onset and peak periods of hatching is thought to result from differences in temperature (Lindley, 1987; Lindley & Kirby, 2010). Relating occurrence of first stage zoea with water temperature in the North Sea, Lindley (1987) has suggested that temperatures must be above 8°C for *Cancer pagurus* to have a successful development of early larval stages. However, the optimal temperature for development is probably higher, as Weiss et al. (2009) only found a complete larval development at temperatures of about 14 °C in the laboratory. Temperature, as well as food availability, influences the duration of each larval stage (Nichols et al., 1982; Lindley, 1984). Estimates from field studies and results from laboratory rearing suggest that the pelagic phase lasts between three weeks and two months (Lebour, 1928; Nichols et al., 1982; Weiss et al., 2009).

Information on larval mortality is scarce and estimates of its magnitude vary. Based on field data and laboratory experiments with larvae held at different temperatures, Nichols et al. (1982) have estimated a daily mortality rate of ~3%, or a total mortality of ~46% during the first four larval stages. Using the occurrence of different larval stages in water samples in combination with estimates of the time spent in each larval stage, Hazlehurst (2007) estimated that only ~7 % of the larvae survived to the sixth larval stage.

The megalopa settles during late summer and autumn and moults into a juvenile crab shortly after. At this first juvenile stage, the crab has a size of about 2.5 mm carapace width (CW) (Cunningham, 1898; Lebour, 1928). It then moults several times during the autumn, reaching a CW of ~1 cm before the onset of winter (Robinson & Tully, 2000a). During these first instar stages a mortality of more than 60 % has been estimated (Robinson & Tully, 2000a). Studies conducted by Williamson (1904) on the eastern shores of Scotland and by Edwards and Brown (1967) off the east coast of England have demonstrated that the crab reaches a size of ~30 mm after one year. Using data from Williamson (1904), Pearson (1908) estimated that crabs moult twice annually during their second and third years but only once each year during the fourth and fifth years. The crabs have by then reached a CW of about 110 mm. During the juvenile phase, moult increment appears to be rather constant at around 20–25% increase from pre-moult size (Williamson, 1900; Williamson, 1904; Edwards, 1965; Tallack, 2002). However, after reaching maturity there is an inverse relationship between size and both moulting frequency and moult increment, which is stronger in females than in males (Bennett, 1979; Bennett, 1995). This change is thought to result from the redistribution of energy from growth towards reproduction (Hancock & Edwards, 1967; Bennett, 1995).

It was recognized early on that the time when adult females moult is also the time for mating (Bell, 1853; Wilson, 1895). Just after exuviation, which is assisted by a male that has followed the female for some time, the male transfers its sperm to the vulva (Williamson, 1900; Edwards, 1966a). The sperm is encapsulated within a fluid secreted by the female oviducts, which solidifies in contact with seawater (Williamson, 1904), forming a sperm plug that is visible in the opening of the oviduct several

weeks after mating (Edwards, 1979). The plug is believed to prevent leakage from the spermatophore (Williamson, 1904), and it probably also prevents other male crabs from copulating with the female (Edwards, 1966a). The belief that females only mate once after moulting is supported by studies investigating multiple paternity (Burfitt, 1980; McKeown & Shaw, 2008). Seasonal occurrence of soft crabs (and the presence of sperm plugs) indicate that the main season for mating in northern European waters is between June and November (Pearson, 1908; Edwards, 1966b; Edwards, 1967; Brown, 1975; Tallack, 2007b), with some variation in peak periods between areas and years (Bennett, 1995).

Moulting and post-moult calcification are energy-demanding processes (Paul & Sharpe, 1916). During the autumn and early winter, the female therefore feeds to refill its oversized exocuticle. Although it is possible for the crab to spawn the coming winter, it is believed that many crabs spend more than a year after mating gaining the energy needed to produce offspring (Wilson, 1895; Pearson, 1908; Edwards, 1979). While males generally stay within a relatively small area throughout the year (Mason, 1965; Bennett & Brown, 1983), females make extensive migrations once they are ready to spawn, often to deeper offshore areas (Bennett & Brown, 1983; Latrouite & Le Foll, 1989; Ungfors et al., 2007; Hunter et al., 2013). Several mark-recapture studies have shown that this migration is predominantly made against the prevailing water currents (Meek, 1916; Gundersen, 1977; Bennett & Brown, 1983; Ungfors et al., 2007; Hunter et al., 2013), and it has been suggested that this counter-current movement allows larvae to drift back to the place from which the female migrated (Meek, 1916). Spawning grounds are usually soft-sediment seabeds, where the female digs a pit in which it rests to incubate the eggs (Howard, 1982; Thompson et al., 1995; Woll, 2003). Once oviposition has occurred, *Cancer pagurus* spawn from a few hundred thousand to three million eggs (Pearson, 1908; Edwards, 1979; Tallack, 2007a), with larger females producing more eggs than smaller individuals (Hankin et al., 1989; Tallack, 2007a). The incubation period lasts from six to eight months, which include a diapause period starting shortly after spawning (Wear, 1974; Naylor et al., 1999). Upon releasing the larvae, the female has spent most of its stored energy (Howard, 1982), and migrates inshore to forage. The sperm stored in the seminal receptacles are used to fertilize at least two batches of eggs (Williamson, 1900; Pearson, 1908; Edwards, 1979), meaning that females only have to moult and mate every second to third year (cf. the biannual reproductive cycle in Figure 2).

It is difficult to determine the age of crustaceans, as most hard structures on which ageing could potentially be based are dissolved and reconstructed during the moulting process. Estimates of age and longevity in *Cancer pagurus* therefore originate from growth studies in the laboratory (Williamson, 1904; Edwards, 1979), analysis of results of tag-recapture experiments (Edwards, 1965; Edwards, 1966c; Edwards & Brown, 1967; Hancock & Edwards, 1967; Edwards, 1972; Bennett, 1974), length frequency analysis (Tallack, 2002; Ungfors, 2008; Klaoudatos et al., 2013), or studies on accumulation of neurolipofuscin in the eye stalk (Sheehy & Prior, 2005; Sheehy & Prior, 2008). Based on these results it has been estimated that *Cancer pagurus* reaches maturity after about 4 to 8 years and has a maximum lifespan of 15 to 20 years.

### Fishery for *Cancer pagurus*

The exploitation of edible crab has a long history, particularly in the UK, where it has been harvested at least since the twelfth century (Edwards, 1979) and possibly even as far back as when the Romans

governed southern parts of the country (~50 AD) (Bell, 1853; Lord, 1867; Edwards, 1979). Currently, the fishery for *Cancer pagurus* is one of the largest crustacean fisheries in European waters, only exceeded in volume by the fishery for Norway lobster (*Nephrops norvegicus*) (FAO, 2018). The total annual landings in the last 10 years have been between 40 and 50 thousand tonnes, of which around ~90% has been harvested by the UK, France, Ireland, and Norway (Figure 3). A large part of the fishery is conducted on small vessels (< 15 m) in coastal waters during late spring to autumn (Brown & Bennett, 1980; Fahy et al., 2002; Woll et al., 2006b; Mill et al., 2009; Aitken, 2018). Some larger vessels target the crab year-around in the English Channel, and in offshore areas off the shores of Scotland and Ireland (Tully et al., 2006; Mill et al., 2009; Carleton, 2016; Mesquita et al., 2017; Aitken, 2018).

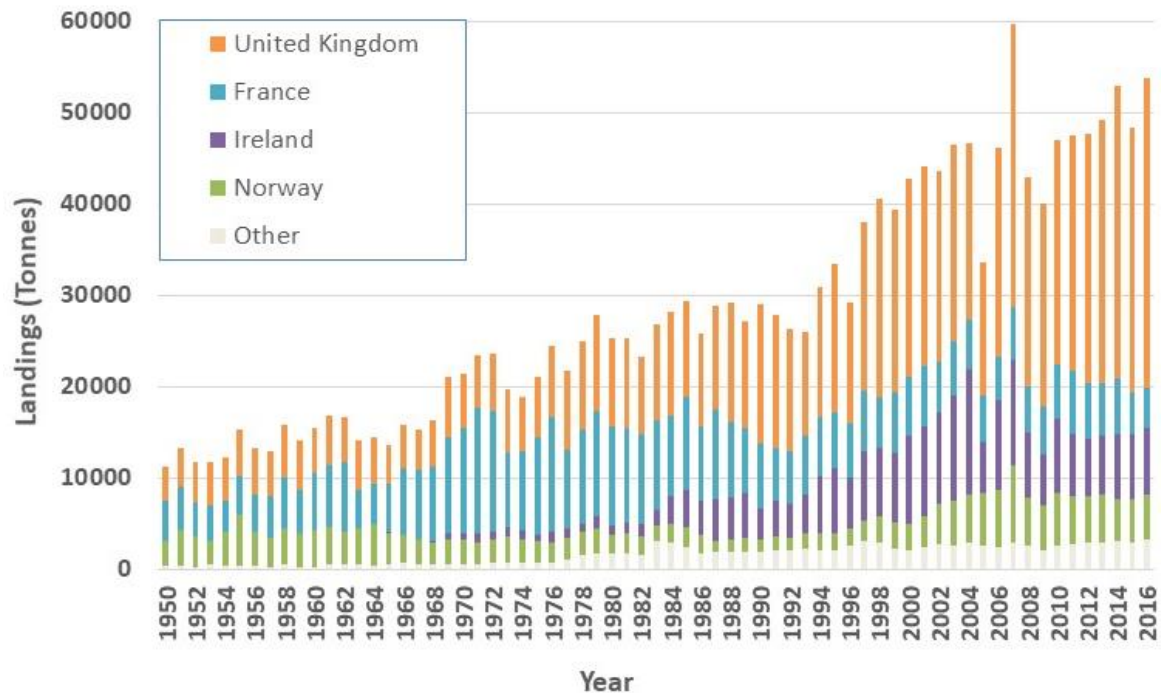


Figure 3 - Landings of *Cancer pagurus* in Europe from 1950 to 2016. Other countries (with landings in 2016) are: the Channel Islands (1073 t), the Netherlands (577 t), the Isle of Man (534 t), Belgium (305 t), Denmark (292 t), Sweden (208 t), Germany (186 t), Spain (66 t), and Portugal (2 t). Data obtained from FishStatJ (FAO, 2018).

With the exception of some anecdotal references in old newspapers to individuals canning crab meat (Andersen, 1877, p. 3), there is little historical information on the extent of fishery or commercial utilization of *Cancer pagurus* in Norway before the 1900s. Wollebæk (1900, p. 5) reported that *Cancer pagurus* was frequently caught by fishermen in gillnets along the coast of Trøndelag (~64 °N), but that the crabs were “seldom utilised”. Bjerkan (1926, p. 143) also commented that the species was considered close to worthless in many districts until the turn of the century. It is likely, however, that crabs were consumed in the larger cities, as about 60 thousand crabs were sold annually between 1902 and 1905 on the fish market in Bergen (Nordgaard, 1912). The major increase in fishery for edible crab in Norway started in the early 1920s, driven by an increased demand for crab meat by the canning industry (Bjerkan 1926). In the 20<sup>th</sup> century the canning industry had its ups and downs, which consequently also affected the fishery for crab (Woll & Van der Meeren, 1997). With the transition from canning to other crab product types (whole crab and filled shells), demand again increased. An important milestone was the building of a new and modern crab factory on the island of Hitra outside

of Trøndelag in 2002. This factory is the largest producer of crab products in Norway, handling about three thousand tonnes annually, which is about 60% of the Norwegian landings (~5000 tonnes, Figure 3 and Figure 4).

The edible crab is currently one of the most important near-shore fisheries for small Norwegian vessels (< 15 m). The crab is fished from the Swedish border north to about 69 °N (Figure 4), but with the largest commercial catches landed along the central western coast (Areas 06, 07, and 08 in Figure 4).

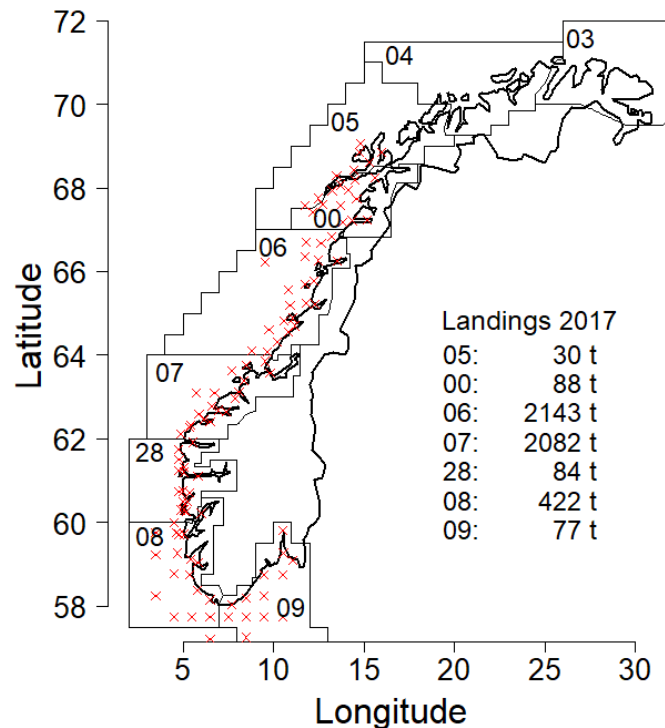


Figure 4 – Landings of *Cancer pagurus* by statistical areas along the coast of Norway. Red crosses denote locations of catch reported by fishers in the period 2001–2017 (Data from the Directorate of Fisheries). Inserted table show landings (in tonnes) for the different areas in 2017.

The main season of the fishery is July to November (Figure 5), with the intensity influenced mainly by the accessibility and quality of crabs. Crabs that have moulted during summer and autumn have low meat content and becomes increasingly difficult to distinguish from a good-quality crabs as the exocuticle calcifies. This affects crab producers, which must discard a large proportion of the landing due to poor quality. Consequently, the main producer of crabs in Norway usually stops buying crabs during late November (Kolbjørn Ulvan, HitraMat AS, pers. com.). Participation in the crab fishery is also regulated by the profitability of available alternative fisheries. Many boats derive their main income from the winter cod fishery, which usually ends in April or May, and then target crab from the summer onwards. In recent years there has been an increase in the number of boats that use pots year-around, typically targeting Norway lobster during winter and spring, edible crab during summer and early autumn, and European lobster (*Homarus gammarus*) during the open season between September and New Year (own observations). About 400 boats landed crabs in Norway in 2017, with the total catch ranging from less than 100 kg to more than 100 tonnes (Data from Directorate of Fisheries).



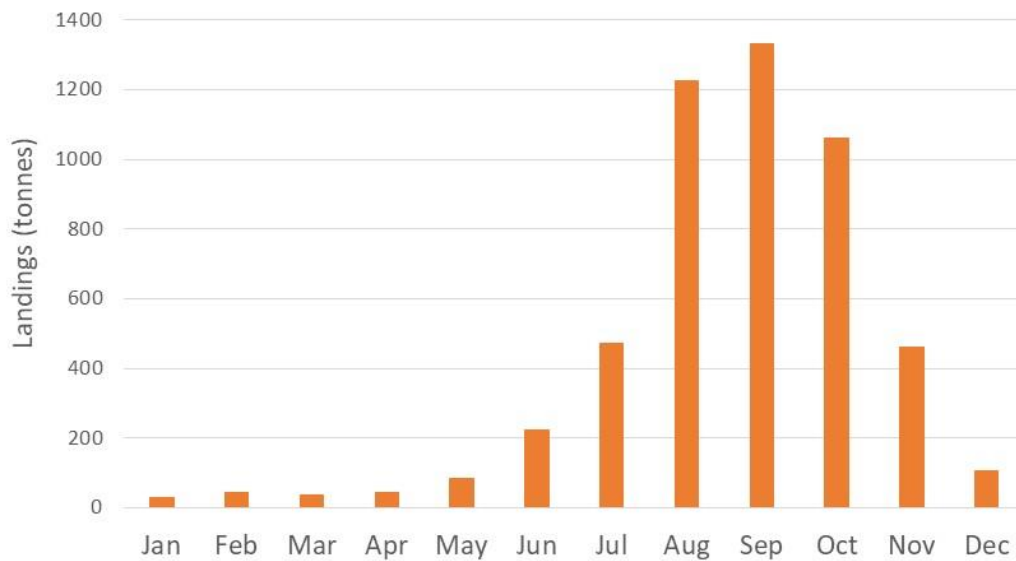


Figure 5 - Monthly landings of *Cancer pagurus* in Norway. Values are averaged for the years 2001 to 2017.

## Management of fishery

In the UK, the first implementation of regulation relating specific to *Cancer pagurus* came in the wake of early fisheries investigations by Francis Buckland in Norfolk, England (Buckland, 1875). Concerns by both fishermen and fishmongers regarding a declining crab stock, thought to be due to small crabs being landed or broken up as bait, led Buckland to suggest a range of conservation measures. Based on his recommendations, the “Fisheries (Oysters, Crabs, and Lobsters) Act” was implemented, banning the landing of berried and recently moulted crabs, and crabs that had carapace widths less than 4 ¼ inches (~108 mm). However, Williamson (1900) reported that the fisheries act in practice was “inoperative”, since it still allowed the harvest of all crabs for use as bait. As a result, several regions in the UK implemented local regulations to protect the crab resource in their district.

Based on his own observations on maturity, and reports by Couch (1832) and Wilson (1895), Williamson (1900, p. 136) suggested that a more appropriate MLS would be 4 ¾ inches (~120 mm) CW. However, the national MLS of 108 ML was maintained until the implementation of the “Sea Fishing Industry Order” of 1951, when the MLS in the UK was raised to 4 ½ inches (~115 mm) CW (Edwards, 1979). The MLSs enforced around the UK have, however, for the most part been higher due to the many regional bylaws (Edwards, 1979; Addison & Bennett, 1992). Currently, the minimum landing size varies both between and within countries across Europe, ranging between 110 and 160 mm CW (Council Directive 1998/850/EC, Tully, 2015). In addition to the size regulation and the ban on landing soft and berried crabs, the fisheries effort in the UK, France, and Ireland is regulated by a limited number of shellfish or crab licences (Tully et al., 2006; Mesquita et al., 2017; Aitken, 2018, Martiel Laurant, IFREMER, pers. com.). For vessels larger than 15 meters there is also an effort regulation in place: EU legislation specifies a maximum number of kilowatt-hours that individual countries can spend within specific regions of the north Atlantic targeting crab (Council Directive 2004/1415/EC).

The regulation of the edible crab fishery in Norway has a similar history to that in the UK, although it starts 50 years later. In the 1920s, fisheries organizations in southern Norway were concerned by

declining crab catches and requested that regulatory measures be implemented (Bjerkan, 1926). Among the suggestions was a closed season (autumn), a means of protecting soft crabs, and a ban on the “sport” of scooping crabs along the shore as they migrated to shallow water during high tide. Bjerkan (1926, p. 162) agreed to the latter of these suggestions (which he later described as “animal cruelty” (Bjerkan, 1927b)), but suggested that an MLS was a more appropriate tool with which to secure the crab population. Referring to the MLS of ~110 mm in the UK, Bjerkan said that his limited investigations indicated that the crab in Norwegian waters was somewhat larger when becoming mature and suggested that an MLS of 120 mm CW would be more appropriate. As in the fisheries act in the UK, he also emphasized that regulations should not prevent the catch of crabs for bait. The implementation of the regulation was, however, delayed until the end of the 1930s, when crabs were included in a separate section of the legislation pertaining to European lobster (Anon, 1939). The legislation set an MLS for crabs of 130 mm CW (likely increased from 120 mm CW after further observations by Bjerkan (1927a)) and banned the aforementioned scooping of crabs at high tide. Legislation pertaining specifically to crab came in 1965 (J-9494-65), in which the MLS of 130 mm CW was maintained, but the ban on scooping crabs rescinded. Further changes to the legislation did not transpire until 1986, when separate MLSs were implemented for different latitudes. North of Rogaland county (~59°30'N), the MLS of 130 mm CW was retained, while the MLS south of the border was lowered to 110 mm CW. Despite extensive searches in the archives of the Directorate of Fisheries, I have not been able to identify an explicit justification for this separation. Personal communication with people who worked with crab fisheries and management at the time indicate that it was due to a request by fishermen, who were complaining about too many crabs and an overrepresentation of small crabs in the catches (pers. com. with Astrid K. Woll, Reidar Vatnaland and Leif Harald Hanssen). The lower MLS south of 59°30'N was thus apparently set with the aim of decimating the population. Throughout the 1980s and 1990s several other regulations were implemented in the pot fishery, but these were exclusively aimed at protecting the European lobster. They included mandatory escape gaps, and depth limitations for pots during certain times of the year. In the crab fishery, there are no licence requirements or effort limitations (except of a maximum number of 20 pots per boat in the recreational fishery), and there is no ban on the landing of berried or soft crabs. Soft and berried crabs are however not landed due to their low economic value. Currently, the only regulatory measure aimed at protecting the crab are the MLSs of 130 mm and 110 mm CW.

Data on landings of crabs in different regions of Norway are collected by the Directorate of Fisheries, which monitors fisheries activity within different statistical areas along the coast (Figure 4). As fishers are not required to provide information on the number of pots they use, there is no information on the effort in the Norwegian fishery. To monitor catch rates, size composition, and discards (soft crabs, berried females, and crabs below the MLS), the Institute of Marine Research therefore cooperate with selected fishermen who measure crabs from four standardized reference pots throughout the main fishing season (June to November). Since the establishment of this reference fleet in 2001, more than 150 thousand crabs have been measured within the main statistical areas for commercial crab fishing (Areas 05, 06, 07, and 08 in Figure 4).

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## Objectives

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The edible crab is an important fishery resource in Norway. Knowledge about its life history parameters are essential for the development of stock assessment models and thus for the construction of a management framework for this resource. However, while the biology, ecology, and physiology of edible crab are well studied, the lion's share of historical studies have come from other European countries. Only a limited number of studies have been conducted on *Cancer pagurus* in Norwegian waters. In contrast to the well-studied crab populations further south (in the UK, Ireland, and France), Norwegian crabs live close to the northern limits of the species distribution and are exposed to quite different physical and biological environments. The crab may therefore play out its biology quite differently in Norwegian waters. The aim of this thesis has therefore been to investigate how the environmental conditions at higher latitude might affect the species biology.

I investigate north-south gradients in sexual maturation and growth of the edible crab along the Norwegian coast and compare my findings with results from more southerly distribution areas (**Paper I** and **Paper II**). As temperature may be important in determining life history processes (Cossins & Bowler, 1987) I study the thermal behaviour and cold-water tolerance of geographically separated individuals of *Cancer pagurus* (**Paper III**). I further present results on depth distribution and migration of *Cancer pagurus* during winter, obtained by analysing video material documenting a high abundance of crabs at depths of ~400 m off western Norway (**Paper IV**).

As male crabs typically constitute only 15–25% of the commercial landings from the most important fishing areas off Norway (Woll et al., 2006b), I have in my studies focused on female crabs. I also hypothesised that female crabs were more sensitive to differences in environmental conditions, due to their complex reproductive cycle (see above). Additionally, more extensive knowledge about the biology and life history of the female crabs (as compared to males) is available from historical studies, providing a better foundation for comparisons between Norwegian waters and other areas.

### **Paper I**

One of my aims was to investigate size at maturity (SAM) in female crabs off Norway and compare these results to findings from other European waters. While preparing for fieldwork in 2014, I was contacted by Dr Jodie Haig (Bangor University), who was coordinating a collaborative effort to conduct a study of SAM in crabs from different areas in northern Europe. This allowed us to compare results between geographical locations, using the same protocol, for crabs collected within the same season. Crabs were collected in 2014 from important fishing grounds in waters off Wales, the Isle of Man, Ireland, England, Scotland, and Norway. In Norway, crabs were collected from statistical area 07 (Figure 4), one of the most important areas for commercial crab fishing. In *Cancer pagurus* various measures are used to determine maturity. The most certain sign that a crab is reproducing is the presence of eggs under the female abdomen (berried crabs). Berried crabs are, however, usually not attracted to baited pots (Williamson, 1900; Edwards, 1979; Howard, 1982), and they are particularly rare in catches in countries such as Norway, where fisheries activity is low during the period when crabs incubate their eggs (winter and spring). The most frequently used criteria for estimating maturity have therefore been signs of mating (presence of sperm in females, indicating behavioural maturity), allometric growth (morphometric maturity) or gonad developmental stage (physiological maturity) (see studies by Williamson, 1900; Edwards, 1979; Le Foll, 1982; Tallack, 2007b; Ungfors, 2007; Öndes

et al., 2017). In **Paper I**, we used gonad developmental stage (physiological maturity) and morphometry (allometric growth) to determine the size at which female crabs mature.

### **Paper II**

In **Paper II** I investigated potential differences in SAM along a south-to-north gradient within Norway. In 2014, crabs were collected within the three statistical areas 05, 06, and 07 (Figure 4). To identify whether changes had occurred after more than 10 years of commercial crab exploitation, I also used raw data collected by Woll and Larssen (2004) during investigations in 2003. Maturity was estimated according to the protocol used in **Paper I** (physiological and morphological maturity), but supplemented with data on the presence of sperm plugs and sperm in seminal receptacles from Woll and Larssen (2004) for analysis of behavioural maturity. I further investigated potential differences in growth between statistical areas (Areas 05, 06, 07, and 08, in Figure 4), by analysing data collected by the reference fleet on the occurrence of soft (recently moulted) crabs.

### **Paper III**

In **Paper III** I studied the thermal preference and lower critical temperature (CT<sub>min</sub>) in *Cancer pagurus*. To investigate potential geographical differences, two groups of crabs were compared, respectively collected close to the northern border of the species distribution, and from the sea outside Ålesund (approximately ~900 km, further south). All crabs were acclimated to the same temperature for a period of four months. Their thermal behaviour was studied in the lab, where crabs fitted with a temperature logger could move freely within a temperature gradient (~5.5 to 14.5 °C). When investigating thermal preference, it is common to distinguish between temperatures selected by individuals' minutes to hours after the onset of experiments ("acute temperature preference") and the temperatures toward which a species will gravitate given sufficient time ("final thermal preferendum") (Fry, 1947; Reynolds & Casterlin, 1979; Jobling, 1981). In my experiments, I investigated final thermal preferendum by allowing crabs to move within the gradient for a period of 40 hours (12/12 light/dark cycle). CT<sub>min</sub> was determined by studying righting reflex in crabs in declining water temperatures (from 7 to ~1 °C).

### **Paper IV**

While presenting my work at a scientific conference, I was contacted by a researcher from the Institute of Marine Research who informed me that during a survey conducted in the winter of 2014 they had filmed a great abundance of *Cancer pagurus* at depths of several hundred meters in Sognesjøen (~61 °N). Since information on the whereabouts and biology of *Cancer pagurus* during winter is limited (particularly in Norway), and because it is commonly stated that crabs are restricted to depths of less than 100 meters (FAO, 2015), we decided to cooperate in making a more detailed analysis of the video material. In our analysis we investigated the density of crabs, the remains of crabs (shell remnants), and apparent crab tracks in the sediment and attempted to determine sex and size.

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## Results and discussion

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My studies show that the size at onset of physiological maturity in female *Cancer pagurus* varies little between areas in northern Europe (**Paper I**) and between latitudinally separated areas within Norway (**Paper II**). Differences in moulting frequency, however, cause slower growth, and consequently higher age at maturity, for crabs at more northern latitudes, a result which is suggested to be due to geographical differences in temperature (**Paper II**). Evidence that crabs in the north live under sub-optimal thermal conditions is found in laboratory experiments showing that individuals from northern and southern latitudes have the same lower thermal tolerance as well as a common and rather warm thermal preference ( $\sim 13$  °C) (**Paper III**). My studies also show that the topography of Norway, with its deep fjords, forces some crabs to move to depths exceeding the depth limitations given in popular fact sheets (**Paper IV**). Results from my studies and implications of my findings are discussed further in this chapter.

### Gonad development and maturity

#### Size at maturity

The results from **Paper I** and **Paper II** suggest that the size at which female *Cancer pagurus* becomes mature is in the range of 100–115 mm CW. This result accords with other estimates of behavioural maturity (Edwards, 1979; Tallack, 2007b; Ungfors, 2007; Öndes et al., 2017) and morphological maturity (Ungfors, 2007), and with some results on physiological maturity (Le Foll, 1986; Öndes et al., 2017). The results however deviates from investigations of physiological maturity made by Tallack (2007b) (Shetland Islands) and Ungfors (2007) (Sweden), both of whom estimated size at 50% maturity of about 130 mm CW. Although this discrepancy might result from geographical differences or indicate a reduction in SAM during the last decade, I suspect that some of the variation is caused by differences in the gonad stage used as a threshold for classifying crabs as immature or mature. In my studies I have used a six-stage (visual) classification of gonads (Larssen et al., 2015). The threshold for maturity was set at early secondary vitellogenesis (stage 2), visually observable as grey or pink ovaries with clear lobe formation. Histologically this corresponds to a gonad with 20–50% secondary oocytes that have a diameter of  $\sim 120$   $\mu\text{m}$  (Larssen et al., 2015). This is the same threshold as used by Le Foll (1982) and Öndes et al. (2017). According to the more detailed methodological description given by Ungfors in her dissertation (Ungfors, 2008, p. 25), and the description given in the master's thesis of one of her students (Sjöström, 2003), it appears that a six-stage classification of gonads, similar to my own, have been used. However, Ungfors set the threshold for maturity at developmental stage 3 (orange to red gonad), excluding crabs with gonads of “pinkish” appearance. As far as I can derive from the study by Tallack (2007b) (which used the gonad classification from Edwards (1979)), a crab was defined as mature only when having “swollen, bright orange to red gonads”. To test whether the differences between these studies and my results could be related to threshold for maturity, I repeated the statistical analysis in **Paper II** on SAM, this time considering crabs as mature only if they had gonad development stage higher than 2. The overall results using data from all three statistical areas and both time periods are presented in Figure 6, and results on estimated size at which 50% of the crabs are mature ( $CW_{50}$ ) in each year/area are presented in Table 1. Black lines and text figure the results when developmental stage 2 is taken as the threshold for maturity (as in **Paper I** and **Paper II**) while red lines and text report the results when developmental stage 3 is taken as the threshold for maturity (to accord with Ungfors (2008)).

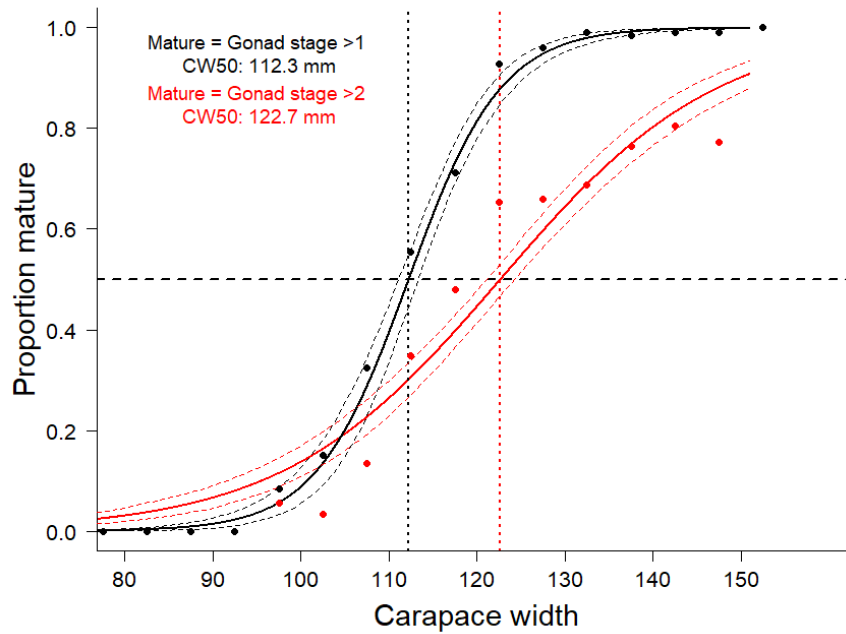


Figure 6 - Maturity ogives for carapace width (CW) of female *Cancer pagurus*. Results based on model using data from **Paper II**, with different threshold for maturity according to scale in Larssen et al. (2015). Black: mature = gonad development stage  $\geq 2$ , Red: mature = gonad development stage  $\geq 3$ . Dots indicate observed proportions of mature crabs within different size groups (5 mm CW interval). Lines denote predicted probability of physiological maturity at a given size.

Table 1 - Estimates of size at 50% maturity for female *Cancer pagurus* using gonad developmental stage 2 (black) and 3 (red) as threshold for maturity. (Areas shown in Figure 4).

	CW <sub>50</sub> (mm)					
	2003	2014	Overall	2003	2014	Overall
Area 05	115.9	108.3	111.0	126.4	114.4	119.6
Area 07	113.9	109.0	111.2	117.9	136.5	123.7
Area 08	116.9	113.9	115.27	129.5	121.2	125
Overall	115.4	109.9	112.3	124.3	121.7	122.7

Using the new threshold for maturity, estimated size at 50% maturity is about 10 mm larger than that reported in **Paper II**. It is thus clear that at least part of the discrepancy between the results found in **Paper I** and **Paper II**, and the studies by Tallack (2007) and Ungfors (2007) is due to the different threshold for maturity. This strengthens the conclusion in **Paper I**, emphasizing the need for a standardized protocol for estimating SAM. Which of the two gonad stages that should be used as a threshold for maturity is difficult to decide, as each has uncertainties and disadvantages. For instance, crabs that have moulted earlier in the year need sufficient time to build up energy to develop gonads. In these crabs, the gonad is usually small and white in colour, sometimes even after the carapace has hardened (own observations). If gonad development stage 3 (orange to red colour) is used as the threshold for maturity, these crabs will be classified as immature, leading to an overestimation of SAM. This partly explains the lower proportion of mature large-sized crabs seen in Figure 6 when gonad stage 3 is used (red dots). At development stage 2, which was used as the threshold in **Paper I**

and **Paper II**, secondary vitellogenesis has started, which means that gonad development should be completed given the right environmental conditions and given that the crab has sufficient resources. However, since these crabs were collected in late autumn, it is likely that they would have needed an additional season to attain the necessary energy to produce eggs. Chances are, then, that they would go through an additional moult, reaching a larger size. This would lead to an underestimation of SAM. On the other hand, in my data, I also had several small crabs (110-120 mm CW) with well-developed gonads that would probably complete their development within the same year. Hence, a large variation in gonad stages within size classes makes maturity estimates uncertain and complicates comparisons among studies.

Since berried crabs (which are occasionally landed) tend to be large (see Öndes et al., 2016, and Table 1 in **Paper I**), several authors have suggested that *Cancer pagurus* becomes functionally mature at a larger size than estimates of behavioural and physiological maturity would indicate (Williamson, 1900; Tallack, 2007b; Ungfors, 2007). Registrations made by the crab reference fleet in Norway also show that the average size of berried crabs is larger than estimates of maturity (Table 2).

*Table 2 - Size of berried female Cancer pagurus registered by the reference fleet between 2001 and 2015. Areas shown in Figure 4.*

Statistical area	Mean CW (mm)	Range CW (min-max) (mm)	n
Area 05	148.3	130 - 185	51
Area 06	147.1	100 - 200	246
Area 07	155.0	105 - 205	99
Area 08	137.7	120 - 155	33
<i>Overall</i>	<i>148.3</i>	<i>100 - 205</i>	<i>429</i>

Whether these sizes are representative of reproducing crabs in different areas is uncertain. For instance, Woll (2003) studied a group of about 20 ovigerous crabs incubating their eggs in a small strait on the north-west coast of Norway (within Area 07, Figure 4). The size of these crabs varied between 122 and 159 mm CW (calculated average: 139 mm CW). This is a smaller average size than estimates based on reference fleet data within the same area (Area 07, Table 2), supporting the claim that the pot fishery is biased towards catching larger individuals (Bennett, 1995; Woll et al., 2006b). Thus, due to the low catchability of berried crabs, it is not possible to conclude at what sizes a given proportion of female crabs becomes functionally mature.

#### Proportion of spawning crabs

Individual variation in gonad developmental stage within the same season should be expected, since many crabs do not spawn every year (Pearson, 1908; Edwards, 1979). During autumn, the gonad of a mature female crab could either be in an early development (stage 2, having just reached maturity or recently moulted), be developed (stage 3 and 4, some time having elapsed since moulting or hatching), or be in a resting stage (stage 6, right after hatching). The proportion of mature female crabs being in these four different stages in my investigations in 2014 is presented in Figure 7.

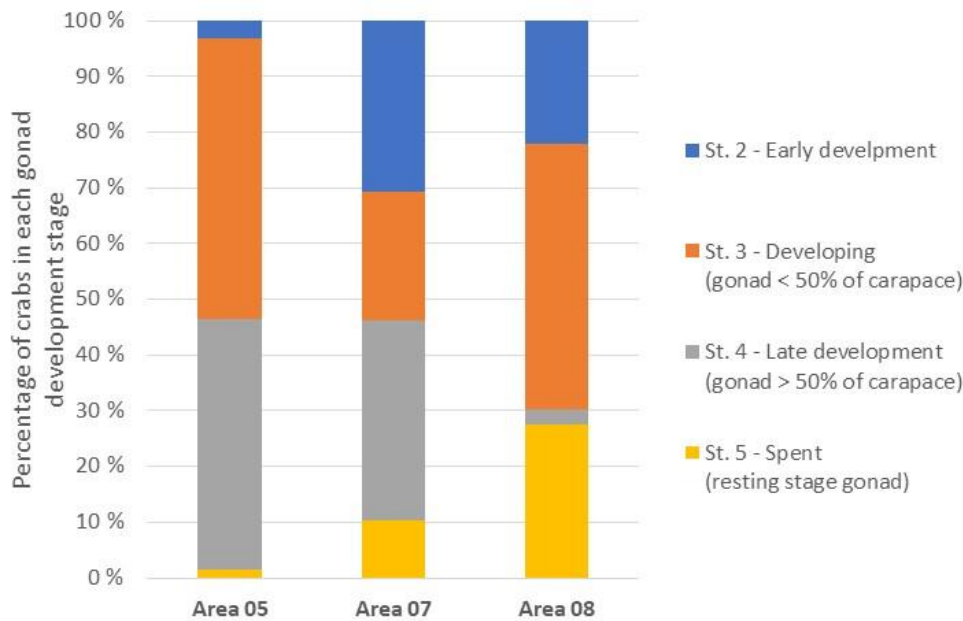


Figure 7 - Proportion of female *Cancer pagurus* in different gonad development stages in the three statistical areas investigated in September and October 2014. Areas shown in Figure 4.

Based on my registrations, there is a higher proportion of recently spawned crabs (gonad in St. 5) in the south than in the north and a higher proportion of crabs with developed gonads as latitude increases. However, it is important to note that some of this variation is likely due to slight differences in the time of sampling. In planning my fieldwork, I hypothesized that development would start earlier in the south than in the north (Woll et al., 2014). Collection of crabs was therefore conducted in a south-to-north order, starting with southern Area 08 in mid-September 2014, continuing with central Area 07 at the end of September, and finishing with northern Area 05 in mid-October (Figure 4). Due to this difference in timing, a direct comparison between areas is difficult. Overall, however, the data do give some indication on the proportion of crabs that might spawn the coming winter. When looking at the data for all areas combined, only about 30% of the crabs I investigated had well-developed gonads (mean of St. 4 in Figure 7). Although it is likely that this proportion would have been higher had the crabs been investigated later in the season, particularly in Area 08 (Figure 4), the number accords with information available from the crab processing industry. HitraMat AS, the largest crab producer in Norway, measures hepatopancreas and roe content of all landed female crabs using a Near Infra-Red (NIR) scanner (Wold et al., 2010). The crabs are sorted into three categories: low quality production crabs (with low meat filling), good crabs and superior crabs. Superior crabs are females that typically have well-developed gonads (Wold et al., 2010; Bakke et al., 2015). During the fishing season (June to the end of November), the factory on average processes about 25–30% of landed females as superior (Kolbjørn Ulvan, HitraMat AS, pers. com). Preliminary investigations conducted by Møreforskning, in which seasonal and spatial variation in quality of crabs have been studied using the NIR-scanner also indicate that the proportion of superior crabs in central Norway (Areas 06 and 07, Figure 4) peaks at around 30 to 40% during autumn (Woll et al., 2014; Bakke et al., 2015). It should be noted that since crabs are sorted on the boat before delivery (with soft or damaged crabs being discarded), the actual proportion of crabs with well-developed gonads is lower. In comparison, Brown and Bennett (1980) reported that up to 90 % of female crabs in the English Channel had well developed gonads by the end of autumn. Similarly, Edwards (1979, p. 72) reported 70% of crabs off the east coast



of England (Yorkshire) to have fully developed gonads when approaching winter, noting it likely that “spawning was imminent”. It would thus appear that there is, annually, a lower proportion of crabs (theoretically) capable of spawning in Norway than in areas further south in Europe. This has also been reported for the Dungeness crab (*Metacarcinus magister*) and is believed to be due to extended inter-mating periods and the longer time required for crabs at high latitudes to fully develop their gonads (Swiney et al., 2003). The generally low brown meat (hepatopancreas and gonad) content in Norwegian crabs is one of the reasons for the many studies on enhancement through artificial feeding (Gundersen, 1970; Gundersen, 1973; Berge & Woll, 2006; Woll et al., 2006a; Woll & Berge, 2007), which support the idea that crabs need a longer time to acquire the energy needed for reproduction.

## Spatiotemporal variation in life history

### Maturity

It has repeatedly been stated that animals tend to reach maturity at a larger size in colder environments (or at higher latitudes) (see Conclusion in **Paper II**). However, a challenging aspect of temperature-size relationship theories is that a large part of their foundation is based on results from studies of terrestrial animals (Kingsolver & Huey, 2008, but see Atkinson 1995). For instance, studies of crustaceans show varying results when relating SAM to temperature or latitude. Using literature search databases (mainly Google Scholar), I collected studies in which SAM of decapod crustaceans has been compared between different geographical areas. Using the search terms “decapoda” and “(size at) maturity”, in combination with either “spatial variation/differences”, “geographical variation/differences”, “latitude” or “temperature”, I found a total of 37 studies, covering 28 different species of decapods. The different species are presented in Table 3, with notations on the method used to determine maturity and whether SAM were concluded to increase with latitude (higher SAM at cold temperatures, denoted with “+”), or to have contrasting or random association with latitude, or whether there was a negative relationship between SAM and latitude (lower SAM at cold temperatures, denoted with “-”). It should be emphasized that this is likely not a complete list of studies in which such comparisons have been made. Also, except for two studies (on *Jasus edwardsii*) reporting contrasting results on the relationship between SAM and latitude, I did not compare results between different studies myself, but included studies in which such comparisons have been made by other authors.

Out of 29 species (including results on *Cancer pagurus* from **Paper I** and **Paper II**), 14 were reported to mature at larger sizes at higher latitudes or lower temperatures, two studies on the same species showed contrasting results, six species showed no difference or random variation, and eight species were reported to have a negative relationship between SAM and latitude. Although this indicates that local thermal condition can influence the size at which some species mature, variations in the direction of this relationship suggest that SAM is affected by other factors more than temperature *per se*. Further, results of several studies are confounded by authors comparing results across studies which were conducted at different times of the year or that use different measures for maturity. As discussed above and in **Paper I**, reliable comparisons between geographical locations should only be made when species are collected at the same time of the year and maturity is assessed using the same criteria.

Table 3 - Studies of decapod crustacea comparing geographical differences in size at maturity

Species	Relationship SAM and latitude	Measure	Reference
<i>Cancer irroratus</i>	+	Gonad maturity Allometric growth Presence of eggs	Campbell and Eagles (1982), comparing own results with other studies
<i>Carcinus maenas</i>	+	Presence of eggs	Berrill (1982), comparing own results with other studies
<i>Callinectes sapidus</i>	+	Terminal moult size	Darnell et al. (2009), Fisher (1999)
<i>Scylla serrata</i>	+	Ovarian development	Quinn and Kojis (1987), comparing results with other studies
<i>Petrolisthes granulatus</i>	+	Presence of eggs	Monaco et al. (2010)
<i>Homarus americanus</i>	+	Presence of eggs Pleopod development	Templeman (1936), Campbell and Robinson (1983), Estrella and McKiernan (1989), Watson et al. (2013), Little and Watson III (2005)
<i>Leptuca uruguayensis</i> *	+	Allometric growth	Hirose et al. (2013)
<i>Artemesia longinaris</i>	+	Ovarian development	Castilho et al. (2007)
<i>Penaeus californiensis</i> *	+	Ovarian development	Aragón-Noriega and Alcántara-Razo (2004)
<i>Panulirus cygnus</i>	+	Pleopod development and presence of eggs or spermatophore (female) Allometric growth and testis development (male)	Melville-Smith and de Lestang (2006) Melville-Smith et al. (2010)
<i>Pachygrapsus crassipes</i>	+	Allometric growth	Hines (1989)
<i>Emerita analoga</i>	+	Presence of eggs	Dugan et al. (1991)
<i>Austrohelice crassa</i> *	+	Presence of eggs	Jones and Simons (1983)
<i>Ovalipes catharus</i>	+	Gonad development	Armstrong (1988), comparing own results with other studies
<i>Jasus edwardsii</i>	Contrasting results	Presence of eggs Pleopod development	Annala et al. (1980) (+) Gardner et al. (2006) (-)
<b><i>Cancer pagurus</i></b>	No difference or random variation	Gonad development	<b>Paper I and Paper II</b>
<i>Metacarcinus magister</i> *	No difference or random variation	Change in moult frequency	Collier (1983) and Wild and Tasto (1983), both comparing results from different studies
<i>Biffarius fiholi</i> *	Random variation	Allometric growth (males) Presence of eggs (females)	Berkenbusch and Rowden (2000)
<i>Hemigrapsus oregonensis</i>	Random variation	Allometric growth	Hines (1989)
<i>Scyra acutifrons</i>	Random variation	Allometric growth	Hines (1989)
<i>Paralithodes camtschaticus</i> *	Random variation	Presence of eggs Allometric growth Gonad maturity	Otto et al. (1990) and Blau (1990), both comparing own results with other studies
<i>Macrophthalmus banzai</i>	-	Presence of eggs and Gonad development	Henmi (1993)
<i>Goniopsis cruentata</i>	-	Allometric growth	de Lira et al. (2015)
<i>Panopeus herbstii</i>	-	Allometric growth	Hines (1989)
<i>Lithodes aequispinus</i> *	-	Allometric growth (males) Presence of eggs (females)	Jewett et al. (1985) Somerton and Otto (1986)
<i>Chionoecetes opilio</i>	-	Terminal moult size	Dawe et al. (2012), Orensanz et al. (2007), Somerton (1981), Burmeister and Sainte-Marie (2010)
<i>Chionoecetes bairdi</i>	-	Allometric growth	Somerton (1981)
<i>Portunus pelagicus</i>	-	Size at pubertal moult	De Lestang et al. (2003)
<i>Callinectes bellicosus</i>	-	Abdominal features Presence of sperm Presence of eggs	Rodríguez-Félix et al. (2015)

\*Species name changed from that used in studies to name accepted by World Register of Marine species.

The results from **Paper I** and **Paper II** show that in female *Cancer pagurus* there is no relationship between latitude and size at onset of physiological maturity. Some authors have, however, stated otherwise. Shields (1991) compared SAM numbers given for *Cancer pagurus* by Brown and Bennett (1980) from British water with results by Le Foll (1986) from the French coast and argued that crabs matured at larger sizes at higher latitudes. This comparison has later been cited by other authors (Cobb et al., 1997; Fischer & Thatje, 2008; Fischer, 2009; Green et al., 2014). However, Shields misinterpreted the results obtained by Le Foll, who gave values in carapace length (CL) rather than CW. (The former size measure is more commonly used in French studies, and we also made this mistake in Table 1 of **Paper I** when presenting results by Latrouite and Noël (1993)). If Le Foll's CL value of 76 mm is converted to CW (using Le Foll's own formula (Le Foll, 1982, p. 89)), estimated size at physiological maturity equals a CW of ~116 mm. This is the same SAM as given by Brown and Bennett (1980) (115 mm CW), and is in accordance with the results from **Paper I** and **Paper II**.

No increase in SAM with latitude is apparent, either, if gonad stage 3 is used as the threshold for maturity (Table 1), with CW<sub>50</sub> values similar or slightly smaller than those reported from Shetland (Tallack, 2007b) and Sweden (Ungfors, 2007). Whether there are geographical differences in functional maturity is more difficult to assess, as berried crabs are so infrequently caught. It has, however, been suggested that such differences exist. Öndes et al. (2016) compared seven studies reporting sizes of berried crabs and found a significant correlation between the smallest size at (functional) maturity and the local minimum seawater bottom temperature. This led the authors to suggest that crabs mature at a smaller size in the colder waters of Sweden, Norway, and the North Sea compared to other areas. However, two of the areas considered "warm water" by the authors have similar reported minimum sizes of berried crabs as those found in northern Norway (Area 05: ~130 mm CW, Table 2). Further, estimates do not include results by Latrouite and Noël (1993) from French waters (min CW of ovigerous female: ~122 mm), by Haig et al. (2015) from Wales (min: 116 mm CW), or by Hines (1991) from Scotland (min: 140 mm CW). Inclusion of results from these studies, and results on berried crabs from the reference fleet in Norway, would likely give a much more random variation in smallest size of ovigerous females across study sites.

It should be emphasized that the variation in onset of maturity observed in several of the species presented in Table 3 are likely real differences, that either result from size-selective fisheries in some areas (Kuparinen & Merilä, 2007; Heino et al. 2015), are caused by phenotypic plasticity in this trait (Stearns, 1992), or are shaped by natural selection optimizing fitness under local environmental conditions (Stearns, 1992; Angilleta, 2009). Using lifetime egg production as a measure of fitness, Bryant (1991) modelled an optimal instar stage for first maturity and a penultimate instar stage for *Cancer pagurus*. The respective instars were found to correspond to sizes of 99.1 mm and 233 mm CW. The predicted size at onset of maturity is very close to the maturity sizes found in **Paper I** and **Paper II**. The predicted penultimate size is, however, slightly overestimated as it corresponds to the largest sizes reported for female crabs (242 mm in the English Channel (Brown & Bennett, 1980), 230 mm in data from the Norwegian reference fleet) and is similar or larger than modelled asymptotic sizes (180-245 mm CW; Tallack, 2002; Sheehy & Prior, 2005; Ungfors, 2008). Overall, however, the model by Bryant fits well with observed values for *Cancer pagurus* and suggests that the species has evolved these traits to maximize offspring production. In fact, *Cancer pagurus* has been estimated to have among the highest fecundities within the Brachyura (Hines, 1991). The advantage of this strategy could be related to high mortality during the early life stages (Nichols et al., 1982; Robinson & Tully, 2000a; Hazlehurst, 2007). The model used by Bryant (1991) depends on several parameters, including

intermoult duration, egg incubation period, and mortality (Hartnoll & Gould, 1988), which for *Cancer pagurus* was derived from laboratory and field studies conducted on the east coast of England (Edwards, 1965; Edwards, 1967). It is therefore likely that the model would provide a completely different outcome if parameters from the northern distributional range of the edible crab were used. However, local adaptations in life history traits require some form of divergent evolution. Genetic studies of *Cancer pagurus* have shown that there is a low degree of spatial genetic structure across the species distribution (Ungfors et al., 2009; McKeown et al., 2017; McKeown et al., 2018), even when comparing crabs from the northern part of the species distribution with crabs from southern Europe (Maria Pan, University of A Coruña, pers. com.). The genetic connectivity between areas is suggested to be due to a high degree of larval dispersal and the long migrations made by female crabs. Thus, high gene flow between geographical locations likely restricts local adaptation in life history traits in this species, which could explain the lack of clear geographical differences in maturity sizes.

### Moulting and growth

In their graduate studies, Eriksen and Moen (1993) studied the ecology of juvenile edible crabs on the coast of Trøndelag, Norway (~66 °N), and estimated that crabs one year after settlement are significantly smaller (~15 mm CW) than reported in studies from the UK by Pearson (1908) and Edwards and Brown (1967) (~30 mm CW). They suggest that this difference is likely due to lower temperatures in Norwegian waters causing longer intermoult periods. Their hypothesis is supported by laboratory studies of juvenile crabs by Le Foll (1986), who found a clear relationship between seasonal temperatures and moulting frequency. The results from **Paper II**, showing declining probability of moulting (and hence a slower growth) with increasing latitude, adds to the evidence, and supports the suggestion made by Bennett (1995) that differences in frequency of moulting between areas are caused by local thermal conditions. Similar conclusions have also been made in studies of the American lobster (*Homarus americanus*) (Templeman, 1936) and the Dungeness crab (Collier, 1983). A temperature-driven geographical difference in growth is supported by the numerous studies showing a significant positive relationship between moulting frequency and temperature (see for instance reviews by Passano, 1960a; Cossins & Bowler, 1987; and Green et al., 2014). With declining temperatures, intermoult periods become longer, for some species, to the point at which moulting is inhibited completely (Passano, 1960b; Miller & Vernberg, 1968). Although the exact mechanisms behind this impediment are not known, it has been suggested to be due to low temperature restraining physiological processes regulating the initiation of moulting (Passano, 1960a). In addition to its direct effect on the moulting process, temperature likely also have an indirect effect on both timing and frequency of moulting by affecting different processes of the reproductive cycle (see below).

The prediction of probability of moulting (see Figure 6 in **Paper II**) shows that an adult female crab from southern Area 08 (Figure 4) is three times more likely to moult during autumn than a crab of same size from Area 05. As we do not, unfortunately, have data on how moulting varies between areas during juvenile development, it is not possible to make estimates of differences in age. A more direct method for determining age would therefore be advantageous. Unfortunately, all of the techniques suggested to be suitable for estimating age in crustaceans have shortcomings. For instance, accumulation of neurolipofuscin, a pigment that is found in several animals (see Vogt, 2012 for a review), is positively correlated with temperature (Sheehy & Prior, 2005). This will cause different rate of accumulation in populations living under different thermal conditions and make comparisons difficult without reliable calibrations. A more recent ageing technique, which has received a lot of

attention, is the counting of apparent growth bands in the eye stalk or calcified structures of the gastric mill of crustacea (Kilada et al., 2012). Although such bands are visible in the gastric mill of the edible crab (Sheridan et al., 2015), more recent studies have cast doubt on the method by showing that structures in the gastric mill are lost during moulting (Sheridan et al., 2016; Becker et al., 2018; Sheridan & O'Connor, 2018). Thus, until a reliable method is found that will allow us to compare ages of crabs across latitudes, efforts should be made to obtain more information on how moulting in different life stages varies across geography (see Conclusion and future perspectives).

The results in **Paper II** also indicate that moulting occurs later in the season at higher latitudes. In Figure 9, I have used data from **Paper II** in a logistic regression model to make a (rough) estimate of the timing of the onset of peak periods for moulting in different statistical areas (Areas 05, 06, 07, and 08 in Figure 4). A threshold of 0.2 was set, estimating the day where the proportion of soft crabs rose above 20%. The threshold was based on observations from other studies of reported seasonal variation in moulting frequency (Edwards, 1967; Tallack, 2007b), and on exploration of the raw data. According to these estimates, the onset of moulting is delayed by about one month for each statistical area when moving from south to north. This accords with results from the investigations of crab meat filling (Woll et al., 2014; Bakke et al., 2015), which show that hepatopancreas and gonad development is delayed by about one month in Area 06 when compared to Area 07.

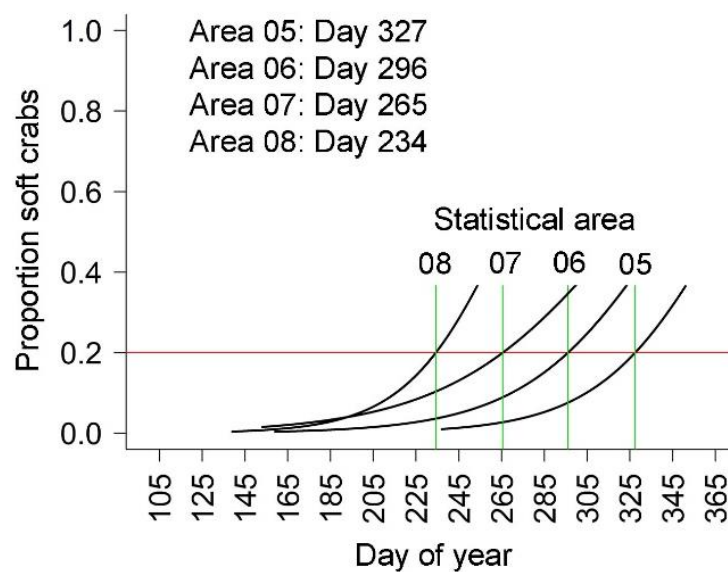


Figure 8 - Estimated timing for onset of moulting periods for female *Cancer pagurus* in different statistical areas. Areas shown in Figure 4.

As crabs first become motile one to two weeks after ecdysis (Edwards, 1979), the onset of moulting occurs slightly earlier than estimated here (and in other studies where moulting frequency has been reported from fisheries). On the other hand, it should be noted that both the rate of increase in occurrence of soft crabs, and the duration of the moulting period are possibly exaggerated in fisheries data: In addition to visual criteria (light colouration of carapace shortly after moulting and presence of sperm plugs in females), the most commonly used method for determining whether a crab has moulted is to investigate whether the carapace recedes if pressure is put on the branchiostegite region

(on the ventro-lateral side of the crab's carapace) (Tallack, 2002; Woll et al., 2006a). This is also the method used by fishers in the reference fleet in Norway to classify a crab as hard- or soft-shelled. Tagging studies have shown that it can take two to three months for the exocuticle of a moulted crab to harden completely (Edwards, 1979). Data on occurrence of soft crabs in catches will therefore be somewhat cumulative, in that it will include both crabs entering pots shortly after moulting and crabs that have moulted some time previously. Consequently, as a decline in the proportion of soft crabs will occur only as crabs become hard-shelled, and given that post-moulting calcification is slower in cold water (Vincent, 1972; Edwards, 1979; Walther et al., 2011), it is possible that this cumulative effect might be stronger in registrations made by the reference fleet in northern Norway (i.e. crabs will remain "soft" longer in cold water). This would cause an overall overestimation of probability of moulting compared to more southern areas.

Although temperature is an important environmental regulator of physiology and behaviour, other factors that could contribute to the observed geographical differences in both frequency and timing of moulting should also be mentioned.

As stated in **Paper II**, since only a limited time of the year was used to model the probability of moulting, a window of increased moulting frequency could have been missed, thereby underestimating the growth of crabs at more northern latitudes. In **Paper IV**, which analyses footage of crabs filmed in deep water in Sognesjøen during winter, the shell fragments observed in several areas were suggested likely to be the remnants of dead crabs. The possibility cannot be excluded, however, that these fragments were the exuviae of moulted crabs (see discussion on depth under "Environmental effects on distribution and behaviour"), which would indicate an extension of the moulting period. However, if these shell fragments were in fact the exuviae of moulted individuals, the fact that the crabs were filmed within the more southern Area 28 (Figure 4) means that the potential extension of the moulting period would have been observed for an area where crabs already exhibit faster growth than northern crabs.

Another factor that could influence moulting is differences in photoperiod. For instance, the southern Area 08 and the northern Area 05 have different lengths of day throughout the year (Figure 9). Within the period investigated in **Paper II** (mid-August to mid-November, arrow Figure 9), there is about two to three hours' difference in length of day between Area 05 and Area 07, but with days becoming shorter in the north compared to the south around mid-September. Whether such slight differences in light exposure could cause variation in moulting frequency is difficult to assess, as the few studies that have investigated the effect of light on moulting in crustacea show contrasting results. For instance, in some species, moult is inhibited during both continuous darkness and continuous light (Bliss, 1954b; Bliss, 1954a; Stephens, 1955), suggesting that a given photoperiod is important for initiation of moulting. Other studies (on shrimp and crayfish) have not been able to identify such a relationship (Westin & Gydemo, 1986; Vijayan & Diwan, 1995; Hoang et al., 2003). Thus, there is too little data to determine whether, and to what degree, day-length directly affects moulting in *Cancer pagurus*. Light can, however, indirectly affect the timing of moulting, possibly by regulating the end of diapause during egg incubation or by affecting foraging behaviour (see below).

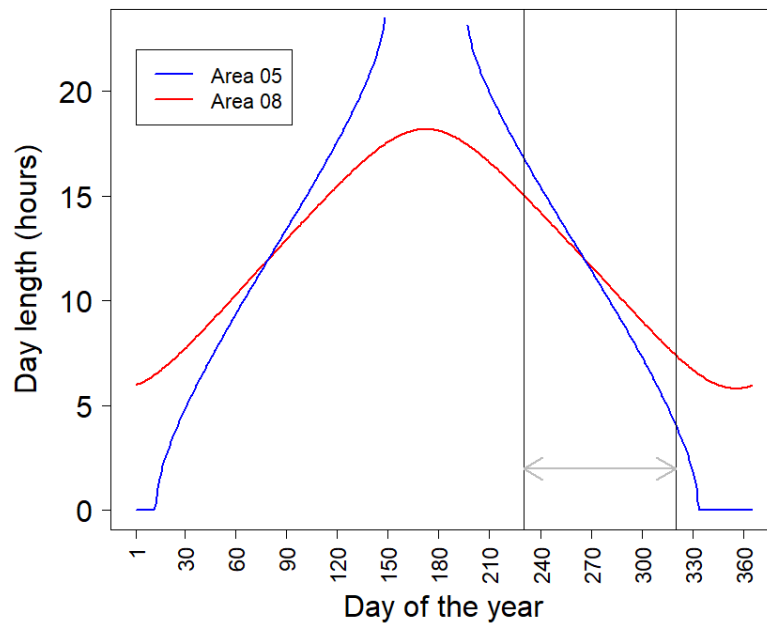


Figure 9 - Day length (difference between sunrise and sunset) in Area 05 (north) and Area 08 (south) (see Figure 4) throughout the year. Arrow between vertical bars show period used to study probability for moulting in **Paper II**. (Curves generated using the *Insol* package (1.1.1) in R, using coordinates from the centre of the statistical areas).

In addition to temperature, food is probably the most influential factor regulating moulting in crustaceans. Limited food availability prolongs the intermolt period and likely reduces moult increment (see Hartnoll, 2001 for a review). Further, studies investigating different types of feed have also shown that nutritional composition can affect frequency of moulting (Brodersen, 1990; Wilber & Wilber, 1989; Petit et al., 1997; Sheen & Wu, 1999). Unfortunately, there is no data on how the diet of *Cancer pagurus* varies in different geographical locations. However, ecological studies provide little evidence that food availability should vary strongly across the distribution area of the species. Although epi-faunal diversity tends to decrease with latitude (Thorson, 1957), northern and southern marine soft-bottom habitats, which are important feeding grounds for the edible crab (Hall et al., 1993), have been shown to be comparable in terms of both species richness (Kendall & Aschan, 1993; Ellingsen & Gray, 2002; Holte et al., 2007) and productivity (Fuhrmann et al., 2015). This benefits the edible crab, which is a highly opportunistic forager that obtains its energy from a range of infaunal and epifaunal invertebrates (Shelton et al., 1979; Hall et al., 1993; Woll, 1995; Hallbäck, 1998; Fagerli et al., 2014). Further, although caloric content will vary among species (Dauvin & Joncourt, 1989), and thus in different types of prey, overall energy content in marine invertebrate communities show little variation across geography (Wacasey & Atkinson, 1987; Brey et al., 1988). Geographical differences in nutritional gain are, however, likely to occur due to the significant effect temperature has on the crabs' feeding efficiency (Gundersen, 1970; Woll et al., 2006a). That is, since female *Cancer pagurus* is a capital feeder (i.e. to a large extent depending on previously acquired energy to develop gonads, **Paper I**), crabs in colder water will require a longer time to gain the energy needed to complete the reproductive cycle, which consequently will affect both frequency and timing of moulting (see below).

### Reproductive cycle

The periods between successive moulting (and mating) events in females are extended due to at least two subsequent spawnings (Williamson, 1900; Edwards, 1979). Due to the significant effect that temperature has on several phases of the reproductive cycle, it is possible that these inter-mating periods will be longer at higher latitudes (Swiney et al., 2003). Specifically, crabs that moult and mate (late) in colder waters are likely to have a longer post-moult calcification period (Vincent, 1972; Edwards, 1979; Walther et al., 2011). Further, feeding activity is significantly reduced at lower temperatures (Gundersen, 1970; Woll et al., 2006a), which affects the rate of gonad development and the build-up during autumn of lipid reserves needed for the long egg incubation period during winter and spring (Howard, 1982; Naylor & Taylor, 1999). Consequently, the timing of oviposition will be delayed at higher latitudes (Shields, 1991). An understudied topic in this part of the reproductive cycle of the edible crab is the function of the diapause during early egg development (Wear, 1974; Naylor et al., 1999). Wear (1974) reported the two-month diapause he observed in *Cancer pagurus* in the lab to be unaffected by temperature. However, a much longer diapause period was reported by Naylor et al. (1999) (November to March), indicating that other environmental cues might be important. Studies of other crustaceans have, for instance, shown photoperiod to be an important regulator of diapause (Alekseev & Starobogatov, 1996). If this also applies to *Cancer pagurus*, it would suggest that the crab has some flexibility in the timing of oviposition (i.e. early oviposition gives a longer diapause and late oviposition gives a shorter diapause period). Further studies are needed, however, to understand whether this arrested egg development is a dormant phase securing the right timing of final egg development (and hatching of larva), or whether it is a necessary resting phase ensuring a successful development of eggs. Still, even if the end of diapause is synchronized, the further development of eggs will also be affected by temperature (Wild, 1980; Wild, 1983; Shirley et al., 1987; Shields & Kuris, 1988; Fischer & Thatje, 2008), with a longer final incubation period and a delayed onset of hatching for crabs in cold water (Park & Shirley, 2008). Late hatching could thus be one of the reasons why crabs moult later in the north than in the south (**Paper II**, Figure 8).

Overall, this suggests that several phases of the reproductive period are delayed in northern crabs. To illustrate this I propose a revised version of the figure made by Bjerkan (1942) showing the timing of important reproductive events for female *Cancer pagurus*, in which I use different colour intensities to illustrate geographical differences in the onset of these events (Figure 10). As suggested by Woll et al. (2014), I have included only one spawning event during the two-year cycle.



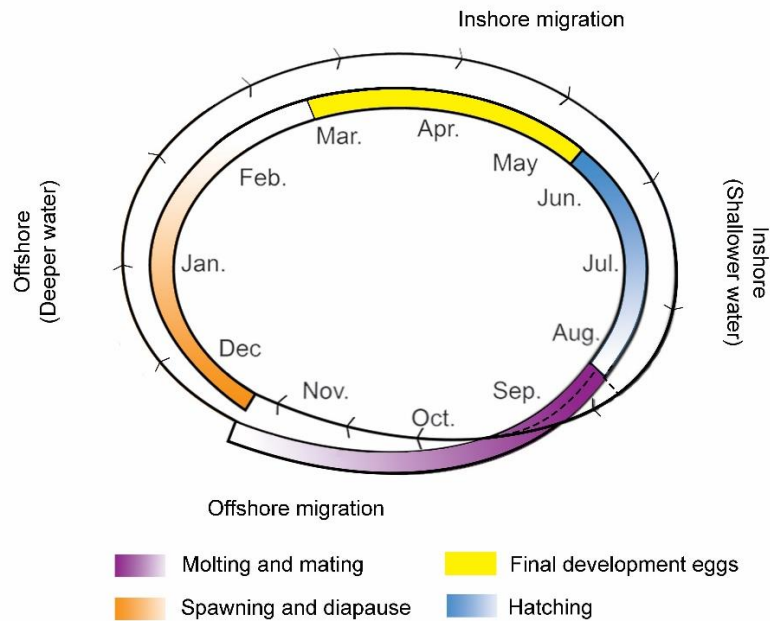


Figure 10 - Proposed reproductive cycle of female *Cancer pagurus*. Different colours denote main periods for particular reproductive events. Different intensities of colours denote geographical differences in onset of events (dark: low latitude/warm water, light: high latitude/cold water). Dotted line illustrates repeated spawning after one mating event and the possibility for early moulting/mating crabs to spawn the following winter. Modified from Bjerkan (1942) and later suggestions by Woll et al. (2014)

The number of times a female will repeat the reproductive cycle will depend on the number of successful moulting and mating events. Cancerid crabs are referred to as species having indeterminate growth (Hartnoll, 1985; McLay & López Greco, 2011). The data from the reference fleet support this, which shows that soft crabs are found within most size classes (Figure 11).

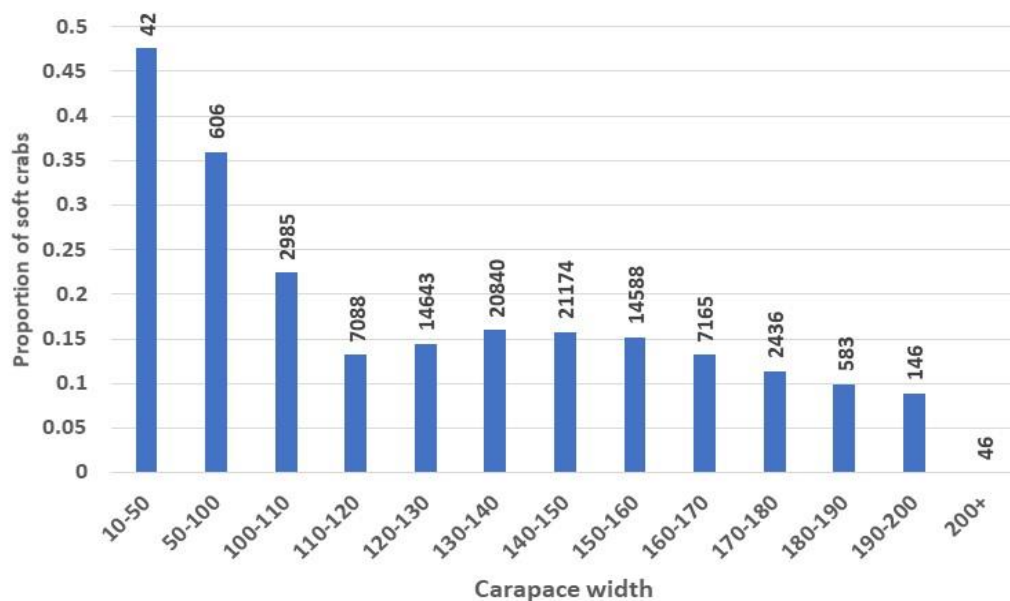


Figure 11 - Proportion of soft female *Cancer pagurus* within 10 mm size groups. Data from registrations made by the reference fleet (combined for all statistical areas). Numbers above bars show number of crabs within each size group.

The proportion of soft crabs, however, decline with increasing size, and no female crabs above 200 mm CW has been registered as recently molted by the reference fleet. Based on all registrations made by the reference fleet, a simple linear probability model predicts zero probability for moulting for females at a CW of 275 mm. This is higher than reported by Bennett (1974) who, based on tag-recapture studies, estimated that crabs would stop molting after reaching a size of 190 mm CW. However, female crabs larger than 200 mm CW are very rare, which suggest that most crabs die before reaching these sizes. This supports the belief that the edible crab has indeterminate growth. On the other hand, individual female crabs will likely not go through more than five mature instars in a lifetime. Using the most conservative regression formula for moult increment suggested by Bennett (1974, post-moult CW (mm) = 14.18 + 1.11\*pre-moult CW (mm)) and assuming maturity is attained at a size of 112 mm CW (Table 1), it can be estimated that the crab will go through four moults before reaching a size of about 235 mm CW (i.e. corresponding to the largest size of female crabs registered by the reference fleet, 230 mm CW). During this time the crab will likely produce only one clutch in the first mature instar, but go through two, or possibly three, breeding events in each subsequent instar stage (Pearson, 1908; Edwards, 1979; Hines, 1991). This suggests that a crab can produce between 9 and 13 clutches of eggs in a lifetime. This is unless the crabs are able to mate without moulting, as is common in some species of brachyuran crabs (Hartnoll, 1969). Although soft-shelled mating (and indeterminate growth) is believed to be an ancestral trait in Brachyura that is sustained in cancerids (McLay & López Greco, 2011), I have occasionally observed hard-shelled crabs with visible sperm plugs extruding from the vulvae. For instance, in the data used to estimate SAM in **Paper II**, the percentage of hard-shelled crabs with visible sperm plugs was around 2% (n=641, considering only crabs larger than 100 mm CW of which visual appearance and shell condition indicated a year or more since moulting). Interestingly, the percentage of hard-shelled crabs with sperm plugs appears to increase with latitude, with a prevalence of 0.8% in Area 08 (n=240), 2.0% in Area 07 (n=148) and 3.6% in Area 05 (n=253). It is tempting to speculate that this trend of increased presence of sperm plugs towards the north is related to a lower moulting frequency in females (**Paper II**). That is, that suppressed moulting causes females to mate in hard-shelled conditions. However, prevalence is low, and when tested statistically the observed difference is not significant (Fisher's exact test, p = 0.12). Further, it cannot be determined whether the presence of sperm plugs in these hard-shelled crabs is a sign of recent mating or if it merely indicates an unsuccessful transfer of the sperm packages to the seminal receptacles. Further studies are thus required to determine whether female *Cancer pagurus* is capable of mating in hard-shelled condition.

## Environmental effects on distribution and behaviour

### Northern distribution

To my knowledge, the first description of the distribution of *Cancer pagurus* in Norwegian waters was made by Michael Sars. In a summary of Norwegian-Arctic crustaceans, he mentioned that his own most northern observation was off the Lofoten Islands (~68 °N) but that he had been told by fishers that they had caught crabs as far north as Tromsø (~69 °N) (Sars, 1858, p. 123). Carl Dons said in his account of “the decapods of northern Norway” that *Cancer pagurus* was a clear boreal species with only limited occurrence in the arctic environment, and he objected to the reports of the fishermen, speculating that they had likely mistaken *Carcinus maenas* or *Lithodes maja* for the edible crab (Dons, 1915, p. 95). Fisheries investigations conducted in the late 1970s by the Institute of Marine Research also suggested that the waters south-east of the Lofoten Islands formed the northern distribution

border for the edible crab (Torheim, 1978; Torheim, 1979). However, during the last 20 to 30 years the crabs have migrated northward, and now support crab fishery as far north as Vesterålen (~69 °N) (Woll et al., 2006b). Currently, the crabs are common in Troms county (~70 °N) and have become a problem in the winter gillnet fishery in several areas, as they get tangled in nets meant to catch halibut and monkfish (Bakke et al., 2016). Having received several reports of this phenomenon over the last few years, I contacted about 20 gillnet fishers operating in Finnmark county, north to North Cape (~71 °N), in an attempt to identify the species' northern distribution border. The most northern location for (by)catch was reported to be just south of the island Rolvsøy (approximately 70°50'N/23°50'E), which is slightly north of other personal observations (Brattegard, 2011, citing personal communication with Hartvig Christie, NIVA).

### Temperature

The northward expansion of *Cancer pagurus* is likely caused by rising ocean temperatures, as seen in a range of marine species (Oviatt, 2004; Hampe & Petit, 2005; Perry et al., 2005; Poloczanska et al., 2013; García Molinos et al., 2016). In the case of the edible crab, the change in distribution has probably also been reinforced by the Atlantic Multidecadal Oscillation, which has been in a positive phase since the 1990`s (Drinkwater et al., 2014). As to what limits the further northward migration of *Cancer pagurus*, it is likely that, north of its current distribution border temperatures become too inhospitable for the crab. Mackay (1943) summarized the geographical distribution of cancerid crabs (including *Cancer pagurus*) and suggested that the genus was limited to latitudes having surface water temperatures above ~4.5 °C (40 °F). His conclusion is in accordance with the average seasonal temperatures measured at the hydrographical station "Ingøy", which is located just north of the most northern registration of crabs by fishers (Table 4).

*Table 4 – Temperature (°C) at "Ingøy" close to the northern distribution border for Cancer pagurus. (Data from the Institute of Marine Research and are average values from 2001 to 2014\*).*

Depth	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
5-10 m	5.8	5.1	4.5	4.5	5.4	7.2	8.3	9.7	9.5	8.2	7.6	6.6
10-50 m	5.9	5.2	4.7	4.7	5.4	6.6	7.1	8.6	9.0	8.3	7.7	6.7
50-100 m	6.3	5.5	5.1	5.0	5.5	6.3	6.4	7.5	8.2	8.2	7.8	6.9
100-200 m	6.5	6.0	5.6	5.3	5.6	6.1	5.9	6.9	7.3	7.6	7.6	7.1

\* Values from 2002,2003,2008,2009 and 2012 was excluded due to abnormal measurements.

The results in **Paper III**, suggesting a functional thermal range for *Cancer pagurus* between 5 and 16 °C, also support temperature being the main factor restricting further northward migration and back Dons (1915) who defined *Cancer pagurus* as mainly a boreal species. This functional temperature range is also in accordance with results by Hunter et al. (2013), who used female crabs fitted with data storage tags to study the depth and temperatures experienced during their migration in the English Channel and the Celtic Sea. A conspicuous observation from the study by Hunter et al. is that the mean temperature measured by crabs during onset of egg incubation was  $13 \pm 1.5$  °C. This is the same temperature as identified preferred temperature in **Paper III** ( $13 \pm 1.1$  °C), strongly suggesting that an optimum temperature for the edible crab falls within this range. Similar, when rearing larvae of *Cancer pagurus*, Weiss et al. (2009) found that a complete development occurred only within a narrow temperature range around a mean of ~14°C. Compensating for potential acclimation effects (i.e. crabs

reared at high temperatures (~16 °C) in the study by Weiss et al. (2009)), this developmental temperature is very close to the preferred temperature found in **Paper III** and the temperature at oviposition found by Hunter et al. (2013). Given their preference for rather warm water, it is quite evident that crabs along the north Norwegian coast live in suboptimal thermal conditions, which will in turn affect both their growth and feeding efficiency.

#### Biotic factors

In addition to a rise in temperature, it is possible that a concomitant change to the crabs' habitat might have contributed to the observed change in distribution. For instance, since the 1980s there has been a significant recovery of kelp forests along the central Norwegian coast (Norderhaug & Christie, 2009). A few studies have suggested that this regrowth might be caused by the northward expansion and increased abundance of the edible crab in the area, which preys on kelp-grazing sea urchins (Fagerli et al., 2014; Rinde et al., 2014; Christie et al., 2019). On the other hand, kelp forests are important nursery grounds for juvenile crabs (Moore, 1973; Eriksen & Moen, 1993; Robinson & Tully, 2000b; Scott et al., 2018), and could also function as an environmental cue upon settlement of megalopae (Forward et al., 2015). It is therefore quite possible that the regrowth of vegetation also has contributed to an increased recruitment of crabs in more northern areas.

#### Light

An interesting question is whether crabs in the north could compensate for their lower feeding efficiency at colder temperatures by having a longer period for foraging during late autumn. In the northern part of the crabs' distribution, the duration of darkness surpasses that of daylight in mid-September (Figure 9), with shallow water still sustaining relatively high temperatures (see Figure 2 in **Paper II**). Given their clear nocturnal foraging behaviour (Skajaa et al., 1998; **Paper III**), the crabs will have longer "nights" in which to hunt for food during late autumn at higher latitudes. On the other hand, constant daylight from around the middle of May until the end of July also indicates that crabs in the north lose precious warm water conditions during summer. Later onset of feeding activity (due to the impediment of daylight) could be one of the reasons for the delay in meat quality of crabs at higher latitudes (Woll et al., 2014; Bakke et al., 2015). However, since day length at a given latitude fluctuates according to the same annual cycle, and given that the industry experiences early and late years in terms of good-quality crabs (Kolbjørn Ulvan, HitraMat AS, pers. com.), foraging and nutritional gain is likely affected by a combination of environmental factors. Thus, further field and laboratory studies are needed to determine the degree to which differences in day length influence this nocturnal forager.

#### Depth

Within their boundaries of tolerance to hydrostatic pressure, many marine crustaceans have evolved life histories that take advantage of the heterogenic environment associated with depth. For instance, most crab species, including the edible crab, have their nursery areas in shallow coastal waters, but move to deeper water habitats when approaching maturity (for some examples in brachyuran species see Bigford, 1979; Hill et al., 1982; Dinnel et al., 1986; Stevens et al., 1993; González-Gurriarán & Freire, 1994; Hines et al., 1995; Robinson & Tully, 2000a; Forward et al., 2003). Conversely, juveniles of deep-water crab species appear to inhabit deeper water than adult conspecifics (Wigley, 1975; Attrill et al., 1990; Macpherson & Abelló, 1991; Blau et al., 1996; López Abellán et al., 2002; Yosho et al., 2009; Keller et al., 2012). Crabs also show diurnal or tidal vertical feeding migrations, usually to take advantage of more biologically productive shallow water habitats (Hill et al., 1982; Stevens et al., 1984; Robles et al., 1989; Hunter & Naylor, 1993; Karlsson & Christiansen, 1996; Silva et al., 2014). The

largest changes in bathymetric distribution, however, occur seasonally, as crustaceans move vertically in response to changes in water temperature or other environmental conditions (Campbell & Stasko, 1986; Ojeda & Dearborn, 1990; Thiel & Darnedde, 1994; Aguzzi et al., 2013) or as animals migrate in connection with particular reproductive events (see reviews by Pittman & McAlpine (2003) and Bauer (2018)).

As opposed to the waters surrounding the British Isles, where depths for the most part are shallower than 100–200 meters, most of the Norwegian coastline is intervened by deep fjords, many of which have depths of several hundred meters. This means that crabs in these areas sometimes encounter great depths during their seasonal migrations (**Paper IV**). The high abundance of shell fragments observed in the videos from Sognesjøen (**Paper IV**) indicate that mortality may be high during the time spent at these depths during winter. However, as mentioned above, the possibility that the observed fragments might be exuviae of moulted crabs should not be excluded. For instance, studies from other countries have shown that recently moulted crabs are found in catches most months of the year (Edwards, 1967; Brown & Bennett, 1980; Tallack, 2002), albeit in much lower numbers than during the peak moulting period of summer and autumn. Assuming that the fragments observed in the video were the exuviae from female crabs (intact remains were from females and most crabs in video had female characteristics), this also indicates that mating might have occurred at these depths. Orensanz et al. (1995) proposed that the breeding system of cancerid crabs could be classified according to the species habitat (gradient from “open” to “structured”, respectively predicted to promote high and low degree of female gregariousness) and the size of the species (determining seasonal synchronism of reproduction; high synchronism in large species and low synchronism in smaller species). The generally high abundance of crabs observed in Sognesjøen (**Paper IV**) fits with the concept of aggregation in open soft-bottom habitats (Orensanz & Gallucci, 1988; Orensanz et al., 1995). However, in terms of its natural habitat (in shallow water), *Cancer pagurus* would be classified as a “structured” species (living on both hard- and soft-bottom substrates (Pearson, 1908; Edwards, 1979; Hall et al., 1991; Hallbäck, 1998), with a fairly restricted season of the year in which moulting and mating occur (i.e. high reproductive synchronism) (Mason, 1965; Tallack, 2007b; **Paper II**). According to Orensanz et al. (1995), species living in such structured habitats should attain a mating system consisting of “resource defence polygyny”, a term derived from Emlen and Oring (1977) who define it as the situation in which “males control access to females *indirectly*, by monopolizing critical resources”. Orensanz and Gallucci (1988) suggest that this “critical resource” could be specific areas within the structured habitat that male crabs control. *In situ* observations of moulting and mating of *Cancer pagurus* is limited, but diver observations (Astrid Woll, pers.com.; Bennett & Brown, 1983, citing personal communication with A. E. Howard) and field samplings (Vogan et al., 1999) suggest that crabs seek shelter in crevices or holes during the moulting and mating process. In his laboratory studies on mating in *Cancer pagurus*, Edwards (1966a, p. 24) also noted that grasping pairs of crabs “moved to a secluded part of the tank and remained stationary”. In the same study, Edwards also reported to observe individual males mating with several receptive females, indicating that polygyny indeed occurs in this species. Thus, if mating locations in the form of crevices and holes are a “limited resource” in the habitat of *Cancer pagurus*, it could promote guarding behaviour in males, which would support the idea of a “resource defence polygyny” mating system in this species (Emlen & Oring, 1977; Orensanz et al., 1995). Consequently, if the use of secluded mating sites is an important part of the reproductive strategy of *Cancer pagurus*, it is difficult to explain the shell remnants observed in open deep-water areas in **Paper IV** as the result of mating activity. Molting and mating in these areas

would mean that female crabs were very exposed during the vulnerable soft state (Edwards, 1989; Bryant, 1991).

The movement of female edible crabs to deeper water during winter, a behaviour that was recognized early (Williamson, 1900; Meek, 1913; Meek, 1914), has in later studies been concluded to be migration to suitable grounds for spawning and incubation of eggs (Bennett & Brown, 1983; Ungfors et al., 2007; Hunter et al., 2013). Such spawning migrations could explain the observed high abundance and aggregation of crabs in Sognesjøen (**Paper IV**). Several crustaceans have been shown to aggregate during egg incubation and release of larvae (McKoy & Leachman, 1982; Armstrong, 1987; Campbell, 1990; Stevens, 2003). Diver observations have also shown that female *Cancer pagurus* congregates in specific areas when incubating their eggs. For instance, Howard (1982) reported on a high abundance of ovigerous crabs on a soft-sediment location in Lyme Bay on the south coast of England. Similar reports have been made by Woll (2003), who observed about 20 partially buried ovigerous crabs within a small area (15 x 20 m) in a strait on the west coast of Norway. Aggregations of ovigerous crustaceans have in other studies been found to be associated with tidal currents (McKoy & Leachman, 1982; Stevens et al., 2000; Stevens, 2003) that might secure a wide dispersal of larvae. Although the dominant contranantant winter migration of female *Cancer pagurus* has been suggested to be related to larval release (Meek, 1916; Bennett & Brown, 1983), it is not known whether sites for oviposition are selected based on hydrographic conditions. Woll (2003) described the strait where she observed ovigerous crabs as having strong tidal currents. Conversely, Howard (1982) described the area where he observed ovigerous crabs to have low impact of tidal currents. On the other hand, it is quite possible that the crabs move from the site of incubation to a more suitable location for release of larvae (Thompson et al., 1995). In terms of selecting sites for oviposition, it is possible that the type of sediment is more important for the crab. During incubation of eggs, *Cancer pagurus* and other cancerid crabs are dependent on soft sediment in which they can burrow (Scarratt & Lowe, 1972; Howard, 1982; Shields, 1991; Scheduling et al., 2001; Woll, 2003). Apparently, this burrowing behaviour is necessary to ensure that the eggs adhere to the pleopods (Wear, 1974; Wild, 1980; Kuris, 1990). In the video from Sognesjøen (**Paper IV**) four crabs were observed to be partially buried in the sediment and thus could have been incubating their eggs. However, the majority of crabs in the video were moving around on top of the sediment and showed no sign of burrowing behaviour. Although it is possible that there were nearby spawning grounds not covered by the video transect (as indicated by the large areas of the seabed covered by apparent crawling tracks of crabs), it is not possible to conclude from the video that crabs actually aggregate in this area to spawn and incubate their eggs.

### Implication of study for management and fishery in Norway

Currently, the only management measures in the Norwegian edible crab fishery are the minimum legal landing sizes of 130 and 110 mm CW for crabs caught north and south of the border between statistical areas 28 and 08 (Figure 4), respectively. The results in **Paper I** and **Paper II** suggest that the northern MLS is sufficient to restrict the catch of immature females. This is also true if the more conservative threshold for maturity is used, with the overall value showing that 50 % of the crabs mature at a size of ~123 mm CW (Figure 6, Table 1). Based on results on SAM in Swedish waters, Ungfors (2007) argued that the current MLS of 110 mm CW in southern Norway should be reconsidered. The results from my studies support her conclusion (**Paper II**, Table 1) and suggest that the MLS set in 1986 to reduce the population likely causes many crabs to be fished before they can reproduce. Although mandatory

escape gaps (to prevent the catch of undersized lobsters) and higher size restrictions made by crab producers likely limit catch of small crabs (**Paper II**), the reported average size of landed crabs in the south is smaller than in areas where the MLS is 130 mm CW (Woll et al., 2006b; Søvik et al., 2017), indicating that these operational safeguards alone are insufficient to limit the landing of undersized individuals. Hence, if the management objective is to conserve the reproductive potential of the stock an increase in MLS from 110 to the same as the rest of the country is recommended.

The results from **Paper II** suggest that crabs in the north are more sensitive to fishing pressure than crabs from more southern areas due to slower somatic growth and lower reproductive potential. In particular, it is likely that the proportion of crabs producing offspring every year is lower at higher latitudes (see above), lowering overall production available for the fishery. Also, natural mortality could possibly be elevated in certain areas where crabs migrate to deep water (**Paper IV**), which could affect the crabs' sensitivity to exploitation.

In a summary of data collected by the reference fleet, Søvik et al. (2017) suggested that the fishing pressure might be too high in Area 06 (Figure 4), as over the last few years there has been a decline in the number of large individuals in the catches, and an overall tendency towards a reduction in catch rates. Although catch rates based on data from the reference fleet only provide rough estimates of landings and catch per unit effort, these trends emphasize the need for better monitoring of the population. To provide better information on how catch rates varies between areas, and to identify potential changes over time, I would therefore recommend that fishers report the number of pots they use, particularly in those areas where fishing activity currently is high (Areas 06 and 07). This information should be quite easy to include in the landing reports fishers and buyers already are obliged to fill out on delivery.

It is worth mentioning that, as opposed to in the UK where crabs in several areas are targeted year-round (Bannister, 2009; Mill et al., 2009; Mesquita et al., 2017), there is almost no winter fishery for edible crab in Norway, with the limited summer and autumn season restricted by boats turning to other species, and factories stopping their production by the end of November (see Introduction). Thus, in most parts of Norway crabs are protected from a targeted fishery for about six months of the year (December–June). There is, however, an interest in extending the crab season (Woll et al., 2014), which would add to the fishing mortality. This development should be followed closely and taken into consideration in future monitoring of this species.

#### New fishing opportunities

For the fisheries industry, the northward spread of crabs could pose an opportunity. In 2015, I coordinated a project that examined the possibility for commercial utilization of crabs in an area of Troms county (~69 – 70 °N) (Bakke et al., 2016). Based on our results, we concluded that the abundance of crabs was sufficient to sustain a profitable fishery in the southern part of this area, but that the development of an industry was hampered by the absence of factories capable of processing the crabs. Investigations of heavy metals also revealed high levels of cadmium in the hepatopancreas of crabs caught, restricting their usability for processing and consumption. The geographical differences in growth reported in **Paper II** have recently been suggested as a possible reason for the elevated levels of cadmium in northern crabs (Wiech, 2018). (The same size crabs are older in the north and therefore have had a longer time for accumulation.) Thus, so far, the development of a fishery on this immigrating species is limited by incomplete infrastructure and high levels of heavy metals.

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## Conclusion and future perspectives

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The overall aim of this thesis has been to provide information on how environmental conditions in Norway affect the life history and distribution of the edible crab. My results suggest that the size at which female crabs reach (physiological) maturity varies little, and only randomly, across northern Europe (**Paper I**) and among areas within Norway (**Paper II**). The discrepancy between my results and some previous studies (Tallack, 2007b; Ungfors, 2007) may relate to different interpretations of the gonad stage that should be used as the threshold for maturity. Future work should therefore aim to identify whether crabs within the estimated range of SAM in **Paper I** and **Paper II** are capable of producing eggs. This could be achieved by holding crabs in tanks under the right environmental conditions, past the time for anticipated spawning.

The results from **Paper II** show that crabs at higher latitudes grow more slowly, and therefore are older when they reach maturity. As age and growth are important parameters in stock assessment (Bennett, 1979; Bennett, 1995), an attempt should be made to quantify these geographical differences. Better information on differences in adult growth will likely be available in the future, as the Institute of Marine Research now have restricted the registrations by the reference fleet to every second year but have increased the number of fishers participating (Søvik et al., 2017). This will provide better data on the occurrence of soft crabs both on a temporal and a spatial scale. However, to gain a more complete understanding of how growth and age vary between regions within Norway, information on geographical differences in juvenile growth is needed. This could be obtained by field studies similar to those conducted by Eriksen and Moen (1993) or through laboratory experiments investigating the effect of temperature and light on moulting in juvenile crabs.

In **Paper III**, a common temperature preference of around 13 °C was found for female *Cancer pagurus* collected from northern Norway and those crabs collected 900 km further south. There was, however, a tendency for northern crabs to spend more time in the cold range of the thermal gradient and a trend for these crabs to have a lower tolerance to cold water compared to crabs from the south. These observations warrant further investigations to determine whether this could be due to inherent physiological differences in these climatically separated individuals. For instance, the sedative effect of circulating magnesium has been suggested to be a protective mechanism to constrain metabolic activity in cold water (Frederich et al., 2000; Frederich et al., 2001), and its haemolymph levels are known to vary between species of crustacean living under different environmental conditions (Walters & Uglow, 1981). Other physiological parameters that could be investigated are geographical differences in mitochondrial density and activity (Pörtner, 2002) and the genes involved in glucose production (Ronges et al., 2012).

The analysis of video transects from Sognesjøen, off western Norway, (**Paper IV**) shows that *Cancer pagurus* can migrate to depths greater than commonly reported depth-limits for this species. To determine sex composition and nutritional status of these individuals, the site should be revisited (in the winter), and crabs collected using gill-nets or pots. Using a dredge or a remotely operated vehicle it will also be possible to collect the shell remnants or intact “dead” bodies of crabs that were observed in the video. This will help to determine whether natural mortality is high during the winter in deep water (if they are remains of dead crabs) or whether the crabs moult during winter at these depths (if they prove to be the exuviae of moulted crabs).



### Other topics for future research

As discussed, it is likely that the proportion of crabs in Norway that have well-developed gonads by the end of autumn is lower than in areas further south in Europe. To estimate the number of crabs that spawn every year in Norwegian waters, more detailed investigations of these differences should be conducted. Such information could be gathered through collaboration between research and industry, using data from Norway's largest crab producer on NIR measurements of brown meat filling of female crabs (Bakke et al., 2015). This large-scale screening of crabs could be combined with laboratory studies to investigate the proportion of females with well-developed gonads that succeed in producing eggs.

The larvae of the edible crab require relatively high temperatures in order to undergo a complete development (above 8 °C (Lindley, 1987), but with an optimum around 14 °C (Weiss et al., 2009)). In northern Norway, the larvae would rarely experience optimal thermal conditions, as the surface water only reaches temperatures above 10 °C for a limited period during autumn (**Paper III**, Table 4). Thus, unless the offspring of northern crabs are better adapted to the colder conditions, as has been reported in the case of the American lobster (Quinn et al., 2013), recruitment in the northern part of the crab's distribution is likely to suffer severely from larval mortality. Also, given that the larva of the edible crab is positive phototactic (Nordgaard, 1912; Rice, 1964), it is also likely that latitudinal variation in day length affects larval behaviour and possibly also growth (Dalley, 1980). Further work should therefore try to understand how the environmental conditions at higher latitudes affect the development and mortality of the earliest life stages of this species.

An interesting ecological question is what effect the northward migrating edible crab will have on the benthic community in northern Norway. With the exception of the deeper-living *Lithodes maja*, and the smaller crab species *Carcinus maenas* and *Hyas sp.*, the northern part of Norway has historically been nearly devoid of large decapod crustaceans. In addition to the edible crab (migrating into northern Norway from the south) is the red king crab (*Paralithodes camtschaticus*), migrating into the same area from the east as an invasive species which already has made significant changes to the ecosystem of north Norwegian fjords (Oug et al., 2010; Fuhrmann et al., 2015; Oug et al., 2018; Pedersen et al., 2018). Reports of fishermen catching both the edible crab and the red king crab in the same gillnet (Røen, 2014) suggest that the two species already have an overlapping distribution. Given the opportunistic foraging behaviour of these benthic scavengers, it is likely that they will have a high impact on the benthic community, which should be monitored in future studies.

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# PAPER I

*"Now, the female differs in no respect from the male except in the circumstance that its operculum is larger, more elevated, and more hairy, and into this operculum it spawns its eggs.."*

Aristotle, 350 B.C.E , The History of Animals. (Translation by D'Arcy Wentworth Thompson)





## PAPER II

*“The more healthy and thriving a crab is, the more frequently he casts his shell”.*

Peter Collinson (1746) Some farther observations on the *Cancer major*. Philosophical Transactions Vol. 44.





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## Size at maturity and molting probability across latitude in female *Cancer pagurus*

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### ABSTRACT

Edible crab, *Cancer pagurus*, is a valuable North Atlantic fishery resource distributed from Morocco to northern Norway, covering a wide range of temperatures and other oceanographic variables. Knowledge on how local environmental conditions affect life history traits like maturity and growth in this species is however lacking, despite its importance in science-based management. Through analyses of field data and fishers' reports from different areas along the west coast of Norway (between 59°N and 69°N), latitudinal differences in size at onset of sexual maturity and molting probabilities of female *C. pagurus* were investigated. The size at which 50% of crabs were found to be mature (CW<sub>50</sub>) did not differ between areas and was consistent with historical investigations, i.e. overall CW<sub>50</sub>: 112.3 mm, and CW<sub>50</sub> for each area/year between 108 and 117 mm. Generalized additive modelling was used to predict probability of molting (occurrence of soft crabs) during late summer/autumn, with 'area' as a categorical variable, and 'day of year' and crab size as continuous non-linear predictors. The predictor variables had low explanatory power (16.4% deviance explained by full model), demonstrating the complexity of the process regulating molting. However, frequency of molting decreases and peak periods of molting occur later at higher latitudes, suggesting that lower temperatures have an impeding effect on growth in northern populations. Overall, our findings suggest that current minimum legal catch sizes for crabs in Norwegian waters are sufficient to restrict the catch of immature females, but that crabs in different geographical regions appear to be variably tolerant to fishing pressure following differences in growth.

### 1. Introduction

Edible crab, *Cancer pagurus*, is distributed along Northeast Atlantic coasts, from Morocco in the south to the northern part of Norway (FAO, 2015), and represents a valuable fishery resource across most of Europe. The fishery for edible crab is conducted using baited pots, with total annual catches in Europe in the order of 50,000 t (FAO, 2015). In Norway, approximately 5000 t are harvested annually, mainly by small vessels (length < 15 m) fishing along the Norwegian coast between ~59 and 69°N. The fishery is managed, with minimum landing size limit (MLS) applied as a primary tool to preserve the reproductive potential, but there are no quota or effort regulations. The MLS is set at 130 and 110 mm carapace width (CW) for crabs caught north and south of 62°N, respectively. When MLS values were first implemented, the scientific basis for their choice was weak, in part dating back to limited studies by Bjerkan (1927a,b). A later investigation by Woll and Larssen

(2004) found that 50% of female crabs were mature (CW<sub>50</sub>) at around 110 mm CW, with no apparent differences among crabs from various geographical areas, adding support to the current MLS. In a study by Haig et al. (2016), investigating *C. pagurus* in several European countries using the same method as Woll and Larssen (2004), CW<sub>50</sub> mean values varied between 97 and 117 mm, but with no obvious spatial structure associated with this variation. Also, a CW<sub>50</sub> of 108 mm was recently reported for female *C. pagurus* from the Isle of Man (Öndes et al., 2017). Thus, these studies indicate that the body size at which the gonads of *C. pagurus* become vitellogenic (i.e. yolk forming) varies little or just randomly across geography. Most historical studies have however been focused around central Europe, with limited knowledge on how size at maturity in this species might vary between areas with distinctly different climatic conditions. In the first part of this study we revisit the question of size at maturity by investigating crabs along a north-south gradient along the Norwegian west coast.

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While size may appear as a general trigger of sexual maturation in female *C. pagurus*, the age at which this size is reached might vary. Slower growth due to lower temperatures at higher latitudes is a general response e.g. in fish (Conover, 1992). In crustaceans, growth is a function of molting frequency (or the duration of the intermolt period) and the growth increment at moult. Although there is evidence of an inverse relationship between moult increment and temperature in crustaceans (see Hartnoll, 2001 for a review), the positive relationship between temperatures and metabolic processes overall results in increased growth at higher temperatures due to shorter intermolt periods (Green et al., 2014; Hartnoll, 2001; Passano, 1960). While the reproductive potential of *C. pagurus* may be conserved by appropriate MLS restrictions, similar across geography, the biomass that can be removed sustainably will depend on growth rate, which, in turn, is likely to vary with temperature and, hence, latitude.

In Norway, *C. pagurus* is distributed along the coast from ~59°N to ~70°N, covering a range of more than 10° latitude and exposed to a wide range of seasonal environmental conditions. The importance of temperature for the complete larval development of *C. pagurus* has been demonstrated by Weiss et al. (2009), but little is known about how growth of adult crabs varies with environmental conditions, such as those experienced at different latitudes. The aim of this study is to provide baseline information on size at maturity and individual growth patterns of *C. pagurus* from climatically different areas along the Norwegian coast. Our hypothesis is that (1) crabs mature at a larger size at higher latitudes (Atkinson, 1994), and that (2) cold temperatures have an impeding effect on the molting process causing lower molting frequency (and hence slower growth) in northern areas. Our results will help to understand how a species life history traits may vary across biogeography, and whether such information needs to be taken into consideration in a management perspective.

## 2. Material and methods

### 2.1. Study area

To obtain information on activity of fishing vessels, the species they target and the volumes landed, the Directorate of Fisheries collects data on coastal fisheries from nine different regions (statistical areas) along the coast of Norway (Fig. 1). For studies of size at maturity we collected crabs from Area 05, Area 06 and Area 08, revisiting the same sites as used by Woll and Larssen (2004) eleven years earlier. (The locations are presented as grey, orange and green dots in Fig. 1.) The areas represent (i) the northernmost extent of the commercial crab fishery (Area 05), (ii) the areas with the most intensive fishery in terms of landings (Area 07), and (iii) the southernmost area from where a significant proportion of the commercially harvested crabs are landed (Area 08). For investigations on molting probability we focused on the areas where the registrations by the reference fleet have been most extensive, and which provided sufficient data for statistical modelling (see below). These were Area 05, Area 06, Area 07 and Area 08 (highlighted in Fig. 1 as grey, blue, orange and green, respectively).

### 2.2. Temperature in different areas

Estimates of the temperature regimes to which crabs are exposed in shallow water were obtained from the Norwegian Institute of Marine Research (IMR) which operates hydrographical stations at different locations along the coast. Stations “Eggum”, “Bud” and “Yttre Utsira” located within Area 05, Area 07 and Area 08, respectively, were used. Data from Area 06 was unfortunately not available as no hydrographical station is located within this region. Temperature measurements at 20 m water depth from 2001 to 2015 were used to calculate mean seasonal temperature for each area by applying a smooth local regression (LOESS) (Cleveland et al., 1992) (Fig. 2).

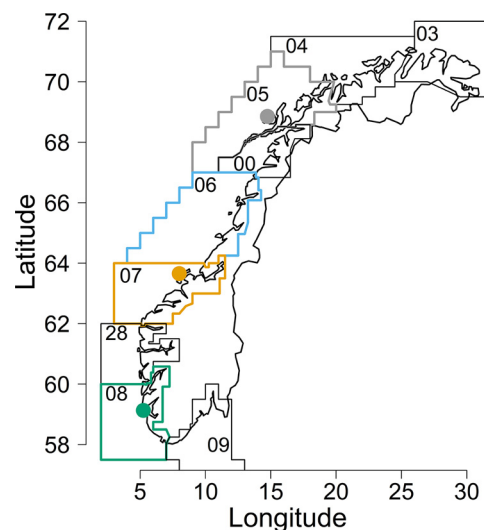
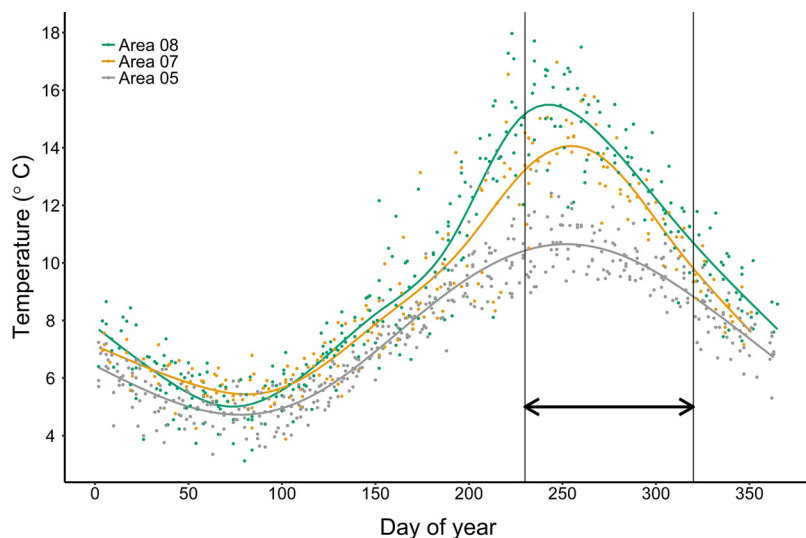


Fig. 1. Map of Norway showing the nine coastal statistical areas used by the Directorate of Fisheries. Areas investigated in our study outlined in grey (Area 05), blue (Area 06), orange (Area 07) and green (Area 08). Dots within each area show locations from where crabs were sampled for size at maturity studies. Polygons for statistical areas represent WMS files obtained from the Directorate of Fisheries online maps services ([www.fdir.no/kart](http://www.fdir.no/kart)). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

### 2.3. Determination of size at maturity

#### 2.3.1. Data collection

In September and October 2014, a total of 621 female crabs were collected (Area 08,  $n = 181$ , Area 07,  $n = 213$  and Area 05,  $n = 227$ ). For each of the three areas, we aimed at collecting a minimum of 20 crabs in each 5 mm size interval from 80 mm to 150 mm carapace width (CW). The crabs were collected from commercial pot catches, at depths of 20–40 m. Fishers in Area 08 are required to have escape gaps on their pots. To increase the likelihood of obtaining small crabs, approval was apprehended from the Directorate of Fisheries to close the escape gaps during the period of collection. The widest part of the carapace was measured in millimetres using a digital calliper. Previous studies on female *C. pagurus* indicate that a change in the width of the abdomen relative to CW occur at onset of maturity (Tallack, 2007; Ungfors, 2007). To investigate if such allometric growth occurred for our crabs, the abdominal width (AW) was also measured to the nearest millimetre. Before dissection, crabs were killed by spiking through one of the eyes (destroying the cerebral ganglia) and through the center of the sternum (destroying the thoracic nerve mass) (Baker, 1955). Individuals were then opened and their gonads stage-determined, following the scale developed by Edwards (1979) and later modified and extended by Larssen et al. (2015) (1 = Immature, 2 = Early mature, 3 = Mature, 4 = Late mature, 5 = Spawning and 6 = Spent). Stage 2 was set as a threshold for maturity, which is characterized by gonads with distinct lobes that are extended in the carapace. Histological investigations by Larssen et al. (2015) defined stage 2 as mature based on the presence of primary oocytes covering 50–80% of the lobes, and the presence of secondary oocytes with yolk. Reference data from Woll and Larssen (2004) on the size at maturity of *C. pagurus* females, which were disseminated only in the grey literature, are also included in this paper for comparison. In their study, 524 female *C. pagurus* were collected in September 2003, from the three areas Area 08 ( $n = 178$ ), Area 07 ( $n = 181$ ) and Area 05 ( $n = 166$ ) (Fig. 1). Woll and Larssen (2004) also investigated if crabs had mated, by registering the presence of sperm plugs or sperm in the spermatheca. These data were used to investigate size at onset of behavioural maturity.



**Fig. 2.** Temperature throughout the year at 20 m depth in areas Area 05 (grey), Area 07 (orange) and Area 08 (green). (Data on temperature from Area 06 was not available). Curves are mean values from measurements conducted weekly to biweekly from 2001 to 2015 (dots). Data were obtained from the Institute of Marine Research database ([www.imr.no](http://www.imr.no)), where data from a series of permanent hydrographical stations along the coast of Norway are gathered. Data for Area 05 was from station “Eggum”, data for Area 07 was from station “Bud” and data for Area 08 was from station “Ytre Utsira”. The area between vertical lines (denoted by arrow) depicts the period used in modelling probability of molting. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

### 2.3.2. Statistical analysis

Estimates of size at 50% physiological maturity ( $CW_{50}$ ) were conducted as recently described by Haig et al. (2016). Individual crabs were categorized as mature (1) or immature (0) based on the gonad developmental stage, where gonads in the stages 2–6 were characterized as mature and gonads in developmental stage 1 were defined as immature (see above). The R script by Harry (2013) was used, which employs the logistic regression model by Roa et al. (1999), reformulated by Walker (2005) to produce

$$P_i = \left\{ 1 + e^{-\ln(19) \left( \frac{CW_i - CW_{50}}{CW_{95} - CW_{50}} \right)} \right\}^{-1}, \quad (1)$$

where  $P(i)$  is the proportion of mature crabs at  $CW_i$ , and where  $CW_{50}$  and  $CW_{95}$  refers to the carapace width at which 50% and 95% of the crabs, respectively, are mature.  $CW_{50}$  and  $CW_{95}$  were calculated from parameters obtained by fitting a generalized linear model with *logit* link function and binomial error structure to the data. Confidence intervals were determined by bootstrapping the model for 10,000 runs. The model was run on the whole dataset and for each of the three areas (Area 05, Area 07 and Area 08), as well as for both time periods (2003 and 2014) separately. The logistic regression model was also used to determine size at behavioural maturity, using data from 2003 on presence (1 = mature) or absence (0 = immature) of sperm plugs or sperm in spermatheca. To investigate size at morphometric maturity for crabs collected in 2014, a piecewise regression model was used (Crawley, 2013):

$$y_i = \begin{cases} \beta_0 + \beta_1 CW_i, & CW_i < c \\ \beta_2 + \beta_3 CW_i, & CW_i \geq c \end{cases} \quad (2)$$

where  $y_i$  is AW of individual  $i$ , and the  $\beta$  parameters intercept and slope from the two linear segments of the piecewise model. The inflection point ( $c$ ) was obtained by an iterative search procedure, selecting the value giving the lowest residual standard error. ANOVA was used to test if a two-line model provided a better fit than a straight line.

## 2.4. Probability of molting

### 2.4.1. Data collection and exploration

As molting frequency can be considered a proxy for growth, we aimed to investigate if and how the probability of molting in female *Cancer pagurus* varied among various regions along the coast of Norway, and as a function of other explanatory variables. Since 2001, the Norwegian Institute of Marine Research (IMR) has overseen data collection on molting (i.e. occurrence of recently moulted, soft-shelled

crabs) by a reference fleet of commercial crab fishers (Woll et al., 2006). Each fisher participating in the reference fleet measures and records the total catch in four standardized reference pots on a weekly basis during the main fishing season (June–December). The data collected include size (CW), sex and discards (soft crabs, berried females and crabs below MLS). Registration of crabs is conducted in the different statistical areas along the coast of Norway (Fig. 1), and since 2001, more than 150,000 crabs have been sampled. For this study, we compiled crab registrations of the reference fleet from 2001 to 2015 into one dataset and explored and corrected for errors (abnormal CW values, date errors and inconsistent geographical information). A subset selecting female crabs from Area 08, Area 07, Area 06 and Area 05, and considering only those years where catch registrations took place in all of these four statistical areas, was used. Data points with missing values for either depth, date of catch, CW, shell condition (soft/hard) were removed. The resulting dataset was visually scanned for outliers and limited observations, and potential dependencies among explanatory variables were tested using Pearson correlation (Zuur and Ieno, 2016). A few registrations where the fishing depth was reported to be more than 100 m were excluded, as we suspected that these resulted from experimental fisheries. Furthermore, in some registrations very long soak times were reported for the reference pots. Since soak times exceeding 96 h may reduce the catch (Bennett, 1974a), such registrations were excluded from the data. When exploring the data, it was found that registrations started and ended earlier in the fishing season in the southern Area 08 compared to Area 07, Area 06 and Area 05. To eliminate this systematic discrepancy, the data subset was limited to registrations conducted between mid August (day 230) and the mid November (day 320) (Fig. 2). Although few observations were conducted in November in Area 08, we did not reduce the time period of the data subset any further, as this would have led to the loss of too many registrations from the other three areas. With regard to size measured as CW, only very few crabs smaller than 80 mm or larger than 200 mm were registered. CW of crabs was therefore restricted to this size interval (80–200 mm). The total number of crabs for each area used in the statistical analysis is presented in Table 1.

In testing for dependencies, collinearity was found between ‘day of year’ and ‘depth’ ( $r = 0.6$ ,  $p = .001$ ). Within the period investigated, there was a gradual change in average fishing depth from about 20 m in the beginning of the period, to about 35 m at the end of the period. This is explained by the fact that fishers track the crabs migrating to slightly deeper waters during autumn. Hence, depth was not used as an explanatory variable in the statistical modelling (see next section). Finally, since close to 80% of soak times were either 24 or 48 h, lumping the majority of data points into just those two categories, we

**Table 1**  
Number of female crabs used in the analysis of the probability of molting.

Area	Year							
	2002	2003	2004	2007	2012	2013	2014	2015
05	604	754	199	322	225	462	547	200
06	8031	6431	2119	1231	1869	1646	814	775
07	5407	5288	1341	552	1259	1397	171	327
08	2203	412	851	522	429	267	518	408

also excluded this variable from the model.

#### 2.4.2. Statistical analysis

In modelling probability of molting, we investigated the explanatory power of ‘statistical area’ (origin of crabs), ‘day of year’ and CW (crab size). The relationship between *C. pagurus* size and molting frequency typically have a reverse S shape, with high molting frequency for small crabs (< ~100 mm CW) and very low molting frequency for crabs above ~170 mm (Bennett, 1995; Hancock and Edwards, 1967). In northern Europe, molting frequency also varies through the year, with a clear seasonal peak during autumn (Mason, 1965; Tallack, 2007; Ungfors et al., 2007). As it therefore was considered likely that both ‘day of year’ and CW would have a non-linear effect on the probability of molting, Generalized Additive Modelling (GAM) was used in the statistical modelling (Hastie and Tibshirani, 1990), a method that allows for identifying non-linear effects of a predictor on a response variable (Wood, 2006). In the full model (3), the binary response “soft” (1 = newly moulted, 0 = hard-shelled) was modelled as a function of the four-level factor “statistical area” (fArea; 5, 6, 7 and 8) with “CW” and “day of year” as smoothing terms (s(CW); 80–200 mm and s(day of year); 230–320). Separate smoothing terms were created for each of the four areas. Since we were interested in the overall differences among areas, ‘year’ was included as a random factor in the model. The final model had the form

$$\text{logit}(\pi_{ij}) = \beta + f_{\text{Area}_{ij}} + f_k(\text{doy}_{ij}) + f_k(\text{CW}_{ij}) + a_i, \quad (3)$$

calculating the probability that crab *j* in year *i* is soft. Index *k* denotes separate smoothers for ‘statistical area’, and *a<sub>i</sub>* random intercept for ‘year’. The model was fitted using the *gam*-function in the *mgcv* package in R (Wood, 2006), with thin-plate regression splines for smoothing terms and automatic selection of smoothing parameters (number of knots) by generalized cross-validation in the *mgcv* package (Wood, 2004). The full model was tested by analyses of variance (ANOVA) against simpler models by a backward stepwise approach, where predictor variables and interactions terms were dropped from the model.

R Version 3.3.1 software (R Core Team, 2016) was used for statistical analyses and graphical illustrations.

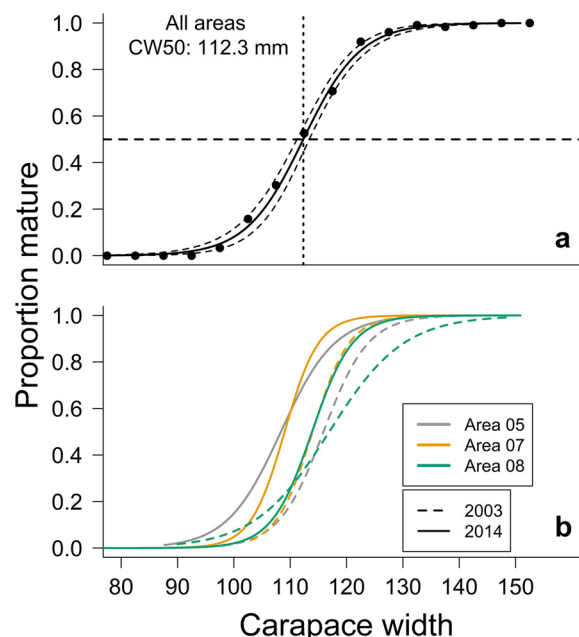
### 3. Results

#### 3.1. Temperature in different areas

The mean temperature at 20 m depth for Area 05, Area 07 and Area 08 is shown in Fig. 2. There is little difference in mean values between the three areas between December (~day 340) and mid June (~day 170). However, during summer and autumn months, there are clear differences in mean temperatures among areas, with peak temperatures of ~15.5 °C in Area 08 (south), ~14 °C in Area 07 and ~10.5 °C in Area 05.

#### 3.2. Size at maturity

The overall mean size (CW) at which 50% of the crabs were physiologically mature was 112 mm (Fig. 3a), with slight differences among areas and years (CW<sub>50</sub> between 108 and 117 mm) (Fig. 3b).



**Fig. 3.** Maturity ogives for carapace width (CW) of female *Cancer pagurus*. (a) Results based on model using data from all areas and years (2003 and 2014) combined. Lines denote predicted probability of physiological maturity, and black dots indicate observed proportions of mature crabs. (b) Separate ogives for each area and year. Solid lines show results from 2014 and dashed lines results from 2003. Different colours denote geographical area. Data from Area 07 in 2014 have previously been published in Haig et al. (2016). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Considering both time periods (2003 and 2014), the smallest CW for which a crab was found to be physiologically mature was 100 mm for Area 05 and Area 07, and 104 mm for Area 08. The largest immature crab was 138 mm CW for Area 05, 128 mm CW for Area 07 and 144 mm CW for Area 08. Results on behavioural maturity (CW<sub>50behavioural</sub>) using data from 2003 on presence of sperm is presented in Fig. S1 (Supplementary material). For the three areas, Area 05, Area 07 and Area 08, CW<sub>50behavioural</sub> was 108, 112, and 107 mm, respectively. Fig. S2 (Supplementary material) present the results on relationship between CW and AW. For Area 05 and Area 07 no allometric growth was evident, with a straight line giving a better fit than a piecewise-model. For Area 08 allometric growth was found, with an inflection point at a CW of 110 mm.

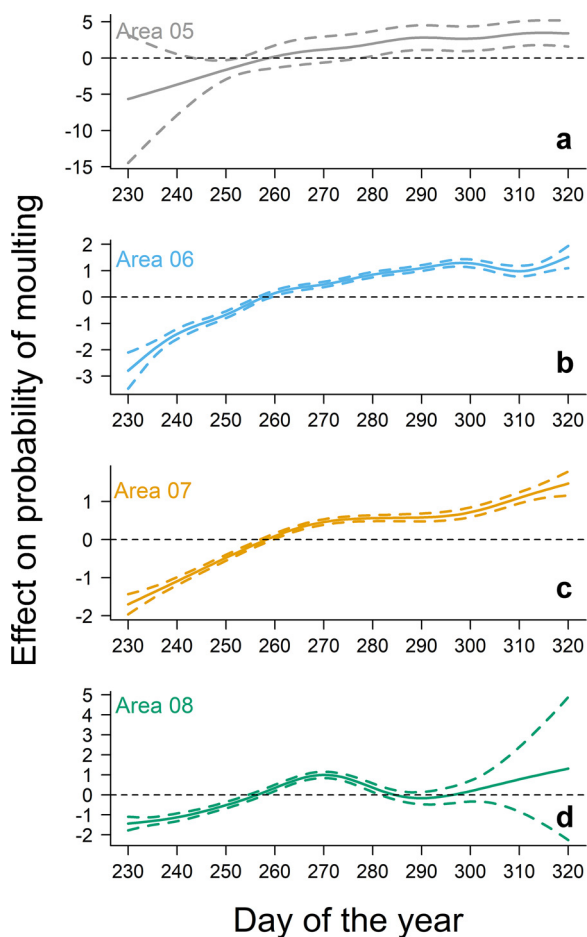
#### 3.3. Probability of molting

‘Statistical area’, and area-specific smoothing terms for ‘day of year’ and CW all had a significant effect on the probability of molting, supporting the full model (2) as the best fit for the available data (parameters of model presented in Table 2). Overall, a low explanatory power was found, with only 16.4% of the variation in the data explained by the model. ‘Statistical area’ had most significant contribution to this deviance explained. There was a lower effect on probability of molting for crabs in Area 05 compared with Area 06, Area 07 and Area 08. Smoothing terms for effect of ‘day of year’ showed a significant non-linear effect on the probability of molting in all areas (Table 2, Fig. 4). A significant non-linear relationship was also found between CW and the probability of molting, i.e. for Area 06, Area 07 and Area 08, a positive but decreasing effect on log odds up to approximately 110–115 mm CW, and an increasing negative effect up to approximately 120–130 mm CW (Fig. 5). The probability of molting through the period investigated was predicted for each area by applying the estimated parameters of the model to a crab size of 112 mm CW

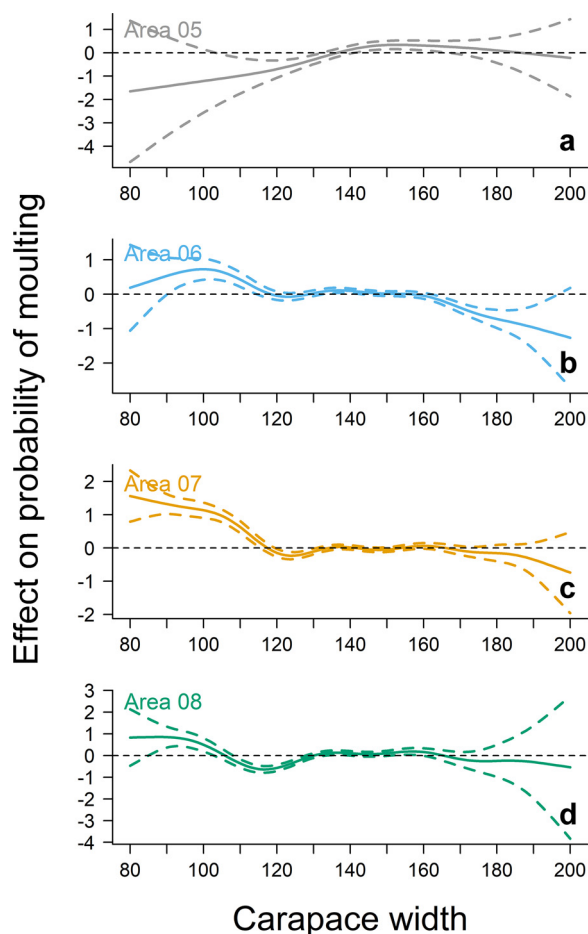
**Table 2**  
Parameters of GAM model – Probability of molting as a function of *statistical area (Area)* and non-linear effects of *day of year (Doy)* and *Carapace width (CW)*.

Parametric coefficients				
Parameter	Estimate	SE	Z	p
Area05	-5.1340	0.8493	-6.046	$1.49 \times 10^{-09}$
Area06	2.7286	0.8438	3.234	0.00122
Area07	3.6003	0.8437	4.267	$1.98 \times 10^{-05}$
Area08	4.8741	0.8456	5.764	$8.22 \times 10^{-09}$
Smoothing terms				
Parameter	edf	Chi.sq.	p	
s(Doy:Area5)	5.563	82.62	$2.56 \times 10^{-15}$	
s(Doy:Area6)	8.420	1029.91	$< 2 \times 10^{-16}$	
s(Doy:Area7)	5.259	814.62	$< 2 \times 10^{-16}$	
s(Doy:Area8)	6.074	679.02	$< 2 \times 10^{-16}$	
s(CW:Area5)	3.004	17.12	0.0019	
s(CW:Area6)	7.260	80.11	$< 2 \times 10^{-16}$	
s(CW:Area7)	8.026	176.25	$< 2 \times 10^{-16}$	
s(CW:Area8)	7.156	95.65	$< 2 \times 10^{-16}$	

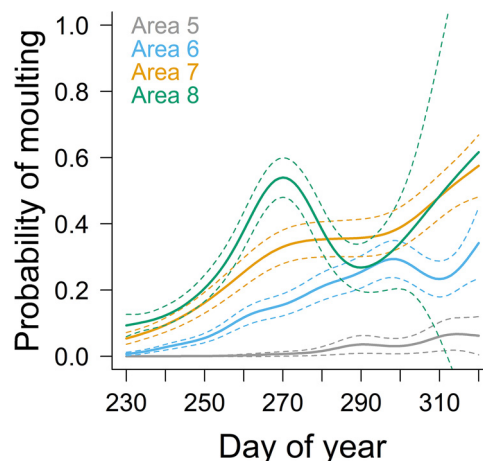
R<sup>2</sup> adj: 0.161; n = 47581; Deviance explained: 16.4%.



**Fig. 4.** Estimated smoothers by Generalized Additive Modelling for the effect of “day of year” on the probability of female *C. pagurus* molting in each of the statistical areas Area 05 (a), Area 06 (b), Area 07 (c) and Area 08 (d). The y-axis denotes the relative effect of the predictor on the probability of molting. Y-values ( $\pm$  95% confidence interval, dashed lines) of zero indicate no effect, values greater than zero indicate a positive effect, while values lower than zero indicate a negative effect on probability of molting. Estimated degrees of freedom for each smoother is presented in Table 2.



**Fig. 5.** Estimated smoother by Generalized Additive Modelling for the effect of carapace width (CW) on the probability of female *C. pagurus* molting in each of the statistical areas Area 05 (a), Area 06 (b), Area 07 (c) and Area 08 (d). The y-axis denotes the effect of the predictor on the probability of molting. Y-values ( $\pm$  95% confidence interval, dashed lines) of zero indicate no effect, values greater than zero indicate a positive effect while values lower than zero indicate a negative effect on probability of molting. Estimated degrees of freedom for smoother is presented in Table 2.



**Fig. 6.** Probability of molting during the period mid-August to mid-November, predicted from model (2) for a female *Cancer pagurus* at 112 mm CW (approx. size at maturity) in Area 08 (green line), Area 07 (orange line), Area 06 (blue line) and Area 05 (gray line). Dashed lines denote estimated 95% confidence intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(approximate to estimated size at 50% maturity, Fig. 6). A clear peak in probability of molting around the end of September (day 270) was identified for Area 08. A clear rise in the probability of molting could also be observed in the other areas, with an earlier and more pronounced rise in probability for Area 06 and Area 07 compared with Area 05. In Area 05, the probability that a crab of 112 mm CW would moult within the investigated period was less than 0.1.

## 4. Discussion

### 4.1. Size at maturity

Fishing pressure may affect marine species at population level, e.g. through changing life history parameters such as size at maturity (Anderson et al., 2008; Sharpe and Hendry, 2009). In the fishery for *C. pagurus* in Norway, more than 70,000 t of crabs have been harvested between 2003 and 2015. Close to 40% of this biomass have been fished in Area 07 where annual landings have been around two thousand tonnes (The Directorate of Fisheries, [www.fiskeridir.no](http://www.fiskeridir.no)). When comparing the investigations on size at physiological maturity conducted in 2003 with the results from the same areas in 2014 (Fig. 3b), a slightly lower  $CW_{50}$  was found for Area 07 and Area 05 in the recent investigations. Although it is possible that this is due to random variation between sampling periods, it does warrant more frequent investigations in the future to determine if these differences could be related to a fishery-induced selection pressure towards maturity at a smaller size.

The data on size at maturity from Area 07 in 2014 (Fig. 3) was included in the study by Haig et al. (2016) where comparisons were made among crabs collected in Ireland, Isle of Man, Scotland, Wales, England and Norway. The  $CW_{50}$  values found for female crabs in that study (overall 105 mm) are similar to both the results obtained by Öndes et al. (2017), as well as data collected in our study, i.e. for both periods and all areas; including Area 05 which is close to the northern border of the distribution for *C. pagurus*. Thus, with variations in  $CW_{50}$  values in the 10 mm range, it is quite evident that the size at which female crabs start to develop gonads is fairly uniform across a large geographical range. Our results on presence of sperm ( $CW_{50}^{\text{behavioural}}$ : 107–112 mm, Fig. S1), are similar to those obtained by Ungfors (2007) on presence of sperm in spermatheca in *C. pagurus* from Swedish waters ( $CW_{50}$  107 mm), and indicate that also behavioural maturity varies little across geography.

The size at onset of physiological maturity found in our study and the studies by Haig et al. (2016) and Öndes et al. (2017) is lower than historical results from Ireland ( $CW_{50}$  ~120 mm, Tully et al., 2006), Scotland ( $CW_{50}$  ~134 mm, Tallack, 2007) and Sweden ( $CW_{50}$  ~132 mm, Ungfors, 2007), and suggest a decline in  $CW_{50}$  during the last decade. However, Haig et al. (2016) concluded that size at maturity was difficult to compare across studies because of differences in methodologies applied, and suggested emphasis on standardizing methods for size at maturity determination to allow for correct comparison in future monitoring. Whether the method used by us and by Haig et al. (2016) is the correct procedure is of course subject for discussion. An obvious uncertainty with the method is that even though the size at onset of (secondary) vitellogenesis is identified (Larsen et al., 2015), it is not guaranteed that crabs will fully develop, fertilize and extrude their eggs. It is a well-known fact that obtaining (enough) berried females for biological investigations is difficult as these rarely enter baited pots (Williamson, 1900). Years of biological investigations with registrations of berried crabs have, however, given some insight, with reports of smallest berried females ranging from 100 to 140 mm CW (see Table 1 in Haig et al., 2016; Öndes et al., 2016). The main season for spawning and incubation of eggs by *C. pagurus* is early winter to early summer, after females migrate to deeper waters (Brown and Bennett, 1980; Edwards, 1979; Tallack, 2007). Obtaining berried females from commercial catches in Norwegian waters is therefore especially challenging as the main season for the fishery is from June to

December, with a small year-round fishery limited for the most part to southern Norway (Woll et al., 2006). Of the more than 150,000 crabs investigated by the Norwegian crab reference fleet, of which close to 96,000 were female, only 455 were registered as berried (data not presented). Of these, the smallest berried crabs found in the four areas in our study were 130 mm (Area 05), 100 mm (Area 06), 105 mm (Area 07), and 120 mm (Area 08). These observations, together with the previous studies, provide evidence for crabs at least being capable of carrying eggs at sizes similar to when gonads start to mature. To confirm this assumption, future studies should aim to collect and track the development of crabs at identified maturing sizes past predicted time of spawning.

Based on our models on size at maturity, the MLS of 130 mm CW in the northern part of Norway will secure that ~97% of the population can reproduce at least once before being targeted in the fishery. The MLS of 110 mm CW in the southern part of Norway (Area 08) on the other hand, is slightly lower than size at 50% maturity for this area (~115 mm, Fig. 3), and will, according to our results, only allow ~25% to spawn once before entering the fishery. Although this MLS was implemented in 1986, there are no indications of changes in catches, as landings in Area 08 have been stable or slightly increasing during the last 15 years (The Directorate of Fisheries, [www.fiskeridir.no](http://www.fiskeridir.no)). The number of landed crabs of sizes close to MLS is probably minimized since most pots used in the fishery have escape gaps (80 mm in diameter) to prevent catch of lobsters; a practice which is also likely to exclude small crabs from the catches. We have also been informed by fishers that one of the main producers of crabs in this region (Area 08) only accepts crabs exceeding 130 mm CW due to production procedures. Thus, there appear to be some operational safeguarding mechanisms against the catch and landing of small crabs. However, monitoring of landings and follow up investigations are recommended, especially if changes in fisheries practices occur.

### 4.2. Probability of molting

The low explanatory power of the full model (Table 2) shows that the variables used ('statistical area', 'day of year' and CW) represent only some aspects of a much more complex process determining molting in *C. pagurus*. Recently moulted crabs are often found on hard substratum in shallow waters where they feed on calcium rich organisms such as mussels and barnacles (Karlsson and Christiansen, 1996, and citations within). The occurrence of soft crabs in the catch therefore likely varies depending of topography and local conditions. In our model, where 'statistical area' is used, such fine-scale spatial differences are not detectable. Further, annual variation in temperatures are probably an important factor governing both the frequency and the timing of molting (Passano, 1960). Much of the unexplained variation in our model is therefore likely connected to inter-annual variation in temporal sampling by the reference fleet, with some years having a potential mismatch between sampling effort and peak molting periods. Thus, it is evident that there are confounding, subtle and interacting factors that remain to be explored further in order to better predict molting in this species. The significance of geographical origin ('statistical area'), 'day of year' and crab size (CW) on the probability of molting should, however, not be neglected, as it improves our understanding of the general biology of *C. pagurus*.

Le Foll (1982) compared seasonal frequencies of *C. pagurus* molting in south Brittany with investigations from other areas in Europe. Whereas molting occurred year-round along the French coast, in the UK and Ireland, a clear peak in molting was detected within the period from early summer to late autumn (Bennett and Brown, 1970; Edwards, 1967; Pearson, 1908; Williamson, 1900). Later studies from both Ireland, Sweden and the Shetland Islands also report summer to autumn as the prominent molting period (Fahy et al., 2004; Tallack, 2007; Ungfors et al., 2007). A clear increase in the frequency of molting during late summer can also be observed in our study. Interestingly, our results also



suggest that the rise in frequency and peak period of molting occur later with increasing latitude (Fig. 6). Since mating in *C. pagurus* occur right after the female's moult (Edwards, 1966), this suggest a slight shift in the crab reproductive cycle from southern to northern Norway. Late molting (and mating) means less time in favourable warm water conditions in order to gain the energy reserves needed to produce gonads. It is thus likely that these late molters would need an additional summer season to complete their reproductive cycle. A more important finding in our study is the overall lower probability of molting in crabs from more northern areas within the period studied. (Table 2, Fig. 6). Similarly, Bennett (1995) in summarizing Bennett (1974b) and Latrouite and Morizur (1988), argued that there was a clear difference in frequency and timing of molting when comparing different geographical areas, suggesting that such differences could be related to different temperatures at these locations. A thermally driven geographical variation in molting frequency is supported by the significant effect temperature has on the molting process in marine crustaceans (see Aiken, 1969; Aiken and Waddy, 1986; Cossins and Bowler, 1987; Green et al., 2014; Kurata, 1962; Passano, 1960; Whiteley and El Haj, 1997). It is therefore likely that the observed geographical difference in molting frequency in our study is related to the different thermal environments the crabs are exposed to. However, as only a limited period of the year was studied, we cannot exclude the possibility of molting occurring at other times of the year in the north, thereby compensating for some of the differences observed. Nevertheless, we do find this unlikely, as the positive relationship between temperature and molting suggests that the ideal time for molting is within the period studied, i.e. when water temperatures are at their annual maximum (Fig. 2). A further delay of moult for females and hence decreasing temperatures, would also be unfavourable in the context of low temperatures having a negative effect on the calcification process post exuviation (Vincent, 1972; Walther et al., 2011). Finally, extended or several molting periods throughout the year are usually associated with warm temperature environments (Conan, 1985). It would therefore be reasonable to assume that crabs in Norway have one seasonal peak period for molting like the one documented for other areas in northern Europe, including Shetland (Tallack, 2007), Sweden (Ungfors et al., 2007) and Scotland (Mason, 1965).

In crustaceans, the generally negative relationship between size and molting frequency (Hartnoll, 1985), has also been demonstrated for *C. pagurus* (Bennett, 1974b, 1979; Edwards, 1965; Hancock and Edwards, 1967), and is concordant also with our results (Fig. 5). From juvenile through adolescence, there is a regular increase in the intermoult period, however the most pronounced reduction in molting frequency is often observed when crabs reach maturity (Hartnoll, 1985). Interestingly, this can also be observed from our results, where there is a change in the effect of CW on the probability of molting close to the size where crabs were found to be mature. An important reason for this is thought to be a change in energetic priorities towards reproduction (Hancock and Edwards, 1967; Hankin et al., 1985; Hartnoll, 1985).

## 5. Concluding remarks and future perspectives

One of the cornerstones in the study of environmental effects on ectotherm life history characteristics is that as temperature decreases, animals tend to reach maturity at larger sizes (Atkinson, 1994). While this is also often the case in several decapod crustaceans (see for instance, Berrill, 1982; Castilho et al., 2007; Hirose et al., 2013; Melville-Smith and de Lestang, 2006; Quinn and Kojis, 1987; Shields, 1991; Watson et al., 2013 (and citations within)), variations exist (Hines, 1989), even within the same species (Annala et al., 1980; Gardner et al., 2006), and the opposite seems to be the case for cold-water crabs (Jewett et al., 1985; Orensanz et al., 2007). The results from our study (Fig. 3) and the recent results by Haig et al. (2016) and Öndes et al. (2017) suggest that *C. pagurus* adds to the exceptions to this rule, as the size at which crabs start vitellogenesis are similar among areas that vary

in thermal conditions. It is well known that mature female crabs during winter venture into deeper waters which have more stable temperatures (Bennett and Brown, 1983; Hunter et al., 2013). Thus, the time of year when geographically separated crabs are exposed to the most prominent differences in environmental conditions is limited to late summer and autumn. In terms of gonad maturity, it is therefore possible that the sub-tidal environmental conditions experienced by female *C. pagurus* across Northern Europe are too similar to influence the adaptive or non-adaptive mechanisms proposed to be responsible for such differences in life history traits (see Angilletta et al., 2004 for a review). Males are less mobile and thus spend more of their time in shallow water (Bennett and Brown, 1983; Karlsson and Christiansen, 1996). This means that male crabs are exposed to larger geographical differences (and fluctuations) in temperature, possibly imposing different constraints on metabolic processes required for transition to maturity. In the study by Haig et al. (2016) where size at maturity was investigated for male crabs from Ireland, Isle of Man, Scotland, Wales and England, no clear trend towards size at maturity being related to geographical origin was found. Unfortunately, maturity data was not compared with male crabs originating from the northern end of its distribution (Norwegian waters). Future studies should therefore identify if environmental conditions affect life history parameters of male *C. pagurus* which potentially experience larger differences of environmental parameters across latitudinal gradients than female conspecifics.

Although we demonstrate that the current MLS in Norway is largely sufficient to prevent catch of undersized (female) crabs, our analyses of molting show that crabs moult less frequently at higher latitudes. This means a higher age at maturity for crabs in the northern areas of the species distribution. In terms of fishery, crabs in the most northerly areas of Norway are therefore more sensitive to exploitation. Fortunately, the fishing pressure on crabs in the north is low, with the participation of fishers very much regulated by catch numbers (i.e. if the fishery yields low income, boats turn to other fisheries.) However, the factories' demand for crabs is increasing and it is recommended that catch rates are monitored closely if the fishery should intensify. This includes strengthening the effort of the reference fleet, and the resolution of the data gathered, in order to gain a better understanding on how molting frequency can be used to determine relative differences in growth, both on spatial and temporal scales.

## Compliance with ethical standards

We, the authors, declare that we have no conflict of interest in these studies. Collection of crabs below MLS, was approved in advance by the Norwegian Directorate of Fisheries and sampled animals killed in accordance with humane practices (Baker, 1955).

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.fishres.2018.03.024>.

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Supplementary material – Behavioral and morphological maturity *C. Pagurus*.

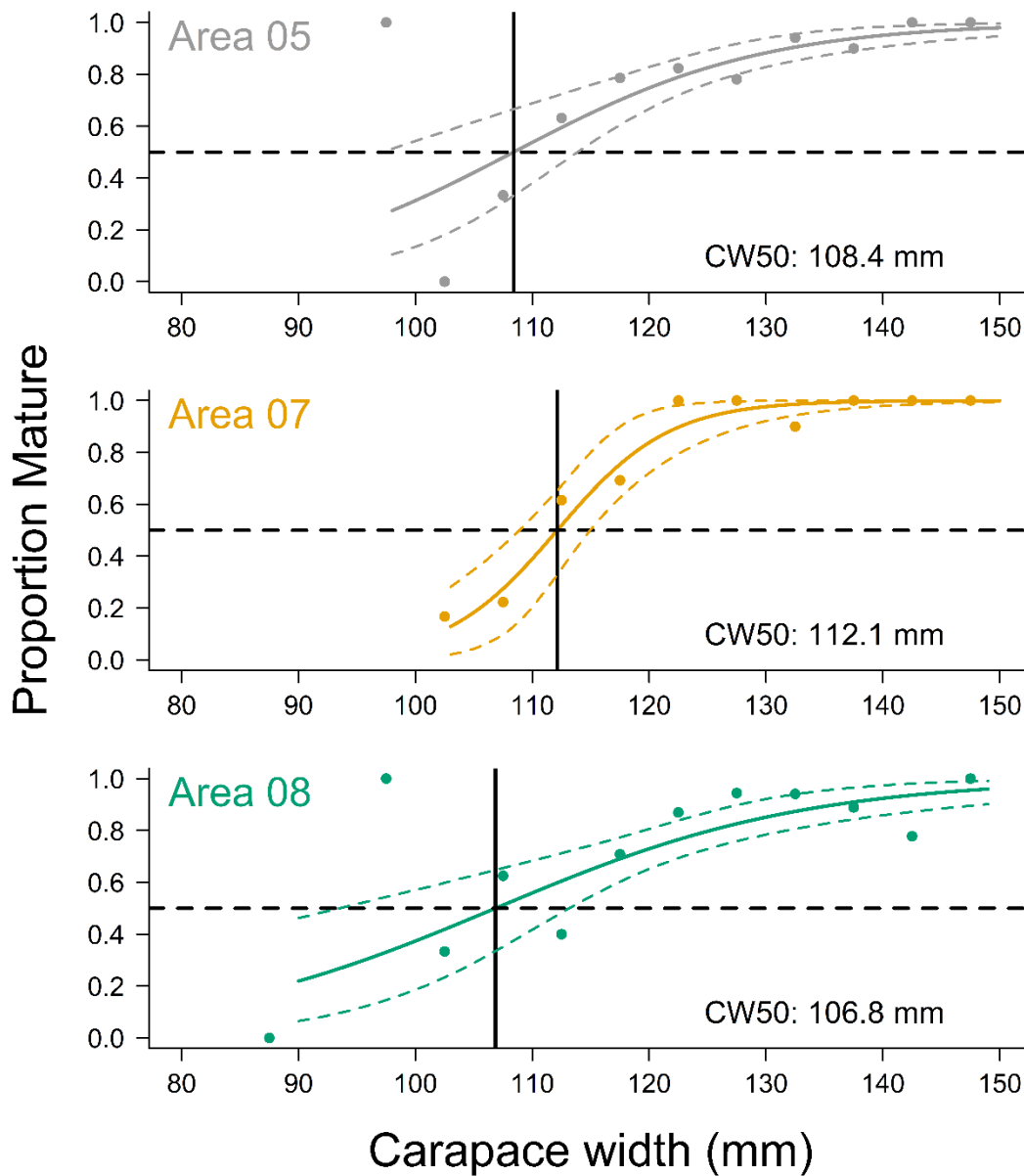
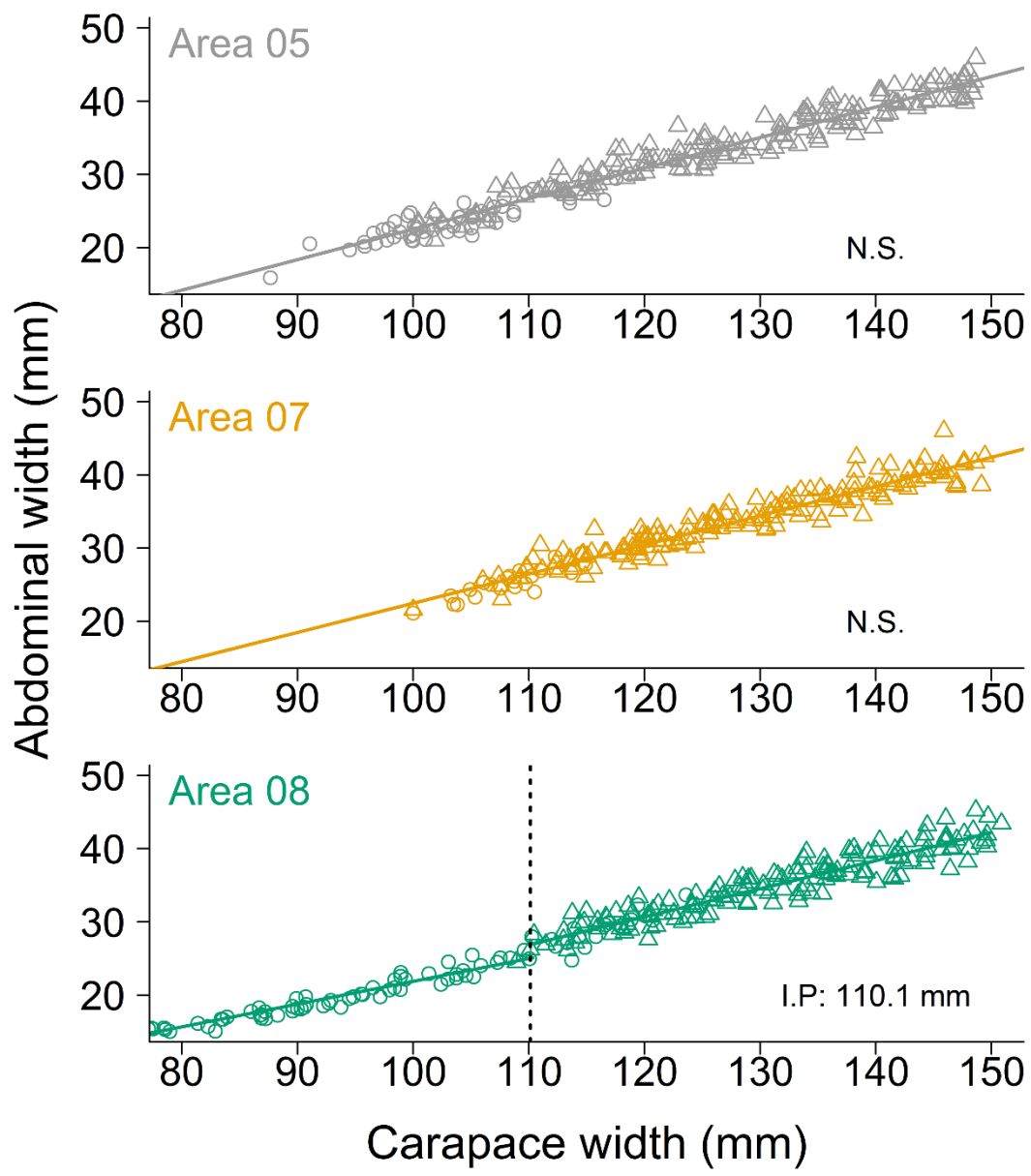


Fig S1 - Maturity ogives for carapace width (CW) of female *Cancer pagurus*. (a) Results based on model using data from 2003 on presence or absence of sperm plugs or sperm in spermatheca. Lines denote predicted probability of behavioral maturity, and black dots indicate observed proportions of crabs with sperm present (mature). Different colors correspond to the geographical areas presented in Fig 1 of the paper.



**Fig S2 – Relationship between carapace width (CW) and abdominal width for female crabs collected in 2014. Different symbols denote if crabs were found to be physiologically mature (rectangles) or immature (circles). Vertical dotted line denotes inflection point (I.P.), giving the lowest residual standard error in a two-segmented piecewise model. N.S. (non-significant) suggest that a straight line is a better fit to the data. Different colors correspond to the geographical areas presented in Fig 1 of the paper.**



## PAPER III

*“In winter they both [crayfish and crabs] choose such parts of the shore as are exposed to the heat of the sun, and in summer they withdraw to the shady recesses of deep inlets of the sea.”*

Pliny the Elder. The Natural History. Book IX “The natural history of fishes.” (Translated by John Bostock and Henry Thomas Riley)





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

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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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## 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

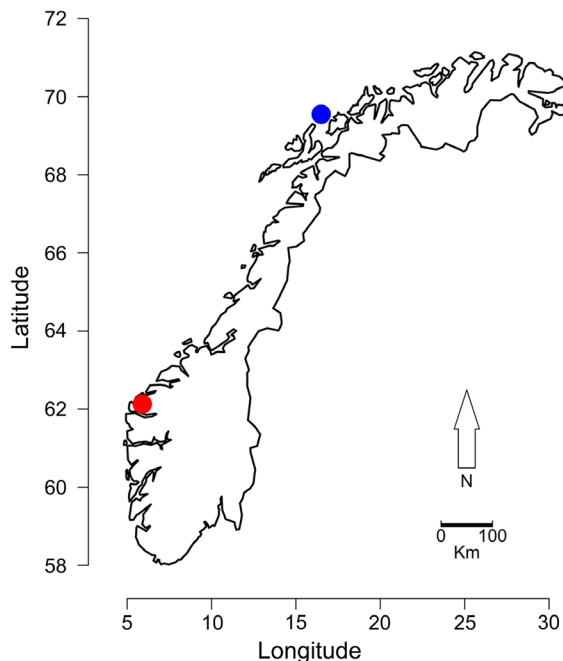


Figure 1. Map of Norway showing origin of edible crab *Cancer pagurus* used in experiments; blue = north and red = south. Details presented in Table 1.

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

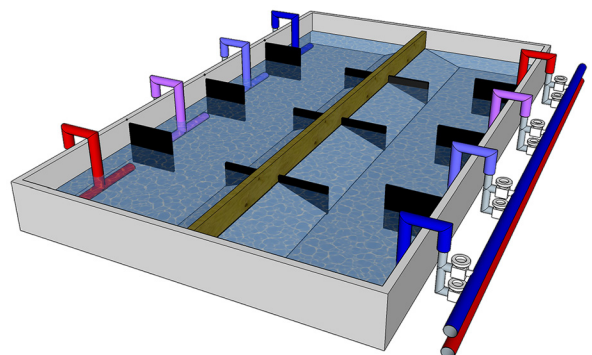


Figure 2. Raceway system with two thermal gradients. Temperature gradients were obtained by mixing cold (blue) and warm (red) water on four inlets along the channel. Ball plug valve at each point and temperature allowed fine tuning of temperature and reversal of the thermal gradient. Flow-meters attached 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.

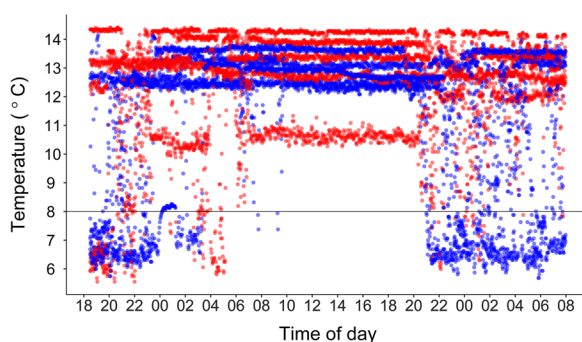


Figure 3. Movement of individual edible crab *Cancer pagurus* in a thermal horizontal gradient. Blue dots show crabs originating from north (n=5) and red dots crabs from south (n=5). Horizontal line denotes acclimation (and introduction) temperature at onset of tests.

towards a lower CTmin 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

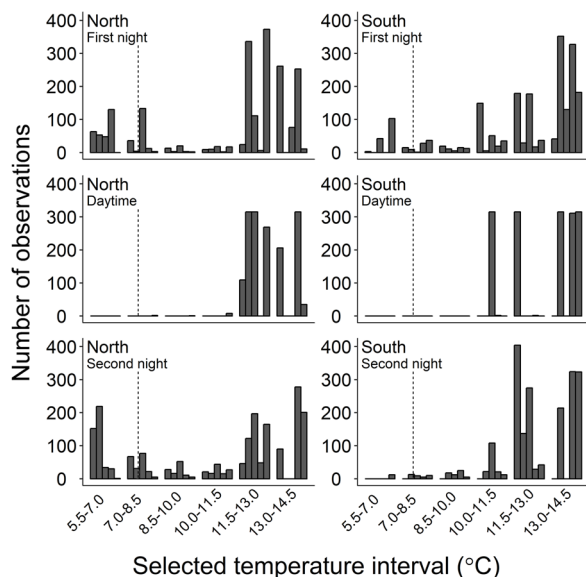


Figure 4. Number of observations at different temperature intervals selected by individual edible crab *Cancer pagurus* during the ~40 hour period within the thermal gradient. One observation equals 2 minutes. Figure shows observations for first night (top), daytime (middle) and second night (bottom) 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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## PAPER IV

*"They [the fishermen] are of the opinion that there are certain "bodies" of crabs restricted to deep water..."*

H. C. Willimason (1900) Contributions to the life-history of the edible crab (*Cancer pagurus*, Linn.)

