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

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A B S T R A C T

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_{50}) did not differ between areas and was consistent with historical investigations, i.e. overall CW_{50}: 112.3 mm, and CW_{50} 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_{50}) 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_{50} mean values varied between 97 and 117 mm, but with no obvious spatial structure associated with this variation. Also, a CW_{50} 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.

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 intermoult 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 intermoult 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).
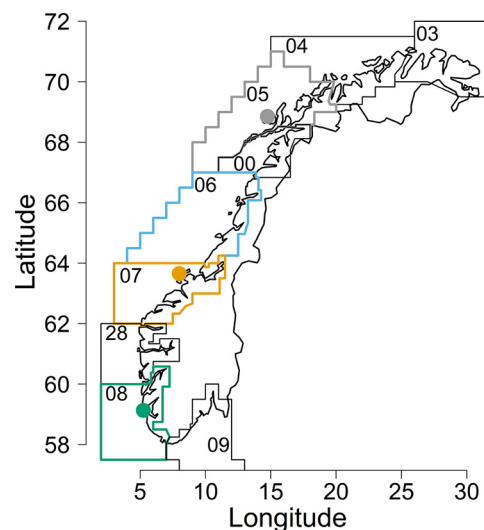

Fig. 1. Map of Norway showing the nine coastal statistical areas used by the Directorate of Fisheries. Areas investigated in our study outlined in grey (Area 05), blue (Area 06), orange (Area 07) and green (Area 08). Dots within each area show locations from where crabs were sampled for size at maturity studies. Polygons for statistical areas represent WMS files obtained from the Directorate of Fisheries online maps services (www.fdir.no/kart). (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 = *Imma*ture, 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 district 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.
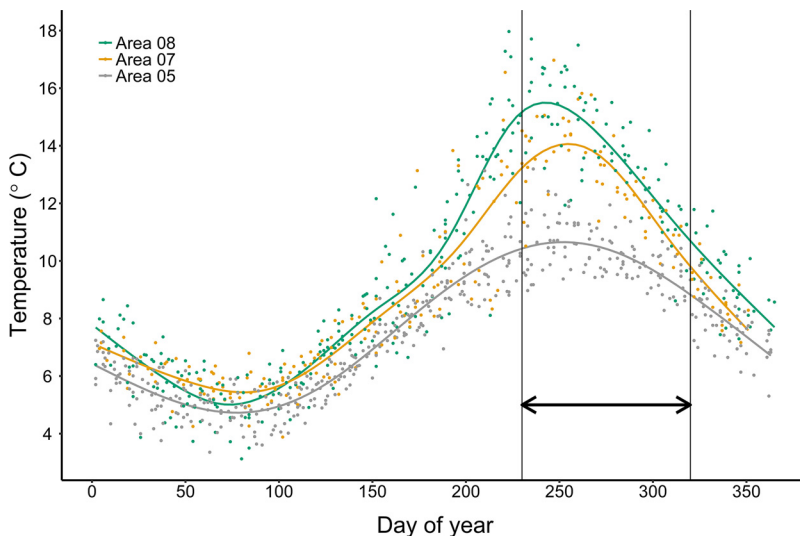
Fig. 2. Temperature throughout the year at 20 m depth in areas Area 05 (grey), Area 07 (orange) and Area 08 (green). (Data on temperature from Area 06 was not available). Curves are mean values from measurements conducted weekly to biweekly from 2001 to 2015 (dots). Data were obtained from the Institute of Marine Research database (www.imr.no), 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

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

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):

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

where y_i is AW of individual i, and the β 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

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

calculating the probability that crab *j* in year *i* is soft. Index *k* denotes separate smoothers for 'statistical area', and a_i 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$_{50}$ between 108 and 117 mm) (Fig. 3b).
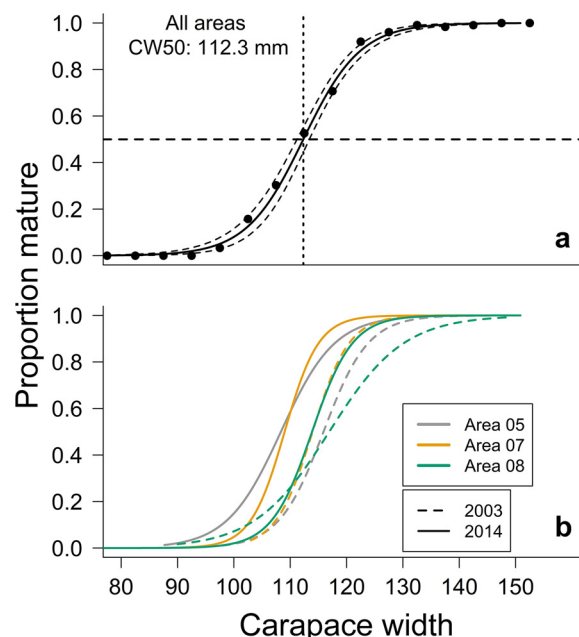

Fig. 3. Maturity ogives for carapace width (CW) of female *Cancer pagurus*. (a) Results based on model using data from all areas and years (2003 and 2014) combined. Lines denote predicted probability of physiological maturity, and black dots indicate observed proportions of mature crabs. (b) Separate 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$_{50\text{behavioural}}$) 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$_{50\text{behavioural}}$ 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	1.49×10^{-09}
Area06	2.7286	0.8438	3.234	0.00122
Area07	3.6003	0.8437	4.267	1.98×10^{-05}
Area08	4.8741	0.8456	5.764	8.22×10^{-09}

Smoothing terms			
Parameter	edf	Chi.sq.	p
s(Doy:Area5)	5.563	82.62	2.56×10^{-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	$< 2 \times 10^{-16}$

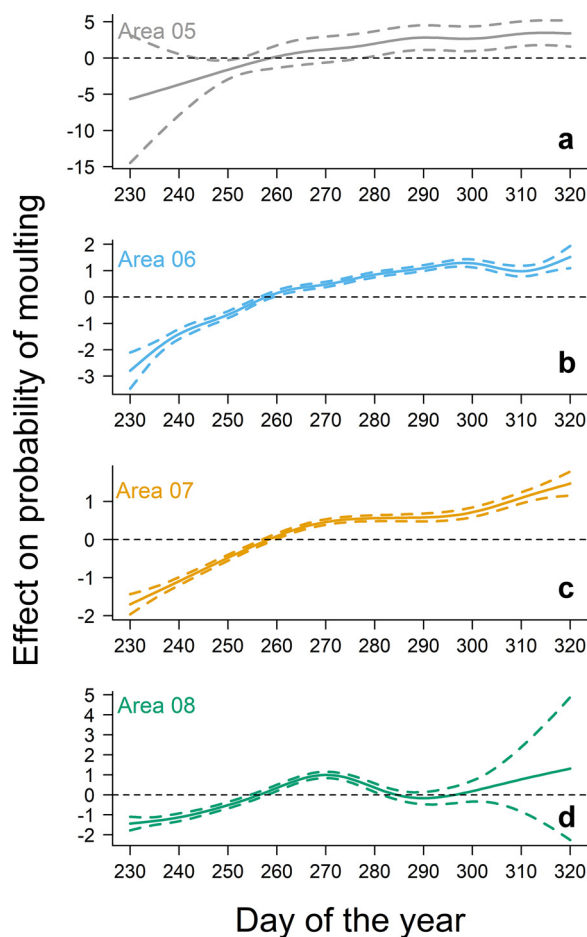R^2 adj: 0.161; n = 47581; Deviance explained: 16.4%.

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 (± 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.
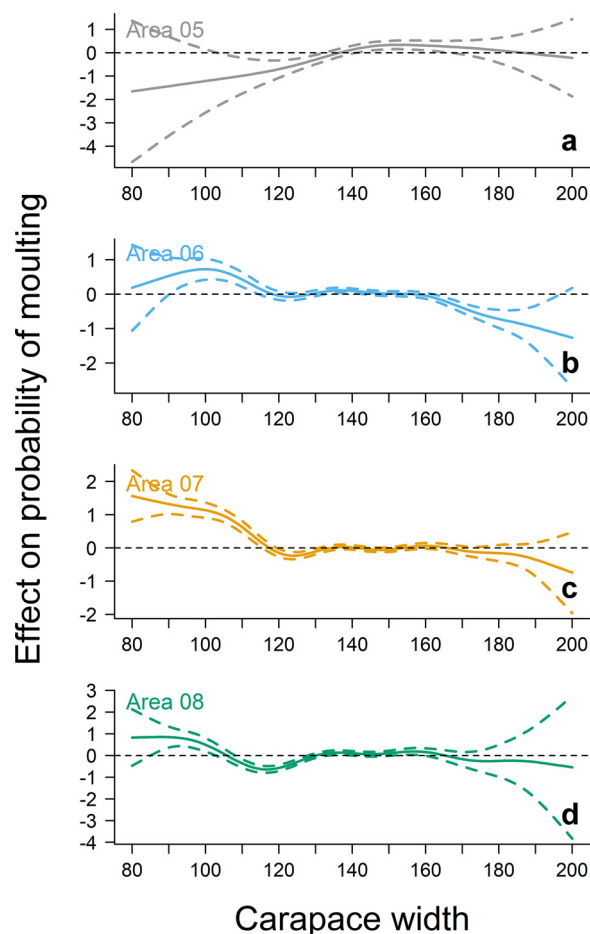

Fig. 5. Estimated smoother by Generalized Additive Modelling for the effect of carapace width (CW) on the probability of female *C. pagurus* molting in each of the statistical areas Area 05 (a), Area 06 (b), Area 07 (c) and Area 08 (d). The y-axis denotes the effect of the predictor on the probability of molting. Y-vales (± 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.
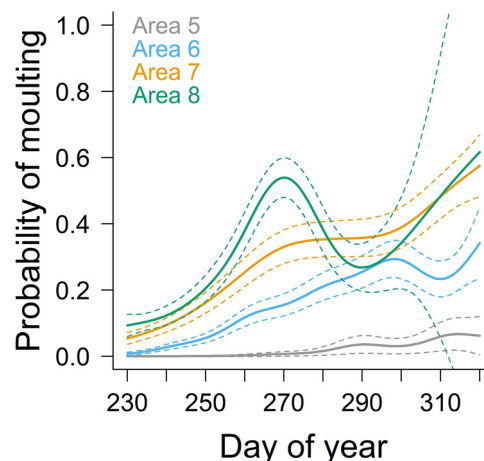

Fig. 6. Probability of molting during the period mid-August to mid-November, predicted from model (2) for a female *Cancer pagurus* at 112 mm CW (approx. size at maturity) in Area 08 (green line), Area 07 (orange line), Area 06 (blue line) and Area 05 (gray line). Dashed lines denote estimated 95% confidence 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). 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 ($CW_{50behavioural}$: 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 (Larssen 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). 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 occurance 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 differencs 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).

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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