



# A first fecundity study of the female snow crab *Chionoecetes opilio* Fabricius, 1788 (Decapoda: Brachyura: Oregoniidae) of the newly established population in the Barents Sea

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## ABSTRACT

The snow crab *Chionoecetes opilio* Fabricius, 1788 is a newly established species in the Barents Sea. Since the first individuals were recorded in 1996, the population has increased and a fishery was initiated in 2012. Mature female snow crab caught in the central Barents Sea were investigated with regards to fecundity. Ovigerous females ( $N = 185$ ) ranged from 48 to 100 mm carapace width (CW). Fecundity was 15,000–184,000 eggs per female with 100% clutch fullness, and was positively related to body size (fecundity =  $0.233 * CW^{2.944}$ ) consistent with relationships described for other snow crab populations. Eight females had less than 100% clutch fullness, two of which had only 10% clutch fullness along with an old shell, indicating senescence. Dry egg weight was on average 0.065 mg and was hardly affected by CW. Females across all sizes invest similarly in individual eggs, and potential size-dependent differences in fitness are more related to the number of eggs produced than to the investment into individual eggs. We conclude that the fecundity-at-size of females is overall comparable to that of other populations, although the presence of large females results in high maximum individual fecundity estimates.

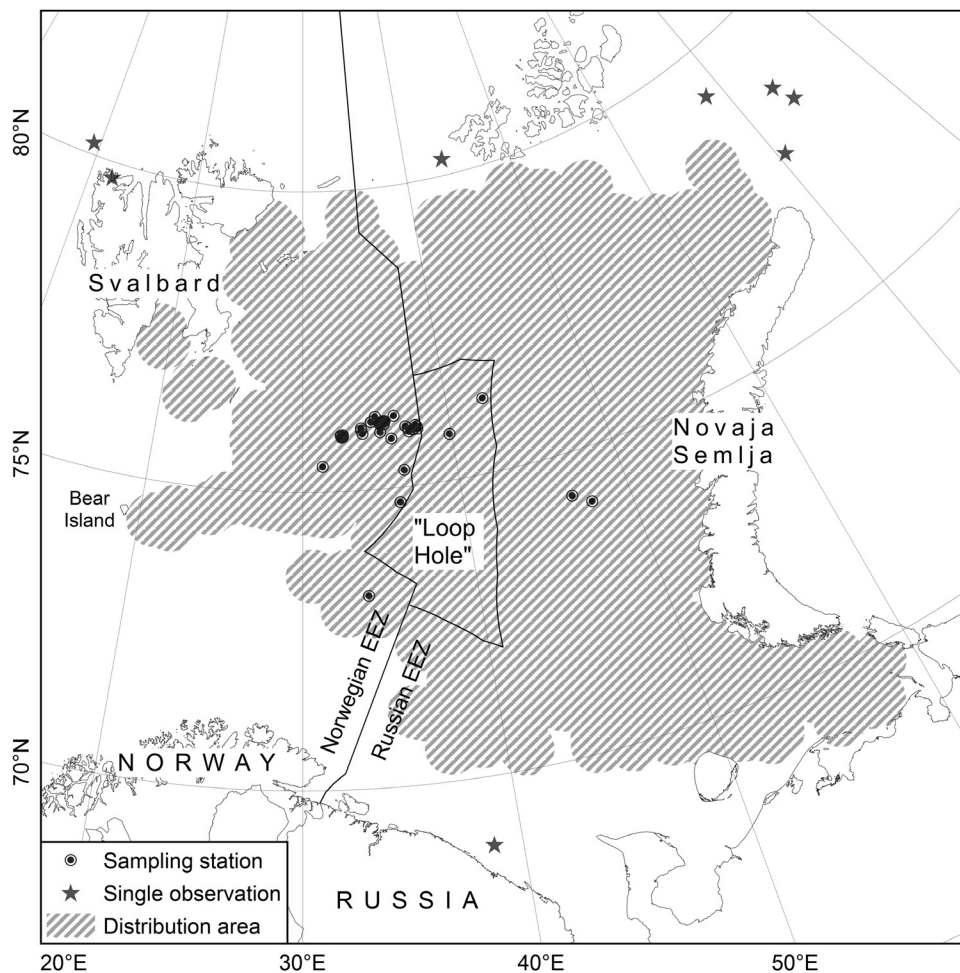
**Key Words:** Arctic Ocean, crab fisheries, life history, non-native species, reproductive potential, size-fecundity relationship

## INTRODUCTION

A female snow crab (*Chionoecetes opilio* Fabricius 1788) was found on the southern slope of Goose Bank in the southeastern Barents Sea in May 1996 (Kuzmin *et al.*, 1999). This was the first record of snow crab in the Barents Sea, drawing attention to the emerging population that since then has grown to inhabit large areas of the Barents Sea. Additional observations of 15 snow crab individuals were made by the end of 1999, and during the last decades a self-reproducing population has established (Alvsvåg *et al.*, 2009). In 2018 snow crab inhabited most areas of the eastern, central, and northwestern Barents Sea (Fig. 1), as well as parts of the Kara Sea (Zimina, 2014). Snow crab have also reached areas around the Svalbard archipelago as observed in 2017 and 2018 (HD, unpublished data). There is no consensus regarding the origin and introduction mechanism of the snow crab to the Barents Sea.

The hypothesis of introduction from the northwestern Atlantic via ballast water was proposed by Kuzmin *et al.* (1999) but genetic analysis shows a closer relationship with the Pacific populations, indicating natural expansion of the species distribution (Dahle *et al.*, 2014; Dahle *et al.*, unpublished data).

The Barents Sea is a shelf sea bordering the Arctic Ocean, Kara Sea, and Atlantic Ocean. The bathymetry is characterised by several banks separated by deeper troughs and basins. The average depth is 220 m, with depths ranging from 20 m at the Spitsbergen Bank to 500 m in the Bear Island Trough (Ozhigin *et al.*, 2011). The water masses in the southwest are dominated by the inflowing North Atlantic Current and bottom temperatures around 5 °C, as opposed to the Arctic-influenced areas in the north and east where bottom temperatures tend to be around 0 °C and can reach below –1 °C in deeper areas (Ozhigin *et al.*, 2011; Jørgensen *et al.*, 2015). Bottom temperature is one essential parameter for management



**Figure 1.** The study area in the Barents Sea, with circles marking stations where mature female *Chionoectes opilio* were caught. The shaded area indicates the 2018 distribution of snow crab; the stars mark single observations of snow crab.

of the snow crab, as it both affects the distribution (Comeau *et al.*, 1998; Ernst *et al.*, 2005) and the length of the female reproductive cycle (Moriyasu & Lanteigne, 1998; Webb *et al.*, 2007).

Snow crab stocks support valuable and regulated commercial fisheries within its native distribution range in the north and northwest Atlantic and the Bering Sea, (Burmeister & Sainte-Marie, 2010; Webb *et al.*, 2016; FAO, 2018). In the Barents Sea, the fishery for snow crab commenced in 2012 and a first quota was set in Norwegian waters to 4000 t in 2017 (Kaiser *et al.*, 2018), and total landings from the Barents Sea in 2017 and 2018 were above 10,000 tones. As the fishery management of this stock is under development the need for knowledge on the biology and production potential of the population is needed to support management decisions.

There are no currently available studies describing the reproductive cycle or spawning areas and season of the Barents Sea populations of the snow crab. Our study therefore largely relies on work conducted in other populations for interpretation of the results. Female snow crab reach morphological and functional maturity at a terminal molt. The size at terminal molt is positively related to temperature (Somerton, 1981; Orensanz *et al.*, 2007; Burmeister & Sainte-Marie, 2010; Dawe *et al.* 2012; Hartmoll, 2015). Reproducing females are termed primiparous during the first reproductive cycle, and multiparous during subsequent cycles (Sainte-Marie *et al.*, 2008). The reproductive cycle can be annual or biennial depending on temperature, with females residing in water  $< 1^{\circ}\text{C}$  brooding their eggs for approximately two years, whereas females residing in warmer water complete the cycle in

approximately one year (Moriyasu & Lanteigne, 1998; Kuhn & Choi, 2011). Individual female fecundity measured as the number of eggs attached to the pleopods is highly related to size (Sainte-Marie, 1993; Comeau *et al.*, 1999; Kolts *et al.*, 2015) and differs between the reproductive stages and shell condition, being highest for a given size in young multiparous females (Webb *et al.*, 2016).

Our research focused on female fecundity of the newly established snow crab population in the Barents Sea. Individual fecundity is directly connected to overall reproductive potential of the population. We present estimates of individual female fecundity in relation to body size as well as other characteristics of reproductive parameters from the newly established population. Our findings are compared to those from the native distribution range of the species.

## MATERIAL AND METHODS

Ovigerous female snow crab were collected during multiple research cruises and two pot deployments by commercial fishing vessels between 2012 and 2017 (Table 1). During the research cruises, we used a Campelen 1800 shrimp trawl and an Alfredo cod trawl. In some cases, a “crab bag” was attached to the trawl’s ground gear to increase the catchability of crab buried in the sediment. On one research cruise a line of 30 small-meshed pots was deployed. The commercial fishing vessels used commercial-size conical pots (bottom diameter of approximately 130 cm) with a top-entrance. The centre of the fishing area was set at the capture

location (Fig. 1) given that the location was not provided for each female snow crab sampled.

A total of 185 ovigerous females was collected at 53 stations in the central Barents Sea, of which 50 were trawl stations and three were pot stations (Fig. 1; Table 1). The depth at the stations was 162–347 m. From each sampled individual, the following parameters were recorded: carapace width (CW), shell condition (only for crab captured in November 2016 and later), clutch fullness, and colour of the egg mass. The females collected at research cruises were measured and characterised at sea prior to freezing, whereas those originating from the commercial pot deployments were frozen directly and measured and characterised on land after thawing.

CW was measured to the nearest millimetre using digital calipers at the widest part of the carapace. The shell condition was determined by visual inspection of the individual with categorization according to [Jadamec et al. \(1999\)](#) and [Sainte-Marie \(1993\)](#), and was based on colour, epi-growth, and wear of the shell and dactyls (Table 2). Females molt to maturity during their terminal molt shortly before their first mating, spawning for the first time (primiparous) in a soft-shell condition ([Watson, 1970](#)). In contrast, females spawning for the second or subsequent times (multiparous) have hard, worn shells. Shell condition was therefore used to differentiate between the reproductive stages of the female: mature females with shell condition 1, 2 were defined as primiparous and those with shell condition 3–5 were defined as multiparous ([Jadamec et al., 1999](#); [Webb et al., 2016](#)).

Clutch fullness was assessed by visual determination ([Jadamec et al., 1999](#)), and was quantified as percentage fullness: 100% clutch fullness meaning that the egg mass completely filled the abdomen, and 0% meaning no eggs or merely traces of egg were detected. The estimates were then rounded to the nearest 10%. The egg clutch was assigned one of two categories according to the colour of the egg mass. The colour gives an indication of the developmental stage of the eggs, and especially the appearance of eye spots in developing eggs darkens the colour of the

egg considerably from a clear orange to brown and consecutively a dark purple or black colour ([Moriyasu & Lanteigne, 1998](#); [Comeau et al., 1999](#)). Orange eggs were thus termed “early stages” and brown or dark brown/black eggs “late stages.”

Fecundity analysis was done in the laboratory following methods by [Hjelset et al. \(2012\)](#). The egg mass was thawed at room temperature before the eggs were detached from the pleopods and three subsamples of approximately 200 eggs each were then removed and counted under a stereomicroscope. The counting was done with the help of a transparent counting chamber using transmitted light. The eggs had to be gently pulled apart to be counted, and some eggs broke during this operation. Eggshell fragments were not counted, but embryos (with two eye spots) were. Both the main egg clutch and the three subsamples were oven-dried for at least 24 h at 60 °C until constant weight was achieved, and cooled before dry weight was recorded to the nearest 0.001 g for the main clutch and to the nearest 0.0001 g for the subsamples. Each subsample from the egg clutch provided one estimate of average individual egg weight (weight of subsample/egg count) and the overall estimate per female was the mean of the three subsample estimates. The fecundity (number of eggs) of every individual was then estimated by dividing total brood dry weight by the overall estimate of individual egg weight. Assuming an allometric relationship between individual female size (CW) and number of eggs produced, fecundity (F) was described as  $F = bCW^a$ , where  $a$  is a normalizing constant and  $b$  is the allometric scaling coefficient. For analytical simplicity, this was modelled as a linear relationship on  $\log_{10}$  transformed data using the linear model procedure (lm) in R. Egg mortality during the brooding period was measured as the difference in size-specific fecundity between females with early and late developmental stages of the broods. This measurement assumes that egg mortality would lead to a lower fecundity at a given size for females with late stage eggs relative to those with early stage eggs ([Comeau et al., 1999](#)). Multiple linear regressions were used to test slope and intercepts for equality by analysis of variance and

**Table 1.** Data collection scheme. Cruises were conducted by the Norwegian Institute of Marine Research (IMR) and UiT the Arctic University of Norway. Some individuals were also collected by commercial fishing vessels. Commercial stations (\*) included several pot deployments per vessel.

Cruise	Year	Month	Gear	Number of stations with mature females	Number of mature females (lower clutch fullness)
IMR	2012	September	Campelen 1800	2	2
IMR	2014	November	Campelen 1800	8	20
IMR	2015	February	Campelen 1800	2	6
IMR	2016	February	Campelen 1800	20	64 (4)
UiT	2016	November	Alfredo3, small-meshed pot	5	7
IMR	2017	September	Campelen 1800	5	11 (1)
UiT	2017	March	Campelen 1800	9	18
Commercial vessels	2017	March	Conical pot	2(*)	57 (3)

**Table 2.** Shell condition staging criteria based on [Jadamec et al. \(1999\)](#) and [Sainte-Marie \(1993\)](#).

Stage	Description
1	New, clean, and soft shell. Otherwise similar to stage 2.
2	New but hard shell. No epi-growth. Evenly distributed color of carapace, white to pink dorsal side, both sides without brown spots. Iridescent chelae and sometimes carapace. Pointed dactyls. No grasping marks.
3	Hard shell with possibly some epifaunal growth. Cream colored dorsal side with some spots/marks. Grasping marks on pereopods visible in females (from mating, most evident on ventral side of posterior pereopods). Slightly worn and rounded dactyls.
4	Hard shell with some epifauna, mostly on carapace. Dark cream to yellow/brown dorsal side with brown and black spots and marks. Distinctly worn dactyls (rounded and often black tip).
5	Brown to black color. Soft shell from decay. Epi-growth and marks. Rounded dactyls.

covariance. Only females with 100% fullness were included in the analysis.

Results suggested a difference in mean body size between females with early and late stage eggs and this was tested using a Welch two-sample t-test. All statistical analyses were carried out using R software (R Core Team, 2017). The significance level used for all statistical analyses was  $\alpha = 0.05$ .

## RESULTS

The carapace width of the 185 ovigerous females collected ranged from 48 to 100 mm, with a mean of 75 mm (SD = 10.4) and a median of 73 mm (Fig. 2). Most individuals (125) were caught by trawl, 57 individuals were caught in commercial pots, and three were caught with small-meshed sampling post. Females caught in commercial pots were generally larger than those caught with trawl. All but eight of the females had 100% clutch fullness. Of those eight, four females had eggs in early stages and four in late stages. Two females had only 10% clutch fullness. These two were also the only ones in shell condition 4 (old shell) and visual inspection showed they had deformed ovaries that were clumpy and partially black, indicating senescence (Kon *et al.*, 2010). Degenerated eggs were not found in this study.

Estimated fecundity ranged from 15,000 to 184,000 eggs in females with 100% clutch fullness. Fecundity increased significantly with increasing CW ( $P < 0.001$ ), following the allometric relationship  $F = 0.2331 * CW^{2.9437}$  (Fig. 3). Given this relationship, the expected fecundity of an average-size crab of 75 mm CW would be about 77,000 eggs. A large proportion of the variation in fecundity was explained by body size ( $r^2 = 0.75$ ).

Mean egg dry weight was 0.065 mg (SD = 0.009 mg). CW explained very little of the variation in egg weight ( $r^2 = 0.059$ ), although there was a slight but significant increase of egg weight with increasing CW ( $P = 0.001$ ) (Fig. 4). After removing two visual outliers, there was no difference in mean egg weight between females with early and late stage broods.

No evidence of egg mortality during the incubation period was found, as females with late-stage broods did not have lower fecundity-at-size compared to females with early stage broods, although these data might be biased by mean CW being significantly smaller in females with early than later stage broods ( $P < 0.001$ ). Females with early and late stage broods were observed simultaneously in November, February, and March, but not in August, when all broods sampled were in early stages of egg development. In November, 88 % of the females had early stage

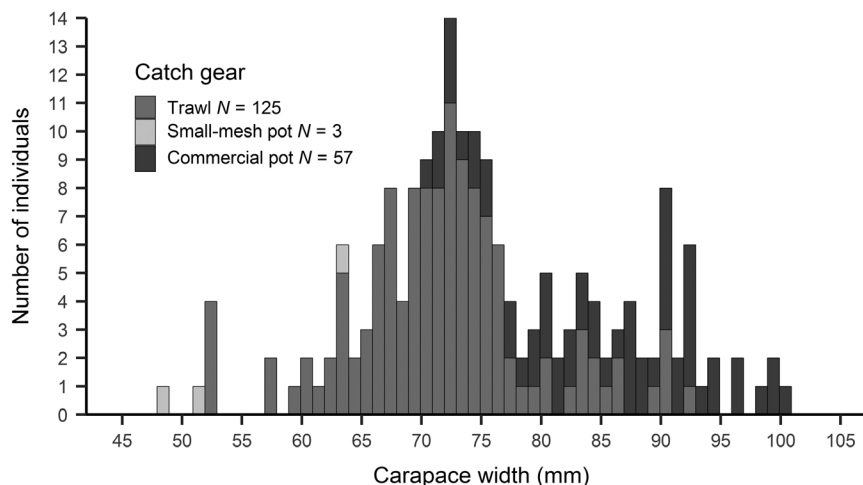
broods, but in February and March combined females with early stage broods constituted only 45% of the sample.

Most of the females that were staged to shell condition 3 or higher were caught by the commercial pots and thus had been frozen prior to staging. The shells of crabs that had been frozen appeared more worn than those of unfrozen crabs; in particular, they were darker in colour, and worn dactyls and other damage appeared to be more pronounced. As freezing had such an impact on shell condition and the females that were staged prior to freezing were few, the data on shell condition was deemed too biased for further analysis.

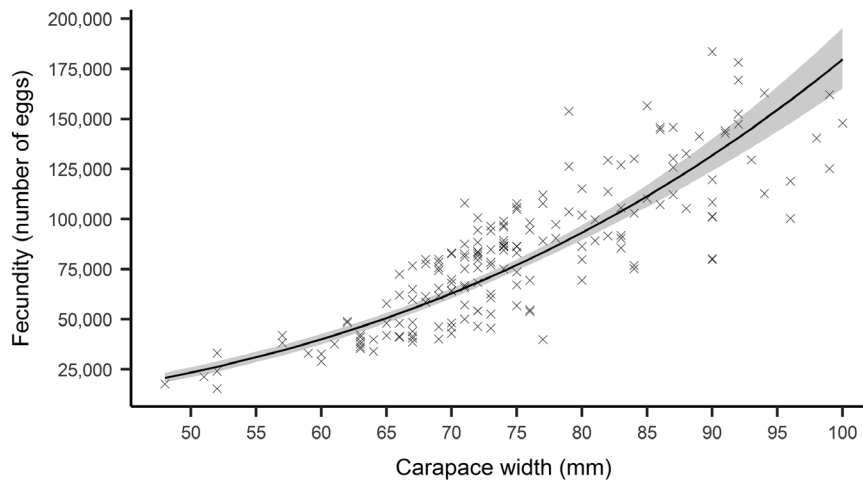
## DISCUSSION

This study provides the first fecundity analysis of female snow crab in the Barents Sea since the species was first observed in the sea in May 1996 (Kuzmin *et al.*, 1999). A positive correlation between body size and fecundity has been demonstrated in many studies on decapods (Somers, 1991). Fecundity in female Barents Sea snow crab is well described by the allometric function and is consistent with reports from other areas for the same species (Fig. 5) (Jewett, 1981; Sainte-Marie, 1993; Comeau *et al.*, 1999; Burmeister, 2002; Kolts *et al.*, 2015). The estimated fecundity of a mean-size female Barents Sea snow crab of 75 mm CW is approximately 77,000 eggs. The corresponding estimates for females differing one SD from the mean size (65 and 85 mm CW) are 51,000 and 112,000 eggs, respectively. Assuming that the number of reproductive events does not vary with size, an 85 mm CW female would on average produce more than twice as many eggs during her life span than a female 65 mm CW.

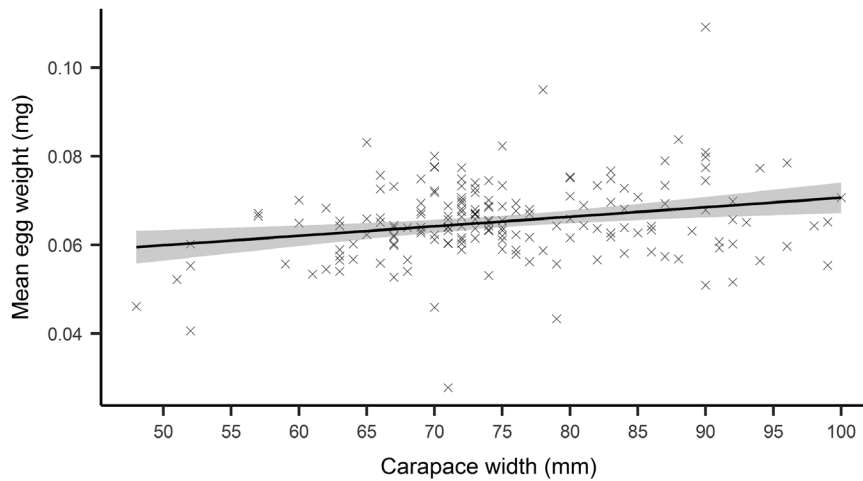
Our data on size-structured fecundity should therefore be taken into consideration in management. This is particularly important if further studies in the Barents Sea confirm the suspected size-specific spatial distribution of mature females related to ontogenetic migrations that is found globally (Mullowney *et al.*, 2018). Knowledge on size-specific distribution could be used to identify potential refuge areas (no-trawl zones or no-fisheries zones) for highly reproductive size-groups to ensure sustainable, high recruitment. Recognizing potential bias in the size distribution in our study resulting from combined collections by different gears, future sampling should expand consistent collections of mature females to allow more detailed partitioning of size-dependent contributions to stock reproductive potential. The low variation in egg weight between females and the weak correlation with maternal size indicate that females across all sizes invest similarly in



**Figure 2.** Size distribution of ovigerous *Chionoecetes opilio* in this study, caught by trawl, small-meshed pots, and commercial pots in the central Barents Sea between November 2012 and November 2017. The shaded area corresponds to the gear used to catch females.



**Figure 3.** Relationship between fecundity (F) and carapace width (CW) in female *Chionoecetes opilio* in the Barents Sea. Black crosses represent the observed values from females with 100% clutch fullness. The black line represents the linear regression with the equation  $\log(F) = -0.63 + 2.94 \cdot \log(CW)$ . The shaded area indicates the 95% confidence interval.

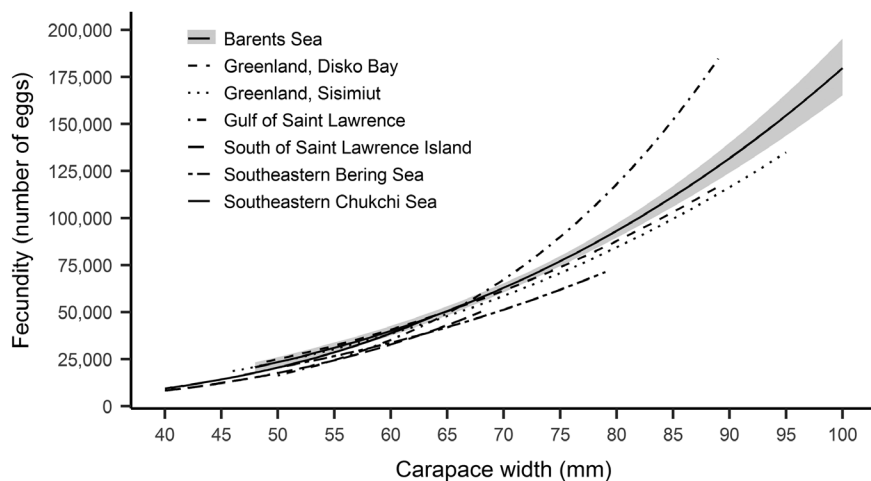


**Figure 4.** Relationship between individual egg dry weight and carapace width in the sampled *Chionoecetes opilio*. Black crosses represent the observed values from females with 100% clutch fullness. The black line represents the linear regression, with the 95% confidence interval (shaded area);  $r^2 = 0.059$ .

individual eggs, and that potential size-dependent differences in fitness are more related to the number of eggs produced than to the investment into individual eggs. As embryos from late-stage eggs could be counted also after breaking whereas early stage eggs could not, there was a concern that the fecundity of females with early-stage broods could be underestimated. This was contradicted as there was no difference in mean egg weight between females with early and late stage broods.

The size-fecundity relationship in the Barents Sea is generally similar to that from other areas, although with some differences. It most closely resembles that reported from the populations in Greenland, although the fecundity estimates from Greenland (Burmeister, 2002) are higher at small sizes, and lower at larger sizes than in the Barents Sea. The maximum fecundity estimates in the Barents Sea and the Gulf of St. Lawrence are higher than those from other areas. This is in part a consequence of the large maximum size of the mature females found in the Barents Sea, whereas in the Gulf of St. Lawrence the slope of the regression is steeper, resulting in higher fecundity for females larger than about 65 mm CW in this area. Fecundity in the Barents Sea is higher than in the Chukchi Sea for the comparable sizes of females, and females in the Barents Sea reach a larger maximum size and thus a much higher maximum fecundity.

Size at terminal molt of snow crab is related to temperature (Burmeister & Sainte-Marie, 2010; Dawe *et al.* 2012). Burmeister & Sainte-Marie (2010) argued that it is the temperature *per se*, and not possible confounding factors such as food availability, density, or season length that is causing the size variation. Temperature seems to be affecting the number of instars individuals go through before reaching terminal molt rather than the relative molt increment (Hines, 1989; Burmeister & Sainte-Marie, 2010). The maximum size of females we report in this study (100 mm CW) indicate a habitat that enables individuals to grow large, presumably through relatively high near bottom temperatures. A female as small as 48 mm CW was nevertheless also found in the same general area. Our sampling was focused on the central Barents Sea in an area where the cold Arctic water meets inflowing Atlantic water, resulting in a gradient in bottom temperature (Ozhigin *et al.*, 2011; Jørgensen *et al.*, 2015), and snow crab in this area might possibly have experienced a range of temperatures through their lifespan. Variation in bottom or near-bottom seasonal temperatures is, to our knowledge, not well studied. Studying potential spatial structure of size at terminal molt throughout the Barents Sea should be prioritized in future studies given the known spatial variation in near-bottom temperature within the distribution area of the populations.



**Figure 5.** Fecundity estimates of female *Chionoecetes opilio* from this and other studies. Black line represents the relationship in the Barents Sea population as described in this study, data from Greenland from Burmeister (2002), and other data summarised by Kolts *et al.*, (2015). The equations for the relationships are as follows: Barents Sea,  $F = 0.2331 \cdot CW^{2.9437}$ ; Disco Bay Greenland,  $F = 0.7244 \cdot CW^{2.6712}$  (Burmeister, 2002); Sisimiut Greenland,  $F = 0.5395 \cdot CW^{2.7295}$  (Burmeister, 2002); Gulf of St. Lawrence,  $F = 0.0012 \cdot CW^{4.20}$  (Kolts *et al.*, 2015); Southeastern Bering Sea,  $F = 0.49 \cdot CW^{2.72}$  (Jewett, 1981; Kolts *et al.*, 2015); southeastern Chukchi Sea,  $F = 0.025 \cdot CW^{3.48}$  (Jewett, 1981; Kolts *et al.*, 2015); Bering Sea south of St. Lawrence Island,  $F = 0.029 \cdot CW^{3.4}$  (Kolts *et al.*, 2015).

The large maximum sizes of female snow crab in the Barents Sea and their related high individual fecundity are in agreement with studies on other non-native species. These shows that species may be larger and more fecund in non-native than in the native ranges (Parker *et al.*, 2013). Examples of this pattern include the gastropod *Crepidula formicata* (Linnaeus, 1758) that had a higher fecundity at size in its non-native range (Pechenik *et al.*, 2017), and the red king crab (*Paralithodes camtschaticus* Tilesius, 1815) grew larger in the Barents Sea than in its native range (Hjelset *et al.*, 2012).

As expected, most of the females examined (177 of 185) had 100% clutch fullness. Two females, however, had only 10% clutch fullness and had old shells, deformed ovaries, and were likely senescent. Sainte-Marie (1993), Ernst *et al.* (2005) and Webb *et al.* (2016) also report multiparous females with relatively small clutches and also argue that this low fecundity could be caused by senescence. Most decapods do not experience physical senescence as they continue to molt throughout their lives, but the snow crab and other members of Oregoniidae and Portunidae experience senescence as a consequence of terminal molt (Vogt, 2012; Hartnoll, 2015; McLay, 2015). The remaining six females with lower clutch fullness (20 to 80%) from this study had seemingly healthy shells and ovaries, and are more likely to have lost parts of the clutch, either during brooding, or during handling or transport. In nature, females might lose parts of the clutch during brooding because of predation or failure in fertilization or development (Elner & Beninger, 1992). An estimated egg mortality during the brooding period of up to 20% was reported by Comeau *et al.* (1999), whereas other authors did not find significant egg mortality (Sainte-Marie, 1993; Webb *et al.*, 2016). No evidence of egg mortality was found in this study.

Difference in female fecundity according to reproductive stage has been reported in snow crab in the Gulf of St. Lawrence (Sainte-Marie, 1993) and the Eastern Bering Sea (Webb *et al.*, 2016), who also report lower fecundity related to senescence. Lower fecundity in primiparous females might be explained by the smaller size of the body cavity prior to the maturity molt which restrict the size of the ovaries and thus the number of eggs produced (Sainte-Marie, 1993). Additionally, a substantial amount of energy is directed by the pubescent females towards molting, and this energy is then not available for ovary growth (Sainte-Marie, 1993). We found that freezing and thawing of the crab prior to

staging the shell makes this procedure difficult and crab that have been frozen should not be compared to unfrozen crab with regard to shell condition. Independent of freezing, other authors (Burmeister, 2002; Bluhm *et al.*, 2015) reported difficulties with assigning females to the primiparous and multiparous categories based on external appearance of the shell, pointing out that the criteria commonly used might not be applicable in all areas. Staging the shell just prior to, or during the mating season, might be difficult as primiparous females that have yet not hatched their eggs will have shells that are nearly one, or even two year, old depending on the length of the brooding period. The potential difference in fecundity between primiparous and multiparous females should nevertheless be considered in management to ensure suitable estimates of the population's reproductive potential with variation in cohort strength and recruitment to the reproductive part of the population.

The simultaneous presence of females with both early and late developmental egg stages might be an indicator of a two-year reproductive cycle in the Barents Sea. Alternatively, it may indicate that sampling was carried out during the mating season, which has been reported to differ between the reproductive stages with primiparous mating occurring earlier in the season (Sainte-Marie, 1993; Moriyasu *et al.*, 1987). A two-year incubation period of the brood between mating events is the most commonly recognized cycle for snow crab populations across its distribution (Sainte-Marie, 1993; Moriyasu & Lanteigne, 1998; Comeau *et al.*, 1999; Burmeister, 2002), but also a one-year cycle has been reported (Burmeister, 2002; Kuhn & Choi, 2011), and has repeatedly been observed in rearing experiments (Moriyasu & Lanteigne, 1998; Webb *et al.*, 2007). Our observations of females with broods in late developmental stages from November, February, and March is an indication that females prepare for the hatching process and multiparous mating during this period. At least two features of the snow crab reproduction make our results difficult to interpret, namely the possible variation in the duration of brooding between annual and biennial cycles and the differing mating period between primiparous and multiparous females. The females that were sampled in February and March with early stage eggs might be primiparous females that had just spawned, or primiparous or multiparous females on a biennial reproductive cycle that have diapausing broods. Females with late-stage broods from the same period might be primiparous or multiparous females having brooded their eggs

for one or two years, preparing to hatch their eggs and start or restart multiparous mating. An understanding of the occurrence of annual *versus* biennial cycles is essential to ensure appropriate estimates of the population's reproductive potential. We recommend studies that may resolve temporal and spatial patterns of egg and ovary developmental stages to further investigate the questions related to breeding cycle. We recognize the limitations in using merely egg colour as a measure of embryonic development and advise future studies to focus on more precise staging of embryonic development and extend sampling throughout the season. The limitations extend to the use of visual shell condition index to distinguish the reproductive stages. Besides the difficulties discussed above, the co-occurrence of an annual and biennial reproductive cycle further complicates the picture. A primiparous female in the second year of a biennial cycle may be indistinguishable in terms of shell condition to a multiparous female in her second annual cycle.

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