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Snow crab (*Chionoecetes opilio*), a new food item for North-east Arctic cod (*Gadus morhua*) in the Barents Sea

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The snow crab (*Chionoecetes opilio*) is a newly established species in the Barents Sea, increasing in both distribution and abundance in recent years. We explore the potential importance of North-east Arctic cod (*Gadus morhua*) predation in structuring the snow crab population expansion in the Barents Sea, through an analysis of cod stomach content data from 2003 to 2018. Spatio-temporal patterns of snow crab within cod diet are assessed across years, between seasons, as well as ontogenetic trends, including predator–prey size relationships. Snow crab represents a new prey item for cod and in recent years the most dominant demersal crustacean species in cod diet. The proportion of snow crab within cod diet increases over time. Primarily 60–110 cm cod prey upon snow crab, mainly during the summer/autumn season. Our results support the idea that the snow crab is still expanding, shifting distribution north and westwards. Cod has the potential to regulate the snow crab population but is unlikely to be in direct competition with the fishery in the Barents Sea. This work suggests that cod can be used as biological sampling tools together with other monitoring programmes to elucidate how new species may affect predator–prey and food-web dynamics within an ecosystem context.

Keywords: diet, ecosystem impact, fisheries, non-native species, predator–prey dynamics, snow crab

Introduction

The native habitat of the snow crab (*Chionoecetes opilio*, Fabricius 1788) is located in the Northern Pacific and adjacent waters of the Chukchi, Eastern Siberian, Laptev, and Beaufort seas, as well as in the North Western Atlantic including waters of western Greenland (Pavlov and Sundet, 2011). However, in recent decades, the snow crab has also been found in the Barents and Kara Seas (Kuzmin *et al.*, 1999; Zimina, 2014), first observed at Goose Bank in the southeastern Barents Sea in 1996 (Kuzmin *et al.*, 1999). The snow crab population has since increased rapidly in both distribution and abundance, maintaining established habitat in areas in the eastern, central, and northwest Barents Sea (Sokolov *et al.*, 2016). The establishment of an abundant, large mega-decapod [defined as a decapod crustacean with a carapace width (CW) >10 cm; Boudreau and Worm, 2012] to the benthic community is expected to have a significant impact on the entire ecosystem, through both trophic interaction and competition (Boudreau and Worm, 2012). As the Barents Sea hosts several valuable fishery resources, e.g. Atlantic cod (*Gadus morhua*), capelin (*Mallotus villosus*), haddock (*Melanogrammus aeglefinus*), red king crab (*Paralithodes camtschaticus*), and deep-sea shrimp (*Pandalus borealis*), an important management concern is how the snow crab expansion may impact existing fisheries, in particular the world's largest cod stock, North-east Arctic cod (hereafter referred to as cod).

Snow crab are largely omnivore feeders, feeding on benthic prey items in their native area/Pacific waters (Tarverdieva, 2001; Squires and Dawe, 2003; Chuchukalo, 2006; Chuchukalo *et al.*, 2011a, b; Kolts *et al.*, 2013), finding food primarily on and within the sea floor. They consume four main prey taxa: polychaetes, decapod crustaceans (crabs, amphipods), echinoderms (mainly ophiuroids), and molluscs (bivalves, gastropods) (Squires and Dawe, 2003; Kolts *et al.*, 2013). Stomach content analyses from the Barents Sea confirm this (Pavlov, 2007; Manushin *et al.*, 2016; Nosova, 2019), suggesting that the snow crab through feeding and burrowing activities may exert a significant impact on the native benthic food web. This may affect other species competing for the same food items. The snow crab also represents a new food item for several benthic feeding species (Benzik and Dolgov, 2016; Dolgov and Benzik, 2016), a pathway to convert inaccessible biomass within the sediment to crab meat available for consumption (Garvey and Chipps, 2012).

In 2019, the Barents Sea snow crab is still considered to be in an expanding phase, expanding its range through adult migration and larval drift (Alvsvåg *et al.*, 2009; Agnalt *et al.*, 2011; Zimina, 2014 Sokolov *et al.*, 2016), and as such, in 2012 commercial harvesting by Norwegian vessels commenced (Norges Råfisklag, 2019). Landings increased rapidly up to 18 000 tonnes in 2015 (Norges Råfisklag, 2019) with vessels from Norway, the EU and Russia participating in the fishery. In 2017 and 2018, landings decreased to 11 000 and 12 500 tonnes, respectively, with only Norwegian and Russian vessels participating in the current fishery. In 2018, the first-hand value of the Norwegian snow crab fishery was ≈158 million NOK (Norges Råfisklag, 2019). Thus, in addition to questions about possible ecosystem effects, and consequences for existing fisheries (e.g. for cod) following the snow crab appearance, fisheries management also needs to consider how to manage an emerging snow crab fishery, as well as address its future scope.

The potential of the snow crab fishery and the overall ecosystem impacts of the snow crab introduction depend on (but is not limited to) its spatio-temporal distribution and population density, as well as predator–prey dynamics. This is partly determined by the availability of suitable snow crab habitat, where for the stenothermic snow crab, habitat space is largely defined by temperature (Slizkin, 1982; Foyle *et al.*, 1989; Mullowney *et al.*, 2014; Ouellet and Sainte-Marie, 2018). Predator–prey dynamics and predation are also important when assessing the impact of the snow crab appearance in the Barents Sea. Gadoid fish, for example are a documented predator of snow crab in Canadian waters (Marcello *et al.*, 2012), while >20 fish species including Pacific cod (*Gadus macrocephalus*) are predators on snow crab in Russian Far East seas (Tripolskaya and Andrievskaya, 1967; Tokranov, 2000; Poltev, 2001; Chuchukalo, 2006; Vdovin *et al.*, 2015). It has been suggested that predation, e.g. by Atlantic cod, may have a top-down effect on both juvenile and adult snow crab (Boudreau *et al.*, 2011; Dolgov and Benzik, 2016), regulating snow crab population size and causing large changes in year-class strength (Dawe and Colbourne, 2002; Marcello *et al.*, 2012). In the Pacific, Pacific cod predation is suggested to be central in determining the distribution of snow crab (Poltev, 2001; Orensanz *et al.*, 2004; Chuchukalo, 2006).

The snow crab distribution in the Barents Sea now co-occurs with cod, with ever increasing spatio-temporal overlap. Cod as a top predator has the potential to control the distribution and further expansion of this species in other seas (e.g. Burgos *et al.*, 2013). In this study, we explore the potential importance of cod predation in structuring snow crab distribution and abundance in the Barents Sea. Through a unique long-term (35 years), high-resolution stomach content database, we quantify how the snow crab establishment is reflected in the diet of the cod, and at what sizes snow crab are the most vulnerable to predation. Finally, we discuss how these findings may impact future snow crab stock assessment and management. A preliminary description of snow crab importance in cod diet in the Barents Sea until 2014 was made by Benzik and Dolgov (2016), as well as in the diet of cod and other fishes (Dolgov and Benzik, 2016). Since then, snow crab occurrence in cod stomachs and the snow crab fishery have increased considerably, and thus, it is timely to provide an updated and extended analysis.

Material and methods

Study area

Within this study we focus on The Barents Sea, an Arcto-boreal sea of ≈1.6 million km^{-2} north of Norway and Northwestern Russia (Figure 1). It is the deepest of the shelf seas surrounding the Arctic Ocean, the geographical extent of which is defined by several boundaries. In the east, the Barents Sea is distinguished from the Kara Sea by a line from Franz Josef Land archipelago to the northern tip of Novaya Zemlya archipelago (Figure 1) (Ozhigin *et al.*, 2011). The coasts of Norway and Russia define the southern boundary. While the shelf break to the north of Svalbard and Franz Josef Land archipelagos defines the northern boundary, and the continental break west of Norway and west Spitsbergen defines the western boundary (Figure 1) (Ozhigin *et al.*, 2011).

Stomach-content data

The joint Norwegian–Russian stomach-content database originates from a study on the diet and food consumption of Barents Sea fish, with cod as the main target species, initiated in the mid-1980s as a joint endeavour between Institute of Marine Research (IMR) and Knipovich Polar Research Institute of Marine Fisheries and Oceanography (PINRO) (since 2019—Polar branch of Russian Federal Research Institute of Fisheries and Oceanography) (Mehl, 1986, Mehl and Yaragina, 1992, Dolgov *et al.*, 2007). This encompassed methods for sampling protocol, stomach-content analysis, and the storing, processing, and exchange of data (Mehl and Yaragina, 1992). An average of 10 884 stomachs were analysed each year (Supplementary Table S1). For each individual sampled, the cod length (size range 5–160 cm) and weight, together with total prey weight (wet weight, g), species (identified to the lowest possible taxonomic level), and prey size composition, were recorded (Supplementary Table S2). Where available size was recorded for individual prey items (Mehl and Yaragina, 1992). Cod length was measured as total length rounded down to the nearest cm. For snow crab prey found in cod stomachs, CW was measured and rounded down to

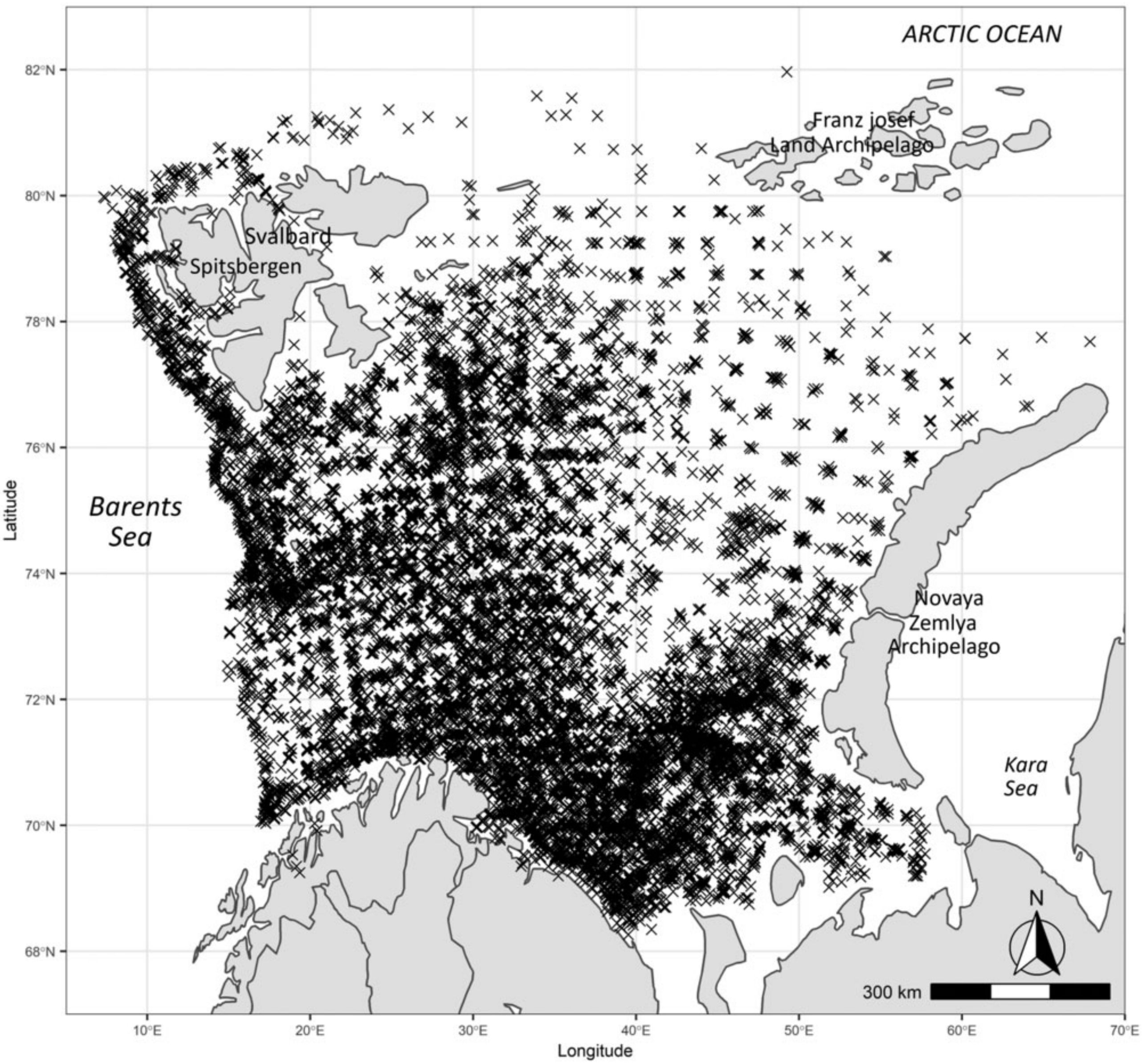

Figure 1. Study area and location of cod stomach samples taken from 2003 to 2018.

the nearest 0.5 or 1 mm depending on crab size. Where possible snow crab fragments were also identified and the degree of digestion recorded (see Mehl and Yaragina, 1992 for details). Length information was not available for all snow crab prey due to the degree of digestion within the cod stomachs, in which case, prey weight was recorded as a sum for the total amount of snow crab found within each individual cod stomach. Data are available for nearly all months each year, in the period 1984–2018; however, a large proportion of stomach samples are concentrated on two seasons: winter from the Norwegian and joint Norwegian–Russian demersal fish survey (January–March) and summer/autumn from various Norwegian, Russian, and joint Norwegian–Russian surveys from July to October (Supplementary Table S3; sample size information). Data were sampled across the Barents Sea (Figure 1), predominantly from these scientific surveys, whereby trawl stations are randomly spread within each stratum of the investigated area (Eriksen *et al.*, 2020). Some additional data from commercial vessels are also included within the dataset (for a comprehensive description of methodology, see Mehl and Yaragina, 1992; Dolgov *et al.*, 2007).

Data delimitation and processing

Cod stomachs sampled used in the analysis are from areas north of 70°N and east of 18°E, all other areas were excluded from our analyses, as snow crab is not found in these regions (Figure 1). The data in the stomach database were thoroughly quality controlled and outliers with inconsistencies between cod size and snow crab weight/prey size were removed. The stomach database ranges from 1984 to date; however, we focus on data from 2003 onwards as snow crab were not found in cod stomachs prior to this year (Dolgov and Benzik, 2016; Holt *et al.*, 2019) (Figure 1).

Snow crab was not present in cod stomachs in 2007; thus, this year is not included in the analyses. Ecosystem survey data for 2018 are included in the stomach content database used for this paper; however, the spatial coverage in the southeastern Barents Sea, where a major proportion of snow crab are found within cod stomachs, was poor for this year. Only 217 trawl stations were sampled in 2018, in comparison to 339 trawl stations sampled in 2017 (Van der Meeren and Prozorkevich, 2019). Thus, the amount of snow crab present in cod diet is likely underrepresented in this year as a result.

Data analysis

Spatio-temporal stomach content analyses

The percentage frequency of occurrence of snow crab $FO_i = \frac{n_i}{n} \cdot 100$ was calculated across size classes and survey years, where n_i is the number of stomachs containing snow crab and n is the total number of stomachs in a given sample, i.e. size class or survey year. The percentage of total prey weight of snow crab found in cod stomachs was calculated for each length class $\frac{\sum W_i}{n}$ and subsequently weighted by an index of length-based biomass of cod for each year of study (S); it was calculated as follows, $S = \frac{\sum W_i}{n} \cdot B$, where W_i is the weight of prey i (snow crab), n is the total number of fish in a given sample (length class for each survey year), and B is an index of length-based biomass for each length class in each survey year. The index of length-based biomass likely underestimates the absolute biomass of 110 cm+ cod due to migration at the time of sampling. To illustrate the relative contribution of snow crab in relation to other prey types within the cod diet, all identifiable preys were aggregated and categorized into broader taxonomic groups for analyses (for details, see Holt *et al.*, 2019).

To illustrate the percentage of total prey weight of snow crab found within cod stomachs by season, data were split into winter (January–March) and summer/autumn (July–October) for all study years (2003–2018). To demonstrate the spatial distribution of different size classes of snow crab found in cod stomachs, data were binned according to maturity and growth information for the Barents Sea (Alvsvåg *et al.*, 2009).

The spatial distribution of snow crab within cod stomachs was analysed using five predetermined strata that cover our study area. Strata were defined according to Hvingel *et al.*, (2008), in which main fishing grounds, latitude, and depth, were used to define strata limits. The percentage frequency of occurrence of snow crab within cod stomachs was standardized by area according to each stratum.

Predator–prey size relationship

Least squares linear regression (OLS) was used to analyse the overall relationship between mean snow crab length and cod length using the model $\mathrm{LC}_i = a + b\mathrm{CWS}_i$ where LC is the length of cod i (cm), a is the intercept, b is the slope, and CWS is the mean CW of snow crab (mm) found in the stomach of cod i. Quantile regression was then used to examine the upper and lower bounds of the distribution, i.e. how minimum and maximum snow crab lengths scale with cod predator length. Lower and upper bounds were represented by 0.05 and 0.95 quantiles. All data manipulation and analyses were conducted in R V3.3.3 (R Core Team, 2017), using the “stats”, and “quantreg” (Koenker, 2017) packages for OLS and quantile regression, respectively.

Cod consumption

In Norway (IMR), cod consumption at the stock level was calculated annually for various prey species/groups using the method described by Bogstad and Mehl (1997) and further explained in the annual ICES Arctic Fisheries Working Group reports [e.g. Table 1.3 as presented in ICES (2018)]. These calculations were based on cod stomach content data, cod abundance estimates from annual ICES stock assessments, together with a gastric evacuation rate model (Dos Santos and Jobling, 1995). Calculations are made separately for cod age groups 1–11+, the first and second half of the year and for three areas of the Barents Sea (east, west, and north), hereafter referred to as the Norwegian method. In Russia (PINRO) consumption, calculations were conducted in a similar way, but for four quarters for each year across the whole Barents Sea area, hereafter referred to as the Russian method (Dolgov *et al.*, 2007). Snow crab has been split as a separate prey species to perform these calculations in recent years (ICES, 2019), whereby it is assumed to have the same digestion rate as deep-sea shrimp. In this paper, we will refer to results based only on composition of stomach content as “diet”, while results from the calculations of consumption described in this paragraph are referred to as “consumption”.

Results

Temporal shifts in the contribution of snow crab to the cod diet

Prior to 2003 snow crab was not present in the cod diet; however, in recent years, it has steadily increased from 0.03% in 2003 to 6.5% in 2018 (Figure 2).

Very little snow crab was present (<5%, prey weight) within small and medium size classes of cod diet (0–60 cm) in all study years (Figures 3 and 4). From 2003 to 2008, snow crab was only found in the diet of 60–90cm cod and no snow crab was preyed upon by cod in 2007 for all size classes (Figures 3 and 4). From 2009 onwards, larger cod individuals (>90 cm) preyed upon snow crab and in more recent years, 2014–2018 the amount of snow crab in large cod (>110 cm) stomachs increased (Figure 3a). The proportion of snow crab in cod diet by length

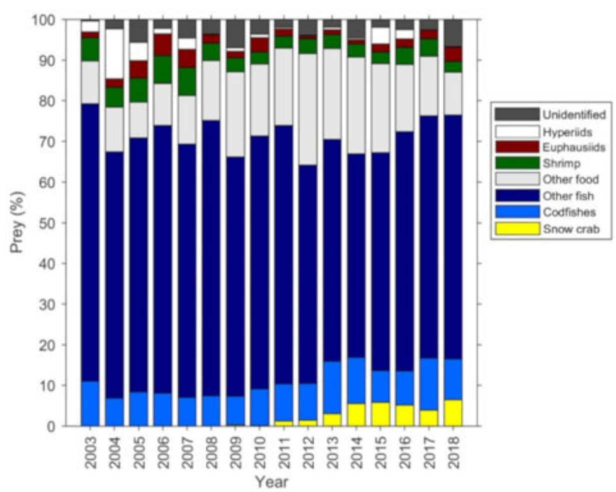

Figure 2. Temporal distribution of percentage (weight, g) of total prey species/species groups found in cod stomachs (all size classes) in 2003–2018 (see Holt *et al.*, 2019 for prey group details).

group was fairly stable from 2013 onwards, although a clear increase in 2018 was seen for cod 100–120cm length (Figure 3). The percentage of snow crab [weight (g), of total stomach contents consisting of snow crab] weighted by length-based biomass illustrates that most of the snow crab is found in stomachs of cod between 60 and 100 cm across all study years (Figure 3). The proportion of the snow crab in cod diet derived from large cod

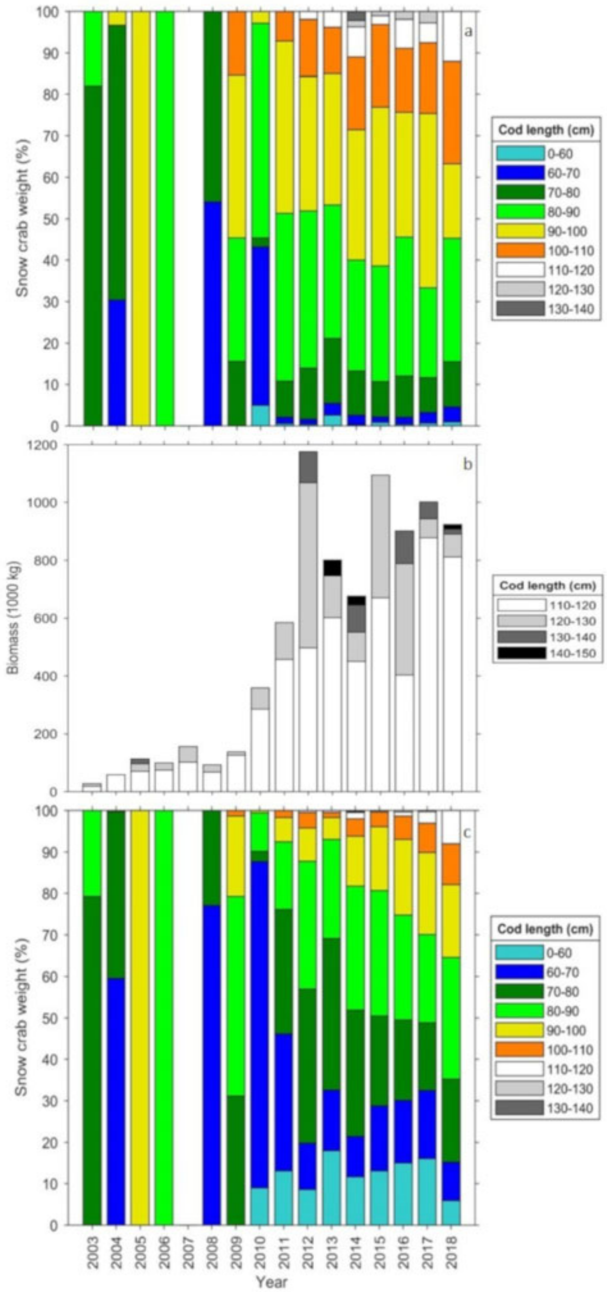

Figure 3. Estimates of snow crab in Barents Sea cod stomachs by cod length group 2003–2018: (a) percentage weight of total stomach content consisting of snow crab; (b) index of biomass of large cod (110 cm+); (c) and percentage weight of total stomach content consisting of snow crab weighted by the biomass of cod in the respective length groups. In (a) and (c), cod length classes 0–60 cm were combined due to low amounts of snow crab preyed upon by these size classes.

(>100 cm) has increased since 2009 (Figure 3) from 1.36 to 17.89% in 2018 [weight (g), of total stomach contents consisting of snow crab] (Figures 3 and 4).

Seasonal variation of snow crab present in cod diet

Long-term seasonal differences in the amount (prey weight; g) of snow crab present within cod stomachs were found between the winter and summer/autumn season (Figure 5). A higher proportion of snow crab was found in the cod diet in the summer/autumn season (July–September) compared with winter months (January–March). In 2016, for example 98.3% of the total snow crab weight (for all size classes of cod) was found in cod stomachs during summer/autumn compared with 0.36% in winter (Figure 5).

Spatial variation in snow crab present in cod diet

The spatial distribution of snow crab found within cod stomachs of all size classes is concentrated along the coast of the southern part of Novaya Zemlya archipelago, Russia (Figures 1 and 6). In later years, the distribution has shifted in a more northeasterly direction (Figure 6). The frequency of occurrence of snow crab within cod stomachs was highest in strata 4 and 5 throughout the time series. In 2018, the frequency of occurrence increased in both strata 3 and 4 indicating a shift towards a more northerly distribution. The spatial distribution of different size classes of snow crab found within cod diets is also more concentrated along the coast of South Island of the Novaya Zemlya archipelago (Figure 7). However, small snow crab (CW 0–50 mm) have a wider and more westerly distribution (strata 4 and 5), whereas snow crab CW >50 mm appear to be concentrated in the south-east, within stratum 5 (Figure 7).

Predator–prey size relationship

Cod prey on a wide range of snow crab carapace widths (CWS) (Figure 8). Least squares regression (OLS) of snow crab prey size (CWS; mm) vs. cod length (TL; cm), $LC_i = a + bCWS_i$ where a is the intercept and bCWS is the slope, is as follows, $y = -15.2985$ (3.884 ± SE) + 0.680 (0.046 ± SE) x ($p < 0.001$, adj r^2 0.3143, $n = 462$, n, number of snow crabs where length measurements were recorded) (Figure 8) shows a significant positive relationship between predator length and carapace prey width. Quantile regression of snow crab size (mm) vs. predator length of each cod prey was calculated for the lower (5%) and upper (95%) quantile slopes: lower [intercept: −13.6653 (0.287 ± SE), slope: 0.384 (0.064 ± SE)] and upper (intercept: −10.7766 (1.0329 ± SE), slope: 1.008 (0.477 ± SE), $n = 462$]. The 95% confidence limit indicates the prey size span by cod size (Figure 8).

Cod consumption

The consumption of snow crab by cod has increased annually, particularly from 2009 onwards (Figure 9a). However, for the annual consumption of snow crab by cod using the Norwegian method, there is no obvious explanation for the dip in consumption in 2016 (Figure 9a). In recent years, snow crab consumption by cod has been at the same level as or higher than the landings from the fishery (Figure 9a and c). When comparing the effect of the fishery and of cod consumption on the snow crab stock, it should be noted that the fishery is on large crabs (CW > 100 mm, which is the minimum landing size), while most of the

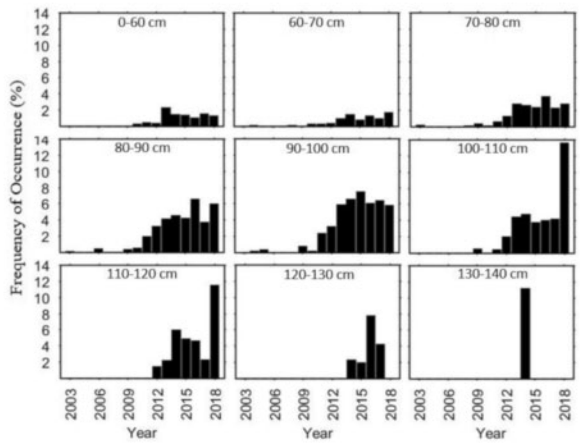

Figure 4. Frequency of occurrence (%) of snow crab in each cod length group in 2003–2018 (cod length classes 0–60 cm were combined due to low amounts of snow crab preyed upon by these cod size classes).

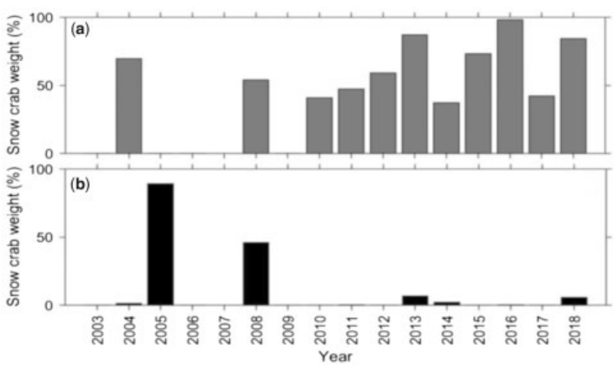

Figure 5. Seasonal distribution of total snow crab biomass found in cod stomachs 2003–2018: (a) in the summer/autumn season (July–October) and (b) winter season (January–March).

consumption by cod is on crabs with CW < 100 mm. The proportion of snow crab in the total consumption by the cod stock increased from 0.20% in 2013 to 1.18% in 2017 and 0.79% in 2018. Cod aged 7 and 8 had the highest level of consumption across all ages (Figure 9b). Annual consumption estimates (both Norwegian and especially Russian method) indicate that cod consumption of snow crab is considerably increased from 2003 to 2018 (Figure 9a), whereas the fisheries landings peaked in 2015 and have decreased somewhat afterwards (Figure 9c). The proportion of snow crab in the cod diet (measured as percentage weight of total stomach content) is much higher than the proportion of total food consumption at the stock level. This difference is due in part to species-specific evacuation rates used in consumption calculations, with the digestion rate of for example capelin being almost twice that of snow crab (which as mentioned earlier is set equal to the evacuation rate for shrimp) (Dos Santos and Jobling, 1995).

Discussion

Our results demonstrate that snow crab is a new prey item for cod, although it does not represent a prominent component of their diet (<10%), e.g. compared to other prey items such as capelin (average: 24.5% from 2003 to 2018) (Figure 2; Holt *et al.*, 2019). However, since 2014, snow crab has become the most important demersal crustacean species in cod diet. This supports and builds upon the findings of previous work (Chabot *et al.*, 2008), where snow crab constituted <10% cod diet across all size classes in both the northern and southern Gulf of St. Lawrence (GSL). Similarly, for Pacific cod (*G. macrocephalus*) in the eastern and western Pacific, snow crab constituted 10–22% (weight, g) of total stomach contents (Livingston, 1989; Burgos *et al.*, 2013), in waters of southeastern Kamchatka and northern Kuril islands 5–10 and $4-15\%$, respectively (Tripolskaya and Andrievskaya, 1967; Poltev, 2001).

The effect of cod on the snow crab population in the Barents Sea

The proportion of snow crab increased within cod diet over time (Figure 2). Since 2014, predation on snow crab by very large cod (>100 cm) has increased (Figures 3 and 4). This is consistent with the increase in large cod individuals in the Barents Sea in recent years (Figure 3b; ICES, 2018). Furthermore, analysis of the relationship between cod length and CW of snow crab (Figure 8) indicated that primarily cod between 60 and 110 cm prey upon snow crab. Snow crab was only marginally present in the diet of cod <60 cm, these small individuals are likely limited by gape size (Chabot *et al.*, 2008). Cod consumed the full-size distribution of snow crab (5–125 mm); however, 20–65mm CW individuals were more prevalent within cod stomachs (Figures 7 and 8). This size distribution is similar to that found in Pacific cod stomachs in northern Kuril Islands (Poltev, 2001) and in the southern GSL, but not in the northern GSL where smaller CWs were found (CW 6–16 mm; Chabot *et al.*, 2008). It is likely that prey of intermediate size are in higher abundance and are more energetically profitable for cod, as handling time is reduced while digestibility is maximized (Scharf *et al.*, 2003). Cod feeds primarily on small-to-intermediate-sized individuals and not on the commercial size harvested within the fishery (CW $\geq$ 95 mm). This smaller size component comprised of juveniles and mature females while the larger-sized component removed by the fishery is mature males only. While a direct competition between cod and fishery for the same specimens of snow crab therefore is small, cod predation may indeed affect the reproductive potential of the snow crab stock as well as recruitment to the fishery.

Snow crab are more readily consumed in the summer/autumn season due to their distribution area and annual seasonal migrations of cod (Figure 5). The highest degree of overlap between predator and prey is observed in the second half of the year when large mature cod migrate to the eastern Barents Sea. This is both due to cod spawning migrations in the first half of the year to the Lofoten area, which is outside the Barents Sea, and because immature cod are distributed more to the north and east in summer/autumn than in winter (Johansen *et al.*, 2013). Furthermore, snow crab in the summer/autumn season have softer shells, having moulted recently and thus may be more easily digested and have a higher evacuation rate compared to their hard-shelled winter counterparts (Sokolov *et al.*, 2016).

The spatial distribution of snow crab found in cod stomachs was consistent with previous studies (Zimina *et al.*, 2015;

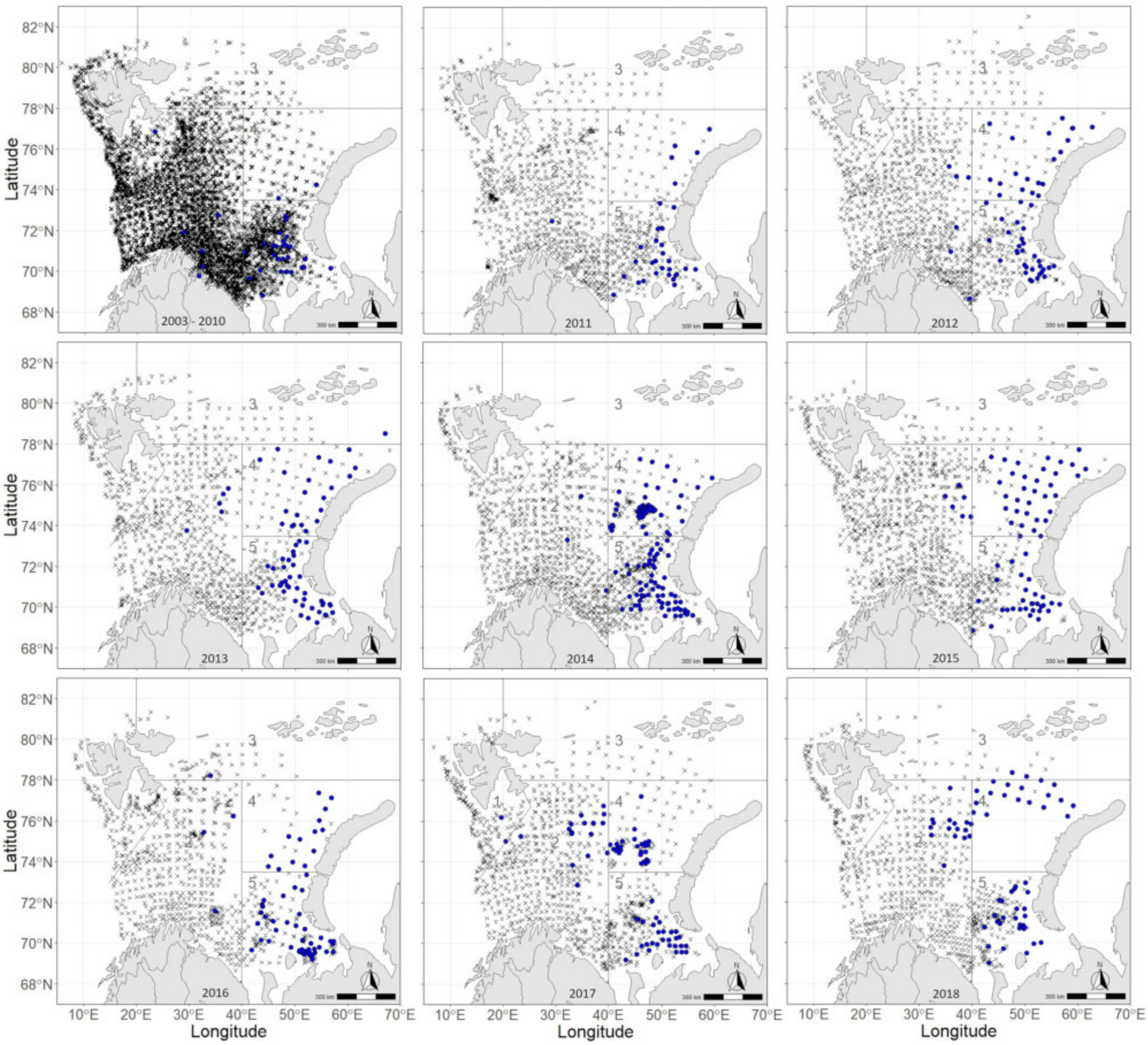

Figure 6. Spatial distribution of snow crab found in cod stomachs in 2003–2018 across all size classes of cod. Blue dots indicate the presence of snow crab within cod stomach samples, black crosses are cod stomach samples where no snow crab was present (data from the study years 2003–2010 are pooled, due to low amounts of snow crab preyed upon by cod within these years). Numbers within the maps, 1–5, detail the study area split into five strata.

Sokolov *et al.*, 2016), where the greatest abundance was found near the North Island of the Novaya Zemlya archipelago (Figure 6). In addition, records of snow crab in the stomachs of other demersal fish are consistent with this spatial distribution and prevalence in the summer/autumn period (Dolgov and Benzik, 2016). Our results support the idea that the newly established snow crab is still in an invading phase, expanding its distribution within the Barents Sea in recent years, and shifting north- and westwards (Figure 6). As such, it is expected that the degree of spatio-temporal overlap with cod will increase, as cod distribution has also shifted in the same direction in recent years due to an expansion of their feeding habitat (Kjesbu *et al.*, 2014).

Predator–prey dynamics

The increasing importance of the snow crab as prey items for cod might suggest a top-down control of the Barents Sea snow crab stock through predation. However, the roles of top-down and bottom-up controls on snow crab populations in the North Atlantic are complex and are still being readily debated (Orensanz *et al.*, 2004; Frank *et al.*, 2005; Boudreau *et al.*, 2011; Émond *et al.*, 2015).

Although cod is often described as the main predator of snow crab (Émond *et al.*, 2015), a number of other species in the Barents Sea eat snow crab, including haddock (*M. aeglefinus*), wolffish (*Anarhichas sp.*), thorny (*Amblyraja radiata*), and arctic (*A. hyperboreus*) skates, long rough dab (*Hippoglossoides*

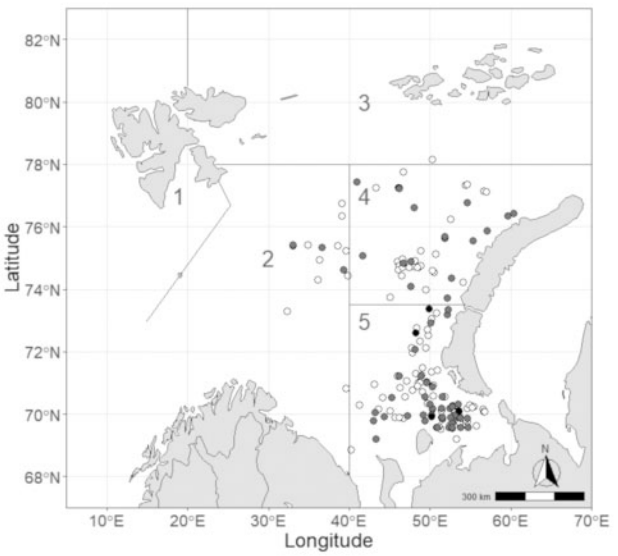

Figure 7. Spatial distribution of different size classes (CW, mm, white: 0–50 mm, grey: >50–100 mm, black: >100–150 mm) of snow crab found in cod stomachs (all size classes) in 2003–2018. Map details the study area split into five strata.

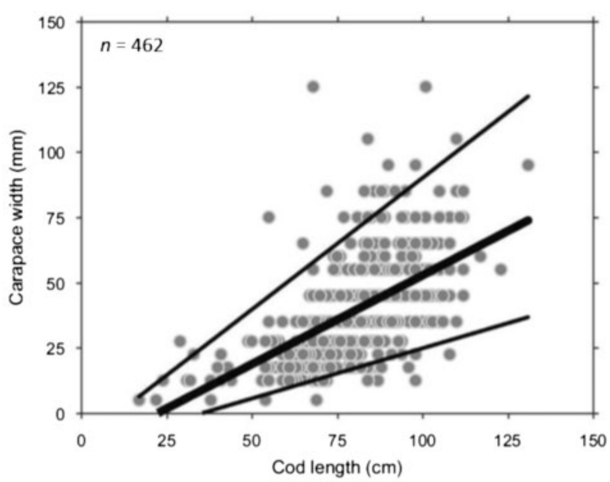

Figure 8. Relationship between cod length (cm) and snow crab carapace width (mm). Regression lines: OLS mean (thick black) and upper and lower bound quantile regressions (thin black) (0.05 and 0.95 regressions).

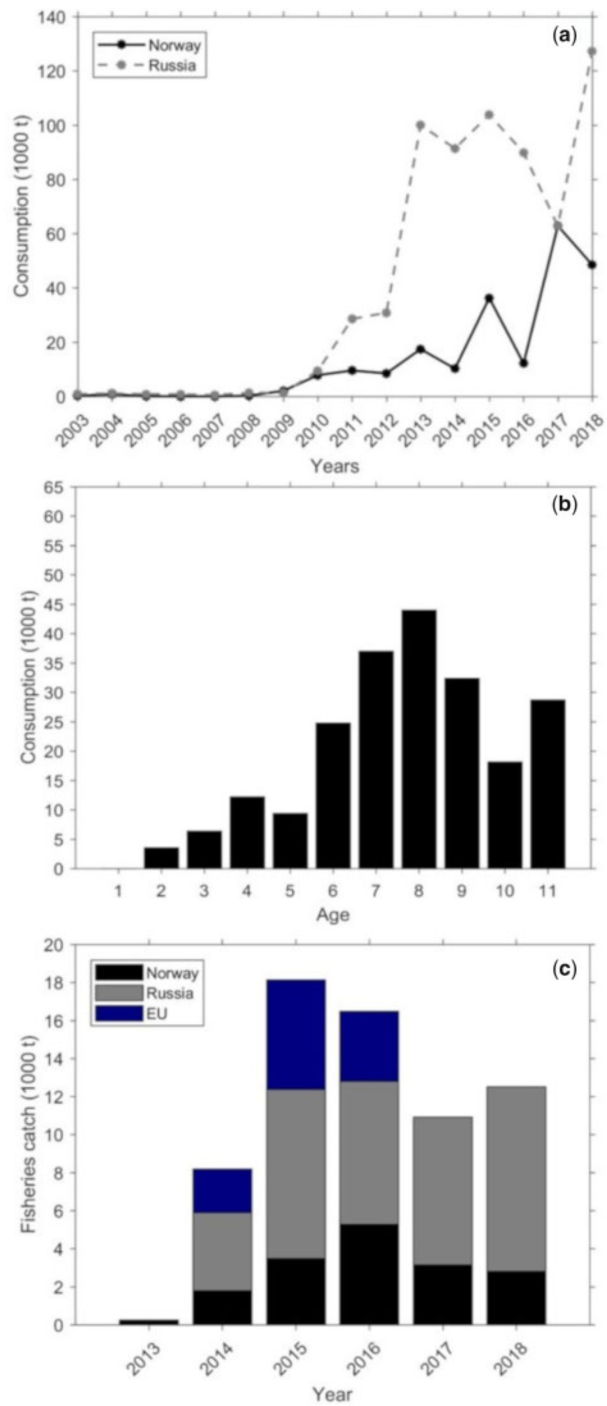

Figure 9. Estimated removal of snow crab biomass from the Barents Sea stock, 2003–2018: (a) total consumption by cod by year (Norwegian method: Black; Russian method: grey dashed); (b) consumption by cod age groups (Norwegian method); and (c) landings of snow crab caught in the Barents Sea by country.

platessoides), shorthorn sculpin (*Myoxocephalus scorpius*), and Arctic staghorn sculpin (*Gymnocanthus tricuspis*) (Pavlov, 2006; Agnalt *et al.*, 2011; Dolgov and Benzik, 2016; Eriksen *et al.*, 2020). Little is known about their predator–prey interactions with snow crab, but they could also be important in regulating the continued expansion of the snow crab population.

One other proposed regulating factor controlling the abundance in snow crab populations that should be noted is cannibalism, representing a major source of post-settlement mortality (Sainte-Marie *et al.*, 1996; Sainte-Marie and Lafrance, 2002; Agnalt *et al.*, 2011; Émond *et al.*, 2015).

Conclusion

The snow crab represents a new prey item for cod in the Barents Sea and has rapidly increased within cod diet since 2003. The increased proportion of snow crab in the cod diets over time is consistent with the increase in population also observed in snow crab landings. Cod has the potential to regulate the snow crab expansion and population increase but is unlikely to be in direct competition with the highly profitable fishery in the Barents Sea. The IMR–PINRO cod stomach content database is a unique, high-resolution time-series, representing a valuable resource in monitoring the expansion of newly established species such as the snow crab, in the Barents Sea ecosystem. Cod can thus be used as a biological sampling tool together with other monitoring programs, not only to corroborate survey results but also to elucidate how new species may affect predator–prey dynamics within an ecosystem context.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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Data availability

For this study, we compliment a published dataset; data are made available by Benzik and Dolgov (2016), Dolgov and Benzik (2016), Holt *et al.* (2019), and Townhill *et al.*, (2020).

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