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Changing winter diet of thick-billed murre *Uria lomvia* in Southwest Greenland, 1990s versus 2010s

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1 Changing winter diet of thick-billed murres *Uria lomvia* in
2 Southwest Greenland, 1990s versus 2010s

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10 Changing winter diet of thick-billed murres *Uria lomvia* in

11 Southwest Greenland, 1990s versus 2010s

12 Abstract

13 Southwest Greenland constitutes an internationally important wintering area for seabirds, including thick-
14 billed murres (*Uria lomvia* Linnaeus, 1758), but their prey may be affected by the general warming of this
15 sub-Arctic region. We compare murre diet collected in winter in the 1990s and 2010s around Nuuk. Fish
16 made up 36% of the diet (wet mass) and crustaceans 63% in the 1990s, changing to 22% and 78% in the
17 2010s, respectively. Capelin (*Mallotus villosus* Müller, 1776) was the dominant fish species, and the smaller
18 contribution in the 2010s coincided with declining densities of capelin around Nuuk. The crustaceans were
19 dominated by two krill species, *Meganyctiphanes norvegica* M. Sars, 1857, and *Thysanoessa inermis* Krøyer,
20 1846. However, *M. norvegica* was only important in the 2010s (51% wet mass), while *T. inermis* was
21 dominating the 1990s with 62% wet mass and only 23% in 2010s. The dominance of *M. norvegica* in the
22 2010s confirmed our expectations of a gradual “borealization” of this region due to the generally warming
23 sub-Arctic. The smaller contribution of fish in the diet may also support the hypothesis of deteriorating
24 winter conditions for murres. Apart from the diet, plastic was found in 15% of the birds and 53% had
25 parasitic nematods.

29 Keywords: seabird winter diet, thick-billed murre, *Uria lomvia*, Southwest Greenland, borealization, krill,
30 capelin

Draft

31 Introduction

32 For migratory bird populations, the non-breeding season represents a very long and usually challenging
33 period of their annual cycle, and their survival and subsequent breeding performance are highly dependent
34 on a predictable and nutritious food base (Scott 1998; Newton 2008; Fort et al. 2009; Milner-Gulland et al.
35 2011). However, changing climatic conditions are currently affecting biological systems worldwide,
36 especially in Arctic and sub-Arctic regions (Edwards and Richardson 2004; IPCC 2013; Fossheim et al. 2015),
37 and birds may be forced into new feeding habits as regularly observed during the breeding season (e.g.
38 Harris et al. 2007; Grémillet et al. 2012; Provencher et al. 2012). Climate induced ecosystem changes have
39 also been observed in the coastal and offshore waters of Southwest Greenland, which constitute an
40 internationally important wintering area for seabirds, with an estimated minimum number of 3.5–5.5
41 million birds, originating from the eastern and western North Atlantic (Lyngs 2003; Boertmann et al. 2004,
42 see also <http://seatrack.seapop.no>). So far, a northerly shift has been documented for Atlantic copepods in
43 this region (Møller and Nielsen 2019) and interdecadal variability of boreal fish abundance was highly
44 influenced by local temperature variability and the dynamics of the subpolar gyre (Post et al. 2021).

45 One species potentially affected by changes in prey composition and distribution is the thick-billed murre
46 (*Uria lomvia* Linnaeus, 1758), which is among the most numerous seabird species wintering in Southwest
47 Greenland (Boertmann et al. 2004). This species is declining in most areas of Greenland, as well as in most
48 regions of the Northeast Atlantic (Merkel et al. 2014; Kuletz et al. 2017). In a transoceanic analysis of
49 migration patterns, Frederiksen et al. (2016) found a strong association among wintering area and breeding
50 population status, in which stable populations were wintering mainly in Canadian waters, while declining
51 populations wintered mainly in Southwest Greenland or around Iceland. This is in line with murre studies in
52 Svalbard, where population decline and reduced adult survival were linked to an abrupt ecosystem shift in
53 the North Atlantic (Descamps et al. 2013; Fluhr et al. 2017). According to a recent modelling study, winter
54 mortality from oiling and harvest in Canada and Greenland also adds demographic stress to the population.

55 The impact, however, appears insufficient to explain the observed population decline, especially in Svalbard
56 and Iceland (Frederiksen et al. 2019).

57 The possible role of the non-breeding season as a central driver for population change in thick-billed
58 murre highlights the need for information about their winter diet. Only one study has previously reported
59 on this and found that murre preyed almost exclusively on capelin (*Mallotus villosus* Müller, 1776) in the
60 southern part of the Greenland wintering area, while crustaceans (mainly euphausiids) played a larger role
61 in more northern wintering areas (Falk and Durinck 1993). Information from Newfoundland waters, the
62 other major Northwest Atlantic wintering area for thick-billed murre, show that capelin was the dominant
63 prey in the 1950s (Tuck 1961), while the diet was more diverse in the 1980s and 1990s, with several fish
64 species, squids, euphausiids and amphipods contributing to the diet (Gaston et al. 1983; Elliot et al. 1990;
65 Rowe et al. 2000).

66 Here, we report on the second study of the winter diet of thick-billed murre in Southwest Greenland,
67 aimed at detecting any major change in the diet since the first study in the 1980s (Falk and Durinck 1993)
68 Based on the indirect evidence that murre are facing deteriorating winter conditions in Southwest
69 Greenland, we expected to find a larger contribution of low quality prey species in the murre diet, and we
70 expected a larger dominance of boreal prey species based on the general larger influx of Atlantic species in
71 sub-Arctic regions. As in the previous study, birds were shot by local hunters, and we analysed the stomach
72 content of birds collected in mid and late winter in the 1990s and the 2010s in the central part of the
73 wintering area west of Nuuk. We explore the influence of sampling decade, month and sex on prey
74 selection, and we discuss the results in relation to previous knowledge about murre winter diet and
75 possible links to ecosystem change.

76 Methods

77 Study area

78 The study area included the coastal area west of Nuuk, Southwest Greenland (Fig. 1). This is a key wintering
79 area for thick-billed murre, common eider, *Somateria mollissima* Linnaeus, 1758, king eider, *S. spectabilis*
80 Linnaeus, 1758, and long-tailed duck, *Clangula hyemalis* Linnaeus, 1758 (Merkel et al. 2019). The murre
81 winter in the shelf region off Southwest Greenland, including the near-coastal archipelago (Boertmann et
82 al. 2004). Seabird hunting is important to Greenlanders during winter in Southwest Greenland, and the
83 thick-billed murre is one of the most important seabird species for hunters in this area (Merkel and
84 Tremblay 2018). The coastal area and the inner shelf region west of Nuuk constitute the main hunting
85 grounds for local hunters (Fig. 1).

86 Sample collections and measurements

87 This study was conducted in accordance with the ethical standards of the Greenland Institute of Natural
88 Resources, and the murre used for diet analyses were shot by local hunters as part of their traditional
89 winter harvest for the local market in Nuuk. Birds were shot by multiple hunters on 26 February 1996 (n =
90 36), 7 January 1997 (n = 13), 5 March 1997 (n = 41), 4 January 2012 (n = 20), 6 January 2012 (n = 14), 1
91 January 2017 (n = 1), 1 February 2017 (n = 9) and 6 February 2017 (n = 11), hereafter referred to as the
92 1990s (n = 90 murre) and the 2010s (n = 55 murre). All birds were shot west of Nuuk (Fig. 1). Birds were
93 stored frozen at -18°C until dissected in 2017, when the stomach, i.e., the proventriculus including the
94 lower part of the oesophagus and the gizzard, was removed and refrozen until diet analysis began in 2019.
95 Birds were aged and sexed during dissection. The sex was determined by the presence of oviduct or
96 testicles. First-winter birds were distinguished from older birds by having an externally measured
97 interorbital skull width of <12.5 mm (Gaston and Hipfner 2000). Where possible, this criterion was

98 combined with the presence or absence of bursa fabricii, the size of the testicles in males and the form of
99 the oviduct (strait or convoluted) in females (Nevins and Carter 2003).

100 Upon opening the proventriculus and the gizzard (separated at the entrance to the gizzard), the content
101 was washed into a tray to make sure that no small objects were missed. Contents from the proventriculus
102 and from the gizzard were analysed separately due to the expectation that quickly digestible species would
103 be under-represented in the gizzard. Food items were identified to species level whenever possible using
104 standard identification literature (Muus 1959; Enckell 1980; Härkönen 1986; Kirkegaard 1992; Muus and
105 Nielsen 1998). Fish were detected by the presence of otoliths, spines, bone fragments and eye lenses. The
106 otoliths were measured to the nearest 0.1 mm on a millimetre paper placed in a petri dish. Crustaceans
107 were measured from the anterior part of the head (tip of rostrum) to the tip of the telson. As they were
108 often fragmented, they were counted by the number of eyes (in pairs). Pebbles and plastic particles were
109 also recorded.

110 As the stomach content in most cases was partially digested, the wet mass composition was estimated
111 from the number of individuals and their length, or the length of the otoliths for the fish. Both the overall
112 percentages of wet mass and the aggregate percentages (the average of individual percentages) were
113 calculated. For all prey species but capelin, it was not possible to assign a mean prey length to individual
114 birds due to the fragmentation of most prey specimens. Instead, the overall mean prey length, measured
115 across samples, was assigned to all birds. In the case of otoliths, we included length measurements from
116 the gizzard content, as otoliths in the proventriculus usually are still inside the fish, while they are retained
117 in the gizzard for some time. For the most frequent prey species, i.e., capelin, the krill (euphausiids)
118 *Meganyctiphanes norvegica* M. Sars, 1857 and *Thysanoessa inermis* Krøyer, 1846 and the amphipod
119 *Themisto libellula* Lichtenstein, 1822, we used the same length-mass regressions as in Falk and Durinck
120 (1993).

121 Unidentified euphausiids were assigned the same length as the most common species in the same sampling
122 period, e.g., *Thysanoessa inermis* in the 1990s and *Meganyctiphanes norvegica* in the 2010s. A single
123 specimen of the amphipod *Anonyx lilljeborgi* Boeck, 1871 was assigned the same mass as an average sized
124 *Themisto libellula*. The same applies for five specimens of unidentified gammarids and four (+1 from
125 gizzard) unidentified amphipods. Two specimens of unidentified gadoids (+ 3 from gizzard) and one (+ 3
126 from gizzard) ragworm (*Nereis sp.*) were assigned a mass of 36 g and 0.5 g, respectively, based on
127 information from Falk and Durinck (1993). Twenty-one specimens of glacier lanternfish (*Benthosema*
128 *glaciale* Reinhardt, 1837) were each assigned a mass of 8 g, corresponding to a medium-sized capelin.
129 Three specimens of unidentified decapods and one pasiphaeid shrimp *Pasiphaea tarda* Krøyer, 1845, were
130 assigned a mass of 2 g (+ 1 penaeid shrimp from gizzard), corresponding to a small/medium sized *Pandalus*
131 *borealis* Krøyer, 1838, the most common shrimp species in West Greenland (A. Burmeister 2020, personal
132 communication). For 11 specimens of *Calanus* spp., one harpacticoid copepod and six unidentified
133 squid/cuttlefish (cephalopods), we used direct mass measurements of the most complete individual found
134 in the diet. Finally, 2.1 g of crustacean fragments (+ 4.1 g from gizzard) and another 2.3 g of unidentifiable
135 diet fragments (+ 0.9 g unknown from gizzard), were not included when calculating the frequency and mass
136 composition.

137 Information about the body condition of the murre, such as total body mass and abdominal fat pad mass,
138 was also collected during dissection. However, these data were strongly influenced by the duration of
139 storage in the freezer prior to dissection, which varied from a few months to 21 years. As we found no
140 reliable method to correct for this bias, we did not use the data.

141 Data analyses

142 Previous studies of the murre harvest in Nuuk have shown that the proportion of first-winter birds is low
143 after 1 January (Frich 1997; Frederiksen et al. 2019). This was also the case in this study. In total we had
144 only 13 first-winter birds, which were all collected in the 2010s. In the diet analysis, these birds were

145 pooled with the older birds as the key prey species and their relative proportions appeared similar for both
146 age-classes.

147 We applied zero-one-augmented beta regression for the observed proportion (by mass) of the three main
148 prey types (capelin, *Meganyctiphanes norvegica*, *Thysanoessa inermis*) separately. Beta regression,
149 including the zero-one-augmented type that allows the presence of zeros and ones in the dataset (Ospina
150 and Ferrari 2012), is a relatively recently developed alternative for analysing proportional data derived from
151 continuous measurements (Ferrari and Cribari-Neto 2004). Such data do not follow standard statistical
152 distributions, and cannot be analysed using binomial or multinomial methods (Douma and Weedon 2019).
153 All models fitted had the same predictors for the beta component of the mixture and for the binomial
154 proportions of zeros and ones. Models were fitted in the R package brms (Bürkner 2017), using four chains
155 of 5000 samples from the posterior distribution with the first 2500 samples discarded as warmup. We used
156 leave-one-out cross-validation in the R package loo (Vehtari et al. 2017) to select the most appropriate
157 model to describe the data. Model convergence was assessed using trace plots and Rhat (Brooks and
158 Gelman 1998). Models fitted included the effects of decade (1990s vs 2010s), month (January, February,
159 March) or both (additive or interactive). An additive effect of sex was added to the model with the best
160 structure for temporal variation, but did not improve the model for any of the prey types (results not
161 shown).

162 Potential differences in the number of prey species per stomach between the two decades were tested
163 using zero-truncated Poisson regression in the R package VGAM (Yee 2015), after removing three empty
164 stomachs from February 1996. Differences in length distribution of capelin between the two study periods
165 were examined using Kolmogorov-Smirnov and Wilcoxon tests in R (R Core Team 2018). Means are
166 reported with standard error (mean \pm SE), unless noted otherwise.

167 Results

168 Diet discrimination

169 The murre stomach content included a total of 29,478 prey items, of which 95% were found in the
170 proventriculus and the remaining 5% in the gizzard (Tab. 1). Except for a few polychaetes (*Nereis* spp.) and
171 squid (cephalopods), the murre were feeding exclusively on fish and crustaceans during winter (Fig. 2).
172 When combining the contents from the proventriculus and the gizzard, a total of 19 species (or taxa) were
173 identified (Tab. 1). In accordance with the expectation that the turn-around time in the stomach differs
174 between prey species, the gizzards contained a larger proportion and higher diversity of fish (otoliths), but
175 in contrast had a lower proportion and fewer species of crustaceans. Most birds (90%) had only one, two or
176 three prey species in the proventriculus (Tab. 2). However, the mean number of prey species per stomach
177 was significantly higher in the more recent sampling decade ($z = 2.829$, $p < 0.005$). In the 1990s, four prey
178 species (6% of birds) was the highest number recorded, while 20% of the birds from the 2010s had between
179 four and six prey species although sample size was smaller and no samples were collected in March (Tab.
180 2).

181 In terms of frequency of occurrence, four species were important in the proventriculus; capelin, the two
182 krill species *M. norvegica* and *T. inermis*, and the amphipod species *Themisto libellula*, being present in 27%
183 - 89% of the birds (Tab. 1). When expressed as estimated wet mass, the capelin and the krill *T. inermis*
184 constituted the two most important species in the 1990s (36% - 62% of the total wet mass), while also the
185 krill *M. norvegica* was important in the 2010s (Tab. 1). In both decades, the amphipod *T. libellula* was no
186 longer important when calculated as estimated wet mass (Tab. 1).

187 Prey sizes

188 The length of the four most common prey species ranged from 11.0 mm to 143.7 mm: with a mean length
189 of 110.1 ± 0.6 mm ($n = 500$) for capelin, 41.2 ± 0.7 mm ($n = 100$) for *M. norvegica*, 25.9 ± 0.4 mm ($n = 23$)
190 for *T. inermis* and 17.6 ± 1.5 mm ($n = 20$) for *T. libellula*. The size distribution of the capelin differed
191 between the 1990s and the 2010s (Kolmogorov-Smirnov test $D = 0.145$, $p = 0.014$, Wilcoxon test $W =$
192 34500 , $p = 0.0014$), although the median length was identical in both periods (112.6 mm). It appears that in
193 both decades the murrelets were feeding on capelin of sizes corresponding to ages of 2 and up, i.e. several
194 age-groups of capelin except the smallest (hatched in the year before the sampling year) (Fig. 3).

195 Temporal variation

196 A shift occurred between the two sampling decades with respect to krill. *M. norvegica* was almost absent in
197 the 1990s, but accounted for 51% of the wet mass in the 2010s (Tab.1). The opposite trend was observed
198 for *T. inermis*, which by mass accounted for 62% in the 1990s, but only 23% in the 2010s. The overall diet
199 contribution from capelin also changed between the two decades, from 36% in the 1990s to 19% in the
200 2010s. The direct comparison between the 1990s and the 2010s is biased by the fact that birds from March
201 were only collected in the first decade. If comparing only birds collected in January and February, the 1990s
202 was almost exclusively dominated by capelin. The beta regression showed that for the two main prey types
203 where all models converged (capelin and *M. norvegica*), models including effects of both decade and
204 month were strongly preferred (Tab. 3), whereas the need for including an interaction term between the
205 two predictors was less clear. For consistency, we display results for all three prey types according to the
206 month*decade model, i.e. separately for each combination of decade and month (Fig. 4). In the 2010s,
207 capelin only contributed significantly to the diet in February. Instead, *M. norvegica* dominated the diet in
208 January in the 2010s. The March samples from the 1990s were completely dominated by *T. inermis* (Fig. 4).
209 The influence of decade and month may include an inherited effect of year; however, this potential effect

210 could not be quantified due to an unequal representation of samples between months and years.
211 According to the beta regression analysis, sex did not influence the diet composition (see Methods).

212 Non-food items

213 Apart from the diet reported in Tab. 1, a number of non-food items were found in the stomachs. Plastic was
214 found in 10 birds from the 1990s and in 11 birds from the 2010s, i.e., in 15% of the birds. All but one piece
215 was found in the gizzard, with a maximum of three pieces per bird. A total of 32 pebbles were found in the
216 gizzard in 14 and 4 birds from the 1990s and the 2010s, respectively. Parasitic nematods (*Nematoda*) were
217 observed in 53% of the birds, usually both in the proventriculus and the gizzard. A total of 737 nematods
218 were found in 55 and 19 of the birds from the 1990s and the 2010s, respectively. Up to 86 nematods were
219 recorded in a single bird.

220 Discussion

221 General food base

222 The present study shows that capelin and krill (*M. norvegica* and *T. inermis*) form the main food base for
223 thick-billed murres in the central part of their wintering area in Southwest Greenland. A similar narrow
224 food base, with capelin as the main fish component, was also reported in Southwest Greenland in the
225 1980s (Falk and Durinck 1993) and in Newfoundland waters in the 1950s (Tuck 1961). Later studies from
226 Newfoundland waters, the Barents Sea and northern Iceland reported only a small or no contribution from
227 capelin (Elliot et al. 1990; Erikstad 1990; Rowe et al. 2000; Lilliendahl 2009).

228 Capelin availability

229 One of the marked changes found in the current diet study was the smaller contribution of capelin in the
230 2010s compared to the 1990s and the 1980s. This may be a result of fewer capelin being available for the

231 murre in the 2010s. Capelin catch data from two stratified random bottom-trawl offshore surveys (see
232 survey data descriptions in Post et al. (2021)) are available for the Nuuk area (63 - 65°N). The surveys take
233 place in the summer, and because adult capelin die after spawning in the spring, it is the catch rates in the
234 summers preceding the bird collections that are relevant as proxies for capelin availability for the sampled
235 murre. Surveys were not conducted in all years; however, the available pieces of information do suggest
236 higher capelin abundance in the relevant years in the 1990s compared to the 2010s. Data from a German
237 survey show that capelin were present in 47% of the trawls in 1996 (N=17), while only in 10% of the trawls
238 in 2011 (N=10). Although catch efficiency is not comparable with the German survey due to differences in
239 sampling gear, data from the Greenland Institute of Natural Resources can be used to add information
240 about 2016 relative to 2011: 64% of the trawls in 2011 contained capelin (N=25) vs. only in 22% in 2016
241 (N=27).

242 Reasons for a possible decline in capelin density could be many: environmental changes, such as suggested
243 for the decline in Iceland/East Greenland (Jansen et al. 2021), or a change in predation pressure from large
244 populations of well-known capelin predators, such as Atlantic cod *Gadus morhua*, harp seal *Pagophilus*
245 *groenlandicus* and humpback whale *Megaptera novaeangliae* (Heide-Jørgensen et al. 2012; ICES 2014,
246 2020). Unlike the stocks that spawn in Canada, Iceland and Norway, these West-Greenland capelin have
247 not been targeted by large scale commercial fisheries, so fishing is not a direct cause for this decline (Vader
248 et al. 1990; Rowe et al. 2000; Gudmundsdottir and Vilhjálmsson 2002; ICES 2020).

249 Capelin versus krill

250 Capelin is high in fatty acids and normally considered a superior prey species for murre compared to
251 invertebrate prey species, including krill (Erikstad 1990; Falk and Durinck 1993, and references therein).
252 This may, however, vary between regions and seasons. Measurements of the energy content of capelin and
253 krill from local stocks in the Nuuk area show that the calorific value of capelin (4.3 kJ/g wet mass) was
254 actually lower than for *M. norvegica* (6.0 kJ/g wet mass) and *Thysanoessa raschii* M. Sars, 1864 (6.4 kJ/g

255 wet mass) when measured in July¹. No local measurements are available for *T. inermis* or for any of the
256 species during mid-winter, when the diet samples were collected for this study. However, based on an
257 Icelandic study, the energy density of capelin can be 2-3 times higher during mid-winter (Engilbertsson
258 2014). The energy value of krill also appears to be higher during winter, but seemingly not to the same
259 degree as for capelin (Falk-Petersen et al. 2000). Furthermore, the mean wet mass of capelin was 7.16 g
260 while only 0.35 g for the largest krill species (*M. norvegica*), and therefore capelin contributed with at least
261 20 times more energy per prey capture than krill. Besides the energy content of the prey, the profitability
262 of feeding on a specific prey type also depends on the energetic costs involved. This is likely a trade-off
263 between predictability of the prey, prey density, prey escape capabilities and how deep the murre has to
264 dive to feed on them (Elliott et al. 2008). According to acoustic surveys in March 2019 and 2021, krill are
265 consistently distributed at greater depth than capelin in the area around Nuuk (T. Jansen, unpublished
266 data).

267 Changes in krill composition

268 Besides the decreased contribution of capelin in the diet in the 2010s, a marked shift in the krill
269 composition has been observed in the murre diet. *M. norvegica* was absent in the 1980s (Falk and Durinck
270 1993), almost absent in the 1990s (this study), but accounted for 51% of the wet mass in the 2010s (this
271 study, Tab. 1). *T. inermis* was important in all three sampling decades. In contrast, *T. raschii* was reported
272 only in the 1980s (Falk and Durinck 1993), although we cannot rule out the possibility that some were
273 present among the unidentified euphausiids in this study (Tab. 1). The fact that both *M. norvegica* and *T.*
274 *inermis* are larger species than *T. raschii* (Agersted and Nielsen 2016 and references therein), resulting in a
275 higher energy gain per prey item for the murre, could perhaps be part of the explanation why *T. raschii*
276 was absent. A study by Agersted and Nielsen (2014) showed that all three species coexist in the Nuuk area,
277 but did not show how they are distributed during winter. However, *T. raschii* is known as a coastal species,

¹ See Supplementary Material

278 whereas *M. norvegica* and *T. inermis* are known to inhabit shelf-regions (see references in Agersted and
279 Nielsen 2014), and this may indicate that the murrelets collected for this study were feeding far from the
280 coast. We do not know how far from the coastline the murrelets were shot, but we know that hunting usually
281 takes place beyond the coastal archipelago. Furthermore, according to local hunters from Nuuk, it happens
282 more and more that murrelets cannot be reached within a safe boating distance (Haastrup 2017).

283 Krill are considered as a good indicator of changes in the food web composition from a bottom-up as well
284 as a top-down perspective (Hempel 1970), and the larger contribution of *M. norvegica*, a boreal Atlantic
285 species, may be a consequence of general “borealization” of the generally warming sub-Arctic (e.g.
286 Vihtakari et al. 2018; Post et al. 2021). A shift towards more Atlantic krill species has been observed in
287 Svalbard and farther east in the Barents Sea, including *M. norvegica* (Eriksen and Dalpadado 2011; Buchholz
288 et al. 2012). A northerly shift has also been documented for Atlantic copepods, the main prey for *M.*
289 *norvegica*, including in the waters off central West Greenland (Hatun et al. 2009; Møller and Nielsen 2019).

290 Conclusion

291 The shift in diet towards boreal Atlantic krill species is in line with the expectations and observations of how
292 global warming affects the sub-Arctic and Arctic regions of the North Atlantic (e.g. Vihtakari et al. 2018;
293 Møller and Nielsen 2019; Post et al. 2021). It is currently not known whether this shift affects the fitness of
294 thick-billed murrelets in our study area, but combined with the observed smaller contribution of the high-
295 energy capelin, the results suggest deteriorating winter conditions for the murrelets, thus supporting earlier,
296 more indirect studies spanning the North Atlantic (Descamps et al. 2013; Frederiksen et al. 2016; Fluhr et
297 al. 2017). Clearly, our results should be treated with caution since they are based on small sample sizes,
298 relatively few sampling years as well as unequal sampling between years and months. Efforts should be
299 made to collect more data in the near future to better understand the temporal and spatial dynamics of
300 these prey species, including their size and energy value, and the consequences for seabird fitness. More
301 data on seabird winter diet can also provide useful indices of fish or invertebrate abundance to supplement

302 the more traditional ship-based surveys in seasons and areas that are difficult to cover. Until then, this
303 study provides a valuable contribution to the limited knowledge about winter diet of seabirds in the
304 Northwest Atlantic.

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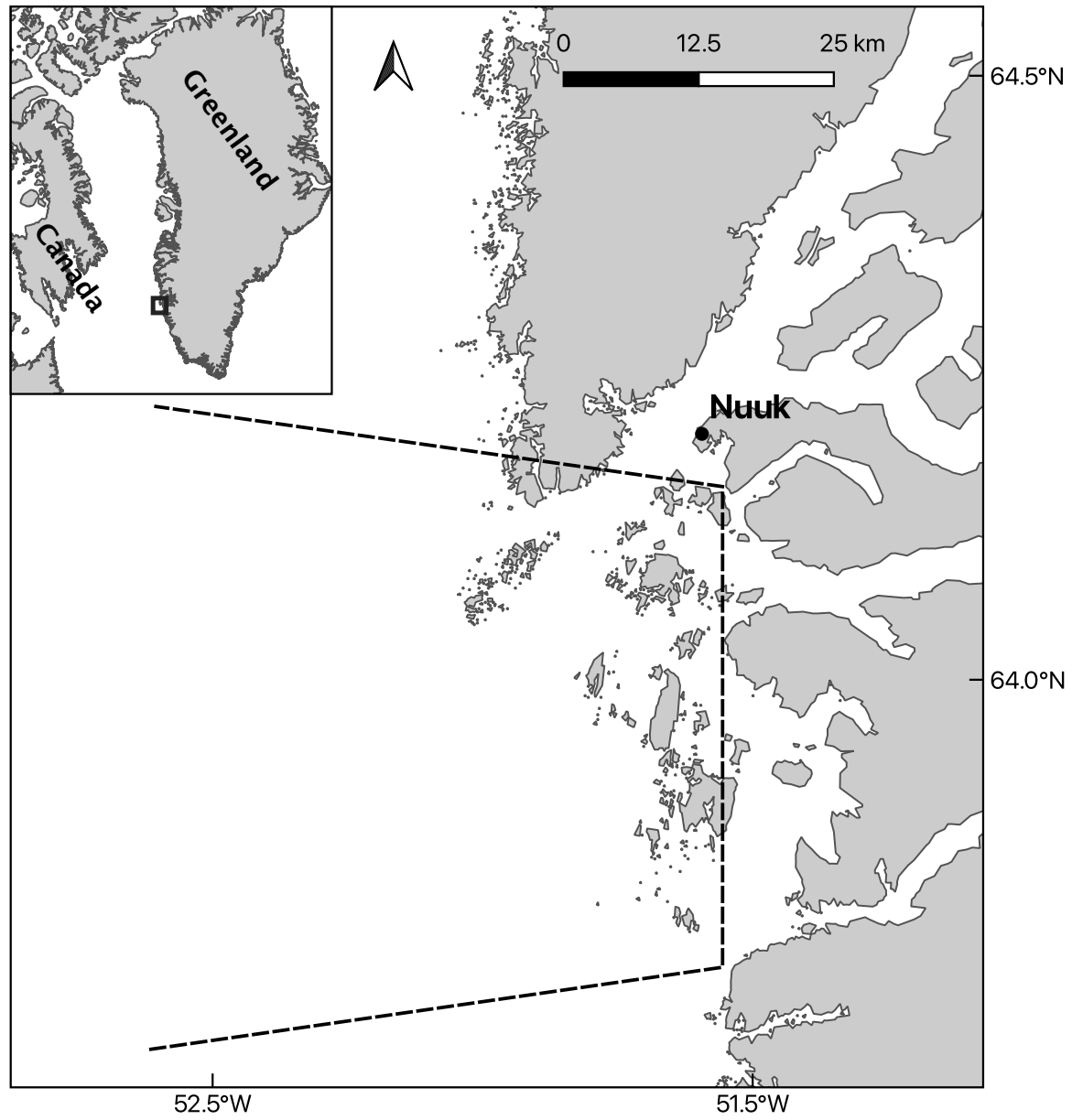
468 Figure captions

469 **Fig. 1.** Map of the study area in Southwest Greenland (dashed line), where thick-billed murres (*Uria*
470 *lomvia*) were shot by local hunters. The western demarcation is unknown, but most likely does not
471 extend beyond the map. Figure was created using QGIS version 3.16 (QGIS Development Team, 2021).
472 QGIS Geographic Information System. Open Source Geospatial Foundation Project
473 <http://qgis.osgeo.org>), using base maps from QGreenland version 1.0.0 (Moon et al. 2021). Map
474 projection is EPSG: 3413.

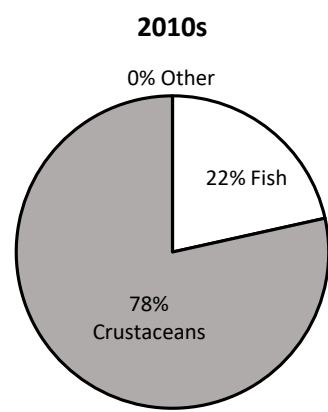
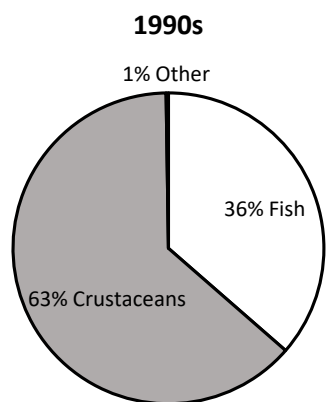
475 **Fig. 2.** The wet mass contribution of crustaceans, fish and other diet in 140 proventriculi samples of
476 thick-billed murres (*Uria lomvia*) collected west of Nuuk, Southwest Greenland, in January – March 1996
477 and 1997 (1990s, n=85) and in January-February 2012 and 2017 (2010s, n=55).

478 **Fig. 3.** Frequency distribution of capelin (*Mallotus villosus*) sizes from the diet of thick-billed murres
479 (*Uria lomvia*) collected west of Nuuk, Southwest Greenland, in January – March 1996 and 1997 (1990s)
480 and in January-February 2012 and 2017 (2010s).

481 **Fig. 4.** Proportions of the three most important prey species in the diet of thick-billed murres (*Uria*
482 *lomvia*) from Nuuk during mid-winter, calculated as the aggregate percentage of wet mass for all the
483 diet and grouped according to months and sampling decades.



	1990s	2010s
Fish	36%	22%
Crustacear	63%	78%
Other	0%	0%
TOTAL	3903	2537.8



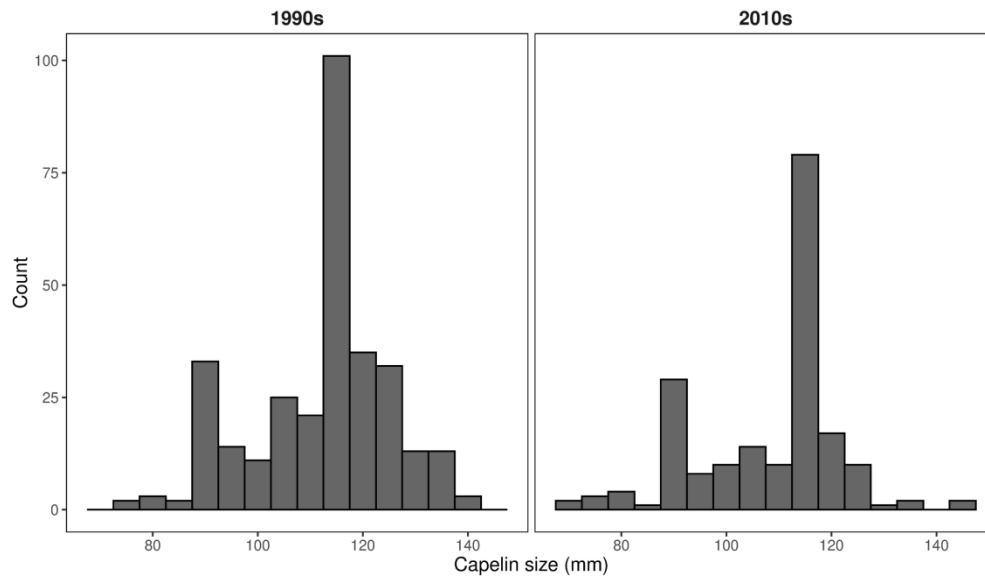


Fig. 3. Frequency distribution of capelin (*Mallotus villosus*) sizes from the diet of thick-billed murres (*Uria lomvia*) collected west of Nuuk, Southwest Greenland, in January – March 1996 and 1997 (1990s) and in January-February 2012 and 2017 (2010s).

238x140mm (300 x 300 DPI)

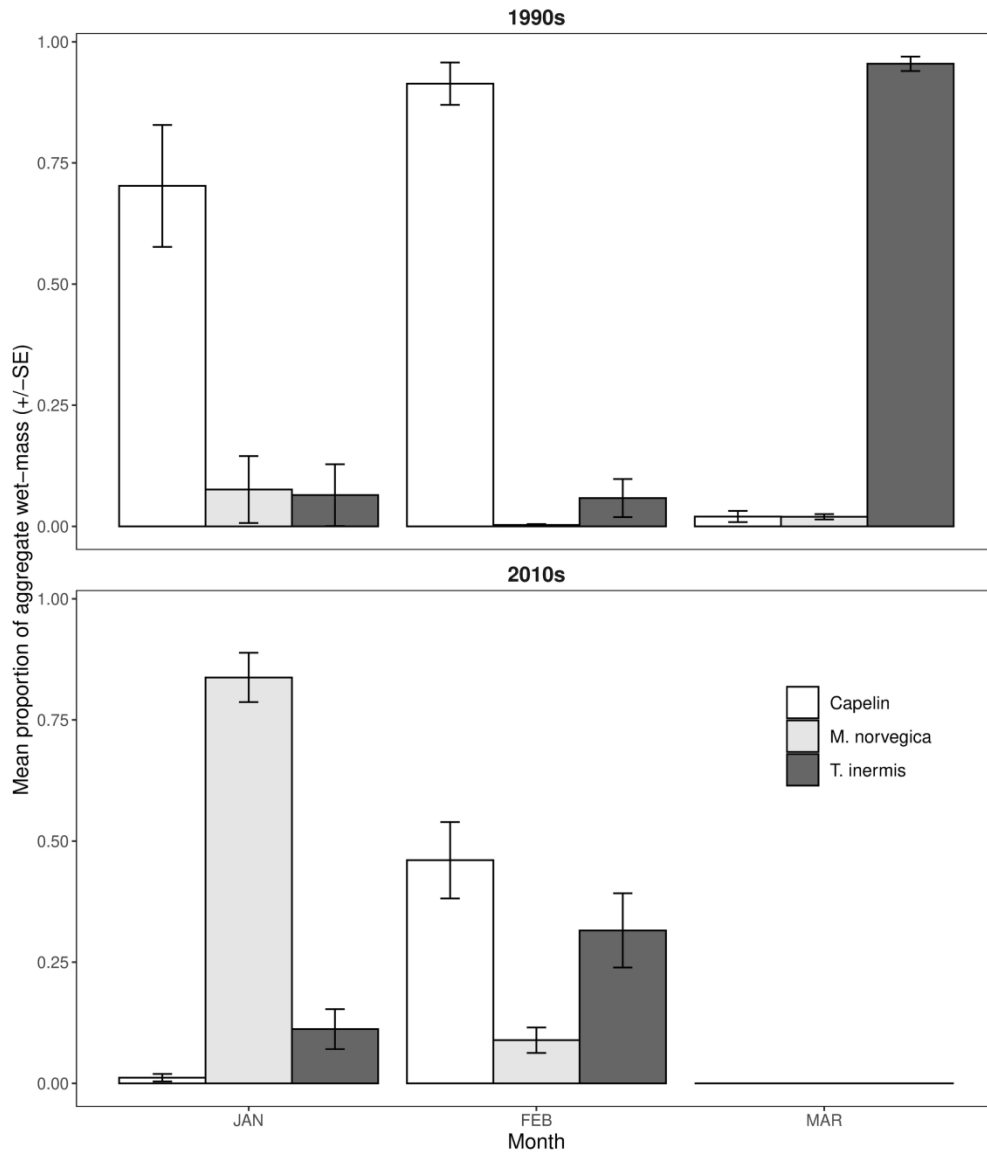


Fig. 4. Proportions of the three most important prey species in the diet of thick-billed murres (*Uria lomvia*) from Nuuk during mid-winter, calculated as the aggregate percentage of wet mass for all the diet and grouped according to months and sampling decades.

238x277mm (300 x 300 DPI)

Tab. 1. The number of prey items, the frequency of occurrence and the estimated wet mass of the diet of thick-billed murre (*Uria lomvia*) from 140 proventriculi and gizzard samples, collected in January – March 1996 and 1997 (1990s, n=85) and in January – February 2012 and 2017 (2010s, n=55) west of Nuuk, Southwest Greenland

	Number Indv. prey	Frequency of occurrence				Estimated Wet Weight (g)			
		1990s		2010s		1990s		2010s	
		N birds	%	N birds	%	Total ww	%	Total ww	%
Proventriculus samples									
Fish									
<i>Mallotus villosus</i>	259	43	51	18	33	1421.5	36	474.3	19
Unid. codfish	2			1	2			72.0	3
Crustaceans									
<i>Meganyctiphanes norvegica</i>	3813	33	39	49	89	38.9	1	1296.8	51
<i>Thysanoessa inermis</i>	23481	46	54	29	53	2415.7	62	584.6	23
Unid. euphausiids	238	2	2	4	7	0.4	<1	82.3	3
<i>Themisto libellula</i>	170	23	27	25	45	9.3	<1	25.9	1
<i>Anonyx lilljeborgi</i>	1			1	2			0.2	<1
Unid. gammarids	5			2	4			1.1	<1
Unid. amphipods	4	1	1	3	5	0.2	<1	0.6	<1
<i>Pasiphaea tarda</i>	1	1	1			2.0	<1		
Unid. decapods	3	2	2			6.0	<1		
<i>Calanus sp.</i>	11	2	2	3	5	0.0	<1	0.1	<1
<i>Harpacticoida sp.</i>	1			1	2			0.0	<1
Other taxa									
Unid. cephalopods	6	4	5			9.0	<1		
<i>Nereis sp.</i>	1	1	1			0.5	<1		
Gizzard samples									
Fish									
<i>Mallotus villosus</i>	319	50	57	19	35	1581.6	79	723.3	79
<i>Benthoosema glaciale</i>	20	5	6	1	2	144.0	7	16.0	2
Unid. codfish	3	2	2			108.0	5		
Unid. fish	6	1	1	2	4	16.0	1	32.0	3
Crustaceans									
<i>Meganyctiphanes norvegica</i>	102	5	6	16	29	4.2	<1	31.5	3
<i>Thysanoessa inermis</i>	159	4	5	7	13	10.0	1	10.3	1
Unid. euphausiids	801	41	47	27	49	77.2	4	69.0	8
<i>Themisto libellula</i>	17	6	7	3	5	2.9	<1	0.6	<1
Unid. amphipods	1			1	2			0.2	<1
<i>Pandalus borealis</i>	1	1	1			2.0	<1		
Penaeid shrimps	2	1	1	1	2	2.0	<1	2.0	<1
Other taxa									
Unid. cephalopods	47	13	15	13	24	40.5	2	30.0	3
<i>Nereis sp.</i>	4	3	3	1	2	1.5	<1	0.5	<1
Proventriculus + gizzard									
Fish									
<i>Mallotus villosus</i>	578	51	57	21	38	3003.1	51	1197.6	35
<i>Benthoosema glaciale</i>	20	5	6	1	2	144.0	2	16.0	<1
Unid. codfish	5	2	2	1	2	108.0	2	72.0	2
Unid. fish	6	1	1	2	4	16.0	<1	32.0	1

Crustaceans

<i>Meganyctiphanes norvegica</i>	3915	35	39	49	89	43.1	1	1328.4	38
<i>Thysanoessa inermis</i>	23640	46	52	29	53	2425.6	41	594.9	17
Remaining species/taxa	1314					153.5	3	212.4	6

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TABLES

Tab. 2. Percentage of proventriculus from thick-billed murre (*Uria lomvia*) containing between one and six different prey species, calculated by sampling decade and for all birds (sample sizes in parentheses).

No. of prey species	1990s (85)	2010s (55)	All birds (140)
1	37.2	18.2	29.8
2	37.2	40.0	38.3
3	19.8	21.8	20.6
4	5.8	12.7	8.5
5		5.5	2.1
6		1.8	0.7

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Tab. 3. Comparison of models fitted for capelin (*Mallotus villosus*) and *Meganyctiphanes norvegica*. All models including month as predictor for *Thysanoessa inermis* failed to converge. Values shown are differences in elpd, or expected log pointwise predictive density, between each model and the best approximating model (Vehtari et al. 2017), and the associated standard error. Differences between models are meaningful if they are several times larger than their standard error.

Model	Prey type	
	Capelin	<i>M. norvegica</i>
Null	73.0 (SE 9.8)	63.6 (SE 15.5)
Decade	59.7 (SE 9.0)	30.2 (SE 13.1)
Month	34.1 (SE 6.8)	29.2 (SE 12.6)
Month + Decade	14.0 (SE 5.6)	1.4 (SE 3.4)
Month * Decade	0	0

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