

# Changing winter diet of Thick-billed Murres (Uria lomvia) in southwest Greenland, 1990s versus 2010s

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

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# Southwest Greenland, 1990s versus 2010s

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# <sup>10</sup> Changing winter diet of thick-billed murres *Uria lomvia* in

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# Southwest Greenland, 1990s versus 2010s

## 12 Abstract

13 Southwest Greenland constitutes an internationally important wintering area for seabirds, including thickbilled murres (Uria lomvia Linnaeus, 1758), but their prey may be affected by the general warming of this 14 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.

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- 28

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

# 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.

The impact, however, appears insufficient to explain the observed population decline, especially in Svalbard
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 murres highlights the need for information about their winter diet. Only one study has previously reported 59 on this and found that murres 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 murres, 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).

Here, we report on the second study of the winter diet of thick-billed murres in Southwest Greenland, 66 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 murres 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 murres 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 murres 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 murres) and the 2010s (n = 55 murres). 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

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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.

As the stomach content in most cases was partially digested, the wet mass composition was estimated 110 111 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 in the diet. Finally, 2.1 g of crustacean fragments (+ 4.1 g from gizzard) and another 2.3 g of unidentifiable 134 135 diet fragments (+ 0.9 g unknown from gizzard), were not included when calculating the frequency and mass 136 composition.

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

#### 141 Data analyses

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

pooled with the older birds as the key prey species and their relative proportions appeared similar for bothage-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, Thyssanoessa 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 proportions of zeros and ones. Models were fitted in the R package brms (Bürkner 2017), using four chains 154 155 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).

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

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## 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 murres 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 prev 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 $\pm$ 0.6 mm (n = 500) for capelin, 41.2 $\pm$ 0.7 mm (n = 100) for <i>M. norvegica</i> , 25.9 $\pm$ 0.4 mm (n = 23)
190	for <i>T. inermis</i> and 17.6 $\pm$ 1.5 mm (n = 20) for <i>T. libellula</i> . 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 murres 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 the 1990s, but accounted for 51% of the wet mass in the 2010s (Tab.1). The opposite trend was observed 197 for *T. inermis,* which by mass accounted for 62% in the 1990s, but only 23% in the 2010s. The overall diet 198 199 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

Apart from the diet reported in Tab. 1, a number of non-food items were found in the stomachs. Plastic was 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 was found in the gizzard, with a maximum of three pieces per bird. A total of 32 pebbles were found in the gizzard in 14 and 4 birds from the 1990s and the 2010s, respectively. Parasitic nematods (*Nematoda*) were observed in 53% of the birds, usually both in the proventriculus and the gizzard. A total of 737 nematods were found in 55 and 19 of the birds from the 1990s and the 2010s, respectively. Up to 86 nematods were recorded in a single bird.

## 220 Discussion

#### 221 General food base

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

#### 228 Capelin availability

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

231 murres 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 murres. 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 sampling gear, data from the Greenland Institute of Natural Resources can be used to add information 239 240 about 2016 relative to 2011: 64% of the trawls in 2011 contained capelin (N=25) vs. only in 22% in 2016 241 (N=27).

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

249 Capelin versus krill

Capelin is high in fatty acids and normally considered a superior prey species for murres compared to
invertebrate prey species, including krill (Erikstad 1990; Falk and Durinck 1993, and references therein).
This may, however, vary between regions and seasons. Measurements of the energy content of capelin and
krill from local stocks in the Nuuk area show that the calorific value of capelin (4.3 kJ/g wet mass) was
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 July<sup>1</sup>. 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 murres have to 264 dive to feed on them (Elliott et al. 2008). According to acoustic surveys in March 2019 and 2021, krill are consistently distributed at greater depth than capelin in the area around Nuuk (T. Jansen, unpublished 265 266 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 murres, 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,

<sup>&</sup>lt;sup>1</sup> See Supplementary Material

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

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

#### 290 Conclusion

The shift in diet towards boreal Atlantic krill species is in line with the expectations and observations of how 291 292 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 murres 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 murres, 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

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

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313

Agersted, M.D., and Nielsen, T.G. 2014. Krill diversity and population structure along the sub-Arctic

## 312 References

314 Godthåbsfjord, SW Greenland. J. Plankton Res. 36(3): 800-815. doi:10.1093/plankt/fbt139. Agersted, M.D., and Nielsen, T.G. 2016. Functional biology of sympatric krill species. J. Plankton Res. 38(3): 315 316 575-588. doi:10.1093/plankt/fbw017. 317 Boertmann, D., Lyngs, P., Merkel, F.R., and Mosbech, A. 2004. The significance of SW Greenland as winter quarters for seabirds. Bird. Cons. Intern. 14: 87-112. doi:10.1017/S0959270904000127. 318 319 Brooks, S., and Gelman, A. 1998. General methods for monitoring convergence of iterative simulations. 320 Journal of Computational Graphical Statistics 7: 434-455. Buchholz, F., Werner, T., and Buchholz, C. 2012. First observation of krill spawning in the high Arctic 321 322 Kongsfjorden, west Spitsbergen. Polar Biol. 35(8): 1273-1279. doi:10.1007/s00300-012-1186-3. Bürkner, P.-C. 2017. brms: An R package for Bayesian multilevel models using Stan [Bayesian inference; 323 324 multilevel model; ordinal data; MCMC; Stan; R]. Journal of Statistical Software 80(1): 28. 325 doi:10.18637/jss.v080.i01. 326 Descamps, S., Strøm, H., and Steen, H. 2013. Decline of an arctic top predator: synchrony in colony size 327 fluctuations, risk of extinction and the subpolar gyre. Oecologia 173: 1271-1282. doi:10.1007/s00442-328 013-2701-0. Douma, J.C., and Weedon, J.T. 2019. Analysing continuous proportions in ecology and evolution: A practical 329 330 introduction to beta and Dirichlet regression. Methods Ecol. Evol. 10(9): 1412-1430. doi:10.1111/2041-331 210X.13234. 332 Edwards, M., and Richardson, A. 2004. Impact of climate change on marine pelagic phenology and trophic 333 mismatch. Nat 430: 881-884. 334 Elliot, R.D., Ryan, P.C., and Lidster, W. 1990. The winter diet of thick-billed murre in coastal Newfoundland 335 waters. Stud. Avian Biol. 14: 125-138. Elliott, K.H., Davoren, G.K., and Gaston, A.J. 2008. Time allocation by a deep-diving bird reflects prey type 336 337 and energy gain. Anim. Behav. 75: 1301-1310. doi:10.1016/j.anbehav.2007.09.024. 338 Enckell, P.H. 1980. Kräftdjur. Fältfauna, Signum, Lund. 339 Engilbertsson, v. 2014. Energy dynamics and recruitment of Icelandic capelin. Master's thesis, Faculty of 340 Life and Environmental Sciences, University of Iceland. Eriksen, E., and Dalpadado, P. 2011. Long-term changes in Krill biomass and distribution in the Barents Sea: 341 342 are the changes mainly related to capelin stock size and temperature conditions? Polar Biol. 34(9): 343 1399-1409. doi:10.1007/s00300-011-0995-0. Erikstad, K.E. 1990. Winter diet of four seabird species in the Barents Sea after a crash in the capelin stock. 344 345 Polar Biol. 10: 619-627. 346 Falk-Petersen, I.B., Hagen, W., Kattner, G., Clarke, A., and Sargent, J. 2000. Lipids, trophic relationships, and 347 biodiversity in Arctic and Antarctic krill. Can. J. Fish. Aquat. Sci. 57: 178-191. 348 Falk, K., and Durinck, J. 1993. The winter diet of thick-billed murres, Uria lomvia, in western Greenland, 1988-1989. Can. J. Zool. 71(2): 264-272. doi:10.1139/z93-038. 349 350 Ferrari, S., and Cribari-Neto, F. 2004. Beta regression for modelling rates and proportions. J. Appl. Stat. **31**(7): 799-815. doi:10.1080/0266476042000214501. 351 352 Fluhr, J., Strøm, H., Pradel, R., Duriez, O., Beaugrand, G., and Descamps, S. 2017. Weakening of the subpolar 353 gyre as a key driver of North Atlantic seabird demography: a case study with Brünnich's guillemots in 354 Svalbard. Mar. Ecol. Prog. Ser. 563: 1-11. doi:10.3354/meps11982. 355 Fort, J., Porter, W.P., and Gremillet, D. 2009. Thermodynamic modelling predicts energetic bottleneck for seabirds wintering in the northwest Atlantic. J. Exp. Biol. 212(15): 2483-2490. doi:Doi 356 357 10.1242/Jeb.032300.

- Fossheim, M., Primicerio, R., Johannesen, E., Ingvaldsen, R.B., Aschan, M.M., and Dolgov, A.V. 2015. Recent
   warming leads to a rapid borealization of fish communities in the Arctic. Nature Climate Change 5(7):
   673–677. doi:10.1038/NCLIMATE2647.
- Frederiksen, M., Linnebjerg, J.F., Merkel, F.R., Wilhelm, S.I., and Robertson, G.J. 2019. Quantifying the
   relative impact of hunting and oiling on Brunnich's guillemots in the North-west Atlantic. Polar Res. 38:
   ARTN 3378. doi: 10.33265/polar.v38.3378.
- Frederiksen, M., Descamps, S., Erikstad, K.E., Gaston, A.J., Gilchrist, H.G., Grémillet, D., Johansen, K.,
  Kolbeinsson, Y., Linnebjerg, J.F., Mallory, M., McFarlane Tranquilla, A.M., Merkel, F., Montevecchi,
  W.A., Mosbech, A., Reiertsen, T.K., Robertson, G., Steen, H., Strøm, H., and Thórarinsson, T.L. 2016.
  Migration and wintering of a declining seabird, the thick-billed murre *Uria lomvia*, on an ocean basin
  scale: Conservation implications. Biol. Cons. **200**: 26-35. doi:10.1016/j.biocon.2016.05.011.
- Frich, A.S. 1997. Lomviefangst i Nuuk vinteren 1995/96. Greenland Institute of Natural Resources, Technical
   Report No. 4, Nuuk, Greenland.
- Gaston, A.J., and Hipfner, J.M. 2000. Thick-billed Murre (*Uria lomvia*). *In* The Birds of North America Online.
   *Edited by* A. Poole, Cornell Lab of Ornithology, Ithaca, NY.
- Gaston, A.J., Goudie, R.I., D.G., N., and MacFarlane, A. 1983. Observations on turr hunting in
   Newfoundland: age, body composition and diet of Thick-billed Murres (Uria lomvia) and proportions of
   other birds killed off Newfoundland in winter. Canadian Wildlife Service, Technical Report 141, Ottawa,
- 376 Canada.
- Grémillet, D., Welcker, J., Karnovsky, N., Walkusz, W., Hall, M.E., Fort, J., Brown, Z.W., Speakman, J., and
   Hardin, J. 2012. Little auks buffer the impact of current Arctic climate change. Mar. Ecol. Prog. Ser. 454:
   197-206.
- Gudmundsdottir, A., and Vilhjálmsson, H. 2002. Predicting total allowable catches for Icelandic capelin,
   1978-2001. ICES J. Mar. Sci. 59: 1105-1115. doi:10.1006/jmsc.2002.1244.
- Haastrup, A. 2017. Appaqanngila? Ingen lomvie? En analyse af forskellige former for viden om lomvien og
   bæredygtighedstanker i Grønland. MA thesis, University of Copenhagen, Denmark.
- Härkönen, T. 1986. Guide to otoliths of the bony fishes of the Northeast Atlantic. Danbio Aps.
- Harris, M.P., Beare, D., Toresen, R., Nøttestad, L., Kloppmann, M., Dorner, H., Peach, K., Rushton, D.R.A.,
   Foster-Smith, J., and Wanless, S. 2007. A major increase in snake pipefish (Entelurus aequoreus) in
   northern European seas since 2003: potential implications for seabird breeding success181. Mar. Biol.
   151(3): 973-983.
- Hatun, H., Payne, M.R., Beaugrand, G., Reid, P.C., Sando, A.B., Drange, H., Hansen, B., Jacobsen, J.A., and
  Bloch, D. 2009. Large bio-geographical shifts in the north-eastern Atlantic Ocean: From the subpolar
  gyre, via plankton, to blue whiting and pilot whales. Prog. Oceanogr. 80(3-4): 149-162.
  doi:10.1016/j.pocean.2009.03.001.
- Heide-Jørgensen, M.P., Laidre, K.L., Hansen, R.G., Burt, M.L., Borchers, D.L., Hansén, J., Harding, K.,
  Rasmussen, M., Dietz, R., and Teilmann, J. 2012. Rate of increase and current abundance of humpback
  whales in West Greenland. J. Cetacean Res. Manag. 12(1): 1-14.
- Hempel, G. 1970. Antarctic. *In* The fish resources of the ocean. *Edited by* J.A. Gulland. Fao Fisheries
   Technical Paper No 97.
- ICES. 2014. Report of the ICES/NAFO Working Group on Harp and Hooded Seals (WGHARP), 17-21
   November 2014, Quebec City, Quebec, Canada. ICES CM 2014/ACOM:20. 62 pp.
- 400 ICES. 2020. North Western Working Group (NWWG). Draft Report. ICES Scientific Reports. 2:51. doi:
  401 10.17895/ices.pub.6051.
- 402 IPCC. 2013. Climate change 2013: The physical science basis. Summary for policymakers. Contribution of
   403 Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change,
   404 Cambridge University Press, Cambridge.

# Jansen, T., Hansen, F.T., and Bardason, B. 2021. Larval drift dynamics, thermal conditions and the shift in juvenile capelin distribution and recruitment success around Iceland and East Greenland. Fish. Res. 236: 1-11. doi:10.1016/j.fishres.2020.105845.

- Kirkegaard, J.B. 1992. Havbørsteorme. 1. Errantia. Danmarks Fauna Bd. 83. Dansk Naturhistorisk Forening,
  København. pp. 416.
- 410 Kuletz, K.J., Mallory, M.L., Gilchrist, H.G., Robertson, G., Merkel, F.R., Olsen, B., Hansen, E.S., Rönkä, M.,
- Anker-Nilssen, T., Strøm, H., Descamps, S., Gavrilo, M., Kaler, R., Irons, D., and Below, A. 2017. Seabirds. *In* State of the Arctic Marine Biodiversity Report, Conservation of Arctic Flora and Fauna International
  Secretariat, Akureyri, Iceland. http://www.caff.is. pp. 129-147.
- Lilliendahl, K. 2009. Winter diets of auks in Icelandic coastal waters. Mar. Biol. Res. 5(2): 143-154.
   doi:10.1080/17451000802279636.
- Lyngs, P. 2003. Migration and winter ranges of birds in Greenland an analysis of ringing recoveries. Dansk
   Orn. Foren. Tidskr. 97(1): 1-167.
- Merkel, F., Labansen, A.L., Boertmann, D., Mosbech, A., Egevang, C., Falk, K., Linnebjerg, J.F., Frederiksen,
  M., and Kampp, K. 2014. Declining trends in the majority of Greenland's Thick-billed Murre (*Uria lomvia*) colonies 1981-2011. Polar Biol. **37**(8): 1061-1071. doi:10.1007/s00300-014-1500-3.
- 421 Merkel, F.R., and Tremblay, J.E. 2018. Living resources. *In* Adaptation Actions for a Changing Arctic:
- Perspectives from the Baffin Bay/Davis Strait Region. *Edited by* A. Mosbech and M. Lemay and M.
  Simon and F. Merkel and T. Christensen and R.B. Jacobsen and P. Egede and K. Falk. Arctic Monitoring
  and Assessment Programme (AMAP), Oslo, Norway. pp. 133-199.
- 425 Merkel, F.R., Johansen, K.L., Nielsen, R.D., Petersen, I.K., Sterup, J., and Mosbech, A. 2019. Wintering 426 seabirds in south-west Greenland, 2017. Polar Res. **38**: 3462. doi:10.33265/polar.v38.3462.
- Milner-Gulland, E.J., Fryxell, J.M., and Sinclair, A.R.E. 2011. Animal migration: a synthesis. Oxford University
   Press, Oxford.
- Møller, E.F., and Nielsen, T.G. 2019. Borealization of Arctic zooplankton—smaller and less fat zooplankton
   species in Disko Bay, Western Greenland. Limnol. Oceanogr. doi:10.1002/lno.11380.
- Moon, T., Fisher, M., Harden, L., and Stafford, T. 2021. QGreenland ver. 1.0.0 (software), National Snow and
   Ice Data Center available from <a href="https://greenland.org">https://greenland.org</a>.
- Muus, B., and Nielsen, J.G. 1998. Havfisk og fiskeri i Nordvesteuropa. 5th ed. Gads forlag, Copenhagen. pp.
  358.
- Muus, B.J. 1959. Skallus, søtænder og blæksprutter. Danmarks Fauna Bd. 65. Gads forlag, Copenhagen. pp.
  239.
- 437 Nevins, H.M., and Carter, H.R. 2003. Age and sex of Common Murres *Uria aalge* recovered during the 1997438 98 Point Reyes Tarball Incidents in central California. Mar. Ornithol. **31**: 51-58.
- 439 Newton, I. 2008. The migration ecology of birds. Academic Press, London.
- 440 Ospina, R., and Ferrari, S.L.P. 2012. A general class of zero-or-one inflated beta regression models.
  441 Computational Statistics & Data Analysis 56(6): 1609-1623.
  442 doi:https://doi.org/10.1016/j.csda.2011.10.005.
- Post, S., Werner, K.M., Núñez-Riboni, I., Chafik, L., Hátún, H., and Jansen, T. 2021. Subpolar gyre and
  temperature drive boreal fish abundance in Greenland waters. Fish Fish. 22: 161-174.
  doi:10.1111/faf.12512.
- Provencher, J.F., Gaston, A.J., O'Hara, P.D., and Gilchrist, H.G. 2012. Seabird diet indicates changing Arctic
  marine communities in eastern Canada. Mar. Ecol. Prog. Ser. 454: 171-182. Available from <Go to</li>
  ISI>://000304605500014 [accessed.
- R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical
   Computing, Vienna, Austria. URL <a href="https://www.R-project.org">https://www.R-project.org</a>.
- Rowe, S., Jones, I.L., Chardine, J.W., Elliot, R.D., and Veitch, B.G. 2000. Recent changes in the winter diet of
   murres (*Uria* spp.) in coastal Newfoundland waters. Can. J. Zool. **78**: 495-500. doi:10.1139/z99-221.
- Scott, D.A. 1998. Global overview of the conservation of migratory Arctic breeding birds outside the Arctic.
   CAFF, Iceland.
- Tuck, L.M. 1961. The murres: their distribution, populations and biology a study of the genus. Canadian
   Wildlife Service Monograph Series No. 1, Minister of Supply and Services Canada, Ottawa, Canada.

- Vader, W., Barrett, R.T., Erikstad, K.E., and Strann, K.B. 1990. Differential responses of Common and Thickbilled Murres to a crash in the capelin stock in the southern Barents Sea. Stud. Avian Biol. 14: 175-180.
- Vehtari, A., Gelman, A., and Gabry, J. 2017. Practical Bayesian model evaluation using leave-one-out cross validation and WAIC. Statistics and Computing 27(5): 1413-1432. doi:10.1007/s11222-016-9696-4.
- 461 Vihtakari, M., Welcker, J., Moe, B., Chastel, O., Tartu, S., Hop, H., Bech, C., Descamps, S., and Gabrielsen,
- 462 G.W. 2018. Black-legged kittiwakes as messengers of Atlantification in the Arctic. Sci. Rep. 8(1): 1178.
  463 doi:10.1038/s41598-017-19118-8.
- Yee, T.W. 2015. Vector Generalized Linear and Additive Models: With an Implementation in R. Springer,
   New York, USA.
- 466

## 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 <u>http://qgis.osgeo.org</u>), 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.



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

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

#### 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 prev	1990s	2010s	All birds
species	(85)	(55)	(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

**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	M. norvegica			
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			