The co-distribution of Arctic cod and its seabird predators across the marginal ice zone in Baffin Bay

Mathieu LeBlanc*, Stéphane Gauthier†, Svend Erik Garbus‡, Anders Mosbech‡ and Louis Fortier*

Arctic cod (Boreogadus saida) is the dominant pelagic fish in Arctic seas and a staple food of many arctic predators including several seabird species. Marginal ice zones are known as important feeding locations for seabirds. The hypothesis that thick-billed murre (Uria lomvia), northern fulmar (Fulmarus glacialis) and black-legged kittiwake (Rissa tridactyla) congregate in areas of high Arctic cod food resource and low ice concentration was tested at different spatial scales. Arctic cod biomass was estimated by hydroacoustics as a resource proxy, and seabirds were counted and sampled for stomach analysis along eight longitudinal transects across the marginal ice zone in southern Baffin Bay in June–July 2016. With increasing length, the epipelagic age-0 Arctic cod migrated from open waters to ice-covered areas. Subsequently, age-1 and age-2 Arctic cod tended to concentrate in a subsurface layer (40–100 m) within the epipelagic layer. Arctic cod 5.7–16.1 cm long (late age-0 to age-5) were the main fish prey of the three seabird species, which preferentially captured age-1 cod (6–11.5 cm). At large spatial scale (western versus eastern Baffin Bay), thick-billed murre, northern fulmar and their Arctic cod resource proxy were generally more abundant on the western ice-covered side of Baffin Bay. No clear spatial match was found, however, when comparing seabird abundances and their food-resource proxy in different ice concentrations across the marginal ice zone or at small scale (5 km). At medium scale (12.5 km), only murre density was influenced positively by its Arctic cod resource. A lack of schooling behavior and a successful strategy to avoid predation by hiding under the ice could explain the absence of any strong spatial match between Arctic cod and its seabird predators at these different scales.

Keywords: Boreogadus saida; Arctic seabirds; Predator-prey interactions; Spatial distribution; Ontogenetic migration; Marginal ice zone

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regions (e.g., Logerwell et al., 1998; Mehlum et al., 1999; Matley et al., 2012a; Suryan et al., 2016). Offshore ice edges and marginal ice zones (where the limit between pack ice and open water is more a gradient than a sharp edge; Smith, 1987) are productive areas (e.g., Mundy et al., 2009) that are often favored feeding locations for seabirds where they feed in openings on invertebrates and fish (Bradstreet, 1982). On the other hand, extensive ice cover can impede foraging (Hunt, 1990).

The degree of association among species typically varies with the spatial scale of observation, and a multiscale approach may help capture the spatial scales at which species are most likely to interact (Schneider and Piatt, 1986; Logerwell and Hargreaves, 1996; Logerwell et al., 1998; Mehlum et al., 1999). In the present study, we tested the hypothesis that seabirds congregate in areas of the marginal ice zone where fish biomass is high and/or ice concentration is low. The stomach contents of thick-billed murre, northern fulmar and black-legged kittiwake were analyzed to identify the fish prey of each species. The co-distribution of seabirds and their potential fish resource was compared at three spatial scales (west vs east Baffin Bay, 12.5 km and 5 km) as well as in relation to percent ice cover across the marginal ice zone of Baffin Bay.

Materials and methods

Study area

Baffin Bay is a large (689,000 km²) seasonally ice-covered sea with relatively narrow continental shelves surrounding an abyssal plain as deep as 2300 m. It is connected to the Arctic Ocean by the narrow and shallow Nares Strait, and to the Labrador Sea and the Atlantic Ocean by Davis Strait. The generally cyclonic circulation carries Atlantic waters northward along Greenland and Arctic waters southward along Baffin Island (e.g., Tang et al., 2004). Except for the North Water polynya and the southeastern part, Baffin Bay is covered with ice for most of the year and completely ice-free in August and September. Typically, ice breakup in April–May progresses from south to north along Greenland, resulting by July in a S–N oriented marginal ice zone with open water to the east and pack ice to the west (e.g., Tang et al., 2004, their Figure 5). As part of the international Green Edge expedition, the research icebreaker CCGS Amundsen conducted an ecosystem survey from 9 June to 12 July 2016 along eight longitudinal transects across the marginal ice zone of southern Baffin Bay (Figure 1). Depth along the transects varied from 144 to 2100 m (average of 928 m). The midnight sun prevailed during the entire duration of the survey.

Sea-ice cover

Satellite-based estimates of daily sea-ice concentration (% cover) were provided by IFREMER/CERSAT at a pixel resolution of 12.5 × 12.5 km (ftp.ifremer.fr/ifremer/cersat). Each 12.5-km segment along the survey transects was assigned the sea-ice concentration of the nearest most overlapping pixel on the sampling day. No sea-ice cover data were available at a resolution scale of 5 km; values were assigned from the 12.5-km resolution data following the same method.

Figure 1: Sampling locations and transects surveyed. Deployment locations of epipelagic net (red circles), bottom trawl (pink circles), simultaneous epipelagic net and pelagic trawl (blue circles), simultaneous epipelagic net and bottom trawl (yellow circles), and locations of seabird sampling (green rectangles). The CCGS Amundsen route (black line), and simultaneous hydroacoustic and seabird sighting transects (teal line) are presented. The order of the completed transects is indicated by 1–8. The background gradient (white–gray scale) represents the mean sea-ice concentration from 9 June to 12 July 2016. Coastal areas with no available ice data are indicated in black. The dashed box shows the domain of Figure 6. DOI: https://doi.org/10.1525/elementa.339.f1
**Fish sampling and acoustic detection**

The abundance and taxonomy of fish along the survey transects were assessed by acoustics validated by deploying a combination of ichthyoplankton sampler and trawls during both day and night. To document the epipelagic fish assemblage, a Double Square Net bearing two square conical nets (1-m² aperture, 500-µm and 750-µm meshes, respectively) was deployed from the surface to depths of 75 to 103 m at 17 locations (Figure 1). The standard length (SL) of up to 50 Arctic cod was measured fresh after each net retrieval. All epipelagic fish were preserved in 95% ethanol. Pelagic fish were sampled with an Isaacs-Kidd Midwater Trawl (IKMT, 9-m² rectangular mouth aperture with mesh sizes of 11 mm in the first section and 5 mm in the last section), deployed from the surface to depths of 244 to 520 m on six occasions (Figure 1). Demersal and benthic fish were sampled with a bottom beam trawl (3-m² rectangular aperture with a headline and a footrope of 4.27 m and a cod-end mesh of 9.5 mm) deployed at sea-floor depths of 199 to 359 m at five locations (Figure 1). The pelagic and bottom trawls were towed at 2–3 knots for 10 to 20 min. All fish collected by the trawls were measured before freezing at –20°C.

Fish density was estimated with a Simrad EK60® split-beam echosounder following the recording and processing methods of Bouchard et al. (2017), except that the acoustic signal was processed with background and impulsive noise removal operators (De Robertis and Higginbottom, 2007; Ryan, et al. 2015) instead of a time-varied threshold. Due to the depth of the transducers on the vessel hull (~7 m); potential vessel avoidance by fish, and acoustic near-field effects (Simmonds and MacLennan, 2005), effective sampling by the echosounder was assumed to start at 12 m; the top 12 m of the water column were excluded from the analysis. The difference in mean volume backscattering strength ∆MVBS (dB re: 1 m⁻²) between 38 and 120 kHz was used to discriminate pelagic fish and dense aggregations of large zooplankton.

In the present study, Arctic cod and 5.0–7.6 cm long *Benthosema glaciale* (mean SL of 6.3 cm) were the only two pelagic species caught in nets with a swim bladder and likely detected at 38 kHz. Arctic cod represented 96% of the total number of the two species captured in the three nets (epipelagic net, pelagic trawl, and bottom trawl). We therefore assumed that echo-integration cells with ∆MVBS₂₀₈₀ in the range –10 dB to 5 dB were dominated by Arctic cod (Benoit et al., 2014; Geoffroy et al., 2016), mixed occasionally with small numbers of *B. glaciale*.

The mean fish target strength (TS, dB re: 1 m⁻²) of each of the two species was estimated from their respective mean SL in net/trawl collections, using $TS = 14.33 \log_{10}(SL) - 65.13$ for Arctic cod (Geoffroy et al., 2016), and $TS = 30 \log_{10}(SL) - 84.5$ for *B. glaciale* (based on Scoulling et al., 2015). Mean TSs were converted to mean backscattering cross-sections ($\sigma_b = 10^{TS/10}$ m²). The total area backscattering coefficient (ABC, m² m⁻¹), integrated over the depth intervals of 12–20 m and 12–200 m, was partitioned to each species based on their relative frequencies in nets/trawls and mean $\sigma_b$ (Simmonds and MacLennan, 2005). The overall density of Arctic cod (individual m⁻²) in each depth interval was estimated by dividing its partitioned ABC for that interval by $\sigma_b$ (Simmonds and MacLennan, 2005; Parker-Stetter et al., 2009). The overall density of Arctic cod was used to calculate the food resource of the three seabird species (see below).

A proxy for availability of Arctic cod to surface-feeding northern fulmar and black-legged kittiwake was estimated in echo-integration cells corresponding to the depth interval of 12–20 m by 5-km transect segments (small scale analysis, $n = 216$ cells) and 12.5-km segments (medium scale analysis, $n = 104$ cells), respectively. The corresponding echo-integration cells for the deep-diving thick-billed murre spanned the depth interval of 12–200 m. A large-scale analysis was also conducted by contrasting western and eastern Baffin Bay, using longitude 60°W as limit between the two regions.

**Estimated in situ length-frequency distribution of Arctic cod**

The length-frequency distribution of Arctic cod *in situ* was estimated from TS of targets detected at 38 kHz as determined by the Echoview® single-echo detection algorithm for split-beam echosounder (method 2: threshold applied on targets after compensation for their position in the beam). Targets detected in the depth intervals of 12–20 m and 12–200 m were assumed to be of Arctic cod, given the overall low frequency of *B. glaciale* (4%) in nets/trawls and its tendency to remain at depths ≥200 m in daylight (Kaartvedt et al., 2009). To eliminate multiple echoes detection, cells 20 pings long and 20 m deep with a Sawada Index >0.04 were removed (Gauthier and Rose, 2001). A lower threshold of ~70 dB and an upper threshold of ~43 dB were set to exclude zooplankton and targets bigger than the largest Arctic cod (Geoffroy et al., 2016). The frequency distribution of SL (based on TS of targets detected) was determined for each echo-integration cell defined for the surface-feeding northern fulmar, black-legged kittiwake (12–20 m by 5 or 12.5 km) and for the deep-diving thick-billed murre (12–200 m by 5 or 12.5 km). When less than 10 targets were detected in a given cell, the length-frequency distribution for that cell was estimated by pooling TS of targets for that cell and the two adjacent cells along the transect.

**Seabird observation, sampling and stomach content analysis**

Seabirds were identified and counted from the bridge of the icebreaker (16 m above sea level) during transit between sampling stations (Figure 1) at speeds ranging from 13 to 18.5 km h⁻¹. The same observer enumerated all birds continuously on one side within a 300-m band perpendicular to the track of the ship using binoculars and a computer-based logger, grouping observations over two-minute blocks following Johansen et al. (2015). The time, coordinates, distance from ship and behaviour of birds (flying or resting on water) were noted for each observation. The analysis was focused on foraging birds that could potentially be influenced by their prey. Therefore, all birds sighted were included (flying or on water) for northern fulmar and black-legged kittiwake as they may dive directly from the air to feed (Matley et al., 2012b), while only thick-billed murre on water were included. Birds suspected to
be ship followers (following or circling around the ship) were excluded from the analysis as well. Seabird numbers were calculated for 5-km and 12.5-km visual transects corresponding to the acoustic echo-integration cells and were converted into abundances (individual [ind.] km⁻¹) for fulmar and kittiwake. Density (ind. km⁻²) was calculated for murre using the distance sampling method (Buckland et al., 2001), as all birds included in the analysis were on water allowing for accurate distance from ship estimation. Overall, 2013 2-minute observation periods, nearly uniformly distributed over 104 12.5-km segments (216 5-km segments), were recorded.

Seabirds were sampled from a zodiac launch deployed from the Amundsen on ten occasions in Greenland waters (Figure 1). Adult individuals were shot in flight or on water by a skilled seabird hunter (with appropriate hunting permit delivered by the Ministry of Fisheries, Hunting and Agriculture of Greenland). In total, 35 thick-billed murres, 30 northern fulmars and 9 black-legged kittiwakes were collected (Table 1). Collected birds were frozen at –20 °C. In the laboratory, the whole stomach (proventriculi and gizzard) was removed. Stomach contents were examined under a dissecting microscope, and fish otoliths were retrieved. Otoliths retained in the stomach were assumed to be sagittae, were identified to the lowest taxonomic level possible (following Härkönen, 1986; Campana, 2004), and their number was divided by two to estimate the number of fish ingested. Total length (TL, mm) of Arctic cod prey was estimated from otolith length (OL, mm) based on TL = 20.6631 + 24.2791 OL, and then transformed into SL (cm) using SL = (–0.2736 + 0.9187 TL) /10 (David et al., 2016). The age of individual Arctic cod prey was estimated with the age-length relationships reported in Falk-Petersen et al. (1986, their Figure 9).

**Estimating the Arctic cod resource available to seabirds**

The Arctic cod food resource (mg m⁻²) available to each seabird species in each echo-integration cell was calculated based on the overall density and length-frequency distribution of Arctic cod in situ in the size range of Arctic cod ingested by seabirds (4–18 cm). For the thick-billed murre, the food resource was calculated in the depth interval of 12–200 m corresponding to the maximum diving range; for the black-legged kittiwise and the northern fulmar, the resource was calculated in the depth interval of 12–20 m as a proxy for food availability in their maximum diving range of 1 and 3 m, respectively. The average weight (W in mg) of Arctic cod in each 2-cm SL interval of the frequency distributions was calculated by integrating the relationship W = (0.0055 SL⁻¹ /2)¹⁰⁰⁰ (Geoffroy et al., 2016) over the length interval. Based on Fortier and Harris (1989) and Ponton and Fortier (1992), the Arctic cod resource (R) available for a given seabird species was

### Table 1: Relative frequency (%) of fish species ingested by seabirds and sampled by the epipelagic net, pelagic trawl and bottom trawl. DOI: [https://doi.org/10.1525/elementa.339.t1](https://doi.org/10.1525/elementa.339.t1)

<table>
<thead>
<tr>
<th>Fish species</th>
<th>Northern fulmar</th>
<th>Thick-billed murre</th>
<th>Black-legged kittiwake</th>
<th>Epipelagic net</th>
<th>Pelagic trawl</th>
<th>Bottom trawl</th>
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<td>94.4</td>
<td>96.4</td>
<td>97.1</td>
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<td>Triglops sp.</td>
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<td>Others†</td>
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<td>0.0</td>
<td>0.9</td>
<td>11.8</td>
<td>14.4</td>
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**Related data**

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<th>Northern fulmar</th>
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<th>Black-legged kittiwake</th>
<th>Epipelagic net</th>
<th>Pelagic trawl</th>
<th>Bottom trawl</th>
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<td>11.3</td>
<td>96.2</td>
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* Category "Others" includes Anarhichas lupus, Anarhichas minor, Artedius atlanticus, Gymnelius viridis, Hypoglossoides platessoides, Leptocephalus maculatus, Leucoraja ocellate, Lumpenus fabricii, Lycenchelys pauxillus, Lycodes terraenovae, Nezumia bairdi, Reinhardti hippoclosoide and Stomias boa.

† Measure of diversity of fish ingested or sampled.

‡ Mean number of fish in stomach (for all birds of a given species, with or without stomach content) and in net samples.
estimated as $R = \sum_{i=1}^{n} W_i D_i$, where $W_i$ is the average weight of Arctic cod in SL interval $i$, $D_i$ is the density of SL interval $i$ in the echo-integration cell (product of overall density by frequency of SL interval $i$) and $n$ is the number of 2-cm length intervals in the frequency distributions (from 4 to 18 cm). Following the same method, the biomass of Arctic cod <4 cm was also estimated in each cell, hereafter referred to as small Arctic cod biomass.

Seabird abundance (fulmar and kittiwake) and density (murre) were then compared to their available Arctic cod food-resource proxy (4–18 cm length) and to small Arctic cod biomass (<4 cm length) at different scales (West-East Baffin Bay, 12.5 km, 5 km) along the survey transects. Seabird abundance/density was non-normal due to frequent 0-values and was rounded for statistical analyses. The influence of Arctic cod resource, small Arctic cod biomass and sea-ice concentration on bird distribution at medium (12.5 km) and small (5 km) scales was tested with zero-inflated negative binomial regressions. To test spatial differences at large scale (West-East Baffin Bay and in different ice concentrations across the marginal ice zone), non-parametric tests (Mann-Whitney U and Kruskal-Wallis tests) were used for Arctic cod food resource and small Arctic cod biomass, whereas negative binomial regressions were used for seabird abundance/density. All statistical analyses were performed with R® version 3.2.3 (R Core Team, 2015).

Results

**Seabird fish prey and in situ fish assemblage**

Northern fulmar ($n = 2242$), thick-billed murre ($n = 2028$) and black-legged kittiwake ($n = 278$), the three most abundant piscivorous seabirds observed along the survey transects, were included in the analysis. Other relatively frequent bird species ($n > 30$) were the glaucous gull (*Larus hyperboreus*), the little auk (*Alle alle*), the black guillemot (*Cepphus grille*) and the common eider (*Somateria mollissima*).

A majority of the northern fulmar, thick-billed murre and black-legged kittiwake sampled at sea presented a stomach content and most contained fish otoliths (Table 1). The mean number of fish ingested per bird was similar for the three species. About two thirds of the fulmars (11/18), murres (13/21) and kittiwakes (5/8) with otoliths in their stomachs also had other discernable fish remnants (e.g., flesh, eyes, bones) indicating that they had been feeding on fish recently (in the last 6 to 24h; Hawkins et al., 1997; Hilton et al., 2000). The low-diversity fish diet of murre and kittiwake (Shannon index = 0.1) was dominated by Arctic cod (>94%), and similar to the fish assemblage in the epipelagic net collections. Northern fulmar also preyed primarily on Arctic cod (~60%) but presented a much more diversified fish diet (Shannon index = 0.6), feeding on no less than 9 fish species including four Liparidae (*Liparis atlanticus*, *L. fabricii*, *L. gibbus* and *Careproctus reinhardtii*). Both surface-feeding fulmar and kittiwake preyed on *B. glaciale*, a bathypelagic species that dominated collections in the deep pelagic trawl (Table 1). The fulmar also captured *Lampanyctus mcdonaldi*, another bathypelagic fish.

The estimated mean SL of Arctic cod prey differed significantly (one-way ANOVA, $p < 0.001$) among the three seabird species (Figure 2). Overall, Arctic cod prey ranged from 5.7 to 16.1 cm in SL (mean = 9.16 cm, $n = 150$) corresponding to age-0 to age-5 fish (mostly age-1). By comparison to seabirds, the epipelagic net captured essentially

![Figure 2: Standard-length frequency distribution of Arctic cod ingested by seabirds and sampled by the nets/trawls.](https://doi.org/10.1525/elementa.339.f2)
small 0.6–1.4 cm (with one 4.9 cm exception) age-0 Arctic cod (Figure 2). The pelagic trawl collected larger age-0 and age-1 Arctic cod 5.2 to 6.8 cm, while Arctic cod in the bottom trawl ranged in SL from 5.7 to 17.2 cm, and from age-0 to age-5.

The distribution of Arctic cod across the marginal ice zone
Coriolis forcing maintained the southward-drifting ice cover on the western side of Baffin Bay, which resulted in a well-defined marginal ice zone (Figure 1). On average over the study period (early June to mid-July), 100% ice cover prevailed on the western Canadian side, thinning progressively to fully open waters on the eastern Greenland side. Despite this general pattern, ice concentration along the survey transects could be highly variable at smaller spatio-temporal scales.

Vertically, Arctic cod distributed in two distinct continuous scattering layers: an epipelagic layer down to about 50 m and a mesopelagic layer above the bottom or between 200 and 300 m in deeper areas (Figure 3). Both scattering layers varied in thickness and density among regions with different ice cover. However, in a given location, scattering density varied little horizontally, and no discrete schools were observed in the scattering layers. Some filament-shaped horizontal aggregations were observed between

Figure 3: Examples of fish distribution in different ice concentrations. Acoustic data ($S_v$) measured at 38 kHz in the depth interval of 12–450 m over a distance of 2 km. Two main scattering layers of fish are present: an epipelagic (red arrow) and a mesopelagic (pink arrow) layer. The hatched part of the echograms represents the top 12 m excluded from the analysis. Areas below the bottom or considered as noise are in black. For each panel (a–e), ice concentration (% ice cover) is followed by local time at the middle of the transect. DOI: https://doi.org/10.1525/elementa.339.f3
the two main scattering layers in echograms recorded at nighttime and early morning (Figure 3a, b, e).

The length of Arctic cod estimated from TS of targets detected at 38 kHz increased with sea-ice concentration (Figure 4). In the depth layer of 12–20 m, the length-frequency distribution of age-0 Arctic cod <5 cm generally shifted to larger sizes with increasing % ice cover. However, the relative frequency of age 1+ Arctic cod (fish > 5 cm), the main fish prey of seabirds, changed little with sea-ice concentration. By contrast, in the depth layer of 12–200 m where the deep-diving thick-billed murre forages, the relative frequency of age-1+ Arctic cod prey increased with sea-ice cover to a maximum at ice concentrations between 40 and 100% (Figure 4).

The length of Arctic cod estimated from TS of targets detected at 38 kHz generally increased with depth over the interval of 12–200 m (Figure 5). Small age-0 Arctic cod dominated the population based on detections. Some age-1 and age-2 Arctic cod, the preferred prey of seabirds, were detected at nearly all depths under each

![Figure 4: Length-frequency distribution of Arctic cod detected in different ice concentrations.](https://doi.org/10.1525/elementa.339.f4)
ice-cover concentration. Moreover, relatively high SL were concentrated in a subsurface layer (40–100 m) for all ice concentration classes, indicating an increased frequency of larger Arctic cod even though small age-0 were preponderant. This subsurface layer of larger fish tended to thicken with ice concentration, spanning the depth interval of 40–80 m at 0–40% ice cover to that of 20–120 m at 40–100% ice cover.

Figure 5: Box and whisker plots of the length of Arctic cod by 20-m deep intervals in different ice concentrations. Box and whisker plots of the length on a log_{10}-based scale measured as target strength (TS, top x-axis) of targets detected at 38 kHz. The black vertical line in the box is the median, the left and right boundaries of the box are the 25 and 75 percentiles, and the whiskers are the minimum and maximum values. The bottom x-axis provides the estimated standard length (SL) of Arctic cod based on TS \( TS = 14.33 \log_{10}[SL]–65.13 \) (Geoffroy et al., 2016). Values for \( n \) are the number of targets detected. Size range corresponding to age-0, age-1 and age-2 are presented. DOI: https://doi.org/10.1525/elementa.339.f5

The co-distribution of Arctic cod and its seabird predators across the marginal ice zone

The three seabirds, their Arctic cod resource proxy and small Arctic cod were widely distributed across the sea-ice gradient of the marginal ice zone (Figure 6). The Arctic cod resource of the deep-diving thick-billed murre and small Arctic cod in the depth layer of 12–200 m were more abundant \( (p < 0.001, \) Mann–Whitney U test) under
the dense ice cover on the western side of Baffin Bay than in the open waters to the east (Figure 6b, c; Table 2). The density of murre was concentrated in southern transects 4 and 8 and roughly followed this longitudinal gradient in food availability along transect 4 (Figure 6a–c). But both low and high concentrations of murre were observed in the resource-rich ice-covered western waters and in the resource-poor open eastern waters. Overall, murre were slightly more abundant in the resource-rich waters on the western side of the Bay (Table 2), although the difference was not statistically significant ($p > 0.05$, Negative binomial regression).

As expected, less Arctic cod food resource seemed to be available to the surface-feeding northern fulmar and black-legged kittiwake, using the depth layer of 12–20 m as proxy, than to the deep-diving thick-billed murre in the depth layer of 12–200 m (Figure 6; Table 2). The resource proxy of both fulmar and kittiwake and small Arctic cod

<table>
<thead>
<tr>
<th>Region</th>
<th>Thick-billed murre (ind. km$^{-2}$)</th>
<th>Food resource (12–200 m) (mg m$^{-2}$)</th>
<th>Small AC (12–200 m) (mg m$^{-2}$)</th>
<th>Northern fulmar (ind. km$^{-1}$)</th>
<th>Food resource (12–20 m) (mg m$^{-2}$)</th>
<th>Small AC (12–20 m) (mg m$^{-2}$)</th>
<th>Black-legged kittiwake (ind. km$^{-1}$)</th>
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$^a$ Differences were not significant for seabird abundance/density ($p > 0.05$, Negative binomial regression).

$^b$ Ice concentration was significantly higher on western side than eastern side ($p < 0.001$, Negative binomial regression).

$^c$ Significantly higher ($p < 0.05$, Mann–Whitney U test).
in the depth layer of 12–20 m were patchily distributed, with high values occurring both in the eastern open waters (e.g., transects 1 and 3) and under the western dense ice cover (transects 6, 7, and 8), with generally lower values in the intermediate ice gradient (Figure 6e, f). At the scale of the survey area, no spatial match between the distribution of fulmar or kittiwake and that of their potential food was obvious (Figure 6d–g). However, northern fulmar was marginally (p > 0.05, Negative binomial regression) more abundant on the western side of the Bay where its Arctic cod food-resource proxy and small Arctic cod were more abundant (p < 0.05, Mann–Whitney U test; Table 2). In contrast, black-legged kittiwake was more abundant on the eastern side (Table 2), although the difference was not statistically significant (p > 0.05, Negative binomial regression).

When grouped according to ice coverage, no clear pattern was found between the abundance/density of seabirds and their Arctic cod food across the marginal ice zone (Figure 7). On average, and despite a highest value in ice concentration 20–40% (p = 0.005, Kruskal-Wallis test), the food resource of thick-billed murre was distributed relatively uniformly across the marginal ice zone (Figure 7a). Small Arctic cod biomass (<4 cm length) in the depth interval of 12–200 m was much lower than

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**Figure 7:** Seabirds density/abundance and Arctic cod biomass in different ice concentrations. Mean thick-billed murre density (a; ind. km<sup>–2</sup>), northern fulmar (b; ind. km<sup>–1</sup>) and black-legged kittiwake (c; ind. km<sup>–1</sup>) abundances, their Arctic cod food-resource proxy (mg m<sup>–2</sup>) and small Arctic cod (AC) biomass (mg m<sup>–2</sup>) in different ice concentrations. Circles represent abundance/density of seabirds and bars represent Arctic cod food resource and small Arctic cod biomass. Asterisks (a) indicate ice concentration class with significant highest value (p < 0.05) of Arctic cod food resource or small Arctic cod biomass (Kruskal-Wallis test) and of murre density (Negative binomial regression). DOI: https://doi.org/10.1525/elementa.339.f7
the food resource in all ice concentrations and was significantly higher in 80–100% ice cover \( (p < 0.001, \text{Kruskal-Wallis test); Figure 7a}.\) Total Arctic cod biomass \( (\leq 18 \text{ cm length}) \) in the depth interval of 12–200 m was mainly dominated by large age-0 and age-1 Arctic cod 4–8 cm across the different ice concentrations \( \text{(Figure 8).} \) Murre density increased from low–medium \( (0–60\%) \) to high ice concentration \( (60–100\%) \), and highest bird density was measured in 80–100% ice cover \( (p < 0.001, \text{Negative binomial regression; Figure 7a}). \)

The Arctic cod food-resource proxy of surface feeders was higher in low ice concentration \( (0–20\%) \), although not statistically significant \( (p > 0.05, \text{Kruskal-Wallis test); Figure 7b, c}. \) Small Arctic cod biomass level in the depth layer of 12–20 m was similar to the food-resource proxy of seabirds (except in the 0–20% ice cover) and generally increased with ice concentration \( \text{(Figure 7b, c).} \) No length interval clearly dominated the total Arctic cod biomass \( (\leq 18 \text{ cm length}) \) in the depth interval of 12–20 m in low–medium ice concentration \( (0–60\% \text{ ice cover}) \) whereas

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**Figure 8:** Frequency of total Arctic cod biomass for each length interval in different ice concentrations. Biomass frequency \( (%) \) of each length interval \( (\leq 18 \text{ cm length}) \) of Arctic cod was calculated for the depth intervals of 12–20 m and 12–200 m under ice conditions of 0–20, 20–40, 40–60, 60–80, and 80–100% ice cover. DOI: https://doi.org/10.1525/elementa.339.f8
2–4 cm Arctic cod (age-0) were predominant in high (60–100%) ice concentration (Figure 8). Both northern fulmar (20–40%) and black-legged kittiwake (0–40%) preferred low to medium ice cover (Figure 7b, c), but the differences were not statistically significant ($p > 0.05$, Negative binomial regression).

**Medium-scale spatial association**

The Arctic cod food resource in the depth interval of 12–200 m had a significant positive effect ($p = 0.03$, Zero-inflated negative binomial regression) on thick-billed murre density at a medium scale of 12.5 km, but this food-resource proxy in the depth interval of 12–20 m had no significant effect ($p > 0.05$) on northern fulmar and black-legged kittiwake abundances (Negative binomial part of the regression models, Table 3). Small Arctic cod biomass in the depth interval of 12–20 m had a significant negative effect ($p = 0.02$) on kittiwake abundance (Negative binomial part of the regression models, Table 3). There was no significant effect of ice concentration on murre density or fulmar and kittiwake abundances ($p > 0.05$).

**Excess in absence of the three seabird species (0-values) at medium scale (12.5 km) was not influenced significantly ($p > 0.05$, Zero-inflated negative binomial regression) by Arctic cod food resource, small Arctic cod biomass or ice concentration (Zero-inflated part of the regression models, Table 3).**

**Table 3:** Zero-inflated negative binomial regression coefficients of the effect of Arctic cod food resource, small Arctic cod (AC) biomass and ice concentration on thick-billed murre density, and northern fulmar and black-legged kittiwake abundances at medium scale of 12.5 km. DOI: https://doi.org/10.1525/elementa.339.t3

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* Significant effect ($p < 0.05$).

**Small-scale spatial association**

Arctic cod food resource and small Arctic cod biomass measured in the depth intervals of 12–20 m and 12–200 m had no significant effect ($p > 0.05$, Zero-inflated negative binomial regression) on thick-billed murre density or on northern fulmar and black-legged kittiwake abundances at a small scale of 5 km (Negative binomial part of the regression models, Table 4). There was no significant effect ($p > 0.05$) of ice concentration on seabird abundance/density.

**Table 4:** Zero-inflated negative binomial regression coefficients of the effect of Arctic cod food resource, small Arctic cod (AC) biomass and ice concentration on thick-billed murre density, and northern fulmar and black-legged kittiwake abundances at small scale of 5 km. DOI: https://doi.org/10.1525/elementa.339.t4

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* Significant effect ($p > 0.05$).
Excess in absence of the three seabird species (0-values) at small scale (5 km) was not significantly influenced (p > 0.05, Zero-inflated negative binomial regression) by Arctic cod food resource, small Arctic cod biomass or ice concentration (Zero-inflated part of the regression models, Table 4).

**Discussion**

**An ontogenetic migration of Arctic cod across the marginal ice zone?**

Over the annual cycle in the offshore Beaufort Sea, Arctic cod were segregated vertically by size and age, with age-0 forming an epipelagic scattering layer (<100 m) and age-1+ distributing progressively deeper in the mesopelagic scattering layer (200–500 m) as their size increased (Geoffroy et al., 2016). The same general distribution into an epipelagic scattering layer dominated by age-0 Arctic cod and a mesopelagic layer dominated by larger fish was observed in southern Baffin Bay (Figure 3). Our TS analysis also confirmed a general increase in the length of Arctic cod with depth (Figures 4 and 5). It further revealed an ontogenetic horizontal migration of age-0 in the depth interval of 12–200 m from the open waters (0–20% ice cover), where small larvae <1.2 cm dominated, to the 40–100% ice pack, where metamorphosing and metamorphosed juveniles (2.3–6 cm) were increasingly frequent (Figure 4). Vertically, age-1 and age-2 Arctic cod were detected at all depths over the interval of 12–200 m, with increased frequency in the subsurface layer of 40–100 m (Figure 5). The emerging pattern is that of a progressive migration of age-0 Arctic cod from the productive open waters to the shelter of the ice cover, followed by some concentration of the developing age-1 and age-2 in the depth interval of 40–100 m. Thereafter, a further ontogenetic migration of age-2+ Arctic cod to depths >200 m occurs (Geoffroy et al., 2016). In this study, this pattern resulted in a general increase in the availability of Arctic cod resource to seabirds from the open eastern waters to the ice-covered western waters, in particular in the depth layer of 12–200 m accessible to the deep-diving thick-billed murre (Figure 6; Table 2). However, this general pattern is not fully supported by the distribution of Arctic cod resource as a function of ice concentration, which shows that, despite higher proportions in biomass of age-1+ Arctic cod (>6 cm) under the ice cover (Figure 8), the food resource for deep-diving seabirds in the layer of 12–200 m can be similar at the ice edge (0–20% cover) and under the ice cover (Figure 7a).

Vertically, we found no indication in the acoustic record that the age-1 and age-2 Arctic cod prey of seabirds were particularly abundant near the ice at the surface, their relative frequency and biomass being much higher in the overall layer of 12–200 m than in the narrow sublayer of 12–20 m (Figures 4 and 8). Yet, age-1 and age-2 Arctic cod with sympagic behavior are present at the ice-water interface and sporadically can swarm immediately under the ice (Gradinger and Bluhm, 2004; Melnikov and Chernova, 2013; David et al., 2016). Such near-surface swarms could not be detected acoustically given the 0–12 m acoustic gap above the effective sampling depths of our echosounder, although some sympagic individuals might have been detected below 12 m as, hypothetically, Arctic cod growing under the ice could migrate vertically to follow their zooplankton prey (see Melnikov and Chernova, 2013). As well, age-1+ fish may have shunned the ice-breaking noise from the ship because higher levels of Arctic cod resource were observed in the depth layer of 12–20 m at low ice concentrations, 0–20% (little or no icebreaking noise), than in medium–high concentrations of 20–100% (frequency noise) (Figure 7). In any case, the biomass of age-1+ Arctic cod detected in the depth interval of 12–20 m likely underestimated the actual food resource available to surface-feeding northern fulmar and black-legged kittiwake. In a given location, however, the epipelagic scattering layer (12 to ~50 m) proved remarkably uniform vertically (Figure 3). Accordingly, we assume that, although prey resource at the very surface might be influenced to some degree by top-down pressure from predators, spatial variations in Arctic cod resource in the depth layer of 12–20 m were a representative proxy of spatial variations in the food available to surface-feeding seabirds.

**A lack of coherence in the spatial co-distribution of seabirds and their Arctic cod food**

As previously reported in the Barents Sea (Mehlum and Gabrielsen, 1993), the fish diet of black-legged kittiwake was comprised of the Arctic cod and the bathypelagic B. glaciale, suggesting that foraging was limited to deep offshore waters, presumably when these two pelagic fish move close to the surface. Northern fulmar preyed on a much wider fish spectrum, including the ice-associated Arctic cod and L. fabricii, the bathypelagic B. glaciale and L. macdonaldi, as well as several benthic or benthopelagic species not captured by the nets and trawls (Table 1). Its fish diet and surface-feeding behaviour suggest that, in addition to feeding in the offshore ice-covered waters, the fulmar likely fed in shallow waters on its way from the colonies to the marginal ice zone and possibly also on discard from trawlers or dead organisms (Hobson and Welch, 1992; Mehlum and Gabrielsen, 1993; Phillips et al., 1999). Although dominated by Arctic cod, the fish diet of thick-billed murre included the infrequent L. atlanticus and Triglops sp., suggesting some limited nearshore feeding as well (Elliott et al., 2009). As the timing of this study (9 June to 12 July) corresponded to the beginning of the breeding season of the three seabird species (McLaren, 1982), some fish ingested may have also been captured during migration from wintering grounds. Anecdotal reports have described how seabirds and marine mammals will congregate on kilometre-long schools of Arctic cod trapped in shallow waters, and deplete the available food resource over several days (Crawford and Jorgenson, 1993, 1996; Welch et al., 1993). In shallow Allen Bay (Nunavut), where Arctic cod form dense schools at depths between 7 and 20 m with small satellite aggregations close to the surface, the presence of schools was a significant predictor of the distribution of northern fulmar but not black-legged kittiwake (Matley et al., 2012a). The relatively weak association of seabirds with Arctic cod schools was attributed to a “local enhancement”
mechanism (Thorpe, 1963) by which predators use memory and the presence of other predators (seabirds and marine mammals) to locate their food. In the offshore marginal ice zone, Arctic cod formed continuous scattering layers rather than dense and discrete schools. Little coherence between the distribution of seabirds and that of Arctic cod was found, despite the observed regional variations in the density of the scattering layers (Figure 6). Predators and prey resource were generally more abundant on the western ice-covered side of Baffin Bay (Table 2), suggesting some spatial match at large spatial scales. However, when comparing seabird abundance/density and their Arctic cod food-resource proxy in different ice concentrations across the marginal ice zone, no clear pattern was found (Figure 7). The only significant positive match was detected at the medium scale of 12.5 km, and only between murre density and Arctic cod resource (Table 3). These results suggest that seabirds respond to the “finer grain” in the spatial variability of their resource, and that local enhancement operates mainly at smaller scales than those resolved in the present study.

Another non-exclusive explanation for the observed lack of spatial match between seabirds and Arctic cod is that the fish prey successfully avoided its predators (Schneider and Piatt, 1986; Logerwell and Hargreaves, 1996). The observed migration of age-0 Arctic cod to ice-covered areas as their length attains the preferred prey length of seabirds suggests an adaptation to minimize avian predation. The subsequent concentration of age-1 and age-2 immature Arctic cod in the 40–100 m depth interval may be a response to limit predation by thick-billed murre and immature ringed seals Phoca hispida (Benoit et al., 2010). The further ontogenetic migration of age-2+ Arctic cod to depths >200 m could reduce predation by deep-diving mature seals and murre (Benoit et al., 2010; Geoffroy et al., 2016).

Seabird predators and their fish prey are more closely associated when prey density is high (e.g., Piatt, 1990; Mehlum et al., 1999; Fauchald and Eriksen, 2002; but see also Vlietstra, 2005). In the present study, as Arctic cod did not form dense schools, the food-resource proxy of seabirds was relatively low, with values ranging from 0 to 325 mg m⁻² (mean value of 5 mg m⁻²) for the surface-feeding northern fulmar and black-legged kittiwake, and from 0 to 550 mg m⁻² (mean value of 53 mg m⁻²) for the deep-diving thick-billed murre, and the biomass of small Arctic cod (<4 cm length) was even lower. Low food levels could be perceived as uniform by the predators, which would explain a lack of strong correlation between seabird and Arctic cod distributions at the different scales.

One could also argue that seabirds analysed in this study might have ingested smaller Arctic cod than the smallest Arctic cod found in bird stomachs (5.7 cm), and that bird distribution was thus more influenced by the distribution of these small Arctic cod than that of larger individuals considered as food resource. Our results at large, medium and small scale suggest, however, that such a greater influence was not the case. Except for the thick-billed murre in the 80–100% ice cover, at no scale was the distribution of seabirds better matched to that of small Arctic cod (<4 cm length) than to their potential food resource based on stomach analysis (4–18 cm length), suggesting that large Arctic cod as found in bird stomachs was their probable target.

Finally, as this study was conducted during the breeding season, the location of the colonies and breeding activity may have influenced seabird foraging behavior and, in addition to ice concentration and food resource, their offshore distribution across the marginal ice zone. Seabirds observed offshore were either non-breeders (immature birds or adults that skip breeding for a year) or breeders on foraging trips from their colonies. However, our observation data cannot distinguish breeding from non-breeding individuals. Foraging trips for breeding murre, kittiwake and fulmar may extend up to 300, 450 and 500 km from their colonies, respectively (Dunnet and Ollason, 1982; Weimerskirch et al., 2001; Falk et al., 2002; Ponchon et al., 2014; Yamamoto et al., 2016), although they have been documented to be mostly ≤100 km for murre and kittiwake in Baffin Bay (Boertmann and Mosbech, 2017). The location of their colonies may have therefore limited the area where observed seabirds could forage and the possibility of encountering high food resources. This situation was potentially the case for the thick-billed murre which was concentrated in the southern transects (Figure 6) relatively close to the Minarets colony on Baffin Island (~130 km to closest sampling transect), but it did not prevent its distribution from matching the highest Arctic cod food resource at medium scale.

**Sea ice and seabirds**

Although ice concentration did not significantly influence the three seabird species at medium and small scales (Tables 3 and 4), our large-scale results suggest that surface-feeding kittiwake and fulmar might avoid zones of high ice concentration as too much ice can impede foraging, which is in agreement with previous reports (e.g., McLaren, 1982; Hunt, 1990; Mehlum, 1997; Mosbech and Johnsson, 1999). Kittiwake and fulmar might prefer low to medium ice concentration (Figure 7), possibly because of the additional availability of sympagic prey compared to open waters (Bradstreet and Cross, 1982; Hobson and Welch, 1992; Lonne and Gabrielsen, 1992; Karnovsky et al., 2008). Thick-billed murre can be associated with higher ice concentration (McLaren, 1982; Laidre et al., 2008), as confirmed by our results (Figure 7). Like fulmar and kittiwake, murre benefit from an ice-covered area by feeding in openings on ice-associated invertebrates and fish (Bradstreet and Cross, 1982; Karnovsky et al., 2008).

**Conclusion**

Matley et al. (2012a) pondered if the association between surface-feeding fulmar and Arctic cod schools observed at scales of hundreds of metres in shallow Allen Bay would hold at larger scales. Our results indicate that it does not. This multiscale study points to a lack of horizontal variability in the offshore distribution of Arctic cod as a cause for the weak spatial correlation between seabird abundance and the biomass of their main food resource. In ice-free nearshore areas, the sporadic occurrence of dense schools of Arctic cod trapped near the surface by
the shallow seafloor represents a trophic bonanza for seabird and marine mammal predators, one that may play a significant role in structuring the ecosystem (Welch et al., 1993; Davoren et al., 2003; Matley et al., 2012a). Offshore, the horizontal migration of age-0 Arctic cod under the ice cover at the precise moment in their ontogeny when they reach the length that makes them vulnerable to seabird predators, followed by the vertical migration of the age-1 to deeper layers, strongly suggests a strategy to minimize avian predation. It is tempting to speculate that this strategy and the lack of schooling behavior both contribute to reduce avian predation and underpin the general lack of spatial correlation between seabirds and their food across the marginal ice zone. We note, however, that the study of the co-distribution of fish and their seabird predators in offshore ice-covered waters is plagued by technical difficulties and potential observational biases, including the intrusive presence of a large research icebreaker. As both autonomous underwater vehicles and unmanned aerial vehicles become available for ecological studies, the coordinated deployment of an upward-looking fish echosounder under the ice and a seabird-observing drone above the ice could provide new insights into the predator-prey relationships between arctic seabirds and their fish prey across the marginal ice zone.

Data Accessibility Statement

- Hydroacoustic data: Available at https://www.polar-data.ca (CCIN Reference No.: 12841).
- Seabird observations data: Can be made available by contacting Anders Mosbech, Aarhus University, Denmark, at amo@bios.au.dk.

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Competing interests

The authors have no competing interests to declare.

Author contributions

- Contributed to conception and design: ML, AM, LF
- Contributed to acquisition of data: ML, SEG
- Contributed to analysis and interpretation of data: ML, SG, SEG, AM, LF
- Drafted and/or revised the article: ML, SG, SEG, AM, LF
- Approved the submitted version for publication: ML, SG, SEG, AM, LF

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