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Original Article

Contrasting assemblages of seabirds in the subglacial meltwater plume and oceanic water of Bowdoin Fjord, northwestern Greenland

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In Greenland, tidewater glaciers discharge turbid subglacial freshwater into fjords, forming plumes near the calving fronts, and these areas serve as an important foraging habitat for seabirds. To investigate the effect of subglacial discharge on the foraging assemblages of surface feeders and divers in a glacial fjord, we conducted boat-based seabird surveys, near-surface zooplankton samplings, and hydrographic measurements at Bowdoin Fjord, northwestern Greenland in July. Foraging surface feeders (black-legged kittiwake *Rissa tridactyla*, glaucous gull *Larus hyperboreus*, and northern fulmar *Fulmarus glacialis*) aggregated within a plume-affected area in front of Bowdoin Glacier. This area was characterized by highly turbid subglacial meltwater and abundant large-sized zooplankton including *Calanus hyperboreus*, chaetognaths, and ctenophores near the surface. Surface feeders fed on these aggregated prey presumably transported to the surface by strong upwelling of subglacial meltwater. In contrast, divers (little auk *Alle alle*, thick-billed murre *Uria lomvia*, and black guillemot *Cepphus grylle*) foraged outside the fjord, where turbidity was low and jellyfish and *Calanus* copepods dominated under the influence of Atlantic water. Our study indicates spatial segregation between surface feeders and divers in a glacial fjord; surface feeders are not hindered by turbidity if taking prey at the surface, whereas divers need clear water.

Keywords: divers, fjord, surface feeders, tidewater glacier, turbidity, upwelling

Introduction

The mass loss of glaciers is accelerating worldwide because of global warming (Bliss *et al.*, 2014). Glacial meltwater provides sediment-laden freshwater and has the potential to alter the physical and chemical properties of the adjacent sea and marine ecosystems. For example, the freshwater runoff from Alaskan glaciers affects large-scale circulation and primary productivity in the coastal waters of the Gulf of Alaska (Weingartner *et al.*, 2005), as well as in the fjords (Etherington *et al.*, 2007). Within fjords, the estuarine circulation, driven by the summer glacial meltwater discharge, transports various zooplankton species with near-bottom currents towards the glacier front where they may be advected to the surface (Węsławski *et al.*, 2000). Therefore, marine predators including fish, seabirds, and marine mammals tend to aggregate to feed at the front of tidewater glacier (Hop *et al.*, 2002; Lydersen *et al.*, 2014; Arimitsu *et al.*, 2016; Dalpadado *et al.*, 2016).

Tidewater glacier fronts are known as an important foraging habitat for seabirds (Lydersen *et al.*, 2014). In western Baffin Bay and eastern Lancaster Sound, Canada, for instance, the densities of surface-feeding seabirds, black-legged kittiwakes (*Rissa tridactyla*), ivory gulls (*Pagophila eburnea*), and northern fulmars (*Fulmarus glacialis*), were significantly higher in front of glaciers than along coastlines during summer and fall (McLaren and Renaud, 1982; Renaud and McLaren, 1982). Previous studies in West Spitsbergen showed that, in summers, large aggregations of black-legged kittiwakes and northern fulmars occurred in meltwater plumes near the front of tidewater glaciers, where they fed on macroplankton, such as krill (*Thysanoessa* spp.) and amphipods (Hartley and Fisher, 1936; Stott, 1936). A recent study revealed that zooplankton is transported to the surface as a part of the large volume of ambient water entrained by rising plumes of subglacial discharge, thereby making them more easily accessible for surface feeders (black-legged kittiwakes; Urbanski *et al.*, 2017). The locations and magnitudes of these subglacial discharges fluctuate in time, thereby affecting the locations of the aggregations of surface-feeding kittiwakes (Urbanski *et al.*, 2017).

In contrast to surface feeders, pursuit-diving seabirds, such as little auks (*Alle alle*) and thick-billed murres (*Uria lomvia*), were generally absent from the areas in front of tidewater glaciers (Hartley and Fisher, 1936; Stott, 1936). Despite these previously reported observations of foraging seabirds, the responsible mechanism is still unknown. One possible interpretation is that the turbid meltwater from tidewater glaciers prevents prey detection by divers at depth (Ainley, 1977; Lydersen *et al.*, 2014). In Prince William Sound, Alaska, two pursuit-diving alcids (Kittlitz's murrelets *Brachyramphus brevirostris* and marbled murrelets *B. marmoratus*) exhibited differences in habitat use; Kittlitz's murrelets preferred turbid glacial water, while marbled murrelets preferred clearer water without glacial influence (Day and Nigro, 2000; Day *et al.*, 2003). Kittlitz's murrelets have proportionately larger-diameter eyes than those of marbled murrelets, which might allow them to capture prey in silty water (Day *et al.*, 1999). Since 2005, after the disappearance of summer sea ice and the increase in coastal glacial meltwater in Franz-Josef Land (80°N), Russian Arctic, little auks have switched foraging sites from ice-edge waters located at a long distance from their breeding site to glacial meltwater fronts within <5 km of their breeding site (Grémillet *et al.*, 2015). Thus, the ways in which glacial meltwater influences the foraging habitats of divers vary among localities and species.

To understand the factors affecting seabird foraging aggregations in glacial fjords, boat-based seabird observations, hydrographic measurements, and near-surface zooplankton (i.e. seabird's main prey) samplings were performed in Bowdoin Fjord, a glacial fjord in northwestern Greenland, in the summer of 2016. During our summer field research activities, carried out in this region since 2013, large seabird aggregations have been frequently observed at the front of tidewater glacier. We compared foraging distributions between surface feeders and divers in relation to oceanographic environments, with special attention to turbidity and prey distributions. We hypothesized that surface feeders forage at the front of the tidewater glacier where their prey, large zooplankton, are transported to the near surface by upwelling of a turbid subglacial discharge plume. On the other hand, divers were expected to avoid turbid meltwater plume at the front of the tidewater glacier and forage in clear water away from the glacier front. To test these hypotheses, we examined (i) the effect of turbidity (a proxy for glacial meltwater) on the density of foraging surface feeders and (ii) the effect of turbidity on the density of foraging divers.

Material and methods

Study area and sampling overview

Bowdoin Glacier (77°41′N, 68°35′W) is a marine-terminating outlet glacier (i.e. tidewater glacier) located in northwestern Greenland (Figure 1). The glacier discharges into Bowdoin Fjord through a 3-km wide calving front. The height of the calving front above the sea surface is between 20–25 m (Sugiyama *et al.*, 2015). At 20 km south of the calving front, Bowdoin Fjord connects to Inglefield Bredning, the largest fjord in this region. In turn, Inglefield Bredning Fjord connects to the western part of Baffin Bay, where warm, saline, and northward-flowing Atlantic water, called West Greenland Current, exists. In front of the glacier centre within 2 km of the terminus, the sea depth ranges between 190 and 210 m (Sugiyama *et al.*, 2015). The sea depth deepens towards the mouth of the fjord, which has no sill, where the average sea depth is 500 m (Sugiyama *et al.*, 2015). Recently, Bowdoin Glacier retreated rapidly with a significant acceleration in ice flow speed (Sugiyama *et al.*, 2015).

The at-sea field surveys were conducted in calm weather on 27 and 29 July 2016 at Bowdoin Fjord in the northwestern Greenland. Sea ice covering the entire fjord began disintegrating in early July and completely disappeared from the fjord before our surveys (approximately on 23 July 2016). Small icebergs were sparsely distributed in the fjord during our survey periods, but they did not disturb our ship navigation and observations. Two small boats of 5 m length were operated in the fjord; one boat was for conductivity-temperature-depth (CTD) observations and surface seawater samplings, and the other one for seabird observations and near-surface zooplankton samplings.

Seabird observations

The at-sea seabird observations were conducted on 27 and 29 July 2016 in Bowdoin Fjord (Figure 1), concurrently with zooplankton samplings. We used the standard strip transect methodology (Tasker *et al.*, 1984) while the vessel was underway. During our observations, a single observer continuously recorded the number and behaviours (flying, sitting on water, sitting on iceberg, and foraging) of all seabirds using the 8× binoculars (eye height above sea surface of 2 m) within a 200-m survey range (from the bow to 90° to port or to starboard) of the side of the boat that offered the best observation conditions (i.e. the lowest sun glare) during daylight hours. The position (latitude and longitude) of the boat during the observations was obtained at 30-s intervals using a handy GPS (eTrex venture HC manufactured by GARMIN). We defined surface feeders sitting on water or foraging as "foraging surface feeders" because they feed on prey at the surface by surface-seizing or surface-plunging (<1 m). We also defined divers sitting on water as "foraging divers" because they were assumed to be about to forage or to be resting from a previous foraging bout (Hunt *et al.*, 1998; Kokubun *et al.*, 2008). Seabirds flying or sitting on icebergs were considered as "non-foraging" in our study. The density of seabirds was defined as the number of individuals per 200 × 200 m cell, which is the highest resolution in our study. We chose this cell size because our study area of Bowdoin Fjord is relatively small (i.e. 3-km wide × 20-km long). The total time of seabird surveys

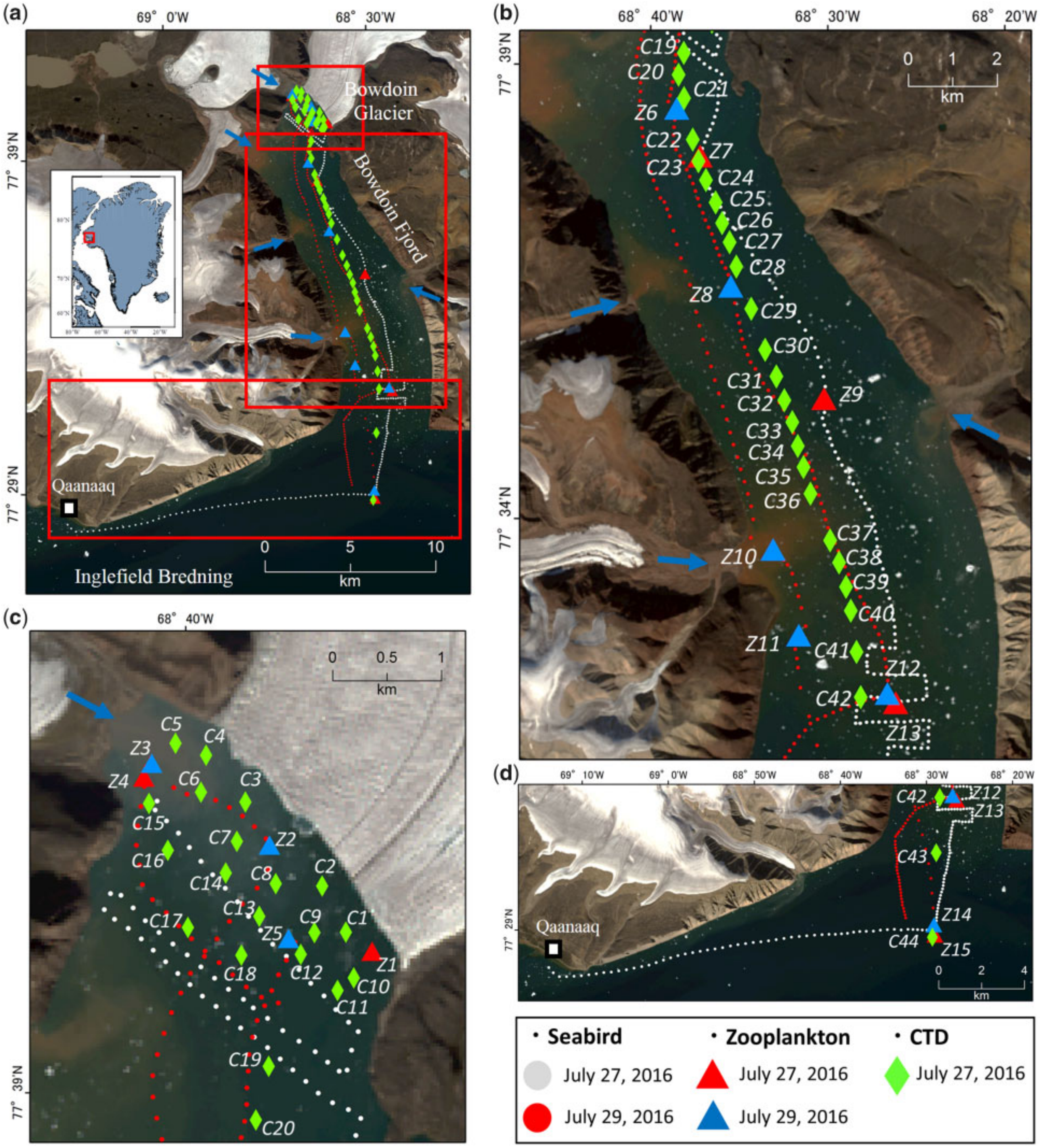

Figure 1. Study area with seabird observation lines (circles), CTD stations (diamonds) with station name (C number), and zooplankton sampling stations (triangles) with station name (Z number). Study area of Bowdoin Fjord in northwestern Greenland (a), details inside fjord (b), the plume-affected at the front of Bowdoin Glacier (c), and outside fjord (d). Arrows denote proglacial streams from land-terminating glaciers. Maps are the natural-color images taken from satellite on July 30 2016.

was 504 min (278 min on 27 July and 226 min on 29 July). The total number of seabird sampling cells (i.e. 200 × 200 m) was 521 (284 on July 27 and 237 on July 29).

Zooplankton sampling

Near-surface zooplankton was collected during daytime on 27 and 29 July 2016, concurrently with seabird observations, at 15 sampling stations (six stations on 27 July and nine stations on 29 July, Figure 1, data from Naito *et al.*, 2019) from the outside of Bowdoin Fjord (23 km from the calving front of Bowdoin Glacier and 4 km from the exit of the fjord) to the front of Bowdoin Glacier (200 m from the calving front of Bowdoin Glacier). The sampling was performed by horizontal tows with a North Pacific Standard Net (NORPAC net; mouth diameter 45 cm, mesh size 335 μm, Motoda, 1957) at a depth of 1.0–2.5 m for 3 min at a ship speed of 5 km h^{-1}. The volume of water filtered through the net was estimated using a flow-meter mounted in the mouth of the net. On the mouth of the net, a 6-kg weight and floater (distance between the net mouth and the floater was 1.35 m) were attached, allowing us to tow the net horizontally in the near-surface layer. The distance from the stern to the net was 20 m when hauling, thereby avoiding the effect of turbulence by the boat propeller during our zooplankton sampling. The net depth was recorded every second with a depth logger (JFE Advantech Co., Ltd., DEFI2-D50, 0.05 m resolution) attached on the mouth of the net. The zooplankton samples were immediately fixed with 4% buffered formalin seawater on the boat. In the laboratory, species identification and enumeration were performed under a stereomicroscope. Subsequently, we weighed the wet mass (WM) of each taxonomic group with a precision of 0.1 μg using an electronic balance (Mettler AE-100). The zooplankton biomass (X: mg WM m^{-3}) was calculated based on the WM and volume of water filtered through the net.

In the fjord on the west coast of Spitsbergen, black-legged kittiwakes feed on large zooplanktons (>5 mg individual WM) abundantly distributed in the vicinity of glacier cliffs (Urbanski *et al.*, 2017). We thus defined "large zooplankton" (mean individual WM >5 mg) and "small zooplankton" (mean individual WM <5 mg) based on the individual mean WM calculated from the biomass and abundance of each taxonomic group. Thereafter, we examined the abundance of large and small zooplankton at each sampling station. Hereafter, the zooplankton sampling stations will be described as "Z number".

Oceanographic measurements and seawater sampling

Surface seawater temperature (resolution 0.001°C) and turbidity [resolution 0.03 FTU (formazin turbidity unit)] were measured at the depth of 0.3 m by a CTD profiler (JFE Advantech Co., Ltd., RINKO-Profiler ASTD102) on-board the boat. The measurements were performed on 27 July at 44 stations in Bowdoin Fjord from the mouth of the fjord to the calving front of Bowdoin Glacier (0.25–23 km from the glaciers, Figure 1, data from Kanna *et al.*, 2018). Surface water sampling was conducted at the CTD stations to measure the salinity. The salinity of the surface water was determined using a salinometer (AUTOSAL 8400B, Guildline Instruments, USA; instrumental accuracy: <0.002). Hereafter, the CTD stations will be described as "C number".

Analyses

Our 2 d (on 27 and 29 July) of observations of seabird and zooplankton samplings were pooled into a single dataset, because the spatial patterns of seabirds were similar for the 2 d (i.e. during both days the highest densities of divers and surface feeders occurred in outside fjord and plume-affected sections, respectively) and the number of the zooplankton sampling stations was small (six stations on 27 July and nine stations on 29 July). Note here again that CTD observations were conducted only on 27 July. In our analysis, we excluded skuas and common eiders (*Somateria mollissima*) from surface feeders or divers because skuas are kleptoparasitic and feed by stealing fish and other prey from other seabirds, such as gulls and terns, and common eiders feed mainly on benthos, such as bivalves and polychaetes (Merkel *et al.*, 2007; Supplementary Table S1).

To explore the relationships among seabird density, turbidity, and abundance of zooplankton, we compared the data from three sections in the study area. We defined the section within 2 km from Bowdoin Glacier (C1–C18) as a "plume-affected" since surface water showed high turbidity (i.e. >5 FTU) in this section (Figures 2 and Supplementary Figure S3). The section between the plume-affected section and the mouth of Bowdoin Fjord (19 km from Bowdoin Glacier) was defined as "inside fjord" and the section on the outside of Bowdoin Fjord as "outside fjord". We then compared the seabird densities, abundances of large and small zooplankton, and surface oceanographic environments (water temperature, salinity, and turbidity) among these three sections using the Steel-Dwass pairwise non-parametric test. Values are expressed as mean ± *SD*.

Based on the finer spatial resolution data obtained at each sampling station, we examined our above-mentioned hypotheses using non-parametric generalized additive models (GAMs). To examine the effect of turbidity on the density of foraging surface feeders and foraging divers, we used turbidities at 44 CTD stations, and the total abundance of foraging surface feeders and divers that occurred within 1 km area from each CTD station. In these GAMs, response variables, such as seabird abundance, were assumed to be negative binomial distributions with log link functions because the data were overdispersed. Moreover, owing to an unequal survey length of seabird observations within the 1 km area from each CTD station, survey effort (i.e. the total survey length in each 1 km area) was treated as an offset term in the GAMs. GAMs were implemented using the mgcv package in the free statistical analysis software R (v.3.1.2, R Development Core Team, 2014) using generalized cross-validation to estimate smoothness parameters (Zuur *et al.*, 2009).

The position of the calving front of Bowdoin Glacier was measured on a natural-colour satellite image from Landsat 8 (bands 4, 3, and 2 were synthesized) on July 30, 2016 (downloaded from http://earthexplorer.usgs.gov/). The spatial resolution of the image was 30 m.

Results

We observed nine seabird species (Supplementary Table S1). Surface feeders included black-legged kittiwake, glaucous gull, and northern fulmar, with black-legged kittiwake being the most abundant (91%; Supplementary Table S1). Divers included little auk, thick-billed murre, and black guillemot, with little auk being the most abundant (80%; Supplementary Table S1).

We collected 20 zooplankton species (Supplementary Table S2). Large zooplankton (>5 mg $ind.^{-1}$) included jellyfish (cnidarians and ctenophores), chaetognaths, appendicularians, thecosomes, and *Calanus hyperboreus* (Supplementary Table S2). Barnacle larvae, classified as small zooplankton (<5 mg $ind.^{-1}$), were collected at all sampling stations and accounted for 6–100% in abundance and <1–87% in biomass.

Comparison between sections

Plume-affected section

The density of foraging surface feeders in the plume-affected section at the front of Bowdoin Glacier was the highest among the three sections (Table 1, Figure 3a). A huge mixed-aggregation of black-legged kittiwakes (930 birds per 200 m^2) and glaucous gulls (100 birds per 200 m^2) was observed within 300 m from the glacier front. These birds exhibited repeated foraging behaviours, such as surface-seizing or surface-plunging. We also observed at least 10 black-legged kittiwakes in the aggregated birds capturing

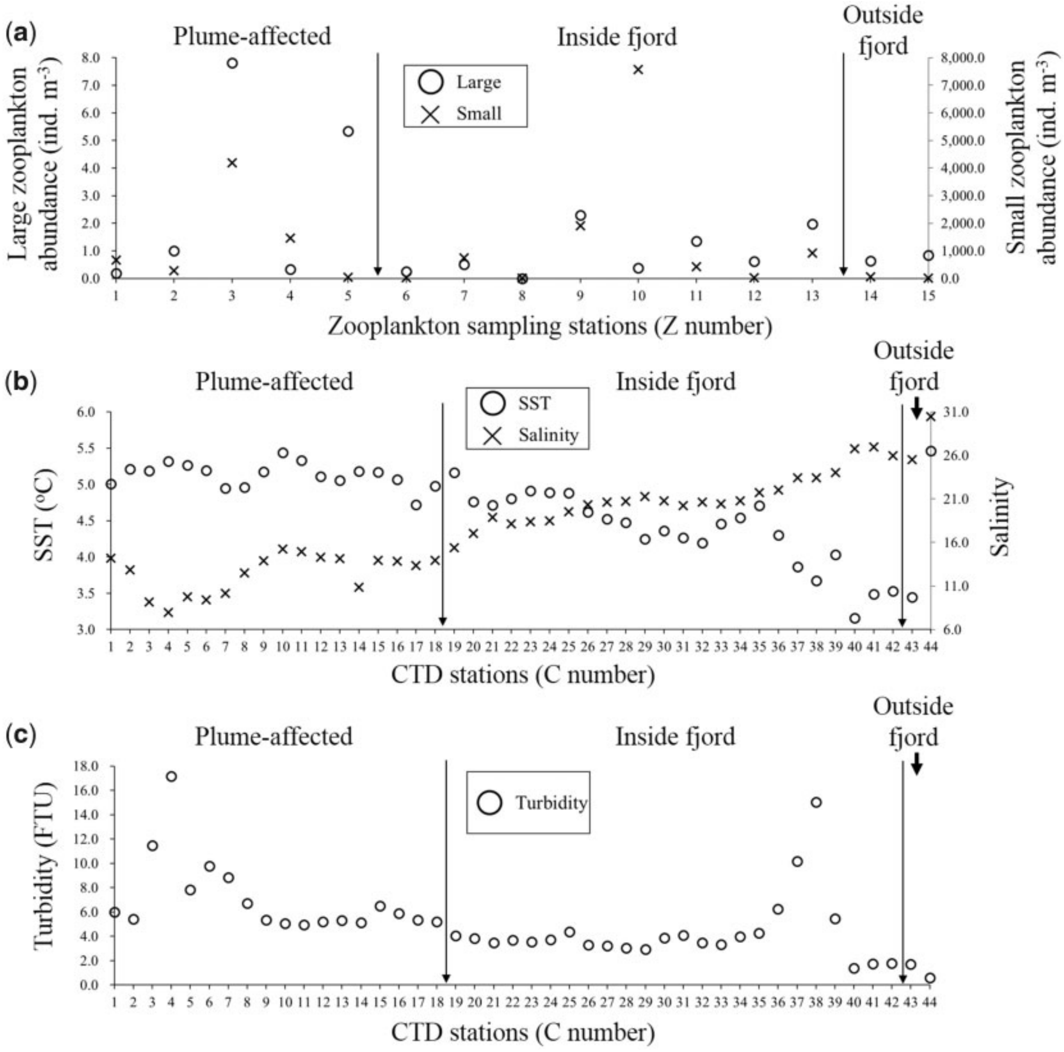

Figure 2. Zooplankton abundance and oceanographic environments in Bowdoin Fjord (plume-affected and inside and outside fjord sections) in northwestern Greenland. Large (>5 mg mean individual WM) and small (<5 mg mean individual WM) zooplankton abundances (a), sea surface temperature (SST) and salinity (b), turbidity (c).

fish (probably polar cod *Boreogadus saida*, ~15 cm in the total length, Supplementary Figure S1). The non-foraging (flying or sitting on iceberg) surface feeders in this section also showed the highest density (Table 1, Supplementary Figure S2a). On the other hand, no divers, whether foraging or non-foraging, were observed in the plume-affected section (Table 1, Figure 3b, Supplementary Figure S2b).

The zooplankton abundance collected in near-surface water was highly variable between the stations (Figure 2a). The average abundance and biomass of total zooplankton in the plume-affected section were similar with those in the inside fjord section (Table 1). The average abundance of large zooplankton, however, seemed to be the highest among the three sections, although the trend was not significant (Table 1, Figure 2a). The large zooplankton (stations Z1–Z5) included ctenophores, chaetognaths (*Parasagitta elegans* and *Eukrohnia hamata*), fish larvae, and copepods (*Calanus hyperboreus*; Supplementary Table S2).

The average surface water temperature in the plume-affected section was the highest, while the surface salinity was the lowest (Table 1, Figure 2b and Supplementary Figure S3). The surface turbidity was the highest, especially at the stations of C3–C8 (Table 1, Figure 2c and Supplementary Figure S3).

Inside fjord section

The densities of both foraging and non-foraging surface feeders and divers in the inside fjord section were quite low (Table 1, Figure 3 and Supplementary Figure S2).

The average abundance and biomass of total zooplankton in the inside fjord were similar with those in the plume-affected section and the large zooplankton seemed to be a low abundance, although the trend was not significant (Table 1 and Figure 2a). Among zooplankton sampling stations in the inside fjord, station Z10 showed the highest density of small zooplankton (Figure 2a), with barnacle larvae as the dominant zooplankton species (Supplementary Table S2).

The average surface water temperature in the inside fjord was lower than that in the plume-affected section and decreased gradually towards the outside fjord section, while the surface salinity showed an opposite trend (Table 1, Figure 2b and Supplementary

Table 1. Density of surface feeders, density of divers, zooplankton abundance (ind. m^{-3}), and zooplankton biomass (mg WM m^{-3}), sea surface temperature (SST, °C), salinity, turbidity [formazin turbidity unit (FTU)] between three sections (plume-affected, inside fjord, and outside fjord), and the results of the Steel-Dwass test (*t*-statistics and *p*-value).

					Steel-Dwass test (*t*-statistics, *p*-value)		
Variables		**Plume-affected**	**Inside fjord**	**Outside fjord**	**Plume-affected *vs.* Inside fjord**	**Plume-affected *vs.* Outside fjord**	**Inside fjord *vs.* Outside fjord**
Density of surface feeders (ind. 200 m^{-2})	Foraging	14.1 ± 109.2 (0.0–1030.0), $n = 88$	0.1 ± 1.1 (0.0–20.0), $n = 317$	0.0 ± 0.2 (0.0–0.2), $n = 116$	5.7, $p < 0.05$	3.5, $p < 0.05$	0.7, $p = 0.78$
	Non-foraging	4.2 ± 17.3 (0.0–150.0), $n = 88$	0.3 ± 0.7 (0.0–4.0), $n = 317$	0.5 ± 0.8 (0.0–4.0), $n = 116$	4.8, $p < 0.05$	2.8, $p < 0.05$	1.6, $p = 0.24$
Density of divers (ind. 200 m^{-2})	Foraging	0 $n = 88$	0.0 ± 0.3 (0.0–3.0), $n = 317$	3.0 ± 8.0 (0.0–50.0), $n = 116$	1.9, $p = 0.15$	6.0, $p < 0.05$	8.7, $p < 0.05$
	Non-foraging	0 $n = 88$	0.1 ± 0.3 (0.0–4.0), $n = 317$	0.6 ± 1.6 (0.0–13.0), $n = 116$	1.9, $p = 0.15$	4.6, $p < 0.05$	5.9, $p < 0.05$
Total zooplankton abundance (ind. m^{-3})		1332.2 ± 1512.6 (39.9–4199.4), $n = 5$	1456.9 ± 2390.9 (7.1–7579.4), $n = 8$	41.5 ± 23.8 (17.7–65.2), $n = 2$	0.4, $p = 0.90$	1.5, $p = 0.27$	1.0, $p = 0.55$
Total zooplankton biomass (mg WM m^{-3})		50.9 ± 30.0 (13.3–90.8), $n = 5$	65.0 ± 78.1 (4.0–259.1), $n = 8$	22.8 ± 7.9 (15.0–30.7), $n = 2$	0.7, $p = 0.74$	0.7, $p = 0.72$	0.5, $p = 0.86$
Large zooplankton abundance (ind. m^{-3})		2.9 ± 3.1 (0.2–7.8), $n = 5$	0.9 ± 0.8 (0.0–2.3), $n = 8$	0.7 ± 0.1 (0.6–0.8), $n = 2$	0.6, $p = 0.83$	0.4, $p = 0.92$	0.5, $p = 0.86$
Small zooplankton abundance (ind. m^{-3})		1328.5 ± 1509.3 (34.6–4187.9), $n = 5$	1455.9 ± 2391.0 (6.2–7579.0), $n = 8$	40.7 ± 23.9 (16.9–64.6), $n = 2$	0.4, $p = 0.90$	1.5, $p = 0.27$	1.0, $p = 0.55$
SST (°C)		5.1 ± 0.2 (4.7–5.4), $n = 18$	4.4 ± 0.5 (3.2–5.2), $n = 24$	4.5 ± 1.0 (3.4–5.5), $n = 2$	5.5, $p < 0.05$	0.0, $p = 1.00$	0.1, $p = 0.10$
Salinity		12.5 ± 2.2 (7.9–15.2), $n = 18$	21.1 ± 2.8 (15.4–27.0), $n = 24$	28.0 ± 2.5 (25.5–30.5), $n = 2$	5.5, $p < 0.05$	2.3, $p = 0.06$	2.0, $p = 0.11$
Turbidity (FTU)		7.1 ± 3.0 (5.0–17.1), $n = 18$	4.3 ± 2.8 (1.4–15.0), $n = 24$	1.2 ± 0.6 (0.6–1.7), $n = 2$	4.2, $p < 0.05$	2.3, $p = 0.06$	2.2, $p = 0.08$

Values are described in mean ± *SD*, range, and sample size.

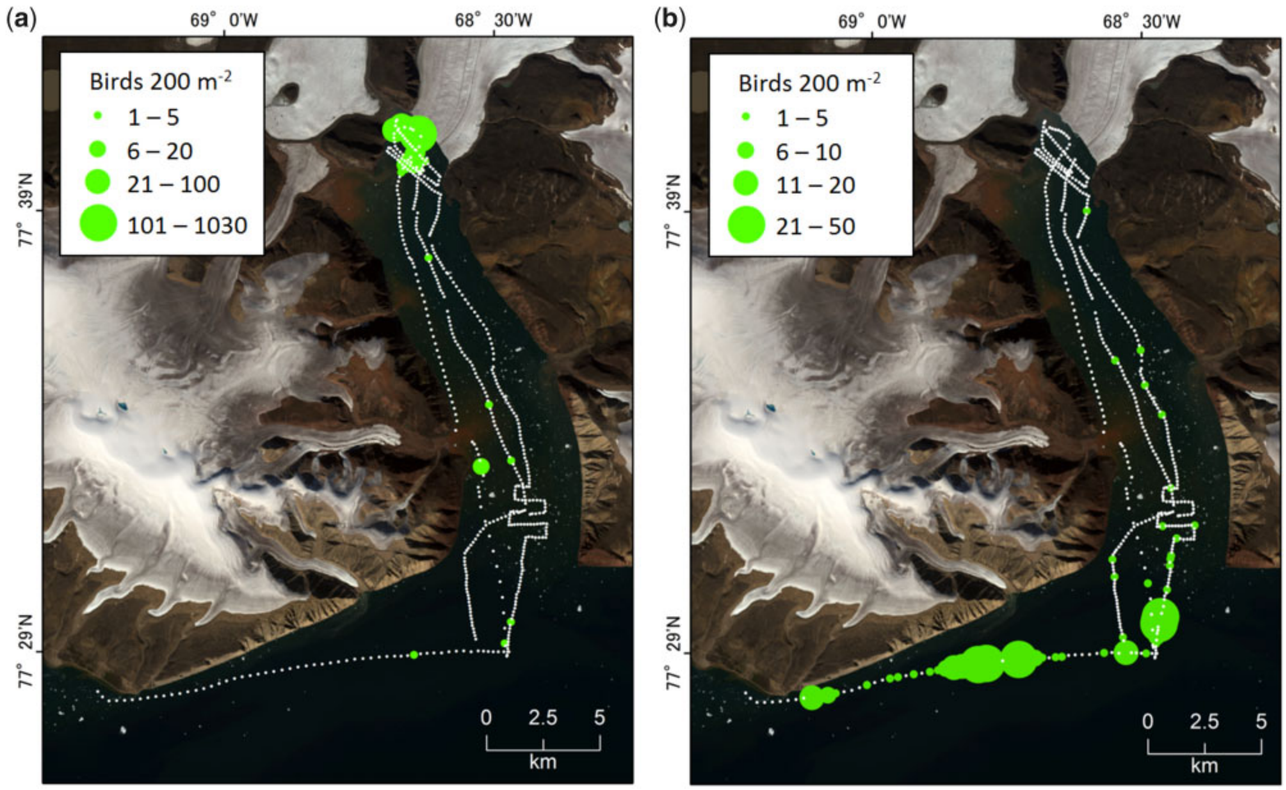

Figure 3. Density (birds 200 m—^{2}) of foraging surface feeders (a) and divers (b) in Bowdoin Fjord in northwestern Greenland. White dots (smallest dots for black/white version) on each map represent nil. Maps are the natural-colour images taken from satellite on 30 July 2016.

Figure S3). The average surface turbidity in the inside fjord showed intermediate values among the sections, with high values recorded at the stations of C36–C38 (12–14 km away from the glacier; Table 1, Figure 2c and Supplementary Figure S3).

Outside fjord section

The density of foraging surface feeders in the outside fjord section was low as observed in the inside fjord (Table 1 and Figure 3a), while the density of foraging divers was the highest (Table 1 and Figure 3b). Similarly, the density of non-foraging surface feeders was low, while the density of non-foraging divers was the highest (Table 1 and Supplementary Figure S2).

The average abundance and biomass of total zooplankton in the outside fjord seemed to be the lowest (Table 1 and Figure 2a).

The average surface water temperature in the outside fjord showed a value similar to that in the inside fjord with high variability between the stations, while the surface salinity was the highest among the sections (Table 1, Figure 2b and Supplementary Figure S3). The surface turbidity measurements in this section were the lowest (Table 1, Figure 2c and Supplementary Figure S3).

Effect of turbidity on the density of surface feeders and divers

The turbidity had a positive effect on the density of foraging surface feeders; in the vicinity of the stations where the turbidity was high, the density of the foraging surface feeders was also high (Figure 4a). On the other hand, the turbidity had a negative effect on the density of foraging divers (Figure 4b).

Discussion

Our study indicated that surface feeders and divers used different foraging habitats with almost no spatial overlap in Bowdoin Fjord, and this segregation was correlated with the varying turbidity level of the subglacial meltwater.

Foraging habitat of surface feeders

In the turbid subglacial meltwater plume near the front of Bowdoin Glacier, surface feeders, including the black-legged kittiwake, northern fulmar, and glaucous gull, aggregated for feeding. In this area, the abundance of large zooplankton (>5 mg ind.$^{-1}$) in near-surface water tended to be higher than in the inside and outside fjord sections. Although the diets of the seabirds were unknown in the present study, they probably fed on large zooplankton similar to those collected at the stations (Z2, Z3, and Z5) within 1 km of a large foraging aggregation of the surface feeders. These zooplankton include copepods (*Calanus hyperboreus*), chaetognaths, and ctenophores. These large zooplankton (>5 mg ind.$^{-1}$) have been frequently observed in the stomach contents of black-legged kittiwake and northern fulmar in the fjords of the Svalbard archipelago, whereas the small zooplankton (<5 mg ind.$^{-1}$), such as barnacle larvae, did not occur in their diets (Hartley and Fisher, 1936; Mehlum and Gabrielsen, 1993, see also Urbanski *et al.*, 2017).

Why were large zooplankton more abundant at near surface in the turbid subglacial meltwater plume? Our small sample of zooplankton supports the previous findings of others; the sediment-rich subglacial discharge that is released at 10–100 m below the

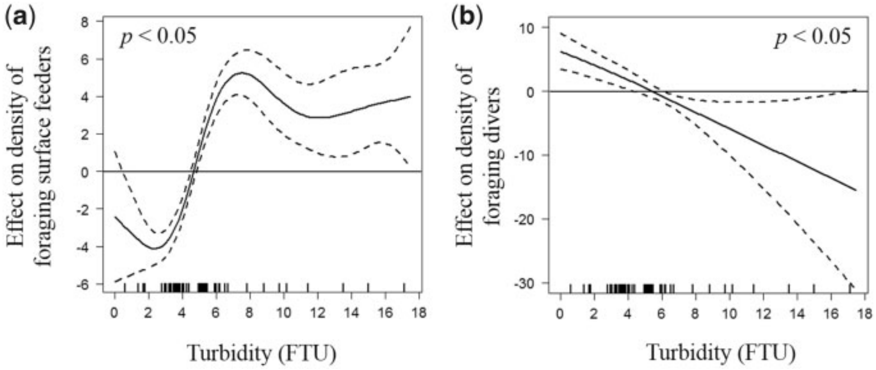

Figure 4. Results of GAM regression for the density of foraging surface feeders (a) and divers (b) as a function of turbidity. Dashed lines are 95% confidence limits. Significance levels (*p*-values) are shown on each plot. Thick marks on the *x*-axis show the locations of data points.

water surface entrains large volumes of water as it upwells to the surface, enabling the transport of zooplankton from the depth to the surface of the fjord (Chu, 2014; Urbanski *et al.*, 2017). This process supplies abundant zooplankton to the plume surface, where surface feeders can easily access them (Urbanski *et al.*, 2017). Elsewhere, an abrupt drop in salinity to <24 PSU was found fatal for zooplankton in glacier bays (Zajaczkowski and Legeżyńska, 2001). Presumably, the zooplankton near the glacier front is transported from outside of the fjord by the estuarine circulation driven by the glacial meltwater discharge (Węsławski *et al.*, 2000). In our study region of Bowdoin Fjord, a clustered near-surface zooplankton group occurring at the plume in front of Bowdoin Glacier comprised large amounts of oceanic species, such as *Calanus* spp. and chaetognaths, suggesting an inflow from oceanic water through the bottom of the fjord and upwelling by plume in front of the glacier (Kanna *et al.*, 2018; Naito *et al.*, 2019). Furthermore, we observed at least 10 black-legged kittiwakes feeding on small fish (probably polar cod) in the plume-affected section, suggesting that fish are also available at the surface near the glacier front. The fish might be either stunned or killed by osmotic shock upon entrainment into glacial meltwater. Polar cod is an important prey (>80% by occurrence and >50% by the total number of prey in stomach samples) of black-legged kittiwakes feeding in the nearby North Water Polynya, northern Baffin Bay, during the months of June and July (Karnovsky *et al.*, 2008). A recent study provides photographic and video evidence of dead redfish and strong upwelling in connection with a tidewater outlet glacier terminating in Godthåbsfjord, west Greenland (Kjeldsen *et al.*, 2014).

High turbidity (>6 FTU) also occurred at stations C36–C38 (12–14 km away from the edge of the glacier) in the inside fjord section (Figure 2c), which might be the result of proglacial streams from land-terminating glaciers (Kanna *et al.*, 2018). In this area, few surface feeders and large zooplankton at near-surface water (at station Z10) were observed (Figures 2a and 3a), presumably because strong upwelling did not occur.

Foraging habitat of divers

Divers, including the little auk, thick-billed murre, and black guillemot, foraged primarily in the areas outside of the fjord, where turbidity was the lowest. The little auks, a pursuit-diving species, feed mainly on energy-rich copepods (*Calanus glacialis* and *C. hyperboreus*) in the oceanic water of the Arctic (Karnovsky *et al.*, 2008, 2011; Frandsen *et al.*, 2014). The accessibility of these prey species might be affected by water clarity that regulates the foraging efficiency in visually hunting aquatic seabirds (Ainley, 1977; Haney and Stone, 1988; Day *et al.*, 2003; Henkel, 2006). Indeed, the little auks inhabiting the shelf of West Spitsbergen preferred the areas where *C. glacialis* was abundant and was clearly visible (Stempniewicz *et al.*, 2013). Little auks dive to a depth of ∼30 m to feed mainly on *Calanus* copepods (Karnovsky *et al.*, 2011; Brown *et al.*, 2012). We have no information on the density of the prey existing at the depth of ∼30 m in Bowdoin Fjord. However, the *Calanus* copepods (*C. hyperboreus*, *C. glacialis*, and *C. finmarchicus*) occurred in the near-surface waters around the mouth of fjord (Z12 and Z13) and in the outside fjord section (Z14 and Z15), suggesting that these *Calanus* copepods might be available for little auks at their foraging depth. Water masses in the outside fjord section showed the highest salinity (28 PSU) and the lowest turbidity (1.2 FTU), indicating under the influences of the oceanic West Greenland currents. A previous study conducted in Svalbard's glacial fjords showed that the density of small copepods, such as *Pseudocalanus* and *Oithona similis*, was high in the inner fjord, whereas the larger copepods, such as *Calanus* spp., were abundant in the outer fjords under the influence of oceanic Atlantic water (Walkusz *et al.*, 2009).

In conclusion, our study showed that surface feeders and divers are segregated in space in a glacial fjord and turbidity of glacial meltwater may explain these differences. Importance of glacial meltwater on seabird habitats has been widely reported from other areas outside Greenland, including Alaska, Canada, Russia, and Antarctic (e.g. McLaren and Renaud, 1982; Smith *et al.*, 2007; Arimitsu *et al.*, 2012; Grémillet *et al.*, 2015). Therefore, careful attention should be paid to the seabird species, which are the marine top predators, while investigating the impact of changes in tidewater glaciers on the fjord ecosystems.

Supplementary data

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

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