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ORIGINAL PAPER

Abundance, habitat use and food consumption of seabirds in the high-Arctic fjord ecosystem

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Abstract
To monitor the rapid changes occurring in Arctic ecosystems and predict their direction, basic information about the current number and structure of the main components of these systems is necessary. Using boat-based surveys, we studied the numbers and distribution of seabirds foraging in Hornsund (SW Spitsbergen) during three summer seasons. The average number of seabirds foraging concurrently in the whole fjord was estimated at 28,000. Little Auks *Alle alle* were the most numerous, followed by Northern Fulmars *Fulmarus glacialis*, Brünnich's Guillemots *Uria lomvia* and Black-legged Kittiwakes *Rissa tridactyla*. The pelagic zone was exploited by some 75% of the birds. Their density was the highest (>400 ind. km^{-2}) in the tidewater glacier bays, where kittiwakes were predominant, and the lowest in the coastal glacier bays. The seabirds in Hornsund daily consumed c. 12.7 tons of food, i.e. c. 0.2% of the summer mesozooplankton and fish standing stocks available in the fjord. This food consisted primarily of copepods, amphipods and molluscs (c. 70%), whereas fish made up < 15%. More than 50% of this biomass was ingested by pursuit divers, while surface feeders took c. 29% and benthophages c. 13%. About three-quarters of the food biomass was taken from the pelagic zone. This paper describes, for the first time in quantitative terms, the structure and function of a seabird community foraging in an Arctic fjord. It also provides a baseline for future studies on climate-induced changes in the importance of seabirds in the Arctic food web.

Keywords Marine birds · Food consumption · Arctic fjord · Spitsbergen

Introduction

Climate-induced changes in environmental conditions are occurring very rapidly and are most pronounced in the Arctic. They are manifested by increasing air and seawater temperatures, resulting in rapid shrinking of the sea ice range and in tidewater glacier retreat (Serreze et al. 2007). The dramatically diminishing area of ice cover in both the sea and the coastal zone will have detrimental consequences for ice-associated algae, invertebrates, fish, and marine birds and mammals (Wassmann et al. 2011; Moody et al. 2012; Sydeman et al. 2012; Post et al. 2013; Barber et al. 2015; Amélineau et al. 2016; CAFF 2017; Pratte et al. 2019). Rapid glacier recession and melting rate are substantially changing the topography of fjords, as well as their hydrology and productivity, including fish and invertebrates, which constitute an important food resource for seabirds (Dahl et al. 2003; Kumar et al. 2018; Błaszczyk et al. 2019). Changing environmental conditions in such waters modify the food resources and foraging habitats used by seabirds, which could affect the magnitudes of their populations and species composition (Kitaysky and Golubova 2000; Willis et al. 2006; Dalpadado et al. 2012; Sydeman et al. 2012; Grémillet et al. 2015; Kortsch et al. 2015; Descamps et al. 2017; Ramirez et al. 2017; Mallory et al. 2018; Renaud et al. 2018; Vihtakari et al. 2018; Hovinen et al. 2019). Nonetheless, the consequences of this process may differ. On the one hand, it may result in a population decline of some vulnerable species, such as the Ivory Gull *Pagophila eburnea* (Gilg et al. 2016) or Kittlitz's Murrelet *Brachyramphus brevirostris*, which has been found to be linked to the retreat of tidal glaciers (Kuletz et al. 2003). On the other hand, rapid glacier melting periodically creates attractive foraging spots for seabirds, and glacier recession unveils new habitats accessible

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to birds, thus enhancing species diversity (CAFF 2017; Stempniewicz et al. 2017; Urbanski et al. 2017).

Arctic fjords are among the most climate-sensitive regions (Serreze et al. 2007; Kumar et al. 2018; Błaszczyk et al. 2013). The response of a fjord ecosystem including marine birds and mammals to a rapidly changing environment is a subject that has been attracting increased attention (Hop et al. 2002; Willis et al. 2006; Stempniewicz et al. 2007, 2017; Arimitsu et al. 2012; Lydersen et al. 2014; Urbanski et al. 2017; Hovinen et al. 2019; Duarte et al. 2019). Baseline information on the abundance and distribution of seabirds is essential if we wish to identify population changes, implement efficient conservation management programmes, and assess their importance in the Arctic ecosystem's food webs (Karnovsky and Hunt 2002; Diemer et al. 2011; Renaud et al. 2018). However, current knowledge of population sizes of seabirds using fjords as foraging grounds is insufficient for most Arctic areas (CAFF 2017; Descamps et al. 2017; Vihtakari et al. 2018). When constructing models of food web/trophic relationships in a fjord ecosystem, one usually uses numbers of local breeding birds. Such an approach, however, does not take into account the fact that some seabirds forage exclusively in the fjord, while others exploit feeding grounds in both the fjord and the open sea in proportions depending on current food availability and weather conditions (Stempniewicz et al. 2017; Urbanski et al. 2017). Our present research has been based exclusively on surveys of seabirds actually foraging in the fjord.

To address the above shortcomings, systematic seabird transect surveys were carried out in Hornsund, SW Spitsbergen, an area of high biological production and species diversity (Węsławski et al. 2006). Hornsund, too, is experiencing the effects of strong global warming, which are manifested in the fastest retreat of tidal glaciers in the whole of Svalbard (Błaszczyk et al. 2013). The objectives of this study were: (1) to estimate the abundances of seabirds foraging in Hornsund, including their principal foraging guilds and habitats; (2) to identify their community structure, distribution and foraging habitat preferences in the fjord; (3) to estimate the biomasses of different food types taken daily by seabirds from the fjord during the chick feeding period.

Study area

Our study area was Hornsund (SW Spitsbergen), a rapidly deglaciating high-Arctic fjord. The largest seabird colonies in the area are at Ariekammen, Dotten, Krykkjestupet, Luciapynten, Skoddefjellet and Sofiekammen. Hornsund hosts one of the largest worldwide concentrations of breeding Little Auks *Alle alle* (ca 6,00,000 breeding pairs; Keslinka et al. 2019). There are also several big colonies of Black-legged Kittiwakes *Rissa tridactyla* (size category: 15–20,000 breeding pairs) and Brünnich's Guillemots *Uria lomvia* (5.5–10,000 pairs). However, due to inaccessibility and hidden nesting sites, the breeding population size of many common seabirds such as the Northern Fulmar *Fulmarus glacialis*, the Black Guillemot *Cepphus grylle* and the Atlantic Puffin *Fratercula arctica* is poorly understood. Common Eiders *Somateria mollissima*, Arctic Terns *Sterna paradisea* and Glaucous Gulls *Larus hyperboreus* are also common though less numerous breeders in the fjord area, with populations consisting of several dozen to several hundred breeding pairs (Norwegian Polar Institute, unpublished database).

The study area comprised both the pelagic and coastal parts of the fjord. The latter consisted of non-glaciated (NGCL) and iced coastline, including glaciers in different stages of retreat. Sea-terminating tidewater glaciers (STTG), calving intensively and receding rapidly, provide substantial amounts of drifting ice. They usually have deep glacier bays and long frontal zones. Glaciers advanced in their retreat, the fronts of which are largely on the coastline (coastline-terminating glaciers, CLTG), have shallow glacier bays and exhibit little if any calving activity (Fig. 1).

Material and methods

Field methods

We conducted systematic boat-based surveys of the coastline and pelagic sectors (Fig. 1) between 12 July and 1 August 2014–2016, i.e. during the chick-rearing period of the seabird species we studied. Two persons, one noting the observations and the other steering the boat (a rubber Bombard dinghy, travelling at about 15 km h^{-1}), conducted the surveys between 11:00 and 18:30 (UTC + 2); the assumption was that seabirds forage more or less evenly throughout the polar day (Wojczulanis-Jakubas et al. 2020). The height of the observer was 1.5 m above the water, which ensured good observation conditions for the identification and counting of birds along the entire width of the transect. Surveys did not take place on windy days with strong wave action. We used line-transect methods (Tasker et al. 1984) to record the species and numbers of all foraging birds observed except geese and waders. To be consistent with data collected during less favourable weather conditions, we truncated all our observations to a distance of 150 m on either side of the boat. The observations during the coastal surveys encompassed a distance of 150 m between the boat and the coastline, and another 150 m on the opposite side of the boat, the bird densities being calculated assuming perfect detection within this 300 m strip.

Based on the fjord's bathymetry, we took a line 300 m from the shore to be the boundary of the coastal zone. This

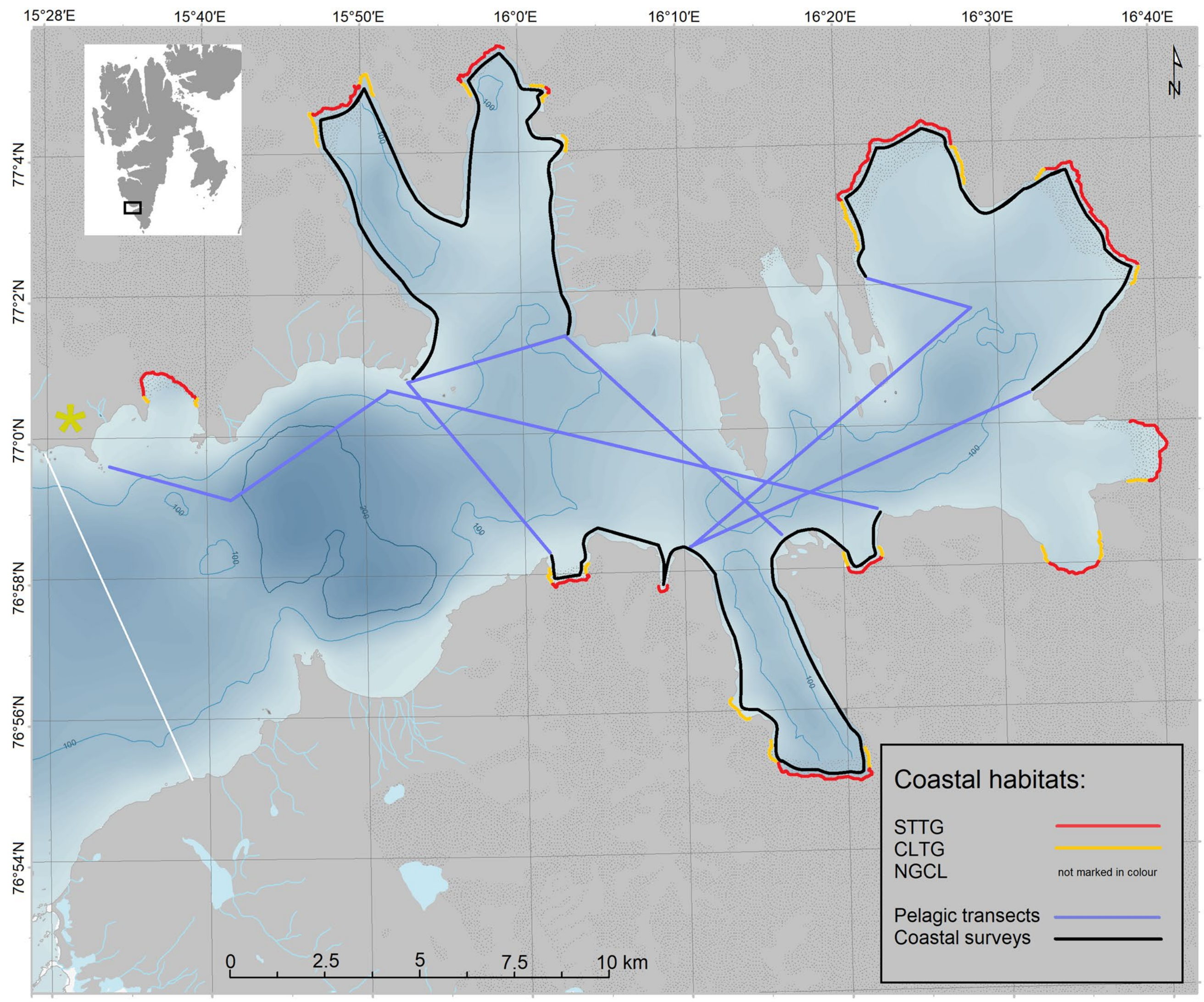

Fig. 1 Study area in Hornsund, SW Spitsbergen showing the coastline sections (black lines) and pelagic transects (blue lines) surveyed. The glaciated coastal habitats are marked by thick coloured lines (red: sea-terminating tidewater glaciers—STTG, orange: coastal glaciers—CLTG). The remaining coastline sectors not marked by a colour are non-glaciated coastline—NGCL. The white line delineates the outer boundary of the fjord, and the yellow asterisk shows the location of the Polish Polar Station

zone is shallow enough (30–40 m) for benthophages to dive and feed on the bottom. Thus, all the surveyed areas farther from the shore and deeper were assigned to the pelagic zone. We included all observations of foraging birds within the surveyed area. Benthophages (ducks, Black Guillemots) and pursuit divers (Little Auks, Brünnich's Guillemots, Atlantic Puffins) observed alternately on the water surface and diving were considered to be foraging. In the case of surface feeders (Black-legged Kittiwakes, Northern Fulmars, Arctic Terns), feeding birds were considered to be those that were picking food off the water surface, or circling over a specific place and diving for food that appeared on the surface. Birds flying over the survey area were not taken into account. All the observers have had many years of experience in conducting marine bird surveys in Svalbard.

The numbers and locations of the surveys were deemed representative of each habitat. The general principle was adopted that the degree of sampling should correspond to the degree of habitat diversity and temporal variability: relatively more surveys were therefore carried out in the more diverse coastal habitats, whereas the very extensive and homogeneous pelagic habitat was sampled relatively less often. As a result, the total area of the relatively small glacier bays (STTG and CLTG) were surveyed often enough that their total surveyed surface area (sum of areas surveyed each time) exceeded their actual area (Table S1).

To estimate the total numbers of seabirds foraging in the particular habitats and in the whole fjord, we calculated the mean density of birds for each habitat (the sum of birds observed during all surveys divided by the accumulated area of the habitats) and then multiplied it by the total area of the given habitat in the fjord. The distribution of habitats and the total area surveyed are shown in Fig. 1 and listed in Table S1. The size of the surveyed areas in particular habitats was large enough to eliminate variation in local bird density within the habitats (foraging hot spots). Based on foraging strategies, we allocated the seabirds to three primary foraging guilds, i.e. surface feeders (SF), pursuit divers (PD) and benthic feeders (BF), and into two groups with regard to habitat foraging preferences, i.e. coastal feeders (CF) and pelagic feeders (PF) (Ainley 1977; Simberloff and Dayan 1991).

The seabird surveys in Hornsund were carried out during three summer seasons in 2014–16. To calculate the total seabird food consumption in the fjord, we used survey data from the 2016 summer season ($n=15$ surveys), as this was the most representative of the habitat coverage. Based on long-term databases from the Polish Polar Station and the Institute of Oceanology (Polish Academy of Sciences), this season also appeared to be typical as regards both meteorological and hydrographical conditions and bird number fluctuations (Promińska et al. 2018; Stempniewicz et al. 2021). Nevertheless, well-sampled data from the coastal habitat surveys performed in all three seasons were compared to demonstrate the interannual variability of seabird numbers and food consumption.

Calculating seabird food consumption

We estimated the food consumption by seabirds on the basis of published values of Daily Energy Expenditure (DEE) or Field Metabolic Rate (FMR) for particular species (adults and chicks), either measured directly (e.g. Gabrielsen et al. 1991; Uttley et al. 1994) or obtained from the equation relating DEE and seabird body mass ($r^2=0.91$): $\log(\text{DEE})=1.1482+0.6521\times(\log \text{body mass})$ or the relationship between body mass and field metabolic rate: $\text{FMR}=16.69\ \text{m}^{0.651}$ (Mehlum and Gabrielsen 1995; Nagy et al. 1999; Crocker et al. 2002; Ellis and Gabrielsen 2002). Next, we calculated the overall daily energy requirements of the "family unit" (ADFFI; two parent birds and their chicks) using our own and literature average values of mean brood size (MBS) in the particular species from the study area (Mehlum and Gabrielsen 1995; Barrett et al. 2002) (Table S2).

To calculate the overall food consumption, we used published information on the dietary composition of each species, with preference given to data from Hornsund or nearby fjords (Stempniewicz 1981; Lydersen et al. 1989; Stempniewicz and Węsławski 1992; Mehlum and Gabrielsen 1993). Most seabirds are opportunistic within the food type as to available prey items. However, the number of prey species available in the high Arctic, and therefore the choice of food type for foraging seabirds, is very limited. Nevertheless, taking into account possible local and temporal variations in the bird's diet, we divided this into just seven rather broad food categories (Table S3).

The calculation of the food biomass taken by birds included calorific values of food, digestive efficiency and water content. The mean energy density and moisture content were calculated for each of the seven food categories. Based on the literature, the following mean calorific values of seabird food were assumed: small fish—6.5 kJ g^{-1}, crustaceans—4 kJ g^{-1} and squid—3.5 kJ g^{-1}. Food moisture contents were assumed to be 71.1% for fish and 77.3% for invertebrates (Mehlum and Gabrielsen 1995; Furness and Bryant 1996; Hunt and Furness 1996; Crocker et al. 2002). The avian assimilation efficiency, i.e. 76% for auks, 79% for gulls and terns, and 87% for Northern Fulmars, was taken from Bairlein (1999). Using these values, we obtained biomass equivalents of particular food types and then calculated the daily consumption by the most numerous seabird species. The daily food intake was calculated using the following equation (Nagy 1999):

$$\text{Daily food intake (wet g)} = \frac{\text{Daily energy expenditure e (kJ)}}{\text{Energy in food}\left(\text{kJ g}^{-1}\right) \times (1-\text{Moisture}) \times \text{Assimilation efficiency}}$$

Having estimated the mean numbers of foraging birds (assuming them to be breeding birds feeding nestlings), we obtained their total daily food consumption in the entire Hornsund fjord, taking account of the species in question, the different guilds and the various habitats.

Statistics

The pattern of multivariate seabird community structure was illustrated using Principal Coordinate Analysis (PCOA). In addition, one-way PERMANOVAs were used to test for differences in the seabird community structure among habitats. The PERMDISP test was used to test the homogeneity of multivariate sample dispersions between the habitats. All the statistical analyses were performed using PRIMER 6 and PERMANOVA (Clarke and Warwick 2001; Anderson et al. 2008).

Results

Seabird numbers, community structure and habitat use

We estimated the average total number of seabirds foraging concurrently in the whole Hornsund area at c. 28,000 with an overall density of c. 90 ind. km^{-2}. Little Auks (c. 13,500; density c. 43 ind. km^{-2}) followed by Northern Fulmars (c. 4500; c. 14 ind. km^{-2}), Brünnich's Guillemots (c. 3700; c. 12 ind. km^{-2}) and Black-legged Kittiwakes (c. 3300; c. 10 ind. km^{-2}) were the most numerous seabird species observed foraging in the fjord and constituted c. 90% of the total seabird community. Pursuit divers, above all Little Auks (c. 48%) and then Brünnich's Guillemots (c. 13%), were predominant in the Hornsund seabird community, making up a total of c. 64%. The proportion of surface-feeders, represented mainly by Black-legged Kittiwakes and Northern Fulmars, was estimated at 28%, while benthic-feeders (almost exclusively Black Guillemots) made up c. 8% (Table 1; Fig. 2c).

The largest habitat, i.e. the pelagic zone, was exploited by the great majority of seabirds (c. 21,000 individuals; c. 75%) with an overall density of c. 86 ind. km^{-2}. Coastal habitats, which provided foraging areas for c. 7000 birds (c. 25%) at an overall density of c. 105 in ind. km^{-2}, included tidal glacier bays (c. 3700), non-glaciated shores (c. 3100) and the least exploited coastline glacier bays (c. 300 individuals) (Table 1).

Table 1 Total estimated number (*N*) and density (*N* km^{-2}) of common seabirds including foraging guilds (benthic feeders—BF, pursuit divers—PD, surface feeders—SF) observed in Hornsund, including the pelagic zone (P) and coastal habitats (sea-terminating tidal glacier bays—STTG, coastal-terminating glacier bays—CLTG, non-glaciated coastline—NGCL) (mean ± SE; *n* = 15 surveys)

Guilds	Species/habitats	Pelagic zone (P)	Coastal zone	STTG	CLTG	NGCL	Whole fjord	% of total
		N (*N* km^{-2})	*N* (*N* km^{-2})	*N* (*N* km^{-2})	*N* (*N* km^{-2})	*N* (*N* km^{-2})	*N* (*N* km^{-2})	
BF	*Cepphus grylle*	374.2 ± 42.3 (1.5 ± 0.4)	1260.8 ± 108.1 (19.0 ± 3.8)	376.3 ± 52.1 (42.7 ± 11.3)	156.3 ± 22.5 (26.3 ± 4.6)	728.2 ± 102.4 (14.2 ± 2.9)	1635.2 ± 132.3 (5.2 ± 1.2)	5.8
BF	*Somateria mollissima*	201.4 ± 36.6 (0.8 ± 0.2)	351.4 ± 50.7 (5.3 ± 1.5)	0.0 ± 0.0 (0.0 ± 0.0)	54.0 ± 7.7 (9.0 ± 1.8)	297.4 ± 41.9 (5.8 ± 1.4)	552.4 ± 88.7 (1.8 ± 0.4)	2.0
BF	Total	**575.9** ± 89.3 (**2.3** ± 0.9)	**1617.3** ± 218.6 (**24.4** ± 4.9)	**376.2** ± 50.9 (**42.7** ± 9.9)	**210.7** ± 32.7 (**35.3** ± 8.7)	**1030.4** ± 102.1 (**20.0** ± 4.8)	**2192.3** ± 148.5 (**7.0** ± 1.8)	**7.8**
PD	*Alle alle*	11,924.1 ± 2012.4 (48.5 ± 10.1)	1658.7 ± 243.7 (25.1 ± 5.2)	38.2 ± 7.1 (4.3 ± 1.0)	25.4 ± 6.3 (4.3 ± 1.0)	1595.1 ± 348.8 (31.0 ± 7.3)	13,582.1 ± 2187.9 (43.5 ± 7.7)	48.2
PD	*Uria lomvia*	3662.3 ± 728.4 (14.9 ± 4.3)	70.8 ± 13.7 (1.1 ± 0.3)	7.2 ± 1.3 (0.8 ± 0.2)	7.1 ± 1.3 (1.2 ± 0.3)	56.5 ± 10.5 (1.1 ± 0.3)	3732.5 ± 702.3 (12.0 ± 3.4)	13.2
PD	*Fratercula arctica*	719.6 ± 101.7 (2.9 ± 1.1)	58.2 ± 7.9 (0.9 ± 0.3)	0.0 ± 0.0 (0.0 ± 0.0)	9.2 ± 1.9 (1.5 ± 0.4)	50.3 ± 11.7 (1.0 ± 0.2)	778.3 ± 113.6 (2.5 ± 0.9)	2.8
PD	Total	**16,306.1** ± 3007.4 (**66.3** ± 14.3)	**1788.8** ± 373.4 (**27.0** ± 5.4)	**45.8** ± 9.9 (**5.1** ± 1.2)	**41.6** ± 9.3 (**6.9** ± 2.2)	**1701.4** ± 366.2 (**33.1** ± 8.9)	**18,093.4** ± 3478.6 (**58.0** ± 10.3)	**64.1**
SF	*Fulmarus glacialis*	4191.8 ± 899.5 (17.0 ± 5.2)	237.2 ± 42.2 (3.6 ± 1.2)	22.4 ± 5.5 (2.4 ± 0.4)	5.2 ± 1.2 (0.9 ± 0.2)	209.6 ± 40.7 (4.1 ± 1.0)	4427.3 ± 908.6 (14.2 ± 3.2)	15.7
SF	*Rissa tridactyla*	69.1 ± 8.8 (0.3 ± 0.1)	3256.8 ± 708.3 (49.2 ± 10.1)	3164.3 ± 702.4 (359.0 ± 79.9)	3.1 ± 1.1 (0.6 ± 0.2)	89.4 ± 21.1 (1.7 ± 0.7)	3 326.2 ± 714.7 (10.6 ± 3.1)	11.8
SF	*Sterna paradisea*	58.4 ± 7.2 (0.2 ± 0.1)	26.5 ± 5.3 (0.4 ± 0.1)	13.2 ± 2.9 (1.5 ± 0.3)	1.1 ± 0.2 (0.1 ± 0.1)	13.1 ± 2.9 (0.2 ± 0.1)	84.4 ± 16.2 (0.3 ± 0.1)	0.3
SF	*Larus hyperboreus*	0.0 ± 0.0 (0.0 ± 0.0)	55.1 ± 10.1 (0.8 ± 0.2)	28.1 ± 6.2 (3.1 ± 1.0)	1.1 ± 0.2 (0.1 ± 0.1)	26.2 ± 5.4 (0.5 ± 0.2)	54.1 ± 10.3 (0.2 ± 0.1)	0.2
SF	Total	**4335.3** ± 914.4 (**17.6** ± 4.3)	**3600.8** ± 712.3 (**54.4** ± 10.2)	**3241.4** ± 655.7 (**367.7** ± 83.2)	**12.2** ± 2.4 (**2.1** ± 0.6)	**347.3** ± 74.8 (**6.7** ± 2.0)	**7936.2** ± 1878.8 (**25.4** ± 5.7)	**28.1**
	Total seabirds	**21,217.4** ± 4004.6 (**86.2** ± 27.4)	**7004.9** ± 1409.6 (**105.9** ± 31.3)	**3662.8** ± 720.6 (**415.5** ± 102.4)	**264.7** ± 51.7 (**44.3** ± 10.3)	**3078.9** ± 689.9 (**59.9** ± 17.2)	**28,221.8** ± 5102.4 (**90.4** ± 24.5)	**100**

*Total values also contain less numerous species, which are not included in the table

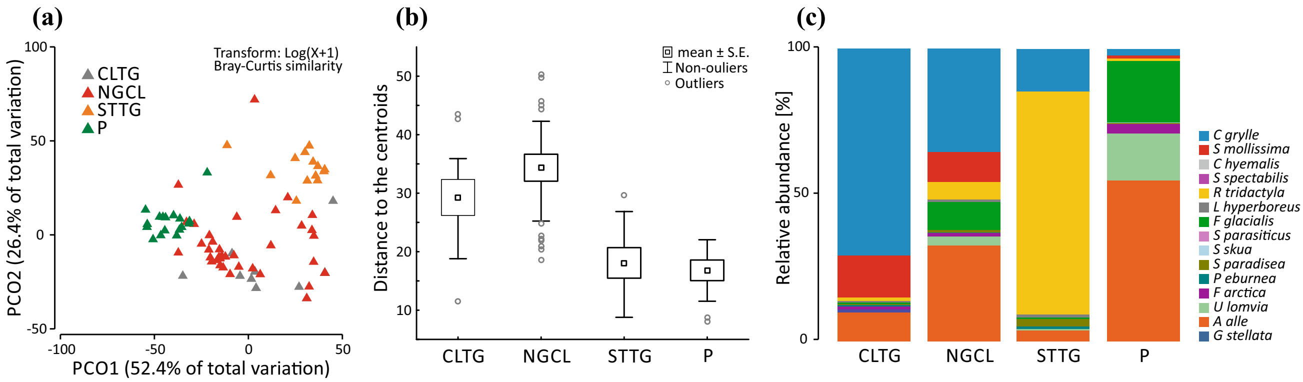

Fig. 2 Seabird community structure (species level) in the four habitat types (STTG—sea-terminating tidal glacier bays, CLTG—coastal glacier bays, NGCL—non-glaciated coastline, P—pelagic zone): **a** Principal Coordinate Analysis (PCO) of Bray–Curtis similarities of relative abundances of seabird species. The symbols represent the habitats; **b** permutational analysis of multivariate dispersions (PERMDISP) showing mean ± SE distances of observations to the centroid of each habitat; **c** average community structure (species composition) for each habitat

Table 2 Habitat effect on seabird community structure (Permanova analysis)

Source of variation	*df*	SS	MS	Pseudo-*F*	*P*(perm)	Unique perms
			Species	Composition		
Habitat	3	77,259	25,753	25.925	**0.001**	999
Residuals	83	82,450	993.37			
Total	86	1.5971E+05				
				Guild structure		
Habitat	3	44,380	14,793	35.662	**0.001**	999
Residuals	83	34,430	414.83			
Total	86	78,811				

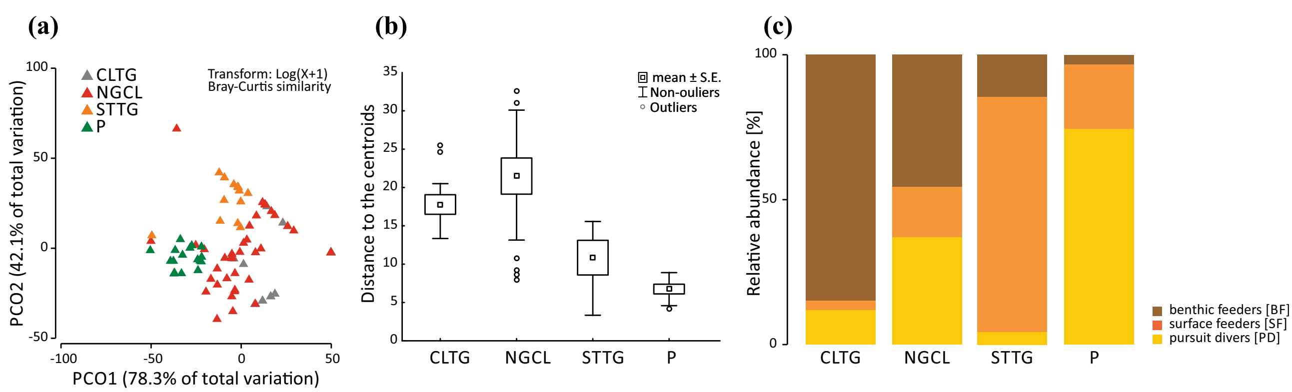

Fig. 3 Seabird community structure (guild level) in the four habitat types: (STTG—sea-terminating tidal glacier bays, CLTG—coastal glacier bays, NGCL—non-glaciated coastline, P—pelagic zone): **a** Principal Coordinate Analysis (PCO) of Bray–Curtis similarities of relative abundances of seabird guilds. The symbols represent the habitats; **b** permutational analysis of multivariate dispersions (PERMDISP) showing mean ± SE distances of observations to the centroid of each habitat; **c** average community structure (guild contribution) for each habitat

We found significant effects of habitat on both the species composition and guild structure of the seabird community (Table 2; Figs. 2a, 3a). The four habitat types distinguished in Hornsund were exploited by different seabirds from different for a ging guilds. The pelagic zone (P) was exploited mainly by pursuit divers, the most common of which were Little Auks. The non-glaciated shore was used primarily by benthic feeding Black Guillemots and Little Auks. Black Guillemots prevailed in the bays formed by retreating glaciers (CLTG), while surface feeding Black-legged Kittiwakes were absolutely predominant in the tidewater glacier bays (STTG). The numbers and densities of foraging seabirds were the highest in the STTG bays, exceeding 3660 birds and 400 ind. km^{-2}, above all Black-legged Kittiwakes, lower in the non-glaciated coastal habitats (over 3000 and c. 60 ind. $km^{-2)}$, and the lowest in CLTG (c. 260 birds and 44 ind. km^{-2}, respectively) (Table 1).

The results of the PERMDISP analysis revealed a statistically significant variation in multivariate dispersion across the habitats in terms of species composition ($F = 10.739$, $df1 = 3$, $df2 = 83$, $p(\text{perm}) = 0.001$) and guild structure ($F = 5.05$, $df1 = 3$, $df2 = 56$, $p(\text{perm}) = 0.009$). Non-glaciated seashore habitats (NGCL) and retreating coastal glacier bays (CLTG) showed greater variability in the community structure than tidal glacier bays (STTG) and the pelagic zone (P) (Table S4; Figs. 2b, 3b).

Interannual variability

During the three study seasons, significant variations in the numbers of birds from different species and guilds feeding in the coastal habitats of the fjord were observed. The most abundant year was 2015, when over 20,000 simultaneously foraging birds were recorded, whereas c. 5390 and 7000 individuals were found in 2014 and 2016, respectively. Black-legged Kittiwakes and Little Auks were the most variable, with numbers varying from 5 to 38 times between the years. Thus, the guilds of pursuit divers and surface feeders were quantitatively the most variable. The number of benthophages in the three seasons remained the most stable. In terms of the numbers of foraging seabirds, the tidal glacier bays (STTG) were the most variable of the habitat types, whereas the coastal glacier bays (CLTG) were the most stable (Table S5).

Food consumption

Based on the mean number of seabirds foraging in Hornsund, their species and guild composition, as well as our own and literature data on their diets and food requirements, we estimated the total amounts of different food types taken daily by seabirds in Hornsund during the chick feeding period. Seabirds foraging in the fjord took c. 12.7 tons of food daily. The most important consumers were Little Auks (35.4%), followed by Brünnich's Guillemots (20.1%), Northern Fulmars (19.1%) and Black-legged Kittiwakes (9.3%). Over half of the food biomass (58%) was ingested by pursuit divers. Surface feeders took c. 29% and benthic feeders c. 13%. About 75% of daily food was taken from the pelagic zone and c. 25% from coastal habitats, including non-glaciated habitats (c. 13%) and tidal glacier bays (c. 11%). Seabirds took less than 1% of their daily food from the coast-terminating glacier bays (Table 3).

Copepods (c. 30%), amphipods (c. 21%) and molluscs (c. 19%) are the most important prey types taken by seabirds in Hornsund. They are followed by fish (c. 14%), polychaetes (c. 10%), euphausids (c. 6%) and mysids (less than 1%).

Table 3 Total estimated wet biomass (*t*) taken daily by seabirds in Hornsund including foraging guilds (benthic feeders—BF, pursuit divers—PD, surface feeders—SF) and particular habitats (sea-terminating tidal glacier bays—STTG, coastal glacier bays—CLTG, non-glaciated coastline—NGCL, pelagic zone—P)

Guilds	Species/habitats	STTG	CLTG	NGCL	Coastal habitats	Pelagic zone P	Whole fjord	% of total
BF	*Cepphus grylle*	0.2	0.1	0.3	0.6	0.2	**0.8**	**6.0**
BF	*Somateria mollissima*	0.0*	0.0	0.5	0.5	0.4	**0.9**	**6.9**
BF	Total	**0.2**	**0.1**	**0.9**	**1.1**	**0.5**	**1.6**	**12.9**
PD	*Alle alle*	0.0	0.0	0.5	0.6	3.9	**4.5**	**35.4**
PD	*Uria lomvia*	0.0	0.0	0.0	0.1	2.5	**2.6**	**20.1**
PD	*Fratercula arctica*	0.0	0.0	0.0	0.0	0.3	**0.3**	**2.5**
PD	Total	**0.02**	**0.02**	**0.62**	**0.65**	**6.74**	**7.39**	**58.0**
SF	*Fulmarus glacialis*	0.0	0.0	0.1	0.1	2.3	**2.4**	**19.1**
SF	*Rissa tridactyla*	1.1	0.0	0.0	1.2	0.0	**1.2**	**9.3**
SF	*Sterna paradisea*	0.0	0.0	0.0	0.0	0.0	**0.0**	**0.1**
SF	*Larus hyperboreus*	0.0	0.0	0.0	0.1	0.0	**0.1**	**0.6**
SF	Total	**1.2**	**0.0**	**0.2**	**1.4**	**2.3**	**3.7**	**29.0**
	Total seabirds	**1.4**	**0.1**	**1.7**	**3.1**	**9.6**	**12.7**	**100.0**

*0.0—values < 0.05 t

Copepods are ingested almost exclusively by Little Auks, amphipods by almost all seabirds, and molluscs by Northern Fulmars (squid) and Common Eiders (gastropods and bivalves). The most important fish consumers appear to be Brünnich's Guillemots, Black-legged Kittiwakes and Northern Fulmars, while polychaetes are taken mainly by Northern Fulmars and Black Guillemots (Table S6).

Discussion

Huge numbers of seabirds (c. 28 thousand individuals) foraged concurrently in Hornsund, which was a result of the unprecedented overall density of foraging seabirds (c. 90 ind. km^{-2}). The density in the pelagic zone (c. 86 ind. km^{-2}) was only slightly lower than that in coastal areas (c. 105 ind. km^{-2}). These values considerably exceeded those obtained in other Arctic fjords. Diemer et al. (2011), using the same survey method and transect width (300 m) in Cumberland Sound fjords (Baffin Island, Nunavut, Canada), recorded 5.5 ind. km^{-2}, while Schoen et al. (2013) found 6.65 ind. km^{-2}in Yakutat Bay, Alaska. The distribution of foraging birds in the Hornsund fjord was patchy; only in the case of tidal glacier bays was it very distinct and constant. Along the non-glaciated coast (NGCL) and in the pelagic zone (P), bird flocks were also observed, but during successive surveys they appeared at different locations. This was probably related to the moving aggregations of available prey on which the birds were feeding.

As a consequence of their high numbers, the seabirds foraging in Hornsund ingested as much as c. 12.7 t. of food daily, which constitutes c. 0.2% (daily) or c. 6% (monthly) of the summer mesozooplankton and fish standing stock available in the fjord (Węsławski et al. 2017). In the North Water Polynya ecosystem, where Little Auks forage in huge numbers (15–30 M breeding pairs), they take only 0.3–0.6% of the primary pelagic production. However, locally and temporarily, this figure could be as high as 5–14% (Karnovsky and Hunt 2002).

The meteorological and hydrological conditions, glacier activity and available food resources in the fjord change significantly from year to year (Kwasniewski et al. 2012; Błaszczyk et al. 2013; Promińska et al. 2018). This results in a different abundance of feeding grounds in different years, and hence, the numbers of seabirds foraging in the fjord (Stempniewicz et al. 2017). During the three study seasons, we noted significant differences in the numbers of seabirds foraging in the coastal habitats of Hornsund. This applied to individual species as well as foraging guilds and habitats. In the most abundant year (2015), an average of over 20,000 birds were foraging simultaneously in the coastal habitats; in the other two years, their numbers were much lower: c. 5390 in 2014 and c. 7000 in 2016 (Table S5). This significant interannual variability in the number of foraging seabirds must have translated into the amounts of food consumed. Thus, the amounts of food consumed daily by seabirds in coastal habitats varied between 2.4 t (2014) and 8.9 t (2015). If the numbers of seabirds foraging in the pelagic zone in the three years varied proportionally with those observed in the coastal habitats, the total food consumption in the whole Hornsund fjord could have ranged from 9.8 t in 2014 to as much as 36.4 t in 2015.

The greatest variability was displayed by the numbers of surface-feeding Black-legged Kittiwakes and pursuit-diving Little Auks, two species which forage alternately in the fjord and on the shelf outside the fjord. The number of benthophages in the three seasons remained the most stable. Tidal glacier bays (STTG) turned out to be the most variable habitat in terms of the numbers of feeding birds, while coastal glacier bays (CLTG) appeared to be the most stable (Table S4).

Food is taken mainly from the pelagic zone (9.6 t) because of its great extent, while the tidewater glacier bays are the most important of the coastal habitats. In the longer term, however, the gradual disappearance of glacier bays will likely reduce the communities of seabirds associated with this habitat. The rapidly progressing deglaciation of the fjord's shores will favour the growth of ice-free coastal habitats (NGCL) and hence, the numbers of mainly benthophagic birds that feed there. Nowadays, the community they form, while not very numerous, is the most diverse (Stempniewicz et al. 2017). Almost 60% of the prey biomass was taken by pursuit divers, with Little Auks alone taking 35.4%. Little Auks, however, avoid glacier bays because of the turbid water occurring there, which makes it difficult or impossible for them to visually search for tiny copepods (Stempniewicz et al. 2013). Water transparency (Secchi depth) and total suspended matter (TSM) near the tidal glacier fronts in Hornsund ranged between 0.6–1.0 m and 220–439 mg d,… m^{-3} (Dragańska-Deja et al. 2020).

Compared to seabirds, the abundance of marine mammals, and therefore, the biomass of food consumed by them in Hornsund are negligible. During the three study years, we recorded four species of marine mammals, represented in total by 20 ringed seals *Pusa hispida*, nine bearded seals *Erignathus barbatus*, 30 belugas *Delphinapterus leucas* and three polar bears *Ursus maritimus*. Their distribution was clearly heterogeneous, with the highest concentrations observed in the tidal glacier bays (Stempniewicz et al. 2017), previously found in the case of ringed seals (Hamilton et al. 2016).

The species composition and proportions of seabirds foraging in Hornsund partly reflected the size of local breeding populations as well as their habitat preferences. The majority of seabirds feed exclusively in the fjord area (e.g. Black Guillemots, Common Eiders, Arctic Terns) (Stempniewicz et al. 2017). However, some of them, including the most numerous Little Auks as well as Brünnich's Guillemots and Black-legged Kittiwakes, exploit alternative foraging grounds situated outside the fjord (Jakubas et al. 2012, 2014; Urbański et al. 2017). Variable proportions of their local populations feed within the fjord, depending largely on the current weather (mainly the direction and strength of the wind and the state of the sea) and the available food resources for a given species (Stempniewicz et al. 2017). Just c. 3% of the 6,00,000 breeding pairs of Little Auks foraged in the fjord during the chick rearing period in the typical 2016 season. On the other hand, no less than 10% of the local Black-legged Kittiwake population usually feeds in the fjord. However, based on observations of c. 10,000 Black-legged Kittiwakes feeding simultaneously on 20 July 2015 in the forefield of the Storbreen glacier, the bulk of the breeding population (c. 15,000 breeding pairs) can feed in Hornsund, making use of exceptionally active subglacial discharges and the calmer fjord waters during bad weather in the open sea. They temporarily exploit the highly attractive tidewater glacier bays as important alternative feeding grounds (Urbanski et al. 2017).

The most visible effect of climate warming in the Arctic is the shrinkage of the extent / area of sea ice (Serreze et al. 2007). In the case of Arctic fjords, this is taking the form of rapid glacier retreat. In Hornsund, this process is the fastest in the whole of Svalbard. In the period 1899–2010, the fjord lost c. 172 km^2 of ice cover. The rate of glacier retreat has increased significantly in recent years to c. 3 km^2 (area) and c. 70 m (linear) per year (Błaszczyk et al. 2013). Since 2000, Hornsund's largest glacier, Hornbreen, has retreated at an average rate of 106 m a^{-1} (Grabiec et al. 2018). So far, the intense melting of glaciers favours the maintenance of attractive feeding grounds for seabirds. However, rapid glacier recession in the Arctic fjords will ultimately result in the disappearance of tidal glacier bays, where subglacial discharges create foraging hotspots with the highest observed foraging seabird densities. As a consequence, we can expect a decrease in surface feeding Black-legged Kittiwakes foraging in the fjord and increasing proportions of pelagic seabirds exploiting planktonic food resources in the fjord (Lydersen et al. 2014; Stempniewicz et al. 2017; Urbanski et al. 2017).

Available food resources, and consequently, the numbers and community structure of seabirds foraging in the fjord and total food consumption can change year to year for reasons such as the irregular advection of oceanic water, the fluctuating input of freshwater of glacial and riverine origin, and the weather conditions (Stempniewicz et al. 2017, 2021; Promińska et al. 2018). Increasing proportions of warm water masses reaching Svalbard fjords by advection will probably transform the proportions of Arctic prey communities into Atlantic ones and will influence the numbers and specific structure of foraging seabirds (Vihtakari et al. 2018; Hop et al. 2019).

Currently, planktonic invertebrates, such as copepods, amphipods and cephalopods, constitute the most important prey of seabirds in Hornsund. The lesser importance of fish in the diet compared to lower latitudes and the predominance of planktonic invertebrates, especially crustaceans, in the trophic web is a specific feature of Arctic marine ecosystems (Hobson and Welch 1992; Wassmann et al. 2011; Kortsch et al. 2015; Renaud et al. 2018). According to future climate-induced scenarios, the proportions of fish in the seabird diet are expected to increase and, consequently, the importance of plankton-feeding seabirds to decrease (Stempniewicz et al. 2007). The results of this paper provide a baseline for future studies on climate-induced changes in the importance of seabirds in the Arctic food web.

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Declaration

Conflict of interest The authors do not have any conflict of interest to declare.

References

Ainley DG (1977) Feeding methods in seabirds: a comparison of polar and tropical nesting communities in the eastern Pacific Ocean. In: Llano GA (ed) Adaptations within Antarctic ecosystems. Smithsonian Institution, Washington, DC, pp 669–685

Anderson M, Gorley RN, Clarke RK (2008) PERMANOVA for PRIMER: guide to software and statistical methods. PRIMER-E Ltd., Plymouth

Arimitsu ML, Piatt JF, Madison EN, Conaway JS, Hillgruber N (2012) Oceanographic gradients and seabird prey community dynamics in glacial fjords. Fish Oceanogr 21:148–169

Amélineau F, Grémillet D, Bonnet D, Le Bot T, Fort J (2016) Where to forage in the absence of sea ice? Bathymetry as a key factor for an Arctic seabird. PLoS ONE 11:e0157764

Bairlein F (1999) Energy and nutrient utilization efficiencies in birds—a review. In: Adams N, Slotow R (eds) Proceedings of the 22nd international ornithological congress, Durban Birdlife South Africa

Barber DG, Hop H, Mundy CJ, Else B, Dmitrenko IA, Tremblay J-E, Ehn JK, Assmy P, Daase M, Candlish LM, Rysgaard S (2015) Selected physical, biological and biogeochemical implications of a rapidly changing Arctic Marginal Ice Zone. Prog Oceanogr 139:122–150

Barrett RT, Anker-Nilssen T, Gabrielsen GW, Chapdelaine G (2002) Food consumption by seabirds in Norwegian waters. ICES J Mar Sci 59:43–57

Błaszczyk M, Jania J, Kolondra L (2013) Fluctuations of tidewater glaciers in Hornsund Fjord (Southern Svalbard) since the beginning of the 20th century. Pol Polar Res 34(4):327–352. https://doi.org/10.2478/popore-2013-0024

Błaszczyk M, Ignatiuk D, Uszczyk A, Cielecka-Nowak K, Grabiec M, Jania J, Moskalik M, Walczowski W (2019) Freshwater input to the Arctic fjord Hornsund (Svalbard). Polar Res. https://doi.org/10.33265/polar.v38.3506

CAFF (2017) State of the Arctic Marine Biodiversity Report. Conservation of Arctic Flora and Fauna International Secretariat, Akureyri, Iceland. 978-9935-431-63-9

Clarke K, Warwick RM (2001) PRIMER v5: User manual. PRIMER-E Limited, Plymouth

Crocker D, Hart A, Gurney J, McCoy C (2002) Methods for estimating daily food intake of wild birds and mammals. Project PN0908, Final Report. Central Science Laboratory.

Dahl TM, Falk-Petersen S, Gabrielsen GW, Sargent JR, Hop H, Millar RM (2003) Lipids and stable isotopes in common eider, black-legged kittiwake and northern fulmar: a trophic study from an Arctic fjord. Mar Ecol Prog Ser 256:257–269

Dalpadado P, Ingvaldsen RB, Stige LC, Bogstad B, Knutsen T, Ottersen G, Ellertsen B (2012) Climate effects on Barents Sea ecosystem dynamics. ICES J Mar Sci 69:1303–1316

Descamps S, Aars J, Fuglei E, Kovacs KM, Lydersen C, Pavlova O, Pedersen ÅØ, Ravolainen V, Strøm H (2017) Climate change impacts on wildlife in a High Arctic archipelago–Svalbard, Norway. Glob Change Biol 23:490–502

Diemer KM, Conroy MJ, Ferguson SH, Hauser DDW, Grgicak-Mannion A, Fisk AT (2011) Marine mammal and seabird summer distribution and abundance in the fjords of northeast Cumberland Sound of Baffin Island, Nunavut, Canada. Polar Biol 34:41–48

Dragańska-Deja K, Błaszczyk M, Deja K, Węsławski JM, Rodak J (2020) Tidewater glaciers as feeding spots for the Black-legged Kittiwake (*Rissa tridactyla*): a citizen science approach. Pol Polar Res 41(1):69–93. https://doi.org/10.24425/ppr.2020.132570

Duarte P, Weslawski JM, Hop H (2019) Outline of an Arctic fjord ecosystem model for Kongsfjorden-Krossfjorden, Svalbard. In: Hop H, Wiencke C (eds) The ecosystem of Kongsfjorden, Svalbard. Advances in polar ecology, vol 2. Springer, Cham

Ellis H, Gabrielsen GW (2002) Energetics of free-ranging seabirds. In: Shreiber E, Burger J (eds) Biology of marine birds. CRC Press, Washington, DC, pp 359–407

Furness RW, Bryant DM (1996) Effect of wind on field metabolic rates of breeding Northern Fulmars. Ecology 77:1181–1188

Gabrielsen GW, Taylor JRE, Konarzewski M, Mehlum F (1991) Field and laboratory metabolism and thermoregulation in dovekies (*Alle alle*). Auk 108:71–78

Gilg O, Istomina L, Heygster G, Strøm H, Gavrilo MV, Mallory ML, Gilchrist G, Aebischer A, Sabard B, Huntemann M, Mosbech YG (2016) Living on the edge of a shrinking habitat: the ivory gull, *Pagophila eburnea*, an endangered sea-ice specialist. Biol Lett 12:20160277. https://doi.org/10.1098/rsbl.2016.0277

Grabiec M, Ignatiuk D, Jania J, Moskalik M, Głowacki P, Błaszczyk M, Budzik T, Walczowski W (2018) Coast formation in an Arctic area due to glacier surge and retreat: the Hornbreen-Hambergbreen case from Spitsbergen. Earth Surf Proc Land 43:387–400

Grémillet D, Fort J, Amelineau F, Zakharova E, Le Bot T, Sala E, Gavrilo M (2015) Arctic warming: nonlinear impacts of sea-ice and glacier melt on seabird foraging. Glob Change Biol 21:1116–1123

Hamilton C, Lydersen C, Ims RA, Kovacs KM (2016) Coastal habitat use by ringed seals *Pusa hispida* following a regional sea-ice collapse: importance of glacial refugia in a changing Arctic. Mar Ecol Prog Ser 545:261–277

Hobson KA, Welch HE (1992) Determination of trophic relationships within a high Arctic marine food web using δ13C and δ15N analysis. Mar Ecol Prog Ser 84:9–18. https://doi.org/10.3354/meps084009

Hop H, Pearson T, Hegseth EN, Kovacs KM, Weslawski JM, Wiencke C, Kwasniewski S, Eiane K, Leakey R, Cochrane S, Zajaczkowski M, Lonne OJ, Mehlum F, Lydersen C, Gulliksen B, Falk-Petersen S, Poltermann M, Wängberg SA, Kendall M, Bischof KY, Voronkov A, Kovaltchouk NA, Gabrielsen GW, Wlodarska-Kowalczuk M, Wiktor J, di Prisco G, Estoppey A, Papucci C, Gerland S (2002) The marine ecosystem of Kongsfjorden, Svalbard. Polar Res 21:167–208

Hop H, Wold A, Vihtakari M, Daase M, Kwasniewski S, Gluchowska M, Lischka S, Buchholz F, Falk-Petersen S (2019) Zooplankton in Kongsfjorden (1996–2016) in relation to climate change. In: Hop H, Wiencke C (eds) The ecosystem of Kongsfjorden, Svalbard. Advances in polar ecology, vol 2. Springer, Cham

Hovinen JEH, Tarroux A, Ramirez F, Forero M, Descamps S (2019) Relationships between isotopic ratios, body condition and breeding success in a High Arctic seabird community. Mar Ecol Prog Ser. https://doi.org/10.3354/meps12886

Hunt GL Jr, Furness RW (1996) Seabird/fish interactions, with particular reference to seabirds in the North Sea. ICES Cooperative Research Report No. 216 ISSN 1017 6195. International Council for the Exploration of the Sea.

Jakubas D, Iliszko L, Wojczulanis-Jakubas K, Stempniewicz L (2012) Foraging by little auks in the distant marginal sea ice zone during the chick-rearing period. Polar Biol 35:73–81

Jakubas D, Wojczulanis-Jakubas K, Iliszko L, Darecki M, Stempniewicz L (2014) Foraging strategy of the little auk *Alle alle* throughout breeding season—switch from unimodal to bimodal pattern. J Avian Biol 45:551–560

Karnovsky NJ, Hunt GL Jr (2002) Estimation of carbon flux to dovekies (*Alle alle*) in the North Water. Deep-Sea Res II 49:5117–5130

Kitaysky AS, Golubova EG (2000) Climate change causes contrasting trends in reproductive performance of planktivorous and piscivorous alcids. J Anim Ecol 69:248–262. https://doi.org/10.1046/j.1365-2656.2000.00392.x

Keslinka LK, Wojczulanis-Jakubas K, Jakubas D, Neubauer G (2019) Determinants of the little auk (*Alle alle*) breeding colony location and size in W and NW coast of Spitsbergen. PLoS ONE 14(3):e0212668. https://doi.org/10.1371/journal.pone.0212668

Kortsch S, Primicerio R, Fossheim M, Dolgov AV, Aschan M (2015) Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists. Proc R Soc B 282:1–9

Kuletz KJ, Stephensen SW, Irons DB, Labunski EA, Brenneman KM (2003) Changes in distribution and abundance of Kittlitz's Murrelets *Brachyramphus brevirostris* relative to glacial recession in Prince William Sound, Alaska. Mar Ornithol 31:133–140

Kumar V, Tiwari M, Rengarajan R (2018) Warming in the Arctic captured by productivity variability at an Arctic fjord over the past two centuries. PLoS ONE 13(8):e0201456. https://doi.org/10.1371/journal.pone.0201456

Kwasniewski S, Gluchowska M, Walkusz W, Karnovsky NJ, Jakubas D, Wojczulanis-Jakubas K, Harding AMA, Goszczko I, Cisek M, Beszczynska-Moller A, Walczowski W, Weslawski JM, Stempniewicz L (2012) Interannual changes in zooplankton on the West Spitsbergen Shelf in relation to hydrography and their consequences for the diet of planktivorous seabirds. ICES J Mar Sci 69:890–901

Lydersen C, Assmy P, Falk-Petersen S, Kohler J, Kovacs KM, Reigstad M, Steen H, Strøm H, Sundfjord A, Varpe Ø, Walczowski W, Węsławski JM, Zajaczkowski M (2014) The importance of tidewater glaciers for marine mammals and seabirds in Svalbard, Norway. J Marine Syst 129:452–471

Lydersen C, Giertz I, Weslawski JM (1989) Stomach contents of autumn-feeding marine vertebrates from Hornsund, Svalbard. Polar Record 25(153):107–114

Mallory ML, Gaston AJ, Provencher JF, Wong SN, Anderson C, Elliott KH, Gilchrist HG, Janssen M, Lazarus T, Patterson A, Pirie-Dominix L (2018) Identifying key marine habitat sites for seabirds and sea ducks in the Canadian Arctic. Environ Rev 27(2):215–240

Mehlum F, Gabrielsen GW (1993) The diet of high-Arctic seabirds in coastal and ice-covered, pelagic areas near the Svalbard archipelago. Polar Res 12:1–20

Mehlum F, Gabrielsen GW (1995) Energy expenditure and food consumption by seabird populations in the Barents Sea region. In: Leinaas HP, Skjoldal HR, Hopkins C, Erikstad KE (eds) Ecology of fjords and coastal waters. Elsevier, Amsterdam, pp 457–470

Moody AT, Hobson KA, Gaston AJ (2012) High-Arctic seabird trophic variation revealed through long-term isotopic monitoring. J Ornithol 153:1067–1078

Nagy KA, Girard IA, Brown TK (1999) Energetics of free-ranging mammals, reptiles and birds. Annu Rev Nutr 19:247–277

Post E, Bhatt US, Bitz CM, Brodie JF, Fulton TL, Hebblewhite M, Kerby J, Kutz SJ, Stirling I, Walker DA (2013) Ecological consequences of sea-ice decline. Science 341:519–524

Pratte I, Braune BM, Hobson KA, Mallory ML (2019) Variable sea-ice conditions influence trophic dynamics in an Arctic community of marine top predators. Ecology and Evolution. https://doi.org/10.1002/ece3.5313

Promińska A, Falck E, Walczowski W (2018) Interannual variability in hydrography and water mass distribution in Hornsund, an Arctic fjord in Svalbard. Polar Res 37:1495546

Ramirez F, Tarroux A, Hovinen J, Navarro J, Afan I, Descamps S (2017) Sea ice phenology and primary productivity pulses shape breeding success in Arctic seabirds. Sci Rep 7:4500. https://doi.org/10.1038/s41598-017-04775-6

Renaud PE, Daase M, Banas NS, Gabrielsen TM, Soreide JE, Varpe O, Cottier F, Falk-Petersen S, Halsband C, Vogedes D, Heggland K, Berge J (2018) Pelagic food-webs in a changing Arctic: a trait-based perspective suggests a mode of resilience. ICES J Mar Sci 75:1871–1881

Schoen SK, Kissling ML, Hatch NR, Shanley CS, Stephensen SW, Jansen JK, Catterson NT, Oehlers SA (2013) Marine birds of Yakutat Bay, Alaska: evaluating summer distribution, abundance, and threats at sea. Mar Ornithol 41:55–61

Serreze MC, Holland MM, Stroeve J (2007) Perspectives on the Arctic's shrinking sea-ice cover. Science 315:1533–1536. https://doi.org/10.1126/science.1139426

Simberloff D, Dayan T (1991) The guild concept and the structure of ecological communities. Annu Rev Ecol Syst 22:115–143

Stempniewicz L (1981) Breeding biology of the Little Auk (*Plautus alle*) in the Hornsund region, SW Spitsbergen. Acta Ornithol 18:141–165

Stempniewicz L, Błachowiak-Samołyk K, Węsławski JM (2007) Impact of climate change on zooplankton communities, seabird populations and arctic terrestrial ecosystem-a scenario. Deep-Sea Res II 54:2934–2945

Stempniewicz L, Darecki M, Trudnowska E, Błachowiak-Samołyk K, Boehnke R, Jakubas D, Keslinka-Nawrot L, Kidawa D, Sagan S (2013) Wojczulanis-Jakubas K (2013) Visual prey availability and distribution of foraging little auks (*Alle alle*) in the shelf waters of West Spitsbergen. Polar Biol 36:949–955. https://doi.org/10.1007/s00300-013-1318-4

Stempniewicz L, Goc M, Kidawa D, Urbański J, Hadwiczak M, Zwolicki A (2017) Marine birds and mammals foraging in the rapidly deglaciating arctic fjord—numbers, distribution and habitat preferences. Clim Change 140:533–548. https://doi.org/10.1007/s10584-016-1853-4

Stempniewicz L, Weydman A, Goc M, Głuchowska M, Kidawa D, Promińska A, Walczowski W, Węsławski JM, Zwolicki A. (2021) Advection of Atlantic water masses influences seabird foraging in a high-Arctic fjord**.** Progress in Oceanography, accepted

Stempniewicz L, Węsławski JM (1992) Outline of trophic relationships in Hornsund fjord, SW Spitsbergen with special consideration of seabirds. In: Opaliński K, Klekowski R (eds) Landscape, life world and man in the high Arctic. Inst. Ekol. PAN, Warszawa, pp 271–298

Sydeman WJ, Thompson SA, Kitaysky A (2012) Seabirds and climate change: roadmap for the future. Mar Ecol Prog Ser 454:107–117. https://doi.org/10.3354/meps09806

Tasker ML, Jones PH, Dixon T, Blake BF (1984) Counting seabirds at sea from ships: a review of methods employed and a suggestion for a standardized approach. Auk 101:567–577

Urbanski JA, Stempniewicz L, Węsławski JM, Dragańska-Deja K, Wochna A, Goc M, Iliszko L (2017) Subglacial discharges create fluctuating foraging hotspots for sea birds in tidewater glacier bays. Sci Rep 7:43999. https://doi.org/10.1038/srep43999

Uttley J, Tatner P, Monaghan P (1994) Measuring the daily energy expenditure of free-living Arctic terns (*Sterna paradisaea*). Auk 111:453–459

Vihtakari M, Welcker J, Moe B, Chastel O, Tartu S, Hop H, Bech C, Descamps S, Gabrielsen GW (2018) Black-legged Kittiwakes as messengers of Atlantification in the Arctic. Sci Rep 8:1178

Wassmann P, Duarte CM, Agustí S, Sejr MK (2011) Footprints of climate change in the Arctic marine ecosystem. Glob Change Biol 17:1235–1249

Węsławski JM, Kwaśniewski S, Stempniewicz L, Błachowiak-Samołyk K (2006) Biodiversity and energy transfer to top trophic levels in two contrasting Arctic fjords. Pol Polar Res 27:259–278

Węsławski JM, Urbański J, Głuchowska M, Grzelak K, Kotwicki L, Kwaśniewski S, Legeżyńska J, Wiktor J, Włodarska-Kowalczuk M, Zaborska A, Zajączkowski M, Stempniewicz L (2017) Can seabirds modify carbon burial in fjords? Oceanologia 59:603–611

Willis K, Cottier F, Kwasniewski S, Wold A, Falk-Petersen S (2006) The influence of advection on zooplankton community composition in an Arctic fjord (Kongsfjorden, Svalbard). J Mar Syst 61:39–54

Wojczulanis-Jakubas K, Wąż P, Jakubas D (2020) Little auks under the midnight sun: diel activity rhythm of a small diving seabird during the Arctic summer. Polar Res 39:3309. https://doi.org/10.33265/polar.v39.3309