ORIGINAL PAPER

Nutrient fluxes from an Arctic seabird colony to the adjacent coastal marine ecosystem

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Abstract

Seabirds are important vectors for nutrient transfer across ecosystem boundaries. In this seasonal study, we evaluate the impact of an Arctic colony (Alkhornet, Svalbard) of Black-legged Kittiwakes (*Rissa tridactyla*) and Brünnich's Guillemots (*Uria lomvia*) on stream nutrient concentrations and fluxes, as well as utilization by coastal biota. Water samples from seabird-impacted and control streams were collected regularly throughout the melt season (June–September) for nutrient and organic carbon analysis. Stable carbon and nitrogen isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) was used to assess whether seabird-derived nitrogen (N) could be traced into filamentous stream algae and marine algae as well as consumers (amphipods). Concentrations of nitrate (NO_3^-) and nitrite (NO_2^-) peaked in July at 9200 µg N L^{-1} in seabird-impacted streams, 70 times higher than for control streams. Mean concentrations of phosphate (PO_4^{3-}) in seabird-impacted streams were 21.9 µg P L^{-1}, tenfold higher than in controls. Areal fluxes from seabird-impacted study catchments of $NO_3^- + NO_2^-$ and PO_4^{3-} had estimated ranges of 400–2100 kg N km^{-2} and 15–70 kg P km^{-2}, respectively. Higher $\delta^{15}N$ was found in all biota collected from seabird-impacted sites, indicating utilization of seabird-derived nitrogen. *Acrosiphonia* sp. from seabird-impacted sites had higher $\delta^{15}N$ values (20–23‰ vs. 3–6‰) and lower C:N ratios (10.9 vs. 14.3) than specimens collected from control sites, indicating reliance on seabird-derived nitrogen sources and potentially higher N-availability at seabird-impacted nearshore sites. Our study demonstrates how marine nutrients brought onshore by seabirds also can return to the ocean and be utilized by nearshore primary producers and consumers.

Keywords Cross-ecosystem fluxes · Runoff · Svalbard · Seabird guano · *Rissa tridactyla* · *Uria lomvia* · Macroalgae

Introduction

Nutrient availability is a strong regulator of marine net primary production (Field 1998). Through fluxes of animals and nutrients, ecosystems are connected, acting as sources and sinks in a dynamic relationship (Polis et al. 1997; Loreau et al. 2003). While passive, abiotic fluxes are limited to transporting nutrients along gradients in potential

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energy, e.g. with river flow or ocean currents, animal-mediated fluxes can go in the opposite direction (McInturf et al. 2019). There are many examples of animals functioning as vectors for nutrient transport, where these fluxes can be of a similar or higher magnitude than passive transport (Varpe et al. 2005; Subalusky and Post 2019). One such example is colonial seabirds, which are responsible for a large part of the animal-mediated nutrient fluxes across the land-sea ecotone (Otero et al. 2018). Seabird droppings, eggs and dead birds scattered around these colonies can be an important nutrient point source for adjacent terrestrial (Anderson and Polis 1999; Breuning-Madsen et al. 2010; Leblans et al. 2014), limnic (Harding et al. 2004; Keatley et al. 2009) and marine ecosystems (Gagnon et al. 2013; Graham et al. 2018; Savage 2019). Seabird-derived nutrients have even been shown to fuel multiple trophic interactions, spanning both marine and terrestrial ecosystems in the Baltic Sea (Hentati-Sundberg et al. 2020). However, many of these interactions can risk weakening, or even disappear, as multiple seabird populations around the world experience declining populations trends (Paleczny et al. 2015; CAFF 2017). Moreover, a recent estimate attributes > 44% of seabird deposited nitrogen (N) and phosphorus (P) to come from species with declining populations (Plazas-Jiménez and Cianciaruso 2020).

The effect of seabird-mediated nutrient fluxes is particularly evident in terrestrial ecosystems surrounding breeding colonies. These areas stand out with intense greenness from increased primary production and change in plant community structure (Eurola and Hakala 1977; González-Bergonzoni et al. 2017; Richter et al. 2017; Duda et al. 2018). Herbivores are attracted to these productivity hotspots which contribute to further nutrient cycling and turnover (Jakubas et al. 2008). Although not as extensively studied in the Arctic, guano deposition from seabird colonies situated close to the shore could be expected to have similar impact on adjacent coastal ecosystems, both through direct deposition in the marine environment, and through runoff of nutrient-rich water from colonies to the coast (Shatova et al. 2017; Bischof et al. 2019).

With large and distinct seabird colonies and a total of around 3 million breeding pairs in the Svalbard area (Anker-Nilssen et al. 2015), combined with a comprehensive understanding of local fjord- and coastal ecosystems (Hop et al. 2002; Bischof et al. 2019), the archipelago is well-suited for studying nutrient fluxes from seabird colonies to the marine ecosystem. In order to understand potential impacts of seabird colonies on coastal ecosystems, there is a need to consider the seasonal processes that may affect the connections between seabird colonies and the coast. Excess nutrients accumulated in the marine system during winter, coupled with a rapid increase in irradiance during spring leads to a large increase in marine primary production. As the summer proceeds, primary production typically becomes limited by nutrient availability, particularly dissolved inorganic forms of nitrogen (DIN), silicate (SiO_2) and to some extent phosphate (PO_4^{3-}) (Rysgaard et al. 1999; Hop et al. 2002; Sakshaug et al. 2009). Meanwhile, the often highly synchronised seabird breeding season (Burr et al. 2016) paired with increased runoff during the summer melt season suggests that the highest intensity of the seabird driven nutrient fluxes may coincide with the onset of the marine nutrient depleted state by June and July (Hodal et al. 2012). Thus, it has been postulated that seabirds can increase primary production in coastal ecosystems in Svalbard, in particular fjord systems where seabirds are numerous (Zmudczyńska-Skarbek et al. 2015; Shatova et al. 2017). In a study comparing Hornsund and Kongsfjorden, two fjords on the west coast of Spitsbergen, Svalbard, it was argued that the higher number of seabirds breeding in Hornsund contributed to a higher annual primary production compared to Kongsfjorden (Smoła et al. 2017).

While several studies (including studies from Svalbard) have estimated seabird-mediated nutrient fluxes from land to sea, the degree to which these nutrients are retained in the terrestrial catchment, released to the atmosphere, or transported to the coast via runoff has received considerably less attention. Some generalisations can be made about the cycling and fate of nitrogen from seabird guano. Loss through runoff during precipitation events and volatilisation of ammonia (NH_3) from uric acid and other nitrogen-compounds in guano are important pathways of nitrogen removal from seabird colonies (Lindeboom 1984). NH_3 emission rates are however dependent on temperature, pH, moisture and substrate type (Zhu et al. 2011). NH_3 typically has a short atmospheric lifetime and will be redeposited within a few hundred meters to a few km (Pitcairn et al. 2002). With increasing distance from the colony, a gradient in seabird impact on terrestrial and limnic environments can be observed, manifested in altered species abundance, composition, and physical characteristics, as well as stoichiometry of soil and water (González-Bergonzoni et al. 2017; Richter et al. 2017; Duda et al. 2018).

Isotope fractionation is widely used in analysis of trophic position and food webs dynamics (Peterson and Fry 1987). The light isotope ^{14}N is preferentially metabolised and excreted relative to the heavier ^{15}N, leading to higher ^{15}N in an organism's tissue relative to its diet. Since seabird species are feeding at high trophic levels in the marine environment, their guano also typically has a much higher $\delta^{15}N$ levels than atmospheric deposited nitrogen and marine DIN. These elevated $\delta^{15}N$ values in guano have been used to trace seabird-derived N into and through impacted ecosystems (Zwolicki et al. 2013; Kazama 2019).

In this paper, we study a seabird colony of Black-legged Kittiwakes (*Rissa tridactyla*) and Brünnich's Guillemots

(*Uria lomvia*) in Svalbard, and the interaction between the breeding birds and the adjacent coastal marine ecosystems, with two objectives: Estimating nutrient fluxes from the colony and assessing uptake in the nearby coastal ecosystem. We test three main hypotheses: (1) The runoff from seabird-impacted streams will have higher concentrations of bioavailable nutrients and organic carbon than control streams; (2) the nutrient and organic carbon concentrations in the seabird-impacted streams will exhibit seasonal variation, with higher concentrations when the seabirds are present in the colony; and (3) The algae in seabird-impacted streams and coastal organisms in adjacent coastal waters will show evidence of reliance on seabird-derived nutrients (i.e. elevated $\delta^{15}N$ values).

Methods

Study area

The bird cliff Alkhornet (Fig. 1) on the west coast of Spitsbergen, Svalbard, was visited five times between June and September 2018 (see Online Resource 1, Table S1, for dates). Alkhornet supports a mixed colony of about 14 000 breeding pairs of Black-legged Kittiwakes (*Rissa tridactyla*) and 15 000 breeding pairs of Brünnich's Guillemots (*Uria lomvia*) (Sebastien Descamps, pers. com.). This can

be considered a medium size colony for Svalbard (Anker-Nilssen et al. 2018). The bird cliffs are situated 700 to 900 m from the shore and consist mainly of marble and calcareous phyllite from Neoproterozoic (Dallmann 2015). *Cochlearia groenlandica* and other nitrophilous species can be found in abundance near and on the rock wall (Fig. 1, I). On the terrace between the rock wall and the coast (Fig. 1, II and III) we find graminoid-moss tundra. The peat here can be 1.5 m deep, which is unusually thick for Svalbard (Låg 1990).

Water chemistry

Water was collected for chemical analysis from three streams impacted by the seabird colony (referred to as B1-B3) and in two control streams (C2 and C3), with little seabird presence. A third control stream (C1) was sampled only once, in July, as there was little surface streamflow on the other sampling occasions. The C1 site will therefore not be included in analyses with a seasonal component. In addition to total concentrations of nitrogen (TN), phosphorous (TP) and organic carbon (TOC), concentrations of SiO_2, PO_4^{3-}, NH_4^+ and $NO_3^- + NO_2^-$ were analysed ($n = 26$). Analyses of water chemistry parameters were carried out using standard and accredited methods (as described in Kaste et al. 2018). A summary of the analytical methods can be found in Online Resource 1, Table S2. Stream water turbidity was measured during the four first visits to the study area ($n = 21$)
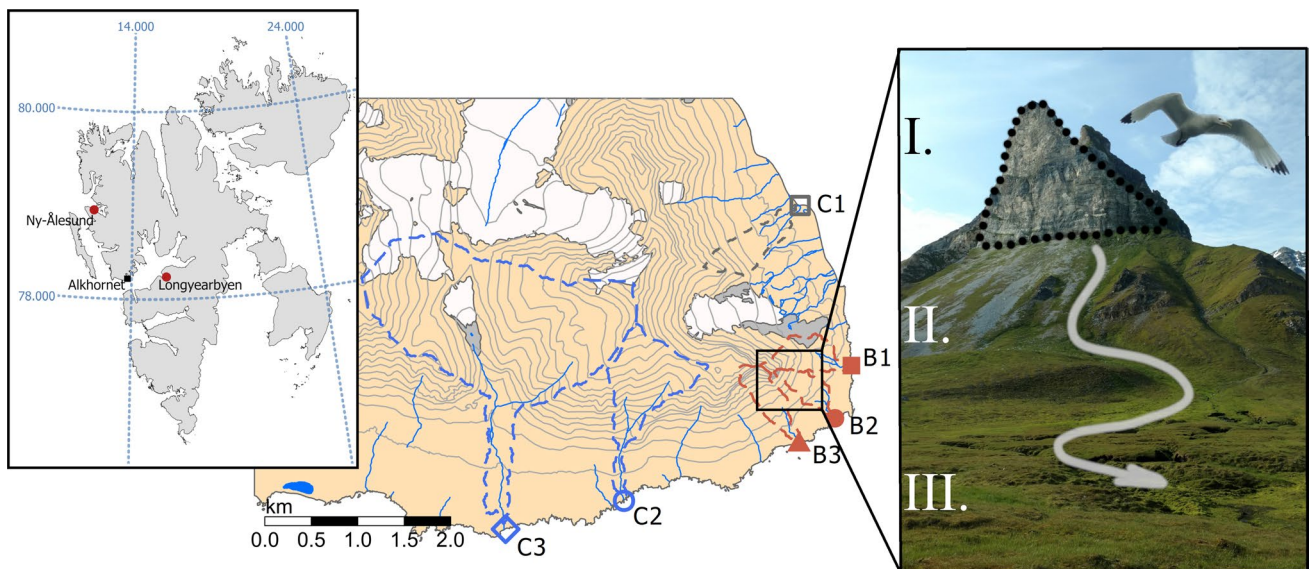

Fig. 1 The study area at Alkhornet, Central-West Spitsbergen in Svalbard (overview map, © Norwegian Polar Institute). Station names correspond to the study streams and marine sampling sites (coordinates in Online Resource 1, Table S1). C1 (only sampled once), C2 and C3 are controls, B1, B2 and B3 are seabird-impacted. A picture is included of the main wall (I) at Alkhornet looking north-westerly, where the main colony is located. Beneath the wall is a scree area (II) before the terrain flattens out to peatlands (III). Dotted lines correspond to the catchment area of each stream (B1 = 0.24 km², B2 = 0.14 km², B3 = 0.22 km², C1 = 0.30 km², C2 = 0.73 km², C3 = 3.74 km²). Approximately 10% of C3 is glaciated, while the other catchment areas are non-glaciated. Stream water were sampled less than 50 m from the shore, at a distance of 0.7–0.8 km from the colony centre for seabird-impacted streams and 2.0–3.5 km from the colony for control streams

with a Eutech TN-100 handheld turbidity meter (Thermo Scientific).

Biotic sampling, stable isotope analysis (SIA), and C:N ratios

Kittiwake guano ($n=3$) was either collected from a piece of plastic (50×50 cm) placed under the colony for 1 h ($n=2$) or scraped off a rock ($n=1$). The sampling was done at the accessible margins of the bird cliff where there is a preponderance of Kittiwake nests, and hence, we assume that Guillemot guano was not obtained. Filamentous, epilithic algae in streams were hand-picked and rinsed in deionized water, while in the adjacent coastal ecosystem, the macroalgae *Acrosiphonia* sp. and *Ectocarpus* sp. were collected in the tidal zone and rinsed with deionized water. Finally, amphipods (*Gammarus setosus* and species from the family Gammarellidae) were hand-picked and stored alive in filtered seawater (filtered through 5 μm pore size) for 24 h in order to clear their guts. Particulate organic matter samples were also collected for streams by filtering stream water onto precombusted glass fibre filters (Whatman GF/F; nominal pore size of 0.7 μm). All samples were stored frozen (-20 °C) until further processing. All biotic samples were freeze-dried and homogenized prior to stable C ($\delta^{13}C$) and N ($\delta^{15}N$) isotope analysis, while filters were freeze dried and analysed for only $\delta^{15}N$. For accurate determination of amphipod and guano $\delta^{13}C$, inorganic carbonates were removed prior to analysis through acidification of homogenized subsamples with 1 M HCl (Brodie et al. 2011; Søreide and Nygård 2012), while $\delta^{15}N$ values were determined through analysis of unacidified subsamples. Analysis of $\delta^{13}C$ and $\delta^{15}N$ was carried out at the UC Davis Stable Isotope Facility (SIF) with a continuous flow Isotope Ratio Mass Spectrometer. Long-term standard deviation at UC Davis is $\pm 0.2\permil$ for ^{13}C and $\pm 0.3\permil$ for ^{15}N. Stable isotope analysis also yielded data on C and N content for analysed samples, which were used to calculate molar C:N ratios for all biotic samples, and particulate N concentrations in stream water.

Runoff estimation

A digital elevation model (DEM) with a ground pixel size of 5×5 m was used for delineation of catchment area (Norwegian Polar Institute 2014). A drainage direction raster was made in QGIS 3.4 with GRASS GIS tools (GRASS Development Team 2017; QGIS Development Team 2019) and from this; the catchments draining towards the coordinates of each station were delineated. Estimation of runoff was made from weather data from the nearby meteorological station at Isfjord Radio (Norwegian Meteorological Institute (MET), http://sharki.oslo.dnmi.no/, accessed January 2019) and the Arctic limited AROME (Application of Research

to Operations at Mesoscale) weather model using median values of a 3×3 cell matrix surrounding the study area. AROME Arctic is METs operational forecasting model for Svalbard with a 2.5 km horizontal resolution (Müller et al. 2017).

A total of 190 mm precipitation was recorded at Isfjord Radio during the sampling period, while 221 mm was recorded from November 2017 to the first sampling in June 2018, and was assumed to be stored in the catchment as snow until the melt-season onset in June. Corresponding numbers based on AROME were higher, at 295 and 400 mm respectively. Precipitation measurements from Isfjord Radio, similarly to other weather stations in Svalbard, are known to often underestimate the true precipitation during winter (Førland and Hanssen-Bauer 2000). Additionally, its location at sea level typically equate to lower precipitation than the higher elevations that constitute much of the catchment basins (Killingtveit et al. 2003). Meanwhile, the AROME weather model accounts for elevation increase, which may explain the deviation between modelled precipitation and measurements at Isfjord Radio.

In order to estimate runoff, we used data on total annual surface runoff from London river (Blomstrandøya) close to Ny-Ålesund, where the ratio of surface runoff to annual precipitation was 0.69 (Killingtveit et al. 2003). Based on this ratio, the total estimated runoff in summer 2018 was 284 mm based on Isfjord Radio data and 479 mm based on AROME data. We used the area under the curve (AUC) function in the package "MESS" in R 3.5.1 (Ekstrøm 2019; R Core Team 2019) with the spline function (Yeh and Kwan 1978) to estimate nutrient and TOC fluxes from the study streams based on the AUC-derived runoff and concentration data for the individual sampling dates. AUC-derived total annual runoff estimates were matched to the ratio-based estimates (284 and 479 mm) by first estimating runoff (excluding snowmelt) for each sampling day by multiplying the 3-day average precipitation prior to the sampling days by 0.69 (Killingtveit et al. 2003). We then adjusted sampling day runoff estimates to account for snowmelt contribution by adding additional runoff for the June and early July sampling days in order to achieve an AUC-derived total annual runoff estimate matching the ratio-based estimate (weighted as two thirds and one third for June and July respectively, based on observations of streamflow and snow cover during fieldwork). Groundwater transport was assumed to be negligible as this only occurs in the permafrost active layer, which is ~ 2 m deep at other coastal sites in Svalbard (Ny-Ålesund and Isfjord Radio; Christiansen et al. 2018). Given the many uncertainties connected to this approach, runoff estimates are given as intervals with the likely underestimation from Isfjord Radio as a low estimate and AROME as a high estimate. Unfortunately, these estimates could not be verified with other catchment areas on Svalbard, as The Norwegian Water Resources and Energy Directorate

had no adequate measurements of waterflow for the 2018 season (Songe, pers. comm.). By pairing catchment areas and runoff estimates with water chemistry data, seasonal yields of the different compounds can be approximated. Seasonal yields were estimated using AUC, following the same method as the runoff calculations.

Normalised difference vegetation index (NDVI) in catchments

The normalised difference vegetation index (NDVI) was used as a measure of seabird impact on the terrestrial vegetation. The index is calculated as follows; $NDVI = [(NIR - red) \times (NIR + red)^{-1}]$, where NIR is near infrared spectral bands (700–805 nm) and red is red bands (635–675 nm). An 8-bit aerial orthophoto from 2009 by the Norwegian Polar Institute with a ground pixel size of 0.4×0.4 m taken with an UltraCam X sensor was used. The NDVI calculation was done with the QGIS "GRASS" package (GRASS Development Team 2017; QGIS Development Team 2019).

Ordination

To identify variation in stream water chemistry among sites and sampling days, we used principal component analysis (PCA). A subset of key parameters was selected for inclusion in the PCA to avoid missing values and to reduce dependence between parameters due to their intrinsic properties, e.g. between TN and $NO_3^- + NO_2^-$. A correlation plot of all parameters can be found in Online Resource 1, Fig. S1. The filtered subset contained 6 variables; TP, NH_4^+, $NO_3^- + NO_2^-$, SiO_2 and $\delta^{15}N$ and particulate N collected on GF/F filters. All parameters were standardised to a mean of 0 and standard deviation of 1. To explain causes of variation in the matrix, the following external environmental variables were available; catchment sizes, NDVI medians of the catchments, the two runoff estimates, sample date, air temperature the last three days and distances from stream sampling points to centre of the colony. Redundancy analysis (RDA) was used to assess explanatory power of these variables. A best model was made using forward selection of a null model, with the pseudo-F value from 10^4 permutations as a selection criterion when p values < 0.05. The best environmental predictors were subsequently fitted to the PCA ordination using the "envfit" function in the "vegan" R package (Oksanen et al. 2019).

Results

Stream water chemistry

N, P and organic C concentrations were generally much higher in seabird-impacted streams than in control streams (Fig. 2). Particulate matter in seabird-impacted streams had a mean $\delta^{15}N$ value of 14.8‰ ± 3.9‰ ($n = 15$), while controls had a mean of 3.7‰ ± 1.2‰ ($n = 11$). The majority of dissolved N was present as $NO_3^- + NO_2^-$, with mean concentrations of 3334 µg L^{-1} ± 2665 µg L^{-1} ($n = 15$) in seabird-impacted streams and 90 µg L^{-1} ± 43 µg L^{-1} ($n = 11$) in control streams. In the seabird-impacted streams, $NO_3^- + NO_2^-$ displayed a seasonal pattern with a clear increase from below 1700 µg N L^{-1} just after snowmelt in June to peak values of up to 9198 µg N L^{-1} at the end of July. Seasonal changes were also observed for TP concentrations, with highest values recorded in June and July. While both stream groups had TP concentrations up to 127 µg L^{-1}, most of the P was dissolved as PO_4^{3-} in seabird-impacted streams, as compared to control streams which never had PO_4^{3-} values above 4 µg P L^{-1}. SiO_2 concentrations were similar between seabird-impacted streams and control, and all streams had low concentrations when the streamflow was high in July. The C1 catchment, which includes a small, glaciated area, had particularly high turbidity linked to the high flow in July (see Online Resource 1, Table S1, for all values).

The variance in stream water chemistry is summarised in the PCA ordination diagram (Fig. 3), highlighting the differences between seabird-impacted and control stations. Median NDVI in the catchment and the estimated discharge were found to be the best environmental predictors for stream water chemistry (permutation test of RDA with 10^4 permutations, pseudo-$F_{1,23} = 18.4$, p value < 0.0001 and pseudo-$F_{1,23} = 5.0$, p value $= 0.0029$, respectively (see Online Resource 1, Fig. S2 for an RDA diagram)). The two runoff estimates based on AROME and Isfjord Radio had negligible difference as environmental predictors.

Flux estimates

Using the 2018 runoff estimate based on Isfjord Radio precipitation measurements and AROME Arctic model output, integrated summer $NO_3^- + NO_2^-$ areal flux in the seabird-impacted streams was approximated to range from 430 to 2500 kg N km^{-2}, and PO_4^{3-} from 5.1 to 21 kg P km^{-2}. For control streams, the corresponding estimates were 19–31 kg N km^{-2} and 0.6–1.7 kg P km^{-2}, respectively (see Table 1 for all estimates). Except for a particularly high value for B3 in July, TOC concentrations remain stable through the season and the integrated summer flux of TOC is at similar magnitude to the $NO_3^- + NO_2^-$-N flux for the seabird impacted streams. This contrasts with C3 where the flux of TOC (760–1300 kg) is one order of magnitude higher than the $NO_3^- + NO_2^-$-N flux.

The catchment areas B1-B3 represent approximately 50% of the total area around the colony with similarly high NDVI values. Furthermore, the Kittiwake guano collected had a N-content between 16 and 28% of the dry weight. By using
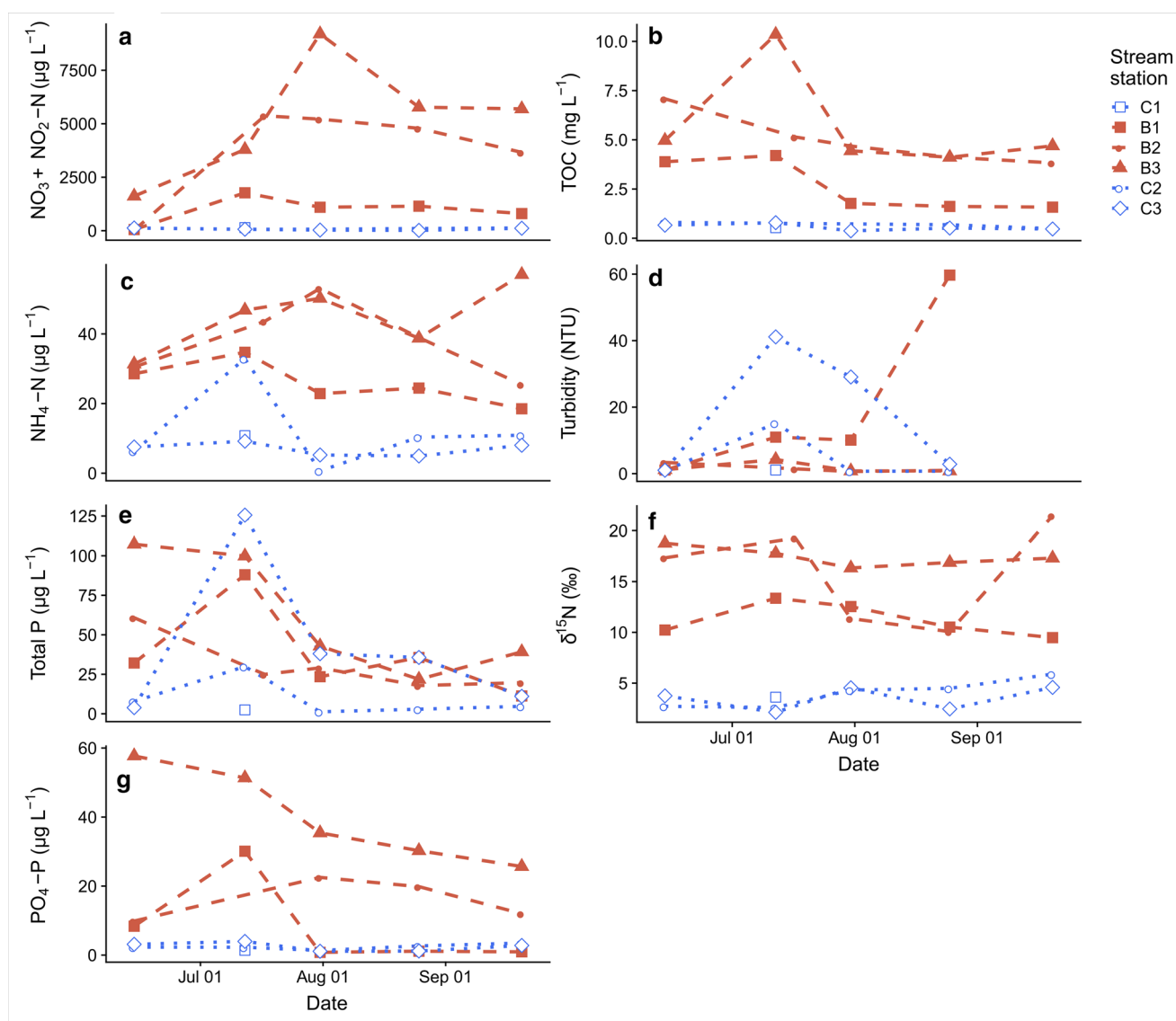
Fig. 2 Seasonal differences in stream water variables at seabird-impacted sites B1, B2 and B3 (red) and control sites C1 (only values from July 12th), C2 and C3 (blue). **a** $NO_3^- + NO_2^-$-N, **b** Total organic carbon (TOC), **c** NH_4^+-N, **d** Turbidity, **e** Total P (TP), **f** δ^{15}N, **g** PO_4^{3-}-P

previous studies of seabirds in Svalbard we have constructed an approximate N and P budget based on the number of seabirds breeding in the Alkhornet colony. From experiments using the doubly-labelled water method to determine field metabolic rates (FMR) and water turnover rates, previous studies have estimated food consumption and assimilation efficiency for Kittiwakes and Guillemots (Gabrielsen et al. 1987; Brekke and Gabrielsen 1994; Mehlum and Gabrielsen 1995; Gabrielsen 1996; Ellis and Gabrielsen 2001). Combining these estimates with time spent in the colony for adults and chicks (Brekke and Gabrielsen 1994; Barrett et al. 2002), a total guano deposition of 118 000 kg dry weight was estimated. The values and equations used for this calculation can be found in Online Resource 1, Table S3. In total,

the Kittiwakes contribute with 37 000 kg and Brünnich's Guillemots with 81 000 kg during the breeding season.

Biota

An ornithogenic signal (higher δ^{15}N) was found in all biota collected from the seabird-impacted sites (Fig. 4 and Table 2). The discrepancy in δ^{15}N values is particularly high for *Acrosiphonia* sp. (see Table 2.) Furthermore, this macroalgae had an atomic C:N ratio that was lower at seabird-impacted sites than controls. The much higher C:N ratio and higher δ^{13}C value of the *Ectocarpus* sp. sample at B1 is likely to reflect taxonomic differences in C:N ratios compared to *Acrosiphonia* sp. Epilithic algae from
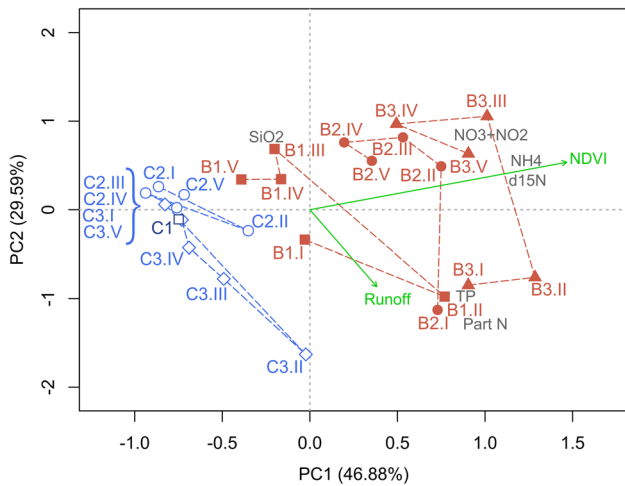
Fig. 3 PCA ordination plot of SiO_2, $NO_3^- + NO_2^-$-N, NH_4^+-N, TP, δ^{15}N amount of particulate carbon nitrogen (PartN) on GF/F filters. The notation of the sample stations corresponds to the name and sampling date (roman numbers from I to V). The red being bird stations B1-B3 and blue being controls C2-C3. C1 is included but does not have a roman number as it was only sampled once. NDVI median of catchment basins and a runoff estimate based on Isfjord Radio weather data were fitted as environmental predictors (green arrows)

seabird-impacted streams B2 and B3 had δ^{13}C values below $-40‰$, potentially indicating a biogenic (and therefore low δ^{13}C) source of CO_2 in these carbon- and nutrient-rich catchments. Amphipods δ^{15}N values were higher at seabird-impacted sites (8.4‰) than at control sites (7.0‰) (Welch's t test, $t_{4.49} = 10.23$, $p = 0.0003$), while δ^{13}C values did not differ significantly (see Online Resource 1, Table S4, for all values).

Discussion

Seabirds play an important role in Arctic nutrient cycling by creating nutrient hotspots around their colonies. While previous research has largely focused on seabird-mediated nutrient transport from sea to land and the impact on terrestrial ecosystems, we show that seabird colonies near the shores can also act as point sources of nutrients to adjacent coastal ecosystems. Despite the presence of a large terrestrial sink in the study site, our results demonstrate substantial seabird-derived nutrient fluxes back to coastal waters, and use of ornithogenic nitrogen in littoral and nearshore coastal organisms.

Stream geochemistry and main drivers

Our first hypothesis proposes elevated nutrient concentrations in streams near the seabird colony. This is well supported by our results, where nutrient concentrations, and especially DIN (dissolved inorganic nitrogen) and DIP (dissolved inorganic phosphorous), were higher in seabird-impacted streams than control streams, and differences between study streams were best explained by the median NDVI values in the catchments (Fig. 3). Maximum NDVI-values in the Isfjorden-area as a whole have increased by 0.015 between 2009 and 2015, which is in accordance with the long term trend (1986–2015) of an NDVI increase of 0.0017 year^{-1} (Vickers et al. 2016), thus we assume the NDVI-change to be negligible between 2009, when the aerial orthophoto was taken, to 2018 when these samples were collected. We also hypothesized that there would be a distinct seasonality in stream nutrient concentrations linked to seabird presence. While we did observe a high degree of seasonality in nutrient concentrations across all streams, much of this seasonality was linked to fluctuations in runoff rather than the timing of seabird presence in the colony.

DIN concentrations in our control streams were similar to those reported by Tye and Heaton (2007) for small non-glaciated catchments in Svalbard, suggesting that the concentrations observed in these streams are within the expected range for non-seabird impacted Svalbard streams. Furthermore, Tye and Heaton (2007) report δ^{15}N values of NO_3^- in their runoffs to lie between -1 and 5‰, which is in congruence with the δ^{15}N values of epilithic stream algae sampled in our

Table 1 Estimates of $NO_3^- + NO_2^-$-N, NH_4^+-N, PO_4^{3-}-P and TOC fluxes from the seabird-impacted (B1-B3) and control (C2-C3) study streams interpolated for the melt season (June–September), both as total mass fluxes and areal fluxes

	B1	B2	B3	C2	C3
$NO_3 + NO_2$-N flux (kg)	100–190	190–350	270–460	15–24	70–110
$NO_3 + NO_2$-N areal flux (kg km^{-2})	430–780	1300–2500	1200–2100	21–32	19–31
NH_4-N flux (kg)	2.2–3.8	1.7–3.0	2.8–4.9	5.3–9.7	8.9–15
NH_4-N areal flux (kg km^{-2})	9.1–16	12–21	13–22	7.3–13	2.4–4.1
PO_4-P flux (kg)	1.6–3.0	0.7–1.3	3.0–5.2	0.5–0.8	3.7–6.4
PO_4-P areal flux (kg km^{-2})	6.5–12	5.1–9.1	14–24	0.6–1.0	1.0–1.7
TOC flux (kg)	260–450	220–360	550–1000	NA	760–1300
TOC areal flux (kg km^{-2})	1100–1900	1500–2500	2500–4500	NA	203–350

These values derived from runoff estimates based on precipitation measured at Isfjord Radio (low values) and the AROME Arctic weather model (high value)
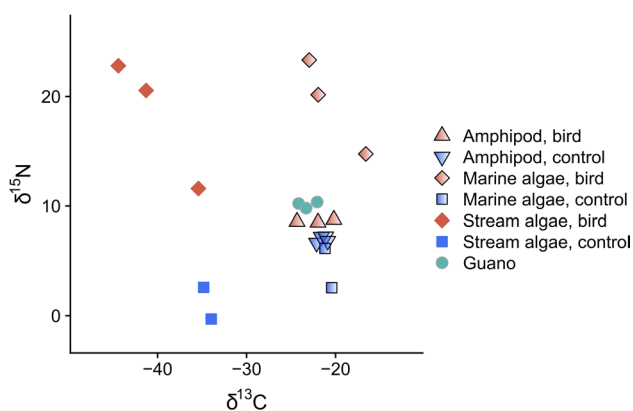
Fig. 4 $\delta^{15}N$ and $\delta^{13}C$ biplot of collected amphipods, macroalgae and Kittiwake guano. Amphipod and guano $\delta^{13}C$ values are from acidified samples, while values for algae are from unacidified samples. All $\delta^{15}N$ values come from unacidified samples. A discrepancy in $\delta^{15}N$ values were found between bird and control stations for all biota, with the algae samples displaying an extreme difference. For both the marine and stream algae, station B1 had the lowest $\delta^{15}N$ value of the bird stations. The terrestrial signal of stream algae is evident as much lower $\delta^{13}C$ values than the other samples

control streams. Similarly, NO_2^- and NO_3^- is the dominant form of nitrogen in the seabird-impacted streams. However, NH_4^+ constitutes a larger percentage of the total N early in the season. Dry deposition of particulate NH_3 to the snowpack from the colony can constitute an important source of NH_4^+ to the streams early in the melt season, as seen in the vicinity of penguin rookeries in Antarctica (Wodehouse and Parker 2013). As the thaw depth increases in July, NO_3^- in soil becomes mobilised which can explain the high values seen here (Yano et al. 2010). Furthermore, we can expect microbial activity to be much greater in the productive and soil-rich surroundings of the bird cliff, which can lead to oxidization of NH_4^+ (Banerjee and Siciliano 2012) or assimilation by vegetation (Yano et al. 2010). Highly different TOC levels between seabird-impacted and control sites are also evident. The elevated TOC concentrations in the seabird impacted streams likely reflects the deep organic-rich soils and abundant vegetation present in the guano-impacted catchments, with the highest concentrations observed early in the season when the flow pathways are shallow and through organic-rich layers (McGovern et al. 2020).

In the present study, Kittiwake guano had $\delta^{15}N$ values higher than 10‰, as expected from previous work

(Wainright et al. 1998). We also expect guano from Brünnich's Guillemots to have similar $\delta^{15}N$ values, as Guillemots occupy the same trophic position as Kittiwakes in the Barents Sea (Hop et al. 2002). However, the extreme $\delta^{15}N$ values in POM and epilithic algae from the seabird-impacted streams reached 20‰. This suggests that further fractioning has occurred in the deposited N. Isotopic fractionation during NH_3 volatilisation from the guano will enrich ^{15}N content of residual nitrogen (Frank et al. 2004). The nitrogen isotopes can be further fractionated in microbial processes e.g. nitrification and denitrification, and after assimilation by autotrophs. Previous work on nitrogen flux through Arctic tundra has shown how efficiently nitrogen is assimilated by vegetation (Odasz 1994; Choudhary et al. 2016), and that most of the N losses through leaching are due to decomposition of organic matter (Yano et al. 2010). The role of soil as a transition step between seabird deposition and release to aquatic ecosystems have been observed in other systems as well (Harding et al. 2009). Although the $\delta^{15}N$ values in the streams were taken from particulate matter, likely reflecting eroded N-enriched catchment soils, the $\delta^{15}N$ of dissolved nitrogen in the seabird-impacted streams is likely similarly high, as evidenced by the extremely high $\delta^{15}N$ in epilithic stream algae relative to the $\delta^{15}N$ values for guano.

Although TP-concentrations were positively associated with streamflow across all study sites, the main drivers for seasonality in observed concentrations are likely different between controls and seabird-impacted catchments. In control streams, TP values were strongly correlated with turbidity, with highest concentrations in C3, where glacial influence and a large catchment area led to elevated turbidity and transport of glacial silt throughout the melt season. Although TP-concentrations were high in this stream, PO_4^{3-} was only a minor contributor to TP concentrations, likely due to a strong contribution of particulate P, which is much less available for uptake by primary producers (Reynolds and Davies 2001). In contrast, PO_4^{3-} was the dominant form of P in seabird-impacted streams, suggesting an important source of bioavailable phosphorus to the coastal environment.

Fluxes and terrestrial retention

Marine-derived nutrients deposited in and around the bird cliff represent a strong point source of nutrients to terrestrial and coastal ecosystems, and originate primarily from the

Table 2 SIA and C:N molar ratios for algae samples for seabird-impacted streams B1, B2 and B3 and for controls C1 and C2. *Ectocarpus* sp. was sampled in absence of *Acrosiphonia* sp. in station B1 (denoted by an asterisk)

	Acrosiphonia sp. (*Ectocarpus* sp.*)*					Epilithic stream algae				
	B1*	B2	B3	C2	C3	B1	B2	B3	C2	C3
$\delta^{15}N$	14.7	20.2	23.3	6.15	2.56	11.6	22.8	20.6	2.6	−0.3
$\delta^{13}C$	−16.6	−22.0	−23.0	−21.2	−20.4	−35.4	−44.4	−41.3	−34.8	−34.0
C:N	17.95	10.41	11.29	14.67	14.00	8.98	10.08	10.97	8.92	8.19

pelagic zone where the surface-feeding Black-legged Kittiwakes and the diving Brünnich's Guillemots hunt. This difference in foraging behaviour impacts their choice of foraging grounds, e.g. with Kittiwakes tending to be more attracted to marine-terminating glacier fronts than Guillemots (Urbanski et al. 2017; Nishizawa et al. 2020). Both species will forage relatively nearby their colonies during the breeding season, commonly within a radius of 20 km from the colony and rarely leaving on foraging trips more than 50 km away from the colony (Mehlum et al. 2001; Falk et al. 2002; Bertrand et al. 2021). The diet of Kittiwakes in Svalbard is dominated by fish, with polar cod (*Boreogadus saida*) being an important food item (Lønne and Gabrielsen 1992), along with crustaceans and other marine invertebrates (Vihtakari et al. 2018). Brünnich's Guillemots prey on fish, with pelagic crustaceans also making up a large portion of their diet (Lønne and Gabrielsen 1992; Anker-Nilssen et al. 2000).

The composition of the guano varies with prey item and quality. The N-content of the Kittiwake guano samples analysed in the present study was in congruence with Brekke and Gabrielsen (1994), who report a mean value of 21% for Svalbard Kittiwakes and Brünnich's Guillemots. Meanwhile, phosphorus concentrations have previously been estimated as approximately 40% of the N content, i.e. 8.8% of guano dry weight (Sakshaug et al. 1994). This translates to an annual seabird-driven flux to Alkhornet of 25 000 kg N and 10 000 kg P, of which 67% originates from the Guillemot colony and 33% from the Kittiwakes. The larger body mass and high wing loading of guillemots contributing to a higher energy expenditure (Gabrielsen 1996) compared to Kittiwakes (Gabrielsen et al. 1987) explains the high guano contribution from this species, despite earlier departure from the colony by Guillemot chicks (fledging at about 25 days of age) and similar number of breeding pairs at Alkhornet (Brekke and Gabrielsen 1994). Arctic ecosystems are typically oligotrophic, with a mean annual wet deposition of only 74 kg N km^{-2} over the past 20 years in Ny-Ålesund, Svalbard, well below deposition rates in more densely populated areas in Europe (Kühnel et al. 2011). The difference between our estimated fluxes and background N deposition rates in Svalbard highlight the potential role of seabird colonies as important nutrient sources to the terrestrial environment.

Based on our estimated nutrient and organic carbon fluxes to the coast, areal fluxes of DIN, DIP and TOC from the seabird-impacted catchment areas were much higher than the controls. While TOC fluxes from seabird streams were elevated relative to fluxes for control streams, the effect of the seabird colony was much more pronounced for dissolved inorganic N and P, highlighting the potential role of these streams as a high-quality nutrient source for downstream ecosystems.

When comparing the estimated fluxes of DIN and DIP with the estimated N and P input from the seabird colony to the terrestrial environment, we see that the majority of estimated nutrient inputs were retained on land (or potentially evaded). The seabird-fertilized, deep peat at Alkhornet is likely to act as a large nutrient sink. Moss communities have been shown to retain virtually all added N in oligotrophic Arctic tundra (Yano et al. 2010). Considering the area of vegetation clearly influenced by seabird fertilization is about twice as large as the B1-B3 catchments, the runoff flux of $NO_3^- + NO_2^-$-N to the coast represents about 4–8% of annual guano-deposition N. Correspondingly, the flux of NH_4^+-N represents 0.05–0.09% of guano-deposited N, and the flux of PO_4^{3-}-P represents 0.1–0.2% of guano-deposited P.

Both concentrations and areal fluxes of DIN and DIP in the control catchment areas are in accordance with other fluvial flux estimates reported from the Arctic (Tye and Heaton 2007; Holmes et al. 2012; Blaen et al. 2014; Wadham et al. 2016). However, the numbers presented in the present study should be interpreted with caution since the stream flow was not measured directly. In our coarse estimates of runoff, variation between catchment areas, such as differences in water holding capacity, evapotranspiration and the rate of snowmelt were not accounted for. Additionally, the fraction of glacial ice in catchment C3 is likely to sustain elevated discharge through the melt season. However, with only five sampling dates, the glacial influence is unlikely to represent a main source of uncertainty for these flux estimates. Although highly uncertain, our goal was to generate preliminary estimates to give insight into the potential scale of the seabird effect on nutrient fluxes.

Coastal impact

Our third hypothesis proposed that impact of seabirds would be detectable in the nearby coastal ecosystem. The *Acrosiphonia* sp. samples show clear signs of utilising seabird-derived N, with high $\delta^{15}N$ values and low C:N molar ratios at seabird-impacted sites compared to control sites. Many macroalgal species, *Acrosiphonia* sp. included, have adapted to the seasonal nutrient availability in the Arctic by endogenic storage of NO_3^- when it is abundant in winter and spring. As the waters become NO_3^- depleted over summer, this reserve is used to maintain photosynthetic activity and a constant tissue C:N ratio (Hodal et al. 2012). Thus, the added NO_3^- flux from the seabird colony might have a larger influence on microalgae which have higher nutrient turnover. Nonetheless, the extremely high $\delta^{15}N$ values from *Acrosiphina* sp. close to Alkhornet and the lower C:N ratios found at the control sites implies a beneficial effect of the seabird colony on this species. Zmudczyńska-Skarbek et al. (2015) found no ornithogenic signal in the coastal benthic

food web close to another mixed seabird colony in Isfjorden. However, their sampling was done 50 m offshore at depths from 5 to 15 m, where the seabird impact can be expected to be more diluted than in the intertidal zone and closer to shore. Furthermore, brown algae such as the *Saccharina latissima* sampled in their study are often more reliant on internally stored nutrients than nitrophilic green macroalgae such as *Acrosiphonia* sp. (Hurd et al. 2014), thus showing a limited response to nutrient enrichment in summer (Gordillo et al. 2006). Still, the lack of a clear signal of seabird-derived nutrients in this earlier study (Zmudczyńska-Skarbek et al. 2015) points towards a limited spatial extent of this nutrient subsidy.

The δ^{15}N values of the amphipods also differed between seabird-impacted stations and controls, but were within the range of values reported for *Gammarus setosus* collected from other areas in Isfjorden during summer 2018 (Skogsberg 2019). The *Gammarus setosus* and Gammarellidae amphipods collected in the present study can feed opportunistically and on a range of food types (Legeżyńska et al. 2012), which, paired with seasonal changes in diet and metabolism, can complicate interpretation of stable isotope values. Different strategies such as phytodetrivory, scavenging and deposit feeding will influence their trophic position and exposure to ornithogenic influence, and the observed variation in δ^{13}C supports such high diversity in feeding strategies. The low variance within the values from both seabird-impacted and control stations, combined with the apparent similarity of habitat, give support to a possible seabird signal in amphipods from influenced sites.

Concluding remarks

The stream catchments investigated in the present study are small compared to the main river systems on Svalbard, and this will generally be the case for other Arctic seabird colonies as well. However, the extremely nutrient rich water draining from these seabird colonies suggests that these colonies can still be important point sources of DIN and DIP to adjacent coastal waters. At the same time, these fluxes are not constant. The size of the breeding seabird population will vary between years. Several seabird species in Svalbard have experienced population decline in recent years (Anker-Nilssen et al. 2015, 2018; CAFF 2017). Climate change in Svalbard, with longer and wetter summers, is likely to have important implications for both seabird-driven fluxes as well as other terrestrial impacts on marine systems (Bilt et al. 2019; McGovern et al. 2020). Increased terrestrial production has the potential to assimilate more of the nutrient input from seabird colonies, while increased microbial activity and runoff, including increased frequency of large rainfall events even during winter (Hansen et al. 2014), could enhance fluxes to the coast. While the present study

focuses on fluvial transport of ornithogenic nutrients to the coast, feathers and droppings from overflying seabirds and other bird activity in the coastal environment constitutes a direct pathway of coastal nutrient enrichment. However, we interpret this direct effect to be of minor importance for this site. The tidal zone in front of Alkhornet is narrow and not heavily used by Guillemots and Kittiwakes. The extremely high δ^{15}N values in the collected marine algae (and epilithic stream algae) relative to guano also indicates that further fractionation of ornithogenic N has taken place, most likely in the terrestrial environment (Hayashi et al. 2018).

There is also a need to further investigate the spatial extent of influence from seabird-derived nitrogen on marine biota, as well as the factors governing the distribution and fate of these nutrients in the marine environment. The extent of this effect will have ecological implications, not only for coastal species but also for species using the coastal environment for part of their life cycle. Still, the work by Zmudczyńska-Skarbek and Balazy (2017) points towards a rather localized effect in most systems. Nonetheless, with 3 million breeding pairs of seabirds in Svalbard (Anker-Nilssen et al. 2015), their combined impact might still be substantial. To generalise our findings to other seabird colonies, there is a need to consider geophysical and geochemical characteristics of the sites. The main colony on Alkhornet is situated approximately 700 m from the coastline, thus reducing direct guano inputs from the colony to coastal waters and leading to increased importance of terrestrial retention and transformation for determining nutrient fluxes from the colony to adjacent coastal ecosystems. Other seabird colonies on Svalbard are located on steep cliffs directly adjacent to coastal waters, where direct nutrient inputs to coastal waters are likely to be larger, and more closely linked to seasonality in bird presence at the cliff. Furthermore, Alkhornet is an exposed site, where marine currents, swells and waves mix the water column efficiently and we would expect rapid dilution and offshore transport of nutrients delivered from land. We would therefore expect to see stronger nutrient retention in more sheltered sites.

This study adds to a new appreciation for the importance of nutrient fluxes from land to sea in the Arctic and their importance for marine primary production (Terhaar et al. 2021). We show that colonial seabirds, particularly larger species, can create coastal nutrient hotspots with ecological effects that may propagate through the food web. However, with declining seabird populations, climate change and other changes in coastal and terrestrial ecosystems, these complex and dynamic nutrient fluxes are also changing (Hansen et al. 2019; Plazas-Jiménez and Cianciaruso 2020). There is a need for further studies to unravel the role of the terrestrial system in the release of seabird-derived nutrients to the coast, and the potential impacts of these nutrient inputs for coastal ecosystem structure and function. There is also a need for a

better understanding of the seasonality of these nutrient fluxes, including the effect of variable seabird presence in colonies and runoff phenology, as well as how the timing of these inputs aligns with key ecological processes in the marine environment (e.g. phytoplankton bloom timing and periods of nutrient limitation). This is particularly relevant in the Arctic, where seabird colonies are common along the coast, and may provide an important 'pulse' of nutrients to nutrient-limited systems during the brief summer growth season.

Declarations

Conflict of interest The authors declare that they have no competing interests.

Ethical approval No approval of research ethics committees was required to accomplish the goals of this study. The sampling of guano was non-invasive, and the collection of biota comprised small quantities of algae and unregulated invertebrate species.

References

Anderson WB, Polis GA (1999) Nutrient fluxes from water to land: seabirds affect plant nutrient status on Gulf of California Islands. Oecologia 118:324–332. https://doi.org/10.1007/s004420050733

Anker-Nilssen T, Bakken V, Strøm H, Golovkin AN, Bianki VV, Tatarinkova IP (2000) The status of marine birds breeding in the Barents Sea region. Norwegian Polar Institute Report Nr. 113

Anker-Nilssen T, Barrett RT, Lorentsen S-H, Strøm H, Bustnes JO, Christensen-Dalsgaard S, Descamps S, Erikstad KE, Fauchald P, Hanssen SA, Lorentzen E, Moe B, Systad RTK, GH, (2015) SEAPOP. De ti første årene. Nøkkeldokument 2005–2014. Norsk institutt for naturforskning, Norsk Polarinstitutt, Tromsø Museum, Tromsø

Anker-Nilssen T, Barrett R, Christensen-Dalsgaard S, Hanssen SA, Reiertsen TK, Bustnes JO, Erikstad K-E, Follestad A, Langset M, Lorentsen S-H, Lorentzen E, Strøm H, Systad GH (2018) Key-site monitoring in Norway 2017, including Svalbard and Jan Mayen. SEAPOP Short Rep 1–2018

Banerjee S, Siciliano SD (2012) Factors driving potential ammonia oxidation in Canadian Arctic ecosystems: does spatial scale matter? Appl Environ Microbiol 78:346–353. https://doi.org/10.1128/AEM.06132-11

Barrett RT, Anker-Nilssen T, Gabrielsen GW, Chapdelaine G (2002) Food consumption by seabirds in Norwegian waters. ICES J Mar Sci 59:43–57. https://doi.org/10.1006/jmsc.2001.1145

Bertrand P, Bêty J, Yoccoz NG, Fortin MJ, Strøm H, Steen H, Kohler J, Harris SM, Patrick SC, Chastel O, Blévin P, Hop H, Moholdt G, Maton J, Descamps S (2021) Fine-scale spatial segregation in a pelagic seabird driven by differential use of tidewater glacier fronts. Sci Rep 11:22109. https://doi.org/10.1038/s41598-021-01404-1

Bischof K, Convey P, Duarte P, Gattuso J-P, Granberg M, Hop H, Hoppe C, Jiménez C, Lisitsyn L, Martinez B, Roleda MY, Thor P, Wiktor JM, Gabrielsen GW (2019) Kongsfjorden as harbinger of the future Arctic: knowns, unknowns and research priorities. In: Hop H, Wiencke C (eds) The ecosystem of Kongsfjorden, Svalbard. Advances in polar ecology, vol 2. Springer, Cham, pp 537–562. https://doi.org/10.1007/978-3-319-46425-1_14

Blaen PJ, Milner AM, Hannah DM, Brittain JE, Brown LE (2014) Impact of changing hydrology on nutrient uptake in high Arctic rivers. River Res Appl 30:1073–1083. https://doi.org/10.1002/rra.2706

Brekke B, Gabrielsen GW (1994) Assimilation efficiency of adult Kittiwakes and Brünnich's Guillemots fed capelin and Arctic cod. Polar Biol 14:279–284. https://doi.org/10.1007/BF00239177

Breuning-Madsen H, Ehlers-Koch C, Gregersen J, Løjtnant CL (2010) Influence of perennial colonies of piscivorous birds on soil nutrient contents in a temperate humid climate. Geogr Tidsskr 110:25–35. https://doi.org/10.1080/00167223.2010.10669494

Brodie CR, Leng MJ, Casford JSL, Kendrick CP, Lloyd JM, Yongqiang Z, Bird MI (2011) Evidence for bias in C and N concentrations and δ^{13}C composition of terrestrial and aquatic organic materials due to pre-analysis acid preparation methods. Chem Geol 282:67–83. https://doi.org/10.1016/j.chemgeo.2011.01.007

Burr ZM, Varpe Ø, Anker-Nilssen T, Erikstad KE, Descamps S, Barrett RT, Bech C, Christensen-Dalsgaard S, Lorentsen S-H, Moe

B, Reiertsen TK, Strøm H (2016) Later at higher latitudes: large-scale variability in seabird breeding timing and synchronicity. Ecosphere. https://doi.org/10.1002/ecs2.1283

CAFF (2017) State of the Arctic marine biodiversity report. Conservation of Arctic Flora and Fauna International Secretariat (CAFF) Akureyri, Iceland

Choudhary S, Blaud A, Osborn AM, Press MC, Phoenix GK (2016) Nitrogen accumulation and partitioning in a High Arctic tundra ecosystem from extreme atmospheric N deposition events. Sci Total Environ 554–555:303–310. https://doi.org/10.1016/j.scitotenv.2016.02.155

Christiansen HH, Gilbert GL, Demidov N, Guglielmin M, Isaksen K, Osuch M, Boike J (2018) Permafrost thermal snapshot and active-layer thickness in Svalbard 2016–2017. SESS Report 2018

Dallmann WK (2015) Geoscience atlas of Svalbard. Norwegian Polar Institute Report 148

Duda MP, Hargan KE, Michelutti N, Kimpe LE, Clyde N, Gilchrist HG, Mallory ML, Blais JM, Smol JP (2018) Breeding eider ducks strongly influence subarctic coastal pond chemistry. Aquat Sci 80:40. https://doi.org/10.1007/s00027-018-0591-2

Ekstrøm CT (2019) MESS: miscellaneous esoteric statistical scripts. R package version 0.5.7. https://CRAN.R-project.org/package=MESS. Accessed 26 Nov 2019

Ellis HI, Gabrielsen GW (2001) Energetics of free-ranging seabirds. In: Schreiber EA, Burger J (eds) Biology of marine birds, 1st edn. CRC Press, Boca Raton, pp 359–408

Eurola S, Hakala AVK (1977) The bird cliff vegetation of Svalbard. Aquil Ser Bot 15:1–18

Falk K, Benvenuti S, Dall'Antonia L, Gilchrist G, Kampp K (2002) Foraging behaviour of thick-billed murres breeding in different sectors of the North Water polynya: an inter-colony comparison. Mar Ecol Prog Ser 231:293–302. https://doi.org/10.3354/meps231293

Field CB (1998) Primary production of the biosphere: integrating terrestrial and oceanic components. Science 281:237–240. https://doi.org/10.1126/science.281.5374.237

Førland EJ, Hanssen-Bauer I (2000) Increased precipitation in the Norwegian Arctic: true or false? Clim Change 46:485–509. https://doi.org/10.1023/A:1005613304674

Frank DA, Evans RD, Tracy BF (2004) The role of ammonia volatilization in controlling the natural ^{15}N abundance of a grazed grassland. Biogeochemistry 68:169–178. https://doi.org/10.1023/B:BIOG.0000025736.19381.91

Gabrielsen GW (1996) Energy expenditure of breeding Common Murres. Can Wild Serv Occas Pap 91:49–58

Gabrielsen GW, Mehlum F, Nagy KA (1987) Daily energy expenditure and energy utilization of free-ranging black-legged kittiwakes. Condor 89:126–132. https://doi.org/10.2307/1368766

Gagnon K, Rothäusler E, Syrjänen A, Yli-Renko M, Jormalainen V (2013) Seabird guano fertilizes Baltic Sea littoral food webs. PLoS ONE. https://doi.org/10.1371/journal.pone.0061284

González-Bergonzoni I, Johansen KL, Mosbech A, Landkildehus F, Jeppesen E, Davidson TA (2017) Small birds, big effects: the little auk (Alle alle) transforms high Arctic ecosystems. Proc R Soc B 284:20162572. https://doi.org/10.1098/rspb.2016.2572

Gordillo FJL, Aguilera J, Jiménez C (2006) The response of nutrient assimilation and biochemical composition of Arctic seaweeds to a nutrient input in summer. J Exp Bot 57:2661–2671. https://doi.org/10.1093/jxb/erl029

Graham NAJ, Wilson SK, Carr P, Hoey AS, Jennings S, MacNeil MA (2018) Seabirds enhance coral reef productivity and functioning in the absence of invasive rats. Nature 559:250. https://doi.org/10.1038/s41586-018-0202-3

GRASS Development Team (2017) Geographic resources analysis support system (GRASS GIS) software, version 7.2. Open Source Geospatial Foundation, Chicago. http://grass.osgeo.org. Accessed 26 Nov 2019

Hansen BB, Isaksen K, Benestad RE, Kohler J, Pedersen ÅØ, Loe LE, Coulson SJ, Larsen JO, Varpe Ø (2014) Warmer and wetter winters: characteristics and implications of an extreme weather event in the High Arctic. Environ Res Lett 9:114021. https://doi.org/10.1088/1748-9326/9/11/114021

Hansen BB, Lorentzen JR, Welker JM, Varpe Ø, Aanes R, Beumer LT, Pedersen ÅØ (2019) Reindeer turning maritime: ice-locked tundra triggers changes in dietary niche utilization. Ecosphere 10:e02672. https://doi.org/10.1002/ecs2.2672

Harding JS, Hawke DJ, Holdaway RN, Winterbourn MJ (2004) Incorporation of marine-derived nutrients from petrel breeding colonies into stream food webs. Freshw Biol 49:576–586. https://doi.org/10.1111/j.1365-2427.2004.01210.x

Harding AMA, Kitaysky AS, Hall ME, Welcker J, Karnovsky NJ, Talbot SL, Hamer KC, Grémillet D (2009) Flexibility in the parental effort of an Arctic-breeding seabird. Funct Ecol 23:348–358. https://doi.org/10.1111/j.1365-2435.2008.01488.x

Hayashi K, Tanabe Y, Ono K, Loonen MJJE, Asano M, Fujitani H, Tokida T, Uchida M, Hayatsu M (2018) Seabird-affected taluses are denitrification hotspots and potential N_2O emitters in the High Arctic. Sci Rep 8:17261. https://doi.org/10.1038/s41598-018-35669-w

Hentati-Sundberg J, Raymond C, Sköld M, Svensson O, Gustafsson B, Bonaglia S (2020) Fueling of a marine-terrestrial ecosystem by a major seabird colony. Sci Rep 10:15455. https://doi.org/10.1038/s41598-020-72238-6

Hodal H, Falk-Petersen S, Hop H, Kristiansen S, Reigstad M (2012) Spring bloom dynamics in Kongsfjorden, Svalbard: nutrients, phytoplankton, protozoans and primary production. Polar Biol 35:191–203. https://doi.org/10.1007/s00300-011-1053-7

Holmes RM, McClelland JW, Peterson BJ, Tank SE, Bulygina E, Eglinton TI, Gordeev VV, Gurtovaya TY, Raymond PA, Repeta DJ, Staples R, Striegl RG, Zhulidov AV, Zimov SA (2012) Seasonal and annual fluxes of nutrients and organic matter from large rivers to the Arctic ocean and surrounding seas. Estuaries Coasts 35:369–382. https://doi.org/10.1007/s12237-011-9386-6

Hop H, Pearson T, Hegseth EN, Kovacs KM, Wiencke C, Kwasniewski S et al (2002) The marine ecosystem of Kongsfjorden, Svalbard. Polar Res 21:167–208. https://doi.org/10.3402/polar.v21i1.6480

Hurd C, Harrison P, Bischof K, Lobban C (2014) Seaweed ecology and physiology. Cambridge University Press, Cambridge. https://doi.org/10.1017/CBO9781139192637

Jakubas D, Zmudczyńska K, Wojczulanis-Jakubas K, Stempniewicz L (2008) Faeces deposition and numbers of vertebrate herbivores in the vicinity of planktivorous and piscivorous seabird colonies in Hornsund, Spitsbergen. Pol Polar Res 29:45–58

Kaste Ø, Skarbøvik E, Greipsland I, Gundersen CB, Austnes K, Skancke LB, Guerrero J-L, Sample JE (2018) The Norwegian river monitoring programme—water quality status and trends 2017. NIVA Report 7313

Kazama K (2019) Bottom-up effects on coastal marine ecosystems due to nitrogen input from seabird feces. Ornithol Sci 18:117–126. https://doi.org/10.2326/osj.18.117

Keatley BE, Douglas MSV, Blais JM, Mallory ML, Smol JP (2009) Impacts of seabird-derived nutrients on water quality and diatom assemblages from Cape Vera, Devon Island, Canadian High Arctic. Hydrobiologia 621:191–205. https://doi.org/10.1007/s10750-008-9670-z

Killingtveit Å, Pettersson L-E, Sand K (2003) Water balance investigations in Svalbard. Polar Res 22:161–174. https://doi.org/10.1111/j.1751-8369.2003.tb00105.x

Kühnel R, Roberts TJ, Björkman MP, Isaksson E, Aas W, Holmén K, Ström J (2011) 20-Year climatology of and wet deposition at

Ny-Ålesund, Svalbard. Adv Meteorol 2011:406508. https://doi.org/10.1155/2011/406508

Låg J (1990) Peat accumulation in steep hills at Alkhornet, Spitsbergen. Acta Agric Scand 40:217–219. https://doi.org/10.1080/00015129009438554

Leblans NIW, Sigurdsson BD, Roefs P, Thuys R, Magnússon B, Janssens IA (2014) Effects of seabird nitrogen input on biomass and carbon accumulation after 50 years of primary succession on a young volcanic island, Surtsey. Biogeosciences 11:6237–6250. https://doi.org/10.5194/bg-11-6237-2014

Legeżyńska J, Kędra M, Walkusz W (2012) When season does not matter: summer and winter trophic ecology of Arctic amphipods. Hydrobiologia 684:189–214. https://doi.org/10.1007/s10750-011-0982-z

Lindeboom HJ (1984) The nitrogen pathway in a penguin rookery. Ecology 65:269–277. https://doi.org/10.2307/1939479

Lønne OJ, Gabrielsen GW (1992) Summer diet of seabirds feeding in sea-ice-covered waters near Svalbard. Polar Biol 12:685–692. https://doi.org/10.1007/BF00238868

Loreau M, Mouquet N, Holt RD (2003) Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. Ecol Lett 6:673–679. https://doi.org/10.1046/j.1461-0248.2003.00483.x

McGovern M, Pavlov AK, Deininger A, Granskog MA, Leu E, Søreide JE, Poste AE (2020) Terrestrial inputs drive seasonality in organic matter and nutrient biogeochemistry in a High Arctic fjord system (Isfjorden, Svalbard). Front Mar Sci 7:542563. https://doi.org/10.3389/fmars.2020.542563

McInturf AG, Pollack L, Yang LH, Spiegel O (2019) Vectors with autonomy: what distinguishes animal-mediated nutrient transport from abiotic vectors? Biol Rev 94:1761–1773. https://doi.org/10.1111/brv.12525

Mehlum F, Gabrielsen GW (1995) Energy expenditure and food consumption by seabird populations in the Barents Sea region. In: Leinaas H (ed) Ecology of fjords and coastal waters. Elsevier, Amsterdam, pp 457–470

Mehlum F, Watanuki Y, Takahashi A (2001) Diving behaviour and foraging habitats of Brünnich's Guillemots (Uria lomvia) breeding in the High-Arctic. J Zool 255:413–423. https://doi.org/10.1017/S0952836901001509

Müller M, Homleid M, Ivarsson K-I, Køltzow MAØ, Lindskog M, Midtbø KH, Andrae U, Aspelien T, Berggren L, Bjørge D, Dahlgren P, Kristiansen J, Randriamampianina R, Ridal M, Vignes O (2017) AROME-MetCoOp: a Nordic Convective-Scale operational weather prediction model. Weather Forecast 32:609–627. https://doi.org/10.1175/WAF-D-16-0099.1

Nishizawa B, Kanna N, Abe Y, Ohashi Y, Sakakibara D, Asaji I, Sugiyama S, Yamaguchi A, Watanuki Y (2020) Contrasting assemblages of seabirds in the subglacial meltwater plume and oceanic water of Bowdoin Fjord, northwestern Greenland. ICES J Mar Sci 77:711–720. https://doi.org/10.1093/icesjms/fsz213

Norwegian Polar Institute (2014) Terrengmodell Svalbard (S0 Terrengmodell). Norwegian Polar Institute. https://doi.org/10.21334/npolar.2014.dce53a47

Odasz AM (1994) Nitrate reductase activity in vegetation below an arctic bird cliff, Svalbard, Norway. J Veg Sci 5:913–920. https://doi.org/10.2307/3236203

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2019) Vegan: community ecology package. R package version 2.5–7. https://CRAN.R-project.org/package=vegan. Accessed 26 Nov 2019

Otero XL, Peña-Lastra S, Pérez-Alberti A, Ferreira TO, Huerta-Diaz MA (2018) Seabird colonies as important global drivers in the nitrogen and phosphorus cycles. Nat Commun 9:246. https://doi.org/10.1038/s41467-017-02446-8

Paleczny M, Hammill E, Karpouzi V, Pauly D (2015) Population trend of the world's monitored seabirds, 1950–2010. PLoS ONE 10:e0129342. https://doi.org/10.1371/journal.pone.0129342

Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. Annu Rev Ecol Evol Syst 18:293–320. https://doi.org/10.1146/annurev.es.18.110187.001453

Pitcairn CER, Skiba UM, Sutton MA, Fowler D, Munro R, Kennedy V (2002) Defining the spatial impacts of poultry farm ammonia emissions on species composition of adjacent woodland ground-flora using Ellenberg Nitrogen Index, nitrous oxide and nitric oxide emissions and foliar nitrogen as marker variables. Environ Pollut 119:9–21. https://doi.org/10.1016/S0269-7491(01)00148-8

Plazas-Jiménez D, Cianciaruso MV (2020) Valuing ecosystem services can help to save seabirds. Trends Ecol Evol 35:757–762. https://doi.org/10.1016/j.tree.2020.06.008

Polis GA, Anderson WB, Holt RD (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annu Rev Ecol Syst 28:289–316. https://doi.org/10.1146/annurev.ecolsys.28.1.289

QGIS Development Team (2019) QGIS geographic information system. Project, Version 3.4.3. Open Source Geospatial Foundation, Chicago. http://qgis.osgeo.org. Accessed 26 Nov 2019

R Core Team (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/. Accessed 26 Nov 2019

Reynolds CS, Davies PS (2001) Sources and bioavailability of phosphorus fractions in freshwaters: a British perspective. Biol Rev 76:27–64. https://doi.org/10.1017/s1464793100005625

Richter D, Matuła J, Urbaniak J, Waleron M, Czerwik-Marcinkowska J (2017) Molecular, morphological and ultrastructural characteristics of Prasiola crispa (Lightfoot) Kützing (Chlorophyta) from Spitsbergen (Arctic). Polar Biol 40:379–397. https://doi.org/10.1007/s00300-016-1966-2

Rysgaard S, Nielsen TG, Hansen BW (1999) Seasonal variation in nutrients, pelagic primary production and grazing in a High-Arctic coastal marine ecosystem, Young Sound, Northeast Greenland. Mar Ecol Prog Ser 179:13–25. https://doi.org/10.3354/meps179013

Sakshaug E, Bjørge A, Gulliksen B, Loeng H, Mehlum F (1994) Structure, biomass distribution, and energetics of the pelagic ecosystem in the Barents Sea: a synopsis. Polar Biol 14:405–411. https://doi.org/10.1007/BF00240261

Sakshaug E, Johnsen GH, Kovacs KM (2009) Ecosystem Barents Sea. Tapir Academic Press, Trondheim

Savage C (2019) Seabird nutrients are assimilated by corals and enhance coral growth rates. Sci Rep 9:4284. https://doi.org/10.1038/s41598-019-41030-6

Shatova OA, Wing SR, Hoffmann LJ, Wing LC, Gault-Ringold M (2017) Phytoplankton community structure is influenced by seabird guano enrichment in the Southern Ocean. Estuar Coast Shelf Sci 191:125–135. https://doi.org/10.1016/j.ecss.2017.04.021

Skogsberg E (2019) Effects of seasonal riverine run-off on coastal contaminant levels in Arctic littoral amphipods. Master's thesis, University of Oslo

Smoła ZT, Tatarek A, Wiktor JM, Wiktor JMW, Kubiszyn A, Węsławski JM (2017) Primary producers and production in Hornsund and Kongsfjorden—comparison of two fjord systems. Pol Polar Res 38:351–373. https://doi.org/10.1515/popore-2017-0013

Søreide JE, Nygård H (2012) Challenges using stable isotopes for estimating trophic levels in marine amphipods. Polar Biol 35:447–453. https://doi.org/10.1007/s00300-011-1073-3

Subalusky AL, Post DM (2019) Context dependency of animal resource subsidies. Biol Rev 94:517–538. https://doi.org/10.1111/brv.12465

Terhaar J, Lauerwald R, Regnier P, Gruber N, Bopp L (2021) Around one third of current Arctic Ocean primary production sustained by rivers and coastal erosion. Nat Commun 12:169. https://doi.org/10.1038/s41467-020-20470-z

Tye AM, Heaton THE (2007) Chemical and isotopic characteristics of weathering and nitrogen release in non-glacial drainage waters on Arctic tundra. Geochim Cosmochim Acta 71:4188–4205. https://doi.org/10.1016/j.gca.2007.06.040

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

van der Bilt W, Bakke J, Smedsrud LH, Sund M, Schuler T, Westermann S et al (2019) Climate in Svalbard 2100—a knowledge base for climate adaptation. Norsk Klimaservicesenter, Norwegian Centre for Climate Services Reports 2019:1

Varpe Ø, Fiksen Ø, Slotte A (2005) Meta-ecosystems and biological energy transport from ocean to coast: the ecological importance of herring migration. Oecologia 146:443–451. https://doi.org/10.1007/s00442-005-0219-9

Vickers H, Høgda KA, Solbø S, Karlsen SR, Tømmervik H, Aanes R, Hansen BB (2016) Changes in greening in the high Arctic: insights from a 30 year AVHRR max NDVI dataset for Svalbard. Environ Res Lett 11:105004. https://doi.org/10.1088/1748-9326/11/10/105004

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. https://doi.org/10.1038/s41598-017-19118-8

Wadham JL, Hawkings J, Telling J, Chandler D, Alcock J, O'Donnell E, Kaur P, Bagshaw E, Tranter M, Tedstone A, Nienow P (2016) Sources, cycling and export of nitrogen on the Greenland ice sheet. Biogeosciences 13:6339–6352. https://doi.org/10.5194/bg-13-6339-2016

Wainright SC, Haney JC, Kerr C, Golovkin AN, Flint MV (1998) Utilization of nitrogen derived from seabird guano by terrestrial and marine plants at St. Paul, Pribilof Islands, Bering Sea, Alaska. Mar Biol 131:63–71. https://doi.org/10.1007/s002270050297

Wodehouse EB, Parker BC (2013) Atmospheric ammonia nitrogen: a potential source of nitrogen eutrophication of freshwater Antarctic ecosystems. In: Parker BB (ed) Terrestrial biology III. American Geophysical Union (AGU), Washington, pp 155–167

Yano Y, Shaver GR, Giblin AE, Rastetter EB, Nadelhoffer KJ (2010) Nitrogen dynamics in a small arctic watershed: retention and downhill movement of ^{15}N. Ecol Monogr 80:331–351. https://doi.org/10.1890/08-0773.1

Yeh KC, Kwan KC (1978) A comparison of numerical integrating algorithms by trapezoidal, Lagrange, and spline approximation. J Pharmacokinet Biopharm 6:79–98. https://doi.org/10.1007/BF01066064

Zhu R, Sun J, Liu Y, Gong Z, Sun L (2011) Potential ammonia emissions from penguin guano, ornithogenic soils and seal colony soils in coastal Antarctica: effects of freezing-thawing cycles and selected environmental variables. Antarct Sci 23:78–92. https://doi.org/10.1017/S0954102010000623

Zmudczyńska-Skarbek KM, Balazy P (2017) Following the flow of ornithogenic nutrients through the Arctic marine coastal food webs. J Mar Syst 168:31–37. https://doi.org/10.1016/j.jmarsys.2016.12.006

Zmudczyńska-Skarbek KM, Balazy P, Kuklinski P (2015) An assessment of seabird influence on Arctic coastal benthic communities. J Mar Syst 144:48–56. https://doi.org/10.1016/j.jmarsys.2014.11.013

Zwolicki A, Zmudczyńska-Skarbek KM, Iliszko L, Stempniewicz L (2013) Guano deposition and nutrient enrichment in the vicinity of planktivorous and piscivorous seabird colonies in Spitsbergen. Polar Biol 36:363–372. https://doi.org/10.1007/s00300-012-1265-5