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ORIGINAL ARTICLE

Bottom-up Effects of Seabird Colonies on Arctic Benthic Communities Mediated by Kelp Forests

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ABSTRACT

Arctic seabird colonies concentrate marine-derived nutrients on land through the deposition of guano, which fertilizes the vegetation and supports local consumers. However, the process in which nutrients derived from seabirds are not fully consumed on land and subsequently return to the sea, accumulating beneath bird cliffs, is not widely recognized, particularly in non-tropical and non-oligotrophic ecosystems. This study aimed to assess the impact of ornithogenic nutrient enrichment on the structure of the benthic community in the shallow, rocky subtidal zone beneath a seabird colony in the Svalbard archipelago. Significant differences in benthic community composition were observed between the seabird and Reference locations, with higher diversity and greater abundance of benthic filter-feeders beneath the bird cliffs. The nitrogen stable isotope ratio values (δ^{15}N) of selected benthic invertebrates were higher in the studied taxa adjacent to colonies than in the reference areas, indicating the uptake of seabird-derived nitrogen. However, the presence of kelp forests modified this effect. Chitons (*Tonicella* sp.) and hermit crabs (*Pagurus pubescens*) appeared to use ornithogenic nutrients effectively beyond the kelp zone, whereas whelks (*Buccinum* sp.) appeared to utilise them closer to the shore among dense kelp. These findings improve our understanding of nutrient transfer processes and the complex interactions between terrestrial and marine ecosystems in the Arctic. The ornithogenic fertilization effect extends beyond the coastline, although it is probably spatially limited and more subtle in nearshore waters than on land as nutrients disperse with waves and currents.

Key words: coastal ecosystems; nitrogen stable isotopes; ornithogenic nutrients; pelagic-benthic coupling; SCUBA; subsidized ecosystem; underwater photography.

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HIGHLIGHTS

- Higher diversity and greater abundance of benthic filter feeders beneath the bird cliffs.
- The seabird colony effect is modified by the presence of kelp forests.
- Pelagic-benthic coupling is crucial for ornithogenic enrichment of the benthos.

INTRODUCTION

The shallow-water coastal regions of the Arctic seas form the interface between typically nutrient-poor, low-productivity land and relatively nutrient-rich, often highly productive deeper waters (Thomas 2021). Seabirds effectively use both the open sea and land: the former as feeding grounds and the latter as nesting sites. The coastal zone between them benefits from being located on bird migration routes, receiving concentrated nutrients from distant areas (Convey and others 2024; Finne and others 2024). Several seabird species, such as the little auks (*Alle alle*), black-legged kittiwakes (*Rissa tridactyla*), Brünnich's and common guillemots (*Uria lomvia*, *U. aalge*), northern fulmars (*Fulmarus glacialis*), and Atlantic puffins (*Fratercula arctica*), nest in large numbers and densities at Arctic coastal cliffs, with their colonies consisting of several hundred thousand breeding pairs (Descamps and Strøm 2021; Ganter and Gaston 2013). By consuming large amounts of zooplankton and fish during their reproductive season, seabirds successfully transport substantial quantities of organic matter produced in the marine environment to the colony and its surrounding areas. This organic matter is primarily in the form of droppings (next referred to as guano), but it can also include feathers, egg shells, and carcasses (Stempniewicz 1990; Zwolicki and others 2013). These seabird products, especially guano, are highly effective fertilizers for terrestrial vegetation growing in and around the colonies (Eurola and Hakala 1977; Roos and others 2025; Zwolicki and others 2013). The ornithogenic nutrients are effectively incorporated and clearly transferred throughout the entire terrestrial food web, triggering changes in vegetation and soil biota communities, and improving feeding grounds for vertebrate fauna (Croll and others 2005; González-Bergonzoni and others 2017; Jakubas and others 2008; Zmudczyńska-Skarbek and others 2024, 2017; Zwolicki and others 2016). However, the seabird-derived organic matter may not be completely utilized on land.

While terrestrial consequences of seabird nutrient input are well documented, little is known about the influence of these nutrients on adjacent marine ecosystems. Our previous survey in Isfjorden (west Spitsbergen) showed that ornithogenic nutrients were successively utilized along the slope beneath the bird cliff (Zmudczyńska-Skarbek and others 2015). Even at the farthest point from the colony, a few metres from the shoreline, they were much more abundant than in the respective reference area, where no birds nested. This suggests that some of the allochthonous nutrients can be returned to the sea through leaching and run-off, with ammonium-containing rainwater after volatilization, as well as through the direct deposition of faeces into the water (Lindeboom 1984; Staunton Smith and Johnson 1995; Wainright and others 1998). Therefore, seabird-derived nutrients from vast marine feeding grounds can become concentrated in a relatively small coastal area beneath a colony. This may constitute an important local resource for marine producers and subsequent consumers, thus exerting a 'bottom-up effect' (Finne and others 2024; Hentati-Sundberg and others 2020; Kazama 2020; Young and others 2011). However, once in the water, the nutrients are diluted, dispersed and flushed out, even after being incorporated into phytoplankton cells. These processes are accelerated in the marine environment by local winds, wave action and ocean currents; therefore, their utility to the entire marine food web is strongly limited in space and time (Kazama 2020; Lorrain and others 2017; Young and others 2011). Consequently, ornithogenic enhancement may be less traceable in the highly dynamic marine environment than on land, where nutrients can be stored in soil and accessed by microbial and plant communities over a longer period (Anderson and Polis 1999; Moss 2017).

The impact of seabirds on marine ecosystems through the local concentration of nutrients has rarely been documented, particularly in the polar regions (De La Peña-Lastra 2021; Kazama 2020; Young and others 2011 and references therein). The environments studied most frequently are semi-closed systems, such as tidal pools and lagoons, and intertidal rocky shores (Healing and others 2024; Methratta 2004; Palomo and others 1999; Signa and others 2012), as well as the nearshore coral reefs of the oligotrophic tropical seas (Graham and others 2018; Savage 2019), which productivity and functioning were enhanced by long-term deposition of nutrients from adjacent seabird colonies. Excessive nutrient subsidies have also been documented, and the coastal ecosystem can deteriorate in response to severe guanotrophication, shifting partially or totally from a system dominated by a benthic food web to a planktonic one (Signa and others 2015; Vizzini and others 2016).

At the same time, seabird colonies are mainly distributed in the polar zones, with a quarter of the global population concentrated in the Atlantic part of the Arctic (209 million breeding individuals, Otero and others 2018). In the Svalbard area, the seabird population is estimated to be 3 million breeding pairs (Descamps and Strøm 2021). The vital role of seabird guano in enriching the otherwise extremely poor Arctic terrestrial ecosystem is relatively well recognized (Eurola and Hakala 1977; Zmudczyńska-Skarbek and others 2024, 2017; Zwolicki and others 2016), yet little is known about ornithogenic nutrients that are not utilized on land and therefore return to nearby seas. Although Arctic waters are generally considered nutrient-rich, they are also subject to extreme seasonality and primary production is restricted to short time windows when light is available. However, the intensive spring bloom of phytoplankton utilizes the resources accumulated during the winter. By summer, nutrients such as nitrogen, phosphorus and silica have become depleted again, thereby limiting further primary production (Daase and others 2021). Nevertheless, spring and summer are the periods when seabirds breed on coastal cliffs; therefore, nutrients derived from their colonies may be of major importance to nearshore marine food webs.

There are few studies on this phenomenon in the Arctic, and the results are inconclusive. Higher nutrient content and productivity of phyto- and zooplankton were observed around seabird colonies in the Russian Arctic (Golovkin 1967; Golovkin and Garkavaya 1975; Zelickman and Golovkin 1972), and the ornithogenic signal was detected in selected macroalgae and amphipods in the tidal zone beneath a seabird colony in Spitsbergen, Svalbard (Finne and others 2024). Nonetheless, other studies suggest that, while still detectable, ornithogenic supplies are insignificant for the overall requirements of local producers (Kurle and others 2008; Marmen and others 2017; Wainright and others 1998). However, these latter studies were conducted close to the highly productive Bering Sea shelf or at depths of over 120 m and relatively far from the coast. Meanwhile, Shatova and others (2017), (2016) conducted experiments in the Southern Ocean that clearly demonstrated a significant increase in the biomass of natural phytoplankton communities, as well as dramatic changes in their structure and composition following the addition of seabird guano.

The most commonly and effectively used proxy for estimating the influence of seabirds is the nitrogen stable isotope ratio (δ^{15}N). The values of this indicator are typically higher in the ornithogenically enriched soil, vegetation or animal tissues due to isotopic fractionation of nitrogen occurring firstly with progression through the food web (seabirds being top predators), and secondly when ammonia volatilizes from guano (González-Bergonzoni and others 2017; Kelly 2000). The carbon stable isotope ratio (δ^{13}C) is also commonly used in trophic ecology to distinguish between different food sources. The δ^{13}C values of typical end members for benthic consumers, such as macroalgae, phytoplankton, and pelagic, sediment and sea ice particulate organic matter (POM), as well as terrestrial supplies, are distinct, and carbon shows much lower fractionation than nitrogen (Budge and others 2008; Tamelander and others 2006). In a previous study in Spitsbergen, the limited isotopic data obtained were not fully conclusive. It was assumed that nutrients returned to the sea and concentrated in the vicinity of a seabird colony, where they were first used by phytoplankton and then entered the bottom food chains through pelagic-benthic coupling (Zmudczyńska-Skarbek and Balazy 2017; Zmudczyńska-Skarbek and others 2015). However, the results suggest that benthic carnivores/scavengers/detritivores such as hermit crabs (*Pagurus pubescens*) and whelks (*Buccinum* spp.), which partly use ornithogenically enriched organic matter originally produced by plankton in spring and summer, might benefit from guanotrophication. Conversely, benthic producers, including microalgae, whose ornithogenic supplies possibly run out after being consumed near the surface, and kelps, which absorb nutrients mostly in late winter/early spring (Dunton 1985, and references therein), that is, before the seabird breeding season and guano delivery start, as well as benthic algivores, may not directly respond to the vicinity of a seabird colony. However, the effect of ornithogenic fertilization on the taxonomic composition of the shallow subtidal benthic community has never been investigated in the Arctic. Apart from scarce data from coral reefs (for example Graham and others 2018), this phenomenon is practically unrecognized worldwide.

Shallow-water benthic ecosystems in the sublittoral zone are among the least recognized parts of polar seas. They are not deep enough to be accessed by most research vessels equipped with advanced sampling and measuring equipment, yet they are too deep to be studied directly from the shore (Renaud and others 2021). Consequently, there is very little understanding of how these ecosystems function, and even basic ecological interactions among the local biota and their relations with the adjacent deeper sea and land are poorly described. The spectacular effects that guano has on the composition of species of Arctic terrestrial biota are well known (Croll and others 2005; Roos and others 2025; Wainright and others 1998; Zmudczyńska-Skarbek and others 2024, 2017; Zwolicki and others 2016), and given that seabird-derived nutrients are not entirely consumed on land and must ultimately sink into the coastal marine zone beneath the seabird colony (Finne and others 2024; Zmudczyńska-Skarbek and others 2015), we hypothesise that the composition and functioning of adjacent benthic communities may also be altered due to ornithogenic enrichment of at least part of the local marine food web.

The aim of the study was to assess the effect of ornithogenic nutrient enrichment on the structure of the benthic community, including its species composition, richness and numerical abundance, in the shallow rocky subtidal zone near a large seabird colony in the High Arctic Svalbard archipelago. We hypothesized that (1) the nitrogen stable isotope ratios (δ^{15}N) of benthic invertebrates would be higher beneath the bird cliff than in a reference area, which was located away from the colony's direct influence, and (2) the benthic community composition would differ, with greater species richness and diversity adjacent to the colony as compared with the reference location. Furthermore, we expected that (3) the impact of the seabird colony on the benthic community would diminish with distance from the coast and eventually cease due to the smaller and increasingly diluted supply of ornithogenic nutrients.

MATERIALS AND METHODS

Study Area

The study was conducted in July 2018 on the south-west coast of Isfjorden (78°13′N 15°20′E), the largest and wide open fjord on the west coast of Spitsbergen, Svalbard archipelago (Figure 1). The fjord's hydrology is shaped by a periodic influx of relatively warm, more saline and nutrient-rich Atlantic water from the West Spitsbergen Current (a branch of the Gulf Stream), and to a lesser extent by cold, nutrient-poor, lower-salinity Arctic water from the East Spitsbergen Current (Loeng 1991). In late spring and summer, the surface waters are locally affected by glacial meltwater and river runoff. Water masses typically circulate counterclockwise around the fjord boundaries (Nilsen and others 2008).

Samples were collected below a large colony of Brunnich's guillemots (*Uria lomvia*) and kittiwakes (*Rissa tridactyla*), situated on Fuglefjella cliff at about 200 m a.s.l. (hereafter referred to as Seabird area). The steep slope beneath the colony was covered in lush vegetation, consisting mainly of the characteristic bird-cliff communities, including mainly *Oxyria digyna*, *Cerastium arcticum*, *Alopecurus borealis* and *Poa alpina* v. *vivipara* (Rønning 1996). A second location (Reference area) was situated at Rusanovoden, to the north-east of the Coleselva outflow and the fjord mouth, and away from the seabird colony, with milder onshore slopes.

In the shallow subtidal zone under study, both locations were characterized by a hard, rocky substrate containing boulders and pebbles, as well as sparse sediment patches. The bottom was overgrown with kelps such as *Saccharina latissima*, *Alaria esculenta* and *Laminaria* spp. (down to ca. 8–10 m), coralline algae and sedentary fauna including sponges, ascidians, polychaetes, barnacles, bryozoans and cnidarians, excluding the shallowest depths (down to ca. 2 m), which were almost devoid of any biota due to tidal, wave and ice action. Benthic predatory and scavenging animals commonly found there included hermit crabs (*P. pubescens*), spider crabs (*Hyas araneus*), whelks (*Buccinum glaciale, B. undatum*), shrimps (*Lebbeus polaris, Eualus gaimardii, Sclerocrangon boreas*), and starfish (*Crossaster papposus, Henricia* sp.). Epibenthic grazers, such as sea urchins (*Strongylocentrotus droebachiensis*) and chitons (*Tonicella* spp.), occurred at high densities at all depths (the former were also likely to be effective detritivores). At depths of 15–20 m, the seabed flattened out and contained a higher proportion of smaller pebbles and rocks.

Sampling Protocol

Two 200-m-long line transects were marked perpendicular to the coast at the Seabird area and one at the Reference area. Scuba divers collected samples at 20-m intervals along each transect, starting 60 m from the coastline (just beyond the wave-breaking zone). A total of eight sampling sites were located along each transect (see Suppl. Table S1 for precise distances and respective depths). The distance from the coast and the depth at each site were measured using a handheld GPS and an echosounder mounted on the rubber boat. Kelp forest covered the first five and four sites of the

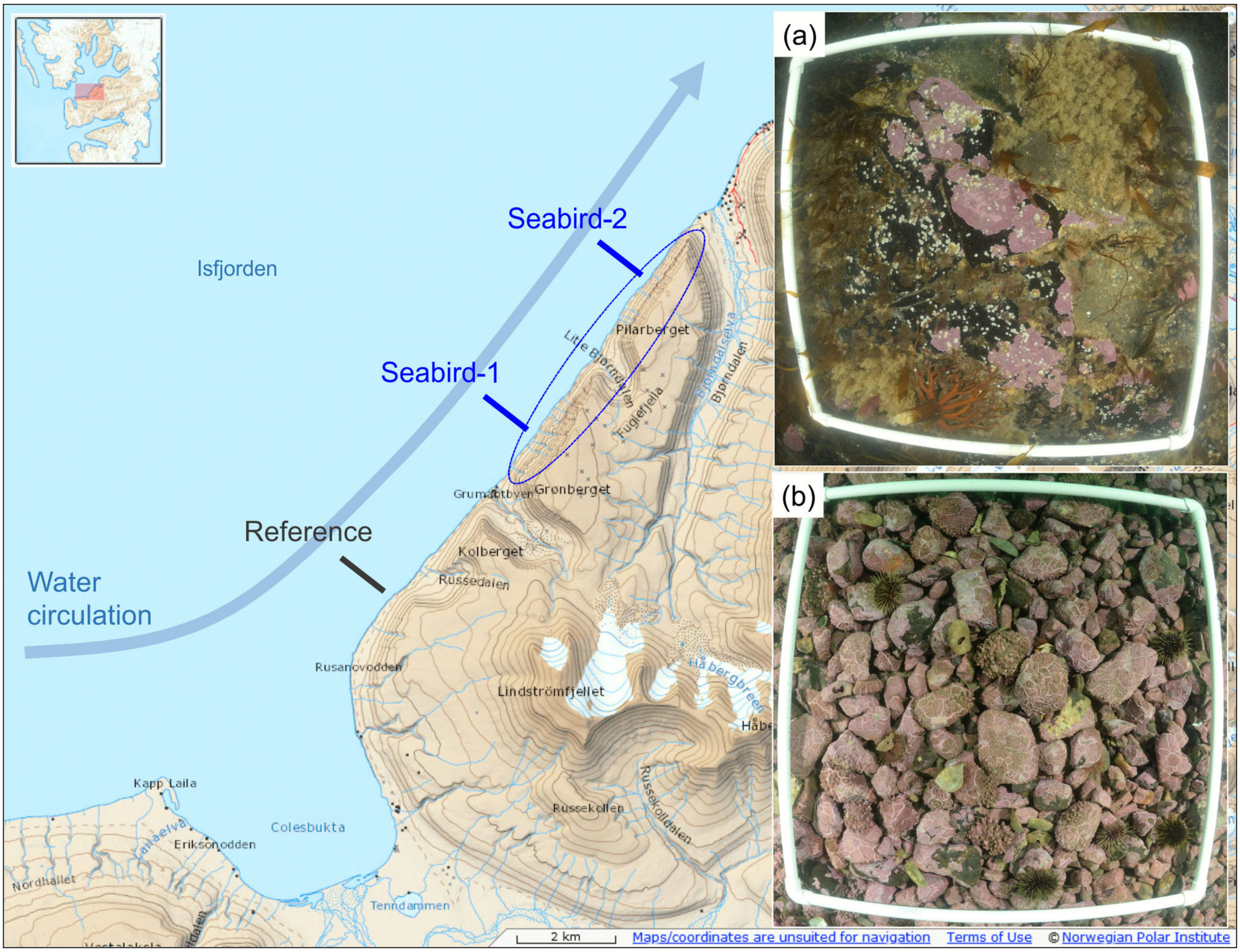


Figure 1. Location of the study transects within the Seabird and Reference areas in Isfjorden, west Spitsbergen (map used with courtesy of the Norwegian Polar Institute). The situation of the seabird colony marked with a blue dashed-line ellipse. Examples of photoquadrats from (a) Seabird-1, distance from the shore 60 m, depth 2.9 m, (b) Reference, distance from the shore 200 m, depth 13.8 m.

Seabird transects and three sites in the Reference area. At each site, three high-resolution digital photoquadrat images (6016 × 4016 pixels) covering a 50 cm × 50 cm area of the seabed were taken. A full-frame Nikon D610 DSLR fitted with a Sigma 15 mm fisheye lens, packed in a Subal housing equipped with two Sea&Sea YS-D2 strobes, was used as the camera. A total of 48 images were collected for the Seabird transects and 25 for the Reference area (with an additional image captured at 180 m from the coastline). At sites densely covered by kelp forests, the kelp was first removed using a diver's knife prior to capturing images, leaving the holdfasts attached to the seabed. Up to six individuals of whelks (a mix of three species: *B. glaciale*, *B. undatum* and *B. polare*; the first two of which showed no differences in δ^{15}N values in a previous study by Zmudczyńska-Skarbek and Balazy, 2017), hermit crabs (*P. pubescens*) and chitons (*Tonicella rubra* and *T. marmorea*) were collected from each site (297 specimens in total). These species were among the most abundant local benthic invertebrates. Moreover, a previous study (Zmudczyńska-Skarbek and Balazy 2017) found that whelks and hermit crabs showed significantly higher δ^{15}N beneath the seabird colony under study than in the reference area.

After collection, the invertebrates were kept in clean seawater for one day to expel any remaining food and waste products from their digestive systems. The whelks and chitons were then extracted from their shells and all the specimens were cleaned and rinsed with fresh water. They were then frozen, oven-dried at 60 °C and ground using a vibrating mill.

Stable Isotope Analyses

The nitrogen and carbon stable isotope ratios of one 2–3 mg sample from each individual (whole bodies ground) were analysed via continuous flow-elemental analysis-isotope ratio mass spectrometry (CF-EA-IRMS) at the University of Liège (Belgium), using a Vario MICRO cube elemental analyzer (Elementar, Hanau, Germany) coupled to the isoprime precisION Elementar (Cheadle, United Kingdom). The results were expressed in the conventional δ^{15}N and δ^{13}C notation (‰), according to the following equation:

$$\delta X = \left(R_{\mathrm{sample}}/R_{\mathrm{standard}} - 1\right) \times 1000$$

where R_{sample} was the stable isotope ratio ^{15}N/^{14}N or ^{13}C/^{12}C, respectively, in the analysed sample, and R_{standard} was the stable isotope ratio ^{15}N/^{14}N or ^{13}C/^{12}C, respectively, in the international standard, that is atmospheric N_2 for nitrogen and Peedee Belemnite for carbon (Kelly 2000). Sucrose (IAEA-C6; mean ± SD: $\delta^{13}C = -10.8 \pm 0.5$‰) and ammonium sulphate (IAEA-N2; $\delta^{15}N = 20.3 \pm 0.2$‰) were used as certified reference materials. A laboratory reference material—glycine (Sigma-Aldrich, Overijse, Belgium; $\delta^{13}C = -47.5 \pm 0.3$‰, $\delta^{15}N = 2.5 \pm 0.4$‰)—and a sample replicate, used as quality control, were inter-spread every 15 samples. The mean standard deviation for the sample replicates was ± 0.3‰. δ^{13}C values were normalized for the effects of lipid concentration using the following equation: $\delta^{13}C_{\mathrm{normalised}} = \delta^{13}C_{\mathrm{untreated}} - 3.32 + 0.99 \times C{:}N$ (Post and others 2007).

Photoquadrat Analysis

To accurately describe the benthic communities, all taxa visible in the images were identified at the highest possible taxonomic level and their individuals counted. Each colonial organism was considered a single individual, except coralline algae (most likely *Lithothamnion glaciale*), the coverage of which was recorded as a percentage. The Laminariales group included *Saccharina latissima* and *Alaria esculenta* (both of which occurred across the Seabird and Reference areas), as well as all the unidentified kelps that had to be removed prior to taking the photo.

Statistical Analyses

Graphs of species numbers, the Shannon diversity index (H') and invertebrate δ^{15}N and δ^{13}C values (means ± SE) at different distances from the shore were created using MS Excel. Species accumulation curves were calculated and visually presented in the R 4.1.0 environment (R Core Team 2021) using the following packages: 'tidyverse' (Wickham and others 2019), 'ggpubr' (Kassambara 2020), and 'vegan' (Oksanen and others 2020). We calculated the species accumulation curves for the Seabird and Reference areas separately using the specaccum function in the 'vegan' package. We then used a permutation test to compare the curves between the two areas (Suppl. Material S2). To ensure comparability, we interpolated the species richness values to the same number of samples. The permutation test involved calculating the mean difference in species richness between the two areas and comparing this to a distribution of differences obtained by randomly shuffling the species richness values between the two groups and recalculating the mean differences 999 times. The *p*-value was determined as the proportion of permuted differences that were as extreme or more extreme than the observed difference. This approach enabled us to test the null hypothesis that there is no difference in species richness between the two areas.

To investigate differences in: (i) the number of benthic species and the Shannon diversity index with a natural logarithm (H'; Shannon and Weaver 1947), as the measures of alpha diversity, (ii) species composition (with each image treated as a separate sample), and (iii) δ^{15}N and δ^{13}C values of chitons, hermit crabs, and whelks (analysed separately for each invertebrate species) between the Seabird and Reference areas, we performed PERMANOVAs with 9999 permutations of residuals under a reduced model, considering kelp forest presence and distance from the shore. The fixed factors tested sequentially using Type I sum of squares were Seabird (representing seabird colony presence), Kelp (representing kelp forest presence), the Seabird × Kelp interaction and Distance (from the shore, coded as a covariate, but tested as the last variable in the models). To test the impact of the type of food source consumed by an invertebrate on the variability in δ^{15}N values, regardless of the possible ornithogenic enrichment, we also calculated PERMANOVA models with δ^{13}C fitted first, as a covariate.

Prior to analysis, the species composition data were square-root transformed. A Bray–Curtis similarity matrix was used for the species composition data, while Euclidean distances were used for the number of species, the Shannon diversity index and the isotopic data. To identify the contributions of different taxa to the dissimilarity between Seabird and Reference groups, we employed the similarity percentage analysis (SIMPER). To examine (dis)similarities in beta diversity, we used PERM-

DISP to test for homogeneity of multivariate dispersions, based on deviations from centroids, with pairwise comparisons and 9999 permutations between the Seabird and Reference groups, taking into account the presence of kelp forests in each area.

Metric multidimensional scaling (mMDS) with approximate 95% region estimates fitted to bootstrap averages was used to visualise the ordination of the multivariate species composition data. Similarity percentage (SIMPER) analysis was used to identify average similarities within groups and dissimilarities between groups in species composition. It also identified the taxa that contributed most to the dissimilarity. Additionally, group average values of invertebrate species δ^{15}N and δ^{13}C were calculated. All the PERMANOVAs, SIMPER, PERMDISP, and mMDS were performed using PRIMER v7 with the PERMANOVA + add-on (Anderson and others 2008; Clarke and others 2014).

Stable isotope niche widths for each group were quantified using the bias-corrected standard ellipse area (SEA$_{(c)}$), which represents the core isotopic niche encompassing 40% of the bivariate δ^{13}C–δ^{15}N distribution—a conventional probability-based niche width metric in SIBER (and not a statistical significance threshold)—following the approach of Jackson and others (2011). Ellipse coordinates corresponding to the SEA$_{(c)}$ were generated using a custom R 4.1.0 script, and the resulting ellipses were visualized in isotope space (δ^{13}C vs. δ^{15}N), with group-specific centroids indicated. To quantify isotopic niche overlap, the geometric intersection of the SEA$_{(c)}$ ellipses was calculated for all pairwise group combinations. The ellipse coordinates were then converted into spatial polygons, and the overlap area was computed using the sf package in R (Pebesma 2018). All calculations, visualizations, and summary tables were generated using custom, fully reproducible R code (Suppl. Material S3).

RESULTS

Alpha Diversity and Species Richness Patterns

A total of 56 taxa of benthic algae and invertebrates (including one unidentified species) were recorded. Of these, 52 were found in the Seabird area and 39 in the Reference area. Species accumulation curves, calculated separately for each area, were asymptotic, confirming that the amount of sampling was sufficient for further analysis (Suppl. Figure S4). The curves indicated significantly higher taxonomic diversity beneath the bird cliffs (permutation test: $p = 0.012$) and revealed that the difference in species number between the two areas increased as more samples were collected.

Univariate PERMANOVAs confirmed that the presence of both seabird colony and kelp forest had a significant effect on alpha diversity ($p < 0.001$ in all cases; Figure 2a, full results presented in Suppl. Table S5). Regarding the number of species, the Kelp factor explained 25.0% of the variance, while the Seabird factor accounted for 24.9%. Additional, albeit smaller, contributions were made by distance from the shore (12.7%, $p = 0.015$) and the Seabird × Kelp interaction (12.2%, $p = 0.035$). For the Shannon diversity index (H′), seabird colony presence accounted for 27.1% of the variance, while kelp forest presence explained 24.3%. Their interaction accounted for a further 16.6% ($p = 0.006$), while Distance was not significant. As shown in Figure 3 and Table 1, the average number of species and the Shannon diversity index were virtually equal in the Seabird and Reference areas within the kelp forest. Differences between the two locations became apparent at 120 m from the shore, where the kelp forest disappeared in the Reference transect, and both measures decreased there. Outside the kelp zone, 12 species on average occurred at the Seabird sites, compared to 7 at the Reference sites. The Shannon diversity index was also almost twice as high beneath the colonies (1.53 versus 0.83).

Community Composition, Beta Diversity and Key Taxa

Patterns in alpha diversity were accompanied by significant differences in overall community composition between the Seabird and Reference areas, as revealed by multivariate PERMANOVA. The Seabird factor accounted for 20.1% of the variation explained ($p < 0.001$; Figures 2a and 4, full PERMANOVA results presented in Suppl. Table S5). However, the largest proportion of the variability in the community was explained by the presence of kelp forest (28.6%, $p < 0.001$). The significant interaction between the Seabird and Kelp factors, which covered 13.7% of the variation ($p < 0.001$), confirmed that the benthic assemblages responded differently to the seabird colony vicinity within *versus* outside the kelp forest. Furthermore, no differences in beta diversity were observed between the entire Seabird and Reference areas (PERMDISP, $F = 2.91$, $p = 0.113$), nor between the kelp zones of the two areas ($F = 12.06$, $p < 0.001$; $t = 1.12$, $p = 0.337$). Nevertheless, within-group multivari-

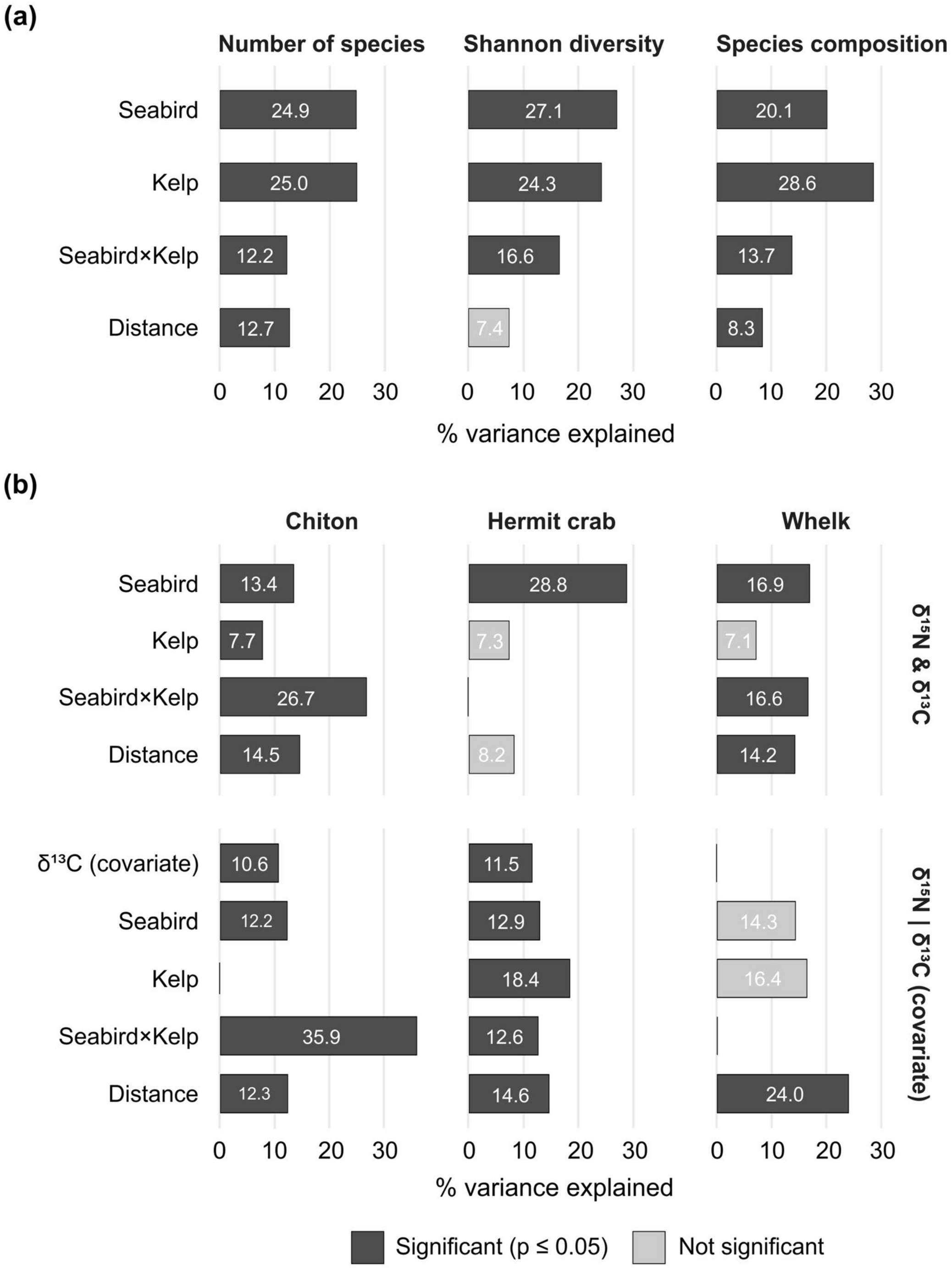


Figure 2. Summary of PERMANOVA results for (a) the number of species, Shannon diversity index (H'), and overall species composition, and (b) δ^{15}N and δ^{13}C values of chitons *Tonicella* sp., hermit crabs *Pagurus pubescens*, and whelks *Buccinum* sp. Bars show the percentage of variance explained by each predictor (Seabird, Kelp, Seabird × Kelp, Distance) and by the covariate (δ^{13}C). Dark grey indicates significant effects ($p \leq 0.05$), and light grey non-significant effects.

ate dispersions differed outside the kelp forest ($t = 5.40$, $p < 0.001$). Since the factors were included in the PERMANOVA model sequentially (SS type I), some of the variation in the community composition was also explained by distance from the coast (8.3%, $p = 0.006$).

The average dissimilarity in benthic taxonomic composition between the Seabird and Reference

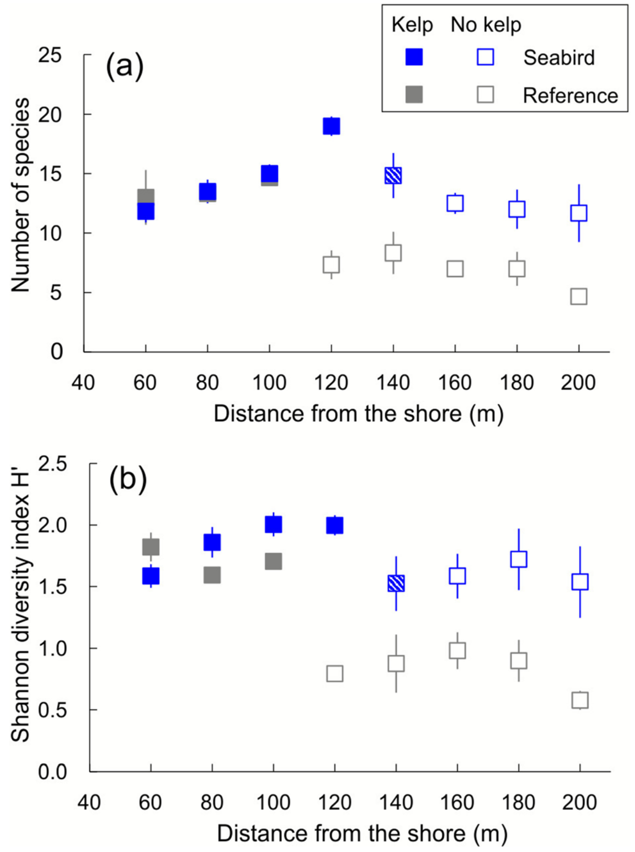


Figure 3. Mean ± SE of (a) the number of species and (b) Shannon diversity index (H') along the distance from the shore in the Seabird (blue) and Reference (grey) areas. Filled and open symbols indicate sites within the kelp forest and outside it, respectively (hatching at the Seabird 180 m site denotes it was overgrown by kelp in one of the two Seabird transects).

Table 1. Mean and Standard Error Values of the Number of Species, Shannon Diversity Index (H') and δ^{15}N and δ^{13}C (‰) of Chitons *Tonicella* sp., Hermit Crabs *Pagurus pubescens*, and Whelks *Buccinum* sp., Within and Outside the Kelp Forest in the Seabird and Reference Areas

	Kelp				No kelp			
	Reference		Seabird		Reference		Seabird	
	n	Mean ± SE	n	Mean ± SE	n	Mean ± SE	N	Mean ± SE
Number of species	9	13.7 ± 0.75	27	15.3 ± 0.68	16	6.9 ± 0.57	21	11.9 ± 0.83
Diversity (H')	9	1.71 ± 0.05	27	1.88 ± 0.05	16	0.83 ± 0.07	21	1.53 ± 0.12
δ^{15}N (‰)								
Chiton	14	8.32 ± 0.16	41	8.08 ± 0.10	15	7.36 ± 0.12	33	8.44 ± 0.10
Hermit crab	15	7.64 ± 0.06	38	7.78 ± 0.06	24	7.72 ± 0.08	34	8.19 ± 0.07
Whelk	10	10.89 ± 0.19	29	11.13 ± 0.15	16	10.76 ± 0.15	28	10.74 ± 0.14
δ^{13}C (‰)								
Chiton	14	− 20.73 ± 0.74	39	− 20.88 ± 0.85	15	− 20.22 ± 0.57	31	− 20.64 ± 0.51
Hermit crab	15	− 17.75 ± 0.83	38	− 18.43 ± 1.00	24	− 17.55 ± 1.01	34	− 18.37 ± 1.60
Whelk	10	− 17.83 ± 1.32	28	− 18.95 ± 0.87	15	− 18.28 ± 0.51	25	− 18.43 ± 0.85

areas, as calculated with SIMPER, was 50.4%. Composition was more similar between the two areas within the kelp forest (average dissimilarity = 47.5%) than outside it (av. dissimilarity = 52.6%). Overall, 31 out of 49, and 34 out of 43 taxa recorded in the kelp forest and outside it, respectively, were more abundant in the Seabird than in the Reference area. The taxa contributing

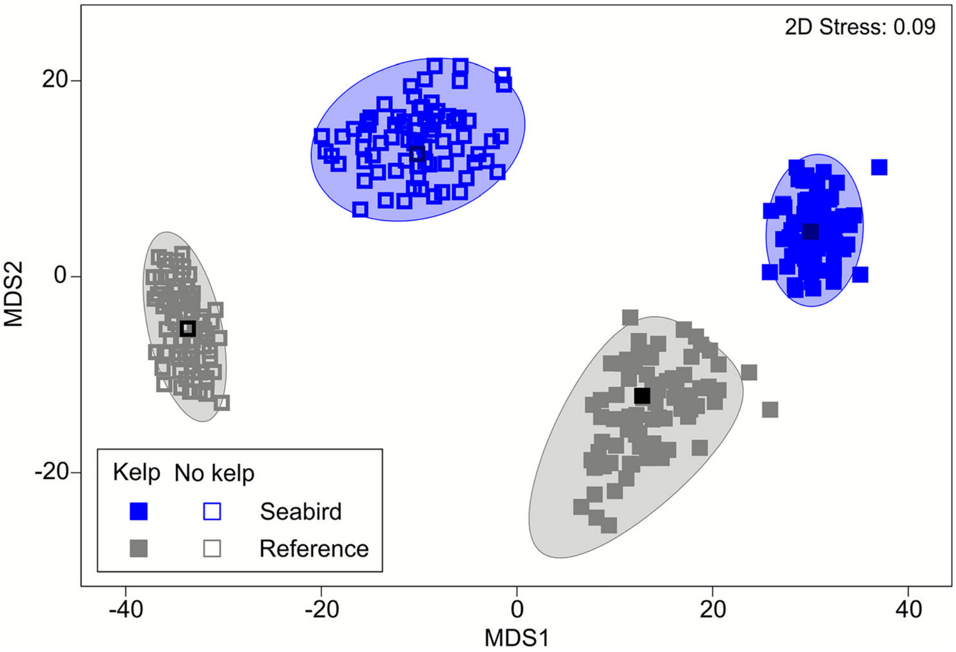


Figure 4. Metric MDS ordination of bootstrap averages (darker symbols indicating group patterns) and the corresponding 95% bootstrap regions for benthic species composition within the kelp forest (filled symbols) and outside it (open symbols) in the Seabird (blue) and Reference (grey) areas

the most to the overall dissimilarity between the Seabird and Reference areas within the kelp forest were: Cirripedia (contributing 14.4% to the total dissimilarity), *Balanus crenatus* (9.8%), and Laminariales, (7.5%), which were more abundant in the Seabird sites; as well as one of *Haliclona* species (7.7%) and coralline algae (7.0%), which were more abundant in the Reference sites (Figure 5a and Suppl. Table S2 for the contributions of the remaining taxa). Outside the kelp zone, coralline algae contributed the most to the overall dissimilarity (13.8%), and were also more abundant in the Reference sites, as were *Strongylocentrotus* sp. (8.8%). In contrast, *Tonicella* sp. (6.3%) and *Balanus balanus* (6.0%) were more numerous in the Seabird area (Figure 5b, Suppl. Table S6).

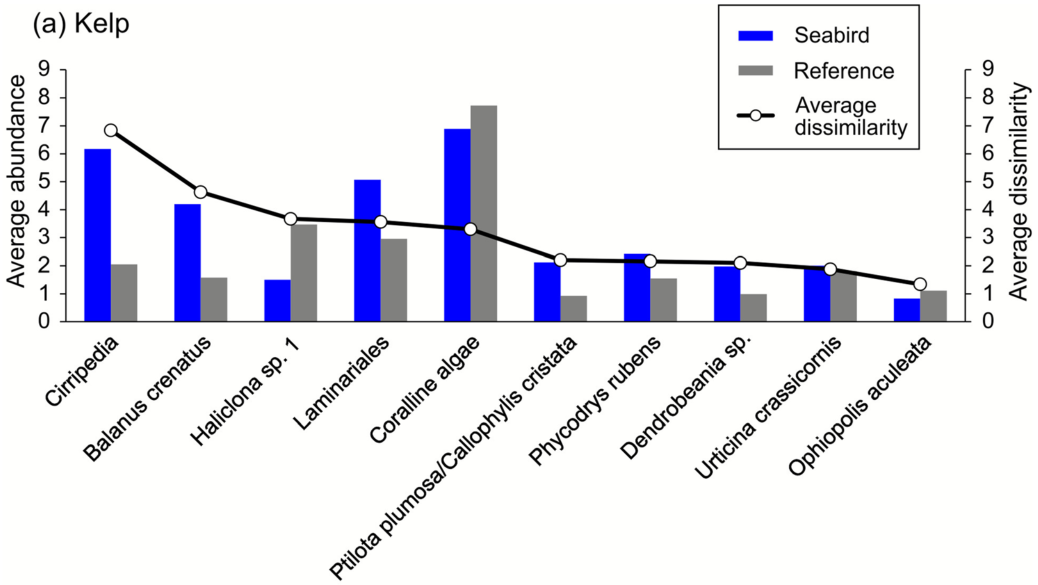
Nitrogen and Carbon Stable Isotope Ratios in Benthic Invertebrates

PERMANOVA confirmed that the presence of seabirds significantly influenced the δ^{15}N and δ^{13}C values of all three taxa ($p < 0.005$ in all cases; Figure 2b). The Seabird factor accounted for the greatest proportion of variance in hermit crabs (28.8%), followed by whelks (16.9%) and chitons (13.4%). For chitons and whelks, additional significant effects were observed for kelp forest presence (only for chitons), the Seabird × Kelp interaction, and distance from the shore, together explaining nearly 50% of the isotopic variability in chitons and over 30% in whelks. In contrast, these additional factors were non-significant in hermit crabs. When δ^{13}C was included as a covariate, the enrichment of ^{15}N in the Seabird area remained significant for chitons and hermit crabs ($p < 0.05$). In these models, the Seabird × Kelp interaction had a much stronger influence on δ^{15}N values in chitons (35.9%, $p < 0.001$) than in hermit crabs (12.6%, $p < 0.05$), however, Kelp also contributed to this variation in hermit crabs (18.4%, $p < 0.001$). Additional significant contributions came from Distance in all three species (full results of the above-described PERMANOVAs, as well as those performed separately for δ^{15}N and δ^{13}C values, are presented in Suppl. Table S5).

SIMPER analysis indicated that these differences were primarily driven by chitons and hermit crabs outside the kelp zone. Here, the dissimilarity in δ^{15}N and δ^{13}C values between the Seabird and Reference sites was higher (2.38 and 4.66, respectively), compared with sites within the kelp forest (2.07 and 2.26; Table 2). The opposite pattern was found for whelks, with higher dissimilarity observed within the kelp forest (4.61) than outside it (1.70).

Descriptive comparisons of group means supported these results (Figure 6, Table 1). The δ^{15}N values of chitons and hermit crabs were similar

(a) Kelp



(b) No kelp

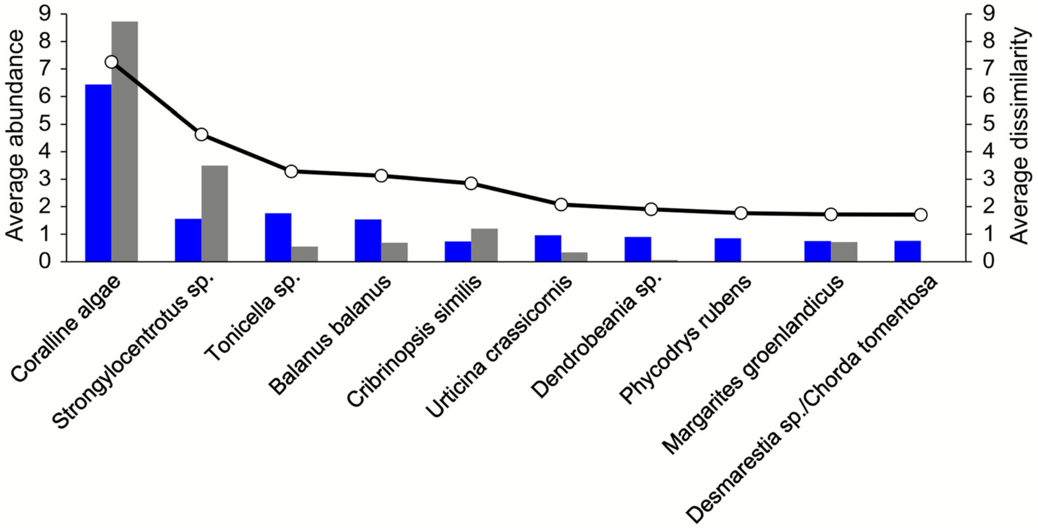


Figure 5. Averages of square-root–transformed abundances of the 10 benthic community components contributing most to the overall dissimilarity between the Seabird and Reference areas, shown separately for sites within the kelp forest (a) and outside it (b). The components presented accounted for 65% (a) and 57% (b) of the overall dissimilarity (SIMPER).

within kelp forests in the Seabird and Reference areas, but outside the kelp zone, they were enriched by ~ 1.1‰ and ~ 0.5‰, respectively, beneath seabird colonies. The δ^{15}N values of whelks were less consistent, with small differences (0.6–0.8‰) recorded nearshore that often inverted or disappeared with distance. Across all taxa, the δ^{13}C values were lower in the Seabird area. The largest differences were observed in hermit crabs (on average 0.8‰), followed by whelks (~ 0.6‰) and chitons (~ 0.3‰).

Finally, isotopic niche ellipses visualized these contrasts (Figure 7). There was no overlap between the Seabird and Reference sites outside the kelp forest for chitons (0.00%) and it was low for hermit crabs (13.5%), but higher for whelks (30.8%). Within the kelp zone, however, niche overlap increased for chitons (33.4%) and hermit crabs (25.2%), and decreased for whelks (15.7%) (Table 2).

DISCUSSION

The results obtained show that seabirds are an important environmental factor affecting the benthic realm on a local scale by concentrating extra

Table 2. Average Squared Distance (SIMPER Analysis) and Isotopic Niche Overlap (%) Between the Seabird and Reference Areas, Within the Kelp Forest and Outside it, for Chitons *Tonicella* sp., Hermit Crabs *Pagurus pubescens*, and Whelks *Buccinum* sp.

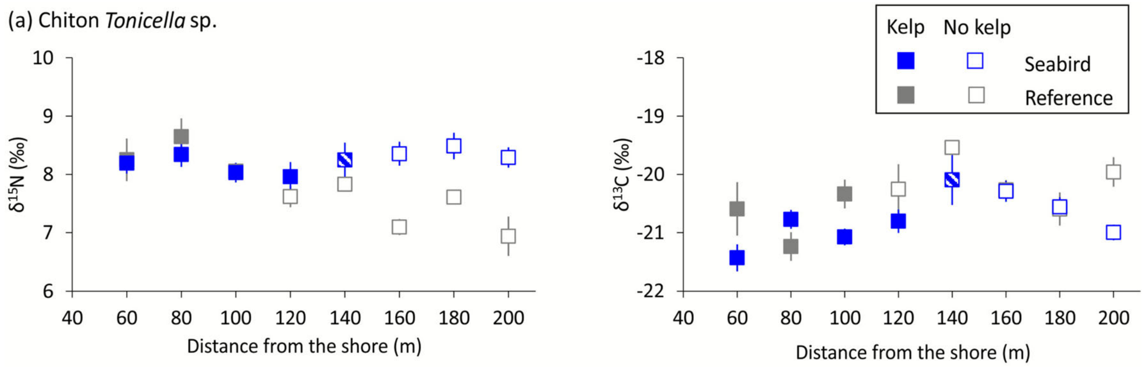
	Kelp	No kelp
	Average squared distance	
Chiton	2.03	2.44
Hermit crab	1.83	4.28
Whelk	3.74	2.33
	Isotopic niche overlap (%)	
Chiton	33.35	0.00
Hermit crab	25.24	13.52
Whelk	15.66	30.84

nutrients beneath their colonies. Significant differences in taxonomic composition were found between the Seabird and Reference locations, with higher diversity observed beneath the bird cliffs, particularly outside the kelp forest. The nitrogen stable isotope ratio values of the studied biota indicated that the invertebrates living adjacent to the colonies were enriched with seabird-derived substances. However, the presence of the kelp forest modified this for different species in different ways. Chitons and hermit crabs appeared to utilise ornithogenic nutrients effectively beyond the kelp zone, whereas whelks could benefit from them closer to the shore amidst dense kelp.

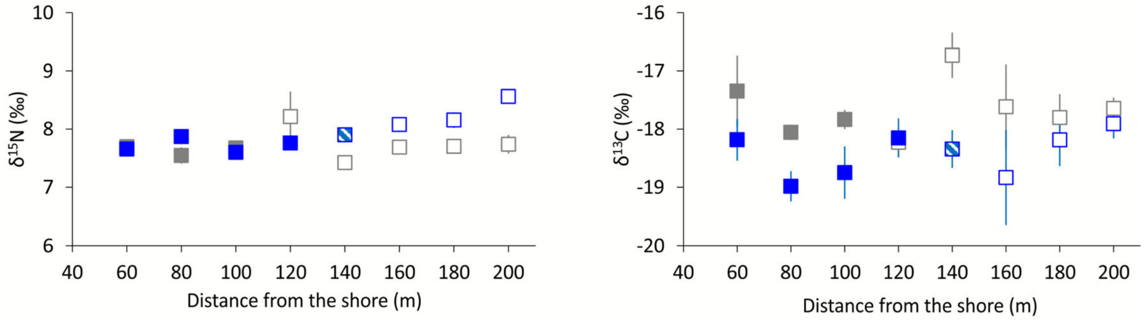
The habitat-forming role of large perennial brown macroalgae is widely recognized worldwide (Christie and others 2009; Schiel and Foster 2015). In the Arctic, these algae also play a central role in enhancing ecosystem functioning, productivity and biodiversity (Bischof and others 2019; Thomas 2021). As in previous studies (for example Teagle and others 2017; Włodarska-Kowalczuk and others 2009), more taxa were recorded within than outside the kelp forest in both studied areas (49 vs. 43). An interesting finding of our analyses is that the Seabird factor significantly interacted with the Kelp factor in explaining variability and diversity in species composition in the studied region. Benthic assemblages were more dissimilar between the Seabird and Reference areas beyond the kelp zone than within it. Clear differences in taxonomic diversity were also evident between the two areas outside the kelp forest. This was due to a pronounced decrease in the number of species and the Shannon diversity index values outside the kelp forest compared to inside it in the Reference area. In contrast, there was only a slight decline in both the parameters' values in the Seabird area. To the best of our knowledge, no studies have been conducted to compare our results on benthic species composition and diversity around seabird colonies. Only a few reports exist on shifts in macroalgae and seagrass community compositions towards fast-growing, ephemeral species, which lead to lower diversity, and increased abundance of selected invertebrates (Gagnon and others 2016; Powell and others 1989).

The highly seasonal conditions of the High Arctic result in kelps maximising their growth and nutrient acquisition very early in the season, in winter and early spring (Dunton 1985; Wiencke and others 2009). This phenomenon occurs either before or concurrently with the onset of the birds' reproductive cycle that is before they can deliver substantial quantities of guano into the surrounding water bodies. In this way, kelps and their few direct consumers, certainly sea urchins *S. droebachiensis*, appear relatively independent of the ornithogenic supplies, showing no δ^{15}N enrichment in previous studies (Zmudczyńska-Skarbek and Balazy 2017). Furthermore, Gordillo and others (2006) demonstrated that Arctic seaweeds, except for few nitrophilic chlorophyte species, did not respond to experimental nitrate and phosphate enrichment in summer with respect to their biochemical composition. This indicates a high degree of resilience of the algal community to a disruption in the typical nutrient availability pattern, and thus supposedly also to ornithogenic fertilization. Nevertheless, both brown (*Desmarestia* sp./*Chorda tomentosa*, cf. Ectocarpaceae, Laminariales) and red (*Phycodrys rubens*, *Ptilota plumosa*/*Callophylis cristata*) macroalgae were more abundant, or simply present in the Seabird area, and were scarce or totally absent across the Reference area. This suggests that the conditions adjacent to the seabird colonies are more favourable for many algal species. A contrasting response was exhibited by the coralline red algae, which were found to be less abundant below the bird cliffs. This is presumably because the coralline red algae lose out in the competition for space with other species when conditions improve (Lebrun and others 2022). Unfortunately, we do not have isotopic data for the specified taxa, except for the absence of differing δ^{15}N values in the laminarian *S. latissima* between the two areas (Zmudczyńska-Skarbek and others 2015). However, Finne and others (2024) revealed that the chlorophytes (*Acrosiphonia* sp.) and the filamentous brown algae (*Ectocarpus* sp.) in the tidal zone on the opposite coast of Isfjorden did show the ornithogenic enrichment, as measured by δ^{15}N. This may

(a) Chiton *Tonicella* sp.



(b) Hermit crab *Pagurus pubescens*



(c) Whelk *Buccinum* sp.

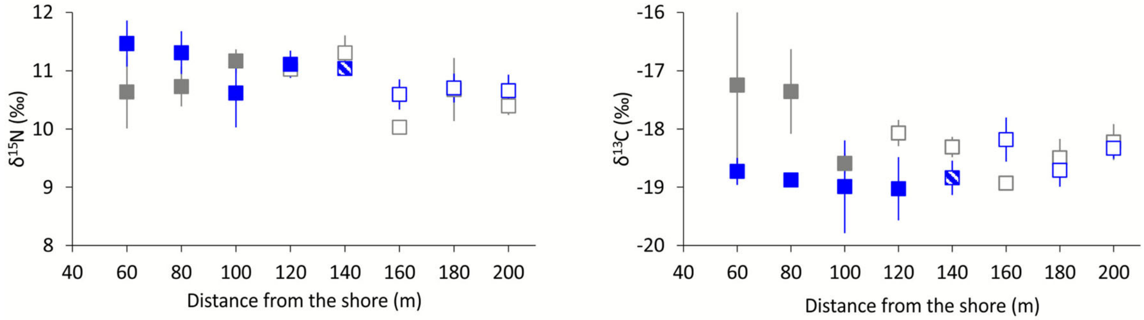


Figure 6. Mean ± SE of δ^{15}N and δ^{13}C (‰) for (a) chitons *Tonicella* sp., (b) hermit crabs *Pagurus pubescens*, and (c) whelks *Buccinum* sp. along distance from the shore in the Seabird (blue) and Reference (grey) areas. Filled and open symbols indicate sites located within and outside the kelp forest, respectively. Hatching at the Seabird 180 m site denotes that this site was overgrown by kelp in one of the two Seabird transects.

be attributed to the close proximity to seabird-derived nutrient sources and the facilitated transfer of allochthonous nutrients to the intertidal zone via seabird-impacted streams, as well as higher capability of these species to absorb excessive nutrients. Similarly increased δ^{15}N values in macroalgal tissues were recorded in temperate European coastal waters on the first few metres from the shoreline (Gagnon and others 2013; Healing and others 2024), as well as on tropical coral reefs (Graham and others 2018; Honig and Mahoney 2016; Thibault and others 2022). This could be due to the availability of seabird subsidies for a much longer period of the year. In the Arctic, in addition to the proximity to the seabird colonies, the phenology of nutrient intake by different algal groups, or even individual species, may play a pivotal role in the response to seabird subsidies.

The process that appears to be essential for providing ornithogenic nutrients to the benthic ecosystem is pelagic-benthic coupling. This is primarily due to the constant high nutrient demand and the ability of phytoplankton to immediately absorb guano-derived compounds throughout the season (Browning and others 2020; Methratta 2004; Vizzini and others 2016; Zmudczyńska-

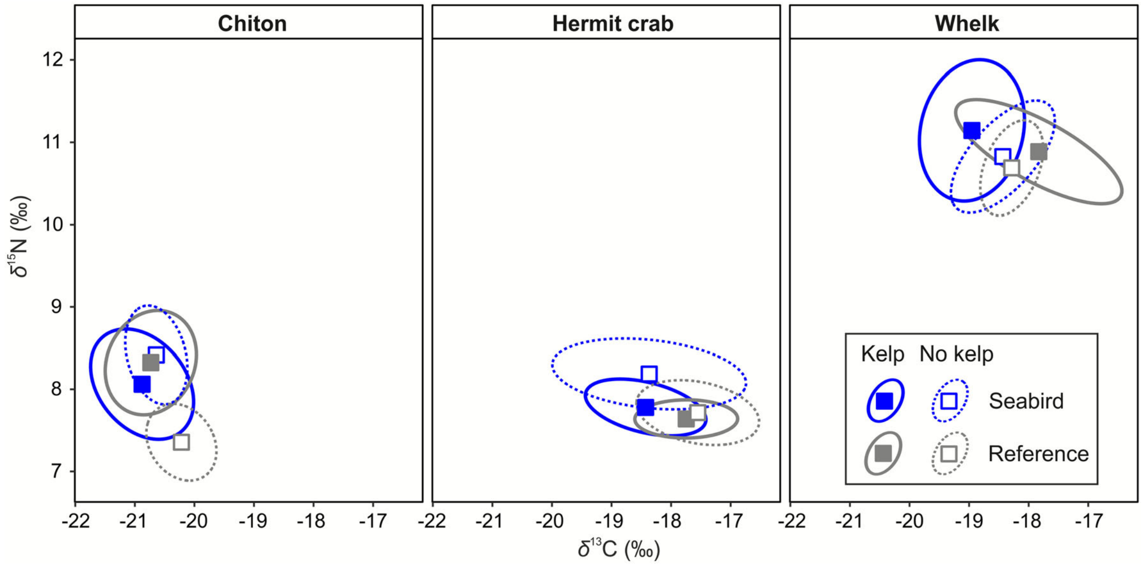


Figure 7. δ^{15}N and δ^{13}C biplots illustrating the isotopic niche widths (bias-corrected standard ellipse areas, $\mathrm{SEA}_{(c)}$) and group-specific centroids of chitons *Tonicella* sp., hermit crabs *Pagurus pubescens*, and whelks *Buccinum* sp., within the kelp forest (solid line, filled symbols) and outside it (dotted line, open symbols) in the Seabird (blue) and Reference (grey) areas. For the corresponding biplot with individual samples plotted, see Suppl. Figure S7.

Skarbek and Balazy 2017). Although the present study did not directly investigate the coupling between pelagic and benthic communities, the higher abundance of most filter-feeders below the bird cliffs, particularly within kelp forests, suggests that the water column contained more abundant and/or higher-quality organic matter. The forest-forming kelps reduce water mixing and flow through their physical density, thus enhancing microbial activity and nutrient cycling locally (Kosek and Kukliński 2023; Pfister and others 2019). Kelps are highly productive by nature, enabling them to effectively fix both inorganic carbon and other nutrients, including nitrogen and phosphorus. However, since kelps grow earlier in the season than seabirds return to their colonies to deliver nutrients to the water beneath, they should not deplete local resources provided by birds in summer (Dunton 1985; Wiencke and others 2009). Instead, it is hypothesized that kelps may facilitate phytoplankton production on site, subsequently preventing living cells and particulate organic matter (in the form of plankton carcasses, faecal pellets and other detritus) from drifting away. This would ultimately direct them downwards to the seabed, thus fostering effective pelagic-benthic coupling. The shallow depths of the local kelp forest (down to approximately 8–10 m in the study area) suggest that there may not be much time for the plankton cells and organic particles to be grazed or decomposed en route to the benthos. This implies that the benthic filter-feeders, such as barnacles, may effectively capture both living and dead food particles originating from the surface layer. This may explain their greater abundance beneath the bird cliffs. *Balanus crenatus* and Cirripedia were the taxa that differed most between the two study areas within the kelp zone (positions 1 and 2, respectively, on the SIMPER rank of taxa based on their average dissimilarities between the Seabird and Reference areas), while *B. balanus* was the fourth consecutive taxon on the corresponding taxa list for outside the kelp forest. Among the other benthic filter-feeders, the bryozoans, including *Dendrobeania* sp., were also found to be more abundant in the vicinity of the seabird colony. Conversely, the sponge *Haliclona* sp. exhibited the opposite trend. Sponges typically filter smaller food particles, including bacteria and nanoplankton measuring less than 10 µm, as well as dissolved organic matter, whereas barnacles and bryozoans are effective at catching larger cells (up to 150 µm), such as diatoms and microzooplankton, and detritus (Hamann and Blanke 2022). Experiments have also shown that following fertilization with guano, the marine phytoplankton community shifts towards larger-celled organisms such as diatoms and prymnesiophytes, which can avoid grazing more effectively. This results in an increased export of organic matter to the seabed (Browning and others 2020; Shatova and others 2017). Consequently, it can be hypothesized that the size of food particles ingested is a contributing factor to the ornithogenic enrichment of suspension-feeders. Nevertheless, further research incorporating the isotopic data of various filter-feeding animals is necessary to ascertain the precise pathways through which these nutrients are transferred to bottom-dwelling communities.

The Seabird factor had a significant effect on the δ^{15}N and δ^{13}C values of the three benthic taxa selected for isotopic analysis: hermit crabs, whelks and chitons (Figure 7). For chitons and hermit crabs, the effect of ornithogenic enrichment, as measured by higher δ^{15}N values, was significant despite the presumed diversity in their feeding strategies, as indicated by the variation in δ^{13}C values (yet, δ^{13}C values were generally lower in the Seabird compared to the Reference sites, consistent with the patterns observed in the nearby terrestrial vegetation, Zmudczyńska-Skarbek and others 2015, and in macroalgae at the opposite coast of Isfjorden, Finne and others 2024). Although the differences in δ^{15}N values were numerically small, they were statistically robust and ecologically consistent. As with the results for species composition, the impact of guano on the nitrogen stable isotope ratio of chitons and hermit crabs was differentiated by the kelp forest. Outside the kelp forest, δ^{15}N values were higher in the Seabird than in the Reference area (the whelk tissues were enriched in the kelp zone, but only in the first two study sites of the Seabird transects). Furthermore, all three invertebrate species were more abundant across the Seabird sites, but only beyond the kelp zone (within the kelp forest, only the group 'buccinids' showed such a difference). Higher abundances of carnivorous and/or scavenging hermit crabs and whelks corroborate with our previous study results from the area (Zmudczyńska-Skarbek and Balazy 2017; Zmudczyńska-Skarbek and others 2015). We hypothesized that these invertebrates primarily acquired seabird-derived nutrients via pelagic-benthic coupling, that is, from guano-subsidized, plankton-derived detritus that had fallen and been deposited in sediments, or from the live or dead bodies of other benthic filter- or deposit-feeding detritivores, at least where kelp-derived organic matter was not dominant. In those investigations, we concluded that seabird-derived substances were first assimilated by phytoplankton in the surface water, which is consistent with other studies (McCauley and others 2012; Methratta 2004; Vizzini and others 2016). However, the substances were insufficient for benthic microalgae. Consequently, these nutrients were not incorporated into the tissues of microherbivorous molluscs grazing on kelp or other hard substrates, as demonstrated by *Margarites helicinus*. However, for the chitons studied here, which are known to feed on microalgae and bacteria (Paar and others 2019), this appeared to be true only when they were living within the kelp forest. Outside the kelp zone and at a greater depth than within the kelp forest, the chitons showed higher tissue δ^{15}N in the Seabird than in the Reference area. Therefore, it is possible that they may expand their diet to include other food sources, including animal-type sources that are possibly ornithogenically enriched, in response to changing environmental conditions, as suggested by Latyshev and others (2004) and commonly observed in many Arctic fauna (Bridier and others 2021; Renaud and others 2021). In this specific case, within the epiphytic communities, the proportion of microfaunal components capable of benefiting from the sinking ornithogenic organic matter over the non-enriched microphytobenthos may increase with depth due to the lower amount of light required for photosynthesis (Kuklinski 2009). This is particularly significant given that, in the absence of kelps, the only available surface for settlement and grazing is the poorly sunlit rocky bottom. In this way, not only carnivores and scavengers such as hermit crabs and whelks, but also grazers such as chitons can utilise seabird-derived nutrients.

We hypothesized that distance from the coast would influence the distribution of ornithogenic nutrients across the subtidal zone, with nutrient dispersal increasing progressively with distance from the bird cliff. A comparable pattern was observed on land (Odasz 1994; Wainright and others 1998; Zmudczyńska-Skarbek and others 2015; Zwolicki and others 2013) and in surface water (own data, unpublished). Benthic communities showed no or negligible responses to ornithogenic fertilization at distances greater than 10 km from the colonies (Gagnon and others 2020; Marmen and others 2017). However, contrary to our expectations, the benthic communities we studied differed more between the Seabird and Reference locations the farther they were from the colony. Distance and depth are inseparable, and these two factors inherently determine the range of kelp forests (Kvile and others 2022), which appeared to be the most significant variable for the studied benthic taxonomic composition.

The variability of N and C stable isotope ratio values was explained by distance to a small degree and inconsistently among taxa, which may partly reflect the relatively limited spatial extent of our study area and its ability to capture broader nutrient dilution gradients. Interpretation of isotopic patterns was further constrained by incomplete characterization of nutrient sources, as key end-member information was not available. More comprehensive source data, including pelagic phytoplankton and benthic microalgae, would have enabled a clearer understanding of nutrient pathways and strengthened the conclusions drawn from the stable isotope results.

CONCLUSIONS

Our study highlights the important ecological function of seabird-derived nutrients in shaping benthic communities in the coastal ecosystems of the High Arctic. Ornithogenic nutrient subsidies have a significant influence on the composition of benthic species, including alpha and beta diversity, as well as on nutrient dynamics, particularly in kelp forest areas. However, the transfer of nutrients from land to the seabed is more complex than anticipated and is influenced by nutrient dispersion over distance and depth, as well as by interactions within the local food webs. Close to the shore, planktonic autotrophs in the surface waters are likely to be the primary absorbers of seabird-derived nutrients, particularly in shallow, well-lit areas where kelp forests thrive. Here, sinking particulate organic matter from planktonic production subsidized by seabirds supports benthic filter-feeders, which in turn provide resources for their predators. Further from the shore and at greater depths, where light is scarce and kelp cover is limited, benthic grazers may shift from herbivory to omnivory, consuming enriched microinvertebrates as a guano-linked nutrient source. At the same time, any sinking, subsidized POM may be trapped by suspension feeders or buried in the sediment. Ultimately, the greater the supply of ornithogenic nutrients to filter-feeders and detritus-feeders, the greater the enrichment of ornithogenic nutrients in benthic carnivores and scavengers. These insights contribute to a better understanding of nutrient transfer processes and the complex interactions between terrestrial and marine ecosystems in the Arctic. Although the ornithogenic fertilization effect extends beyond the coastline, it is spatially limited and more subtle in the sea than on land due to substantial nutrient dispersion in the water.

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DATA AVAILABILITY

Data are available at: https://doi.org/10.5281/zenodo.17867569.

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