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Uncovering the foraging strategies in two pelagic diving seabird species outside their breeding season using coupled feather stable isotopes and light-based geolocators

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Cover photo by Kristina Emilie Nilssen

Bridled morph of Common guillemot *Uria aalge*, Hornøya

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ABSTRACT

The critical endangered Common and Brünnich guillemot are exhibiting contrasting population trends in the Barents Sea region, where the Common guillemots are increasing, while Brünnich guillemots are declining. The non-breeding season is regarded as the main mortality period among seabirds, especially in winter, as climate conditions may be harsh and prey availability rather limited. The contrasting trends seen in the Barents Sea Common and Brünnich guillemot populations are believed to be related to the two species different non-breeding ecology, although little is known about the bird's ecology in this particular period, as the species are out at sea, unavailable for scientists. However, the development of light-weighted tracking equipment has made it possible following small migrating species, such as birds, throughout the entire year-cycle. In combination with stable isotopes, such methods can be used to investigate species ecology non-invasively. This study used combined feather stable isotopes and light-based geolocation data of the two sympatric seabird species to investigate intra- and interspecific dynamics in their non-breeding strategies (i.e., changes in foraging distribution and isotopic niche) in the Barents Sea. Differential responses were found between the species foraging distribution and isotopic niches, as they showed no overlap in isotopic niches when their distribution overlapped, and vice versa, which might indicate an avoidance mechanism for equal resource utilization during the non-breeding season. The species responded differently to limitations in food conditions in the Barents Sea during winter, as Common guillemot exhibited smaller degree of change in isotopic niches compared to the Brünnich guillemot, indicating that the Brünnich guillemot change from having a generalized foraging strategy in winter, to become more specialized during autumn when food is more abundant.

Key words: Geolocation, stable isotopes, non-breeding, distribution, foraging, guillemot, murre, *Uria aalge*, *Uria lomvia*

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1 INTRODUCTION

How seabirds forage and cope during the non-breeding season is today not fully understood. Many seabirds are known to share their non-breeding distribution, but how they share the resources is not well known. Increasing our knowledge of seabirds' non-breeding ecology is therefore essential for understanding their responses to changes in the environment and to ensure sustainable future management, especially for sympatric species with contrasting population trends. However, information of their diet and link to the marine environment is not always easy to acquire as seabirds spend the non-breeding season out at sea, unavailable for scientists. Consequently, most knowledge of seabirds' diet and ecology is derived from their breeding grounds, and thus their non-breeding ecology are less enlightened and often not fully understood.

Earlier knowledge on seabird's whereabouts outside their breeding season were solely based on ring-observations, where citizens observing ringed birds reported back to researchers (Huettmann and Diamond 2000). This could infer bias in the results of seabirds distribution towards areas with people, and less observations in areas where people were not present. Tracking devices can provide information of seabird's distribution out at sea throughout the year, but earlier these devices size and weight limited the usage on seabirds, especially because of the battery size. However, during the last decades, the equipment for animal tracking has improved, and the development of miniature, lightweight geolocators (Global Location Sensors, hereafter referred as GLS-loggers), have made it possible to also follow small, migrating species, such as seabirds, throughout the entire year cycle. GLS-loggers measure light intensity and record the maximum value in a given time interval, which, after retrieval, allows determination of daily latitudinal and longitudinal position and enables identification of year-round distributions (St. John Glew et al. 2018, St. John Glew et al. 2019, Merkel et al. 2020, Reiertsen et al. 2021). In later years, geolocation data have been used in multiple studies as a proxy of seabird's activity, displaying their non-breeding distribution, migratory paths, movements, and activity patterns outside of the breeding season (e.g., Steen et al. 2013, Dunn et al. 2020, Fauchald et al. 2021, Reiertsen et al. 2021). However, such devices do not provide a complete image of animals' ecology, and hence GLS-loggers are often used in combination with dietary data, such as analysis of stomach content and biochemical methods like analysis of stable isotopes and fatty acid.

Stable isotopes from seabirds feather have been used to investigate seabirds non-breeding resource usage (e.g., St. John Glew et al. 2018, 2019, Fromant et al. 2020), because of their relatively harmless sampling approach, easy access, simple procedure, many application possibilities, long-time aggregation, and low analytical costs. In studies of marine species, stable isotope ratios of carbon (^{13}C : ^{12}C or $\delta^{13}\text{C}$) and nitrogen (^{15}N : ^{14}N or $\delta^{15}\text{N}$) are the most commonly used, due to their high degree of heterogeneity in such environments (Newsome et al. 2010). More specific, values of nitrogen can be used to determine an animal's trophic level of foraging, as predators tends to be 3-4‰ more enriched than its prey, whereas carbon can provide information about the animal's habitat utilization, as benthic and coastal food webs tend to be more enriched than offshore and pelagic food webs (Peterson and Fry 1987, Post 2002, Inger and Bearhop 2008, St. John Glew et al., 2018). During the last two decades, stable isotope of carbon and nitrogen have been widely used to display species or populations isotopic niches, a two-dimensional space, plotted in a coordinate system, where $\delta^{13}\text{C}$ on the x-axis and $\delta^{15}\text{N}$ on the y-axis (Inger and Bearhop 2008). The isotopic niche is often interpreted as a proxy of species or populations real world niche and have in several ecological studies been used to test predictions of ecological theory (i.e., optimal foraging theory, competition theory and niche variation hypothesis), by detecting dynamical changes at different scenarios, e.g., at limiting food resources, and/or competition, both inter- and intraspecific (in e.g., Planque et al. 2020, Almela et al. 2021, Garcia-Rodriguez et al. 2021). Seabirds, as most bird species, need to moult and replenish their feathers to maintain feather function (St. John Glew et al. 2018). Feather moult is an extremely energy depleting event, which for most bird species happens outside their breeding season (St. John Glew et al. 2018). Thus, the birds regrown feathers only contain accumulated records of their resource utilization in a period which for most seabird ecologists is unknown.

Upon optimal foraging theory, it is assumed that species must, as a consequence of evolution and natural selection, act in the most economical fashion in order to reproduce and stay alive (MacArthur and Pianka 1966). What an animal includes and excludes in its diet, should therefore be determined by the overall profitability of the food, i.e., the energetic intake must exceed the energetic costs of finding, capturing, and handling the feed (MacArthur and Pinaka 1966). Thus, in a productive environment where food is dense and/or reliable, optimal foraging theory predicts that species should include few dietary items, display increased specialization, and a reduction in niche size. Whereas, under unstable conditions where food

might be scarce and/or unreliable, species should display low dietary restrictions, reduced specialization, and an increase in niche size (Klopfer and MacArthur 1960, MacArthur and MacArthur 1961, MacArthur and Pianka 1966). In a situation of interspecific competition, however, niche variation hypothesis predicts that species should become more specialized, by reducing their intraspecific variation in resource utilization, and thus shrink in their niche area (van Valen 1965). Contrastingly, in a situation of release from interspecific competition, niche variation hypothesis predicts that species should expand their niche, and thus become less specialized, either by increasing intraspecific variation in their resource utilization or by overall utilizing a greater range of resources (Bolnick et al. 2007). The competitive exclusion principle, on the other hand, predicts that when two species exhibit equal requirements to the environment, the outcome may either be exclusion of the inferior opponent, or niche differentiation in such way that both species are able to coexist (Gause 1934; Slobodkin 1961a; Levin 1970). As competition may have negative effects on growth, reproduction and survival, species with the potential to compete, tend, historically, to exhibit some degree of character displacement behaviourally, physiologically and/or morphologically, that ensures less or no competition (MacArthur 1958; Connell 1961, Slobodkin 1961b; Levin 1970). It is therefore assumed that species experiencing a reduction in their niche exclusiveness, increased niche overlap and competition, should respond by reduce and/or separate their habitat utilization, spatially and/or temporally, rather than changing their diet (Beauchamp and Ulliyott 1932; Connell 1961, Begon et al. 2014). Another response may be that when distributional overlap is large, they may segregate their dietary niche more strongly if competition is present.

The Common and Brünnich guillemots are two close-related (Smith and Clarke 2015), sympatric Auk species, that have been exhibiting contrasting population trends in the Barents Sea region the last decades; where the Common guillemots are increasing, while the Brünnich guillemots declining (Fauchald et al. 2015, Frederiksen et al. 2016, Merkel et al. 2021). The Common and Brünnich guillemots are two of the most abundant seabird species in the Barents Sea (Steen et al. 2013), however both species are included in the Norwegian Red List of species in risk of extinction categorized as Critically endangered (Artsdatabanken 2021). The Brünnich guillemot is characterized as an arctic species, due its abundance increases with the northern latitudes (Tuck 1961; Spring 1971, Watanabe et al. 2016), but both species are

often breeding in the same colonies, and Brünnich guillemots on Hornøya in north-eastern Finnmark is the southernmost breeding colony in the Barents Sea.

During the non-breeding season, the two seabirds are known to be out *at sea*, gathering in large flocks, foraging (Steen et al. 2013), and although some distributional overlap occurs, some differences also appear. GLS-data of Barents Sea guillemots have revealed that Common guillemots non-breeding areas lies in the southern to central parts of the sea (Erikstad et al. 2018, Anker-Nilssen et al. 2019), whereas Brünnich guillemots have been found utilizing more north-eastern areas (Steen et al. 2013). Studies of diet and prey preference have indicated that Brünnich guillemot are more of a generalist, feeding on a variety of species – including pelagic schooling fish, squid, and different benthos and crustaceans, while Common guillemot have been suggested to be more of a specialist – being mainly piscivorous (Spring 1971, Gaston and Jones 1998, Smith and Clarke 2015). But whether they are competitor or utilizes different feeding niches during the non-breeding season is less known.

The non-breeding season is considered to be the main mortality period among seabirds (Reynolds et al. 2011), especially in winter, as climate conditions may be harsh and prey availability rather limited (Frederiksen et al. 2008, Smith and Gaston 2012). The contrasting trends seen in the Barents Sea Common and Brünnich guillemot populations may be related to the two species different non-breeding ecology, i.e., related to their foraging niches and conditions during their non-breeding distribution. But knowledge of their ability to handle environmental changes is scarce (e.g., SEATRACK??, Desprez et al. 2018; Merkel et al. 2021). The Barents Sea is considered to be of great importance for many seabird species (Steen et al. 2013), as it acts as an important nursery area for many fish species, and is therefore very rich in food (Eriksen et al. 2020). Thus, the Barents Sea is known to host some of the largest seabird colonies in the world (Erikstad 1990, Anker-Nilssen et al. 2000). However, in recent decades of climate change, the ongoing oceanic warming have been inducing distributional changes in water masses and plankton communities (Eriksen et al. 2017) and allowed boreal migrants to establish further north (Ingvaldsen and Gjørseter 2013, Fossheim et al. 2015, Eriksen et al. 2017), with the possibility to replace endemic prey species, enable new interactions, while disable others (Ozhigin et al. 2011, Johannesen et al. 2012, Fossheim et al. 2015, Frainer et al. 2017, Pecuchet et al. 2020).

Increasing our understanding of the non-breeding ecology, through the autumnal and winter distribution and diet of the two study species is therefore important in order to understand how they are linked to the marine environment and to gain knowledge of how they will cope with changes in relation to climate induced ecosystem change. The aim of this study was to investigate intra- and interspecific differences and/or similarities in Common and Brünnich guillemots non-breeding ecology, by comparing their non-breeding distributions and isotopic niches during autumn and winter. The questions in focus are: 1) Do the two species differ in isotopic niches and foraging locations during the non-breeding season? And how? 2) Under the assumption that the conditions in the Barents Sea are poorer during winter compared to autumn, how do the two species respond when conditions are poorer? This will be investigated by comparing the two species foraging distributions and isotopic niches in autumn and winter through the usage of GLS-data and stable isotope ratios of carbon and nitrogen in the birds' feathers, as both species moult and replenish their feathers annually during the non-breeding period. Such knowledge may shed some light upon the birds so far poorly known non-breeding ecology and dynamics, how they share/segregate their world, and might explain whether recent observed changes in the Barents Sea are affecting the birds differently.

2 METHODS

2.1 Study species

The two close-related seabird species, Common and Brünnich guillemot – in the Auk family, are broadly distributed on the Northern Hemisphere, both in Pacific, Atlantic and Arctic waters (Tuck 1961; Watanabe et al. 2016). However, Brünnich guillemots are regarded as more arctic species, due its abundance increases with the northern gradients (Tuck 1961; Spring 1971, Watanabe et al. 2016). With their black/dark brown- and white-coloured plumage, compact, streamlined body, and short limbs, the sympatric birds may – for the untrained eye – appear to be identical. Nonetheless, Brünnich guillemot is slightly smaller than its opponent, and have a shorter and thicker bill, with a white line along its upper mandible (Gaston and Jones 1998). This is morphological differences which may suggest adaptations to different prey preferences (Spring 1971). Stomach content and isotope analyses during breeding season has revealed that adult Common guillemot is mainly piscivorous, feeding on young year classes of cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and capelin (*Mallotus villosus*) (Bugge et al. 2011, Erikstad et al. 2013), whereas Brünnich guillemot are feeding on a variety of preys; including pelagic schooling fish, squid, different epi-benthos, amphipods, mysids, and euphausiids (Gaston and Bradstreet 1993, Hubson et al. 1994; Gaston and Jones 1998). Outside their breeding season, the birds spend most of the year at sea, foraging (Gaston and Jones 1998), often gathering in large flocks with birds from other colonies (Steen et al. 2013). Guillemots in the Barents Sea region have historically been found in central Barents Sea, however GLS-data of Common guillemots from Bjørnøya show that their non-breeding area lies in the southern to central parts of the Barents Sea (Erikstad et al. 2018, Anker-Nilssen et al. 2019), whereas Brünnich guillemots from Hornøya have been found utilizing north-eastern areas of the sea (Steen et al. 2013). Today, most knowledge on the birds non-breeding diet is solely based on stomach analyses, and early studies have found a strong relationship between the birds and capelin, both in pre-breeding season (Erikstad and Vader 1989) and in non-breeding season (Fauchald et al. 2000). However, in years after the capelin collapse in 1986/87, the Brünnich guillemot in the Central Bank of the Barents Sea were seen feeding on a wide variety of species, including: one year old cod and redfish (*Sebastes marinus*/*S. mentella*), and 1-4 years old polar cod (*Boreogadus saida*), in addition to crustaceans (Erikstad 1990).

2.2 Study area

Data sampling and fieldwork was carried out on Hornøya (70.39° N, 31.15° E), an island in the North-eastern Finnmark, Norway (Fig. 1). Hornøya hosts proximately 80 000 breeding birds a year, Common guillemot, Atlantic Puffin (*Fratercula arctica*), razorbill (*Alca torda*), black legged kittiwake (*Rissa tridactyla*), European shag (*Phalacrocorax aristotelis*), herring gull (*Larus argentatus*), great black-backed gull (*Larus marinus*), and Brünnich guillemot, are the most common species. On Hornøya, the Common guillemot population constitutes of 20 000 – 25 000 breeding pairs (T. Reiertsen unpublished data, Erikstad et al. 2013) and has the last decade (2009-2019) been increasing (Anker-Nilssen et al. 2019). Adult survival and population count of Brünnich guillemot, on the other hand, have not been conducted regularly since 2004. However, unpublished counts in 2013, and later impressions, is a decreasing population trend (T. Reiertsen unpublished data/pers. Comm.).

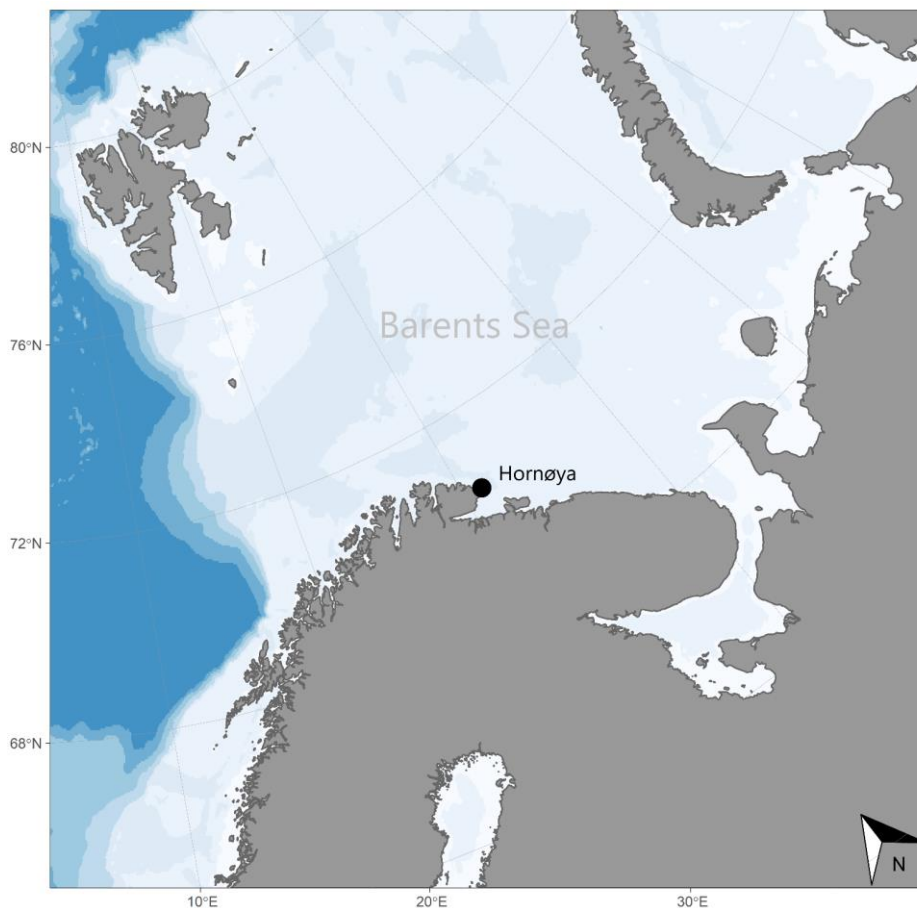


Figure 1. Geographic location of Hornøya (black dot) in southern the Barents Sea.

2.3 Data collection

All data collection followed description in the SEATRACK-protocol (2019) and was annually conducted during the birds breeding season (May to July) 2015, -16 and -17. Both Common and Brünnich guillemot were captured, using extendible poles with nylon snare, and all individuals in the study were random and, in most cases, opportunistically chosen in specific study plots. Thus, the sampling procedure changed depending on whether the birds were “new-capture” or “recaptures”. Newly-captured birds was given a metal ring with its unique number and a plastic ring with a letter code, measured for different biometrics (body mass, tarsus length, culmen length, head-bill-length, and wing length), taken a blood sample of 25 μ l (for sex-determination), equipped with a GLS-logger (on the plastic-ring on its leg, using plastic cable ties, self-adhesive tape, and glue), and, additionally, sampled for feathers from both body (reflecting autumn moult) and head/neck (reflecting winter moult) for isotopic analysing (SEATRACK 2019). Recaptured birds were only weight, sampled for feathers and reequipped with a new GLS-logger (SEATRACK 2019). A minimum of 10 feathers each from body and chin where sampled each time a GLS was retrieved from a bird, in order to compare the birds non-breeding distributions with feather stable isotopes from the same periods. The samples sent to a lab for analysing (SEATRACK 2019). As GLS-loggers may be retrieved several years after equipped, stable isotopes on those birds only represent resource utilization from the non-breeding season prior to retrieval, whereas geolocation data from the same bird might exceed over all three investigated non-breeding years. Furthermore, as feather samples were collected from all captured birds, some birds with stable isotopes might not have geolocation data at all. Thus, number of birds captured during breeding season is not available, however, number of seabirds included in this study that have GLS-data, stable isotope data, or both, in the specific non-breeding periods is listed in Table 1.

Table 1. Number of Common and Brünnich guillemot samples (stable isotope and GLS data) collected on Hornøya during breeding seasons 2014, 2015 and 2016, corresponding to non-breeding seasons 2014/2015, 2015/2016 and 2016/2017, respectively

Species	First non-breeding season, 2014/15 (Sample size, n)	Second non-breeding season, 2015/16 (Sample size, n)	Third non-breeding season, 2016/17 (Sample size, n)
Common guillemot	34	47	68
Brünnich guillemot	38	36	36

2.4 GLS-data: coordinate extraction, geolocation, and data analysis

Common and Brünnich guillemots were tracked using C250 (Migrate Technology Ltd, Cambridge, UK) and Mk3006 (Biotrack, now Lotek, Wareham, UK) GLS-loggers. These loggers measure light levels every minute and stores the maximum value within a 5 or 10-minutes interval, respectively (SEATRACK 2019). Locational accuracy and precision in such equipment varies over time and as a function of latitude, weather, and habitat (Merkel et al. 2016), however, the median value is estimated to be proximately ± 180 km (e.g., Phillips et al. 2004, Merkel et al. 2016).

After logger retrieval, raw light data were downloaded using BASTrack and IntegeorIF softwares for Mk3006 (Biotrack) and C250 (Migrate Tech), respectively (SEATRACK 2019). Subsequent data preparation and coordinate extraction, prior to data analysis was conducted at NINA Trondheim, in the statistical programming software in R v.4.1.0 (R Development Core Team 2021). Coordinate extraction from light-measurements is based on detection of twilight-events, for further determination of length of day or night (latitude), and timing of local midday or midnight (longitude). Twilight-events were determined using the *twilightCalc*-function in the R package *GeoLight*, while latitude and longitude were determined using the *coord*-function and a sun elevation angle ranging from -4.75° to -3° (Lisovski and Hahn 2013). All position estimates were smoothed twice, by running a 3-day mean, in order to improve position accuracy. Unrealistic observations, such as long-distance movements over short time, were filtered out. Additionally, as day length during equinox is more or less equal all around the globe, recordings 2-3 weeks post and prior to autumnal and vernal equinoxes (September 22nd – 23rd and March 20th – 21st) were filtered out to avoid high inaccuracy in latitudinal positions (Lisovski et al. 2012b).

In order to examine the birds geo-spatial foraging distribution in the Barents Sea region in combination with stable isotopes, two periods were defined to reflect the birds' foraging distribution during feather-regrowth: autumn: 11/08 – 07/09 and winter: 01/01 – 31/01. Thus, recordings outside these given seasons were filtered out, in addition to birds not located in the Barents Sea. As Common and Brünnich guillemots moult twice a year, their regrown and retrieved feathers used for stable isotope analyses contain chemical records of their resource utilization soon after moult (i.e., body feathers: September, head/throat feathers: January). Ideally, GLS-data defined to represent the birds foraging distribution during autumn should therefore be 01/09-30/09, but due to the latitude uncertainty during autumnal equinox, position registered from 07/09 – 21/10 were not available.

The bird's seasonal foraging distribution area (i.e., utilization distribution, UD) for the specific years was extracted using the function *kernelUD*, with least square cross validation (LSCV) smoothing and a 10 x 10 km grid, in the package *adehabitatHR* (Calenge 2006), and visualized in maps using the *basemap*-function in the *ggOceaanMaps*-package (Vihtakari 2022). A 50% kernel density contour was used to represent the species core distribution, for the specific seasons and years. The function *kernel.area* was used to estimate area of the 50% kernel, while the *kerneloverlap*-function was used to estimate degree of overlap between the different kernels, if present. Interspecific and seasonal overlap was investigated pairwise, by specifying the method *HR* (for HomeRange) to the overlap-function (Frieberg and Kochanny 2005). As in Reiertsen et al. 2021, overlap was characterized as: absent (< 3% or < 0.03), small (4-20% or 0.04-0.20), medium (21-50% or 0.21-0.5), or high (51-100% or 0.51-1). The function *st_centroid* in the *sf*-package (Pebesma 2018) was used to extract the kernels centre of gravity (i.e., group of interests' centroid position), while *distVincentySphere*, in the *geosphere*-package (Hijmans 2021), was used to calculate centroids distance to colony. Arctic Polar Stereographic projection were used when calculating area of kernels, overlap between kernels and centroids' distance to colony, while distribution in maps were displayed by reprojecting kernels back to WGS84 latitude and longitude coordinates.

2.3 Stable isotope-data: extraction, niche analysis, and statistics

After retrieval, the bird feathers were sent to different laboratories for stable isotope extraction; while the Common guillemot feathers was analysed at the University of Alaska Fairbanks, Brünnich guillemots' feathers were analysed at La Rochelle University in France.

Although the feathers were analysed at different places, the procedure was more or less the equal (see procedure in Will et al. in prep and Rendo et al. 2020). One whole head/throat feather and a half body feather were homogenized, weighed (each weight 0.2-0.6 mg), packed in tin boats and analysed in a continuous flow isotope ratio mass-spectrometer. All stable isotope values were expressed in delta notation (δ), in parts per mille (‰) and compared with international standards: $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = [(\text{R}_{\text{sample}} / \text{R}_{\text{standard}}) - 1] \times 1000$, where R is the ratio of $^{13}\text{C}:^{12}\text{C}$ or $^{15}\text{N}:^{14}\text{N}$, respectively (MEPS and Renedo et a. 2020). The standards used for carbon were the Vienna Pee Dee Belemnite (VPDB), and atmospheric N₂ (AIR) for nitrogen.

Isotopic niches were constructed and investigated following Jackson et al. (2011) descriptions in the vignettes “Introduction to SIBER”, “Ellipse Overlap” and “Comparing Populations” using standardized functions in the SIBER-package (Stable Isotope Bayesian Ellipses R). The package enables construction and fitting of ellipses to groups of data (stable isotope biplots), calculation of total and core niche area, potential overlap between ellipses, and maximum likelihood estimates, among other. Prior to data computation, birds with NAs and incomplete measurements were filtered out, as well as individuals detected, via GLS-data, being outside the Barents Sea region during the specific periods (i.e., autumn: 11/08 – 07/09, and winter: 01/01 – 31/01). As no birds were outside the Barents Sea in autumn, no birds were filtered out. However, during winter several birds (mostly Brünnich guillemot) were outside the Barents Sea, and these were excluded (Appendix, Table A4).

In order to conduct measurements and construct stable isotope biplots in SIBER, the groups of interest were addressed with respective names (“iso1”, “iso2”, “group”, “community”) in an exclusive data frame and transformed into SIBER-object, using the function *creatSiberObject*. Stable isotope biplots were created using the function *plotSiberObject*, where a list of plotting arguments was assigned and passed onward to the model (e.g., ellipses fitting 40% of data). The function *groupMetricsML* allowed computation of summary statistics (TA, SEA, and SEA_C, all expressed in per mille squared, ‰²) for each group displayed by the model. TA is the abbreviation of Total isotopic niche Area, which encircles, as the name implies, all the outermost values within a group or a community (Jackson et al. 2011) and can be interpreted as a measure of the investigated groups total diversity (Layman et al. 2007). However, as TA encompasses all the extremes measures, it is highly sensitive to

sample size and outliers (Layman et al. 2007), and since sample size in this study is highly varying (i.e., ranging from 17 to 61, see Appendix, Table A2), TA will not be discussed. SEA abbreviate Standard Ellipse Area, contains proximately 40% of the data, and thus represent the investigated groups core isotopic niche area (Jackson et al. 2011). SEA_C is SEA corrected for sample size and is considered to be robust for small sample sizes (i.e., 10-30 observations) and when assumption of multivariate normality is not met (Jackson et al. 2011). In this study, the SEA_C was used to quantify and display the species core isotopic niche area and width during the respective seasons and years, and to calculate the degree of overlap between groups core isotopic niches – if present.

When studying interspecific and seasonal differences, pairwise-overlap was used to determine the degree of ones SEA_C overlapping in another's SEA_C , following equation 1 below (modified to percent from the vignette “Comparing populations”). The value simply represents the percentage of ones SEA_C which are included in the overlap area between two ellipses, and thus the overlap needs to be calculated pairwise: first overlap in SEA_{C1} , and then in SEA_{C2} . As in the GLS-data, isotopic niche overlap was characterized as: absent (< 3% or < 0.03), small (4-20% or 0.04-0.20), medium (21-50% or 0.21-0.5), or high (51-100% or 0.51-1).

$$\% \text{ Overlap in } SEA_{C1 \text{ (or 2)}} = \frac{\text{Area of overlap}}{SEA_{C1 \text{ (or 2)}}} \times 100 \quad (1)$$

The uncertainty of core isotopic niche width in all groups was quantified with Bayesian statistics, where a probabilistic approach was used to describe the range of possible values (posterior distribution), the most likely mode (Bayesian standard ellipse area; SEA_B) and its following 50% credible intervals, based on 10 000 iteration sample chain using Gibbs Sampling technique (a Markov-Chain Monte Carlo, MCMC simulation). Prior to analysis, Bayesian multivariate normal distribution was fitted to each group in the data set, using software in the R-package *rjags*.(Plummer 2021). The prior distributions were specified into two list objects: *parms* and *priors*. *Parms* contained parameters defining how the sampling algorithms was to be ran, whereas *priors* contained information about prior distributions parameters which were to be estimated. Posterior estimates of the ellipses were extracted via *jags*-fitting using the SIBER-function *siberMVN* on the SIBER-object, together with *parms* and *priors*. Posterior distribution estimates were further used to calculate the SEA_B , using the

function *siberEllipses*. Value of credible intervals and SEA_B were extracted calling the *hdr*-function from the R-package *hdrcde*. Standard ellipse area was, additionally, compared between groups by calculating the probability of one group's posterior ellipse (SEA_B) being larger (or smaller) than another's, presented in %.

Finally, multivariate analysis of variance (MANOVA) was used to test for differences in the stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) relationship within and between species. A statistically significant MANOVA was further investigated univariately by running ANOVA to find whether $\delta^{13}C$ or $\delta^{15}N$ was “driving” the difference. Intraspecific comparisons were conducted seasonally (e.g., autumn vs. winter), whereas interspecific comparisons were conducted within specific seasons and non-breeding periods (e.g., Common guillemot autumn 2014 vs Brännich guillemot autumn 2014). Residual and Q-Q plots were used to explore homoscedasticity and normality assumptions, outliers, collinearity (i.e., $r > 0.9$), whereas the homogeneity of variance and covariance assumptions were explored by Leven's and Box's M tests, respectively, following the descriptions/procedure at DataNovia (2018). If the data did not display homogeneity of covariance, Pillai's test statistics were used instead of Wilks' in MANOVA, whereas Welch ANOVA was used as an alternative to the Classic ANOVA if homogeneity of variance was not assessed.

3 RESULTS

3.1 Interspecific differences

Autumn

Both species were distributed in central to eastern parts of the Barents Sea in the period of autumnal moult and feather regrowth (i.e., August to September), however Brünnich guillemots were distributed further away from the breeding colony, Hornøya, more north-eastern compared to Common guillemots (Fig. 2 – lower panels). In all three years of this study, Brünnich guillemots were found distributed two distinct areas, in addition that they have a more widely distribution than Common guillemot (Appendix, Table 1). Interspecific overlap between kernel utilization distributions (hereafter referred as kernel UD), fluctuated past the three years; from small overlap in 2014 ($\bar{x} = 10\%$, $HR_{CG} = 0.14$, $HR_{BG} = 0.05$), no overlap in 2015 (0%), to medium overlap in 2016 ($\bar{x} = 41\%$, $HR_{CG} = 0.55$, $HR_{BG} = 0.27$).

The core isotopic niches, represented by the standard ellipse areas corrected for sample size ($SEAC$, $\% ^2$), of Brünnich guillemots were in all three years positioned higher Common guillemots in the bivariate stable isotope plots (Fig. 2 – upper panels). No clear interspecific trends were found between $SEAC$, as Brünnich guillemots were larger in 2014 and 2015, while Common guillemots were largest in 2016 (Appendix, Table 2). Based on Bayesian iterations, there was a 93.6%, 100% and 99.5% probability that the Bayesian standard ellipse area ($SEAB$) display respectively similar pattern as $SEAC$. During all three years, the core isotopic niches were only found overlapping in 2015, with medium degree ($\bar{x} = 40\%$, $CG = 57\%$, $BG = 22\%$). Interspecific segregation between core isotopic niches were mainly seen by higher $\delta^{15}N$ values in Brünnich guillemot.

Stable isotope value ranges, means and standard deviations in Common and Brünnich guillemot, within the respective years and seasons, are given in Appendix, Table 2. Brünnich guillemot showed the widest range in $\delta^{13}C$, all years, and in $\delta^{15}N$, 2014 and 2015. Statistical multivariate significant difference between species were found in all years (Pillai $MANOVA_{2014}$: $F_{2, 45} = 40.142$, $p < 0.0001$; Pillai $MANOVA_{2015}$ $F_{2, 61} = 6.6322$, $p < 0.01$; Pillai $MANOVA_{2016}$: $F_{2, 79} = 71.508$, $p < 0.0001$). Univariately, $\delta^{15}N$ in Brünnich guillemot was found being significantly higher than Common guillemot in 2014 and 2015, whereas both $\delta^{13}C$ and $\delta^{15}N$ were higher in 2016 ($ANOVA_{2014}$: $\delta^{13}C$, $F_{1, 46} = 0.017$, $p > 0.05$; $\delta^{15}N$, $F_{1, 46} =$

47.3, $p < 0.0001$; Welch ANOVA₂₀₁₅: $\delta^{13}\text{C}$, $F_{1,23} = 0.07$, $p > 0.05$; $\delta^{15}\text{N}$, $F_{1,32} = 11$, $p < 0.05$; ANOVA₂₀₁₆: $\delta^{13}\text{C}$, $F_{1,80} = 12$, $p < 0.001$; $\delta^{15}\text{N}$, $F_{1,80} = 139$, $p < 0.0001$).

Winter

During winter moult and feather regrowth (i.e., January), core populations of both Common and Brünnich guillemot remained in the Barents Sea. However, one Common guillemot and several Brünnich guillemot individuals emigrated the sea prior to winter feather moult and did not return until late January/early February (Appendix, Table A3). As this study aimed at investigating the birds non-breeding ecology in the Barents Sea, these individuals were excluded from the study. Nonetheless, Brünnich guillemot were distributed further away from colony, more towards north-east than Common guillemot (Fig. 3 – lower panels). No clear interspecific trends were found between the two species distributions, as Common guillemot were more widely distributed than Brünnich guillemot in 2015 and 2017, while opposite in 2016 (Appendix, Table 1). However, in all three years, interspecific overlap between the species kernel UD_s was characterized as medium (2015: $\bar{x} = 40\%$, $\text{HR}_{\text{CG}} = 0.37$, $\text{HR}_{\text{BG}} = 0.43$; 2016: $\bar{x} = 38\%$, $\text{HR}_{\text{CG}} = 0.39$, $\text{HR}_{\text{BG}} = 0.37$; 2017: $\bar{x} = 49\%$, $\text{HR}_{\text{CG}} = 0.42$, $\text{HR}_{\text{BG}} = 0.55$)

Core isotopic niches of Brünnich guillemots were in all three years positioned above Common guillemots in the bivariate stable isotope plots (Fig. 3 – upper panels). No clear interspecific trends were seen between SEA_{C} , as Brünnich guillemots were slightly larger in 2015 and 2016, while Common guillemots were largest in 2017 (Appendix, Table 2). Based on Bayesian iterations, there was an 80%, 87% and 100% probability that the Bayesian standard ellipse area (SEA_{B}) display respectively similar pattern as SEA_{C} . Interspecific overlap between core isotopic niches were not found in either year. Separation between core isotopic niches were overall driven by Brünnich guillemots higher $\delta^{15}\text{N}$ values. In addition, $\delta^{13}\text{C}$ values of Brünnich guillemot were higher than Common guillemots in 2017, while lower in 2015.

Brünnich guillemot showed the widest range of $\delta^{13}\text{C}$ in 2015 and 2016, while Common guillemot showed the widest $\delta^{15}\text{N}$ range in 2016 and 2017 (Appendix, Table 2). Statistical multivariate significant difference between species were found in all years (Wilks MANOVA₂₀₁₅: $F_{2,45} = 40.14$, $p < 0.0001$; Pillai MANOVA₂₀₁₆: $F_{2,56} = 64.42$, $p < 0.0001$; Pillai MANOVA₂₀₁₇: $F_{2,75} = 39.66$, $p < 0.0001$). Univariately, $\delta^{15}\text{N}$ in Brünnich guillemot significantly higher than Common guillemot in all years, whereas $\delta^{13}\text{C}$ was significantly

lower the 2015, insignificant in the 2016, and significantly higher in the 2017 (ANOVA₂₀₁₅: $\delta^{13}\text{C}$, $F_{1,44} = 49.1$, $p < 0.0001$; $\delta^{15}\text{N}$, $F_{1,44} = 70.4$, $p < 0.0001$; ANOVA₂₀₁₆: $\delta^{13}\text{C}$, $F_{1,57} = 0.33$, $p > 0.05$; $\delta^{15}\text{N}$, $F_{1,57} = 125$, $p < 0.0001$; ANOVA₂₀₁₇: $\delta^{13}\text{C}$, $F_{1,76} = 15.2$, $p < 0.0001$; $\delta^{15}\text{N}$, $F_{1,76} = 58.9$, $p < 0.0001$).

3.2 Intraspecific differences

Common guillemot

During all three years, Common guillemots were distributed further from colony, more easternly, in autumn than the following winters (Fig. 4 – lower panels). No clear trends were found between Common guillemots seasonal utilization distributions, as the birds autumnal distribution were wider than the following winters in 2014/15 and 2016/17, while opposite in 2015/16 (Appendix, Table 1). Kernel UD were found overlapping between autumn and winter in all three years; from high in 2014/15 (2014/15: $\bar{x} = 59\%$, $\text{HR}_{\text{Autumn}} = 0.65$, $\text{HR}_{\text{Winter}} = 0.52$), to medium in 2015/16 and 2016/17 (2015/16: $\bar{x} = 36\%$, $\text{HR}_{\text{Autumn}} = 0.35$, $\text{HR}_{\text{Winter}} = 0.36$; 2016/17: $\bar{x} = 35\%$, $\text{HR}_{\text{Autumn}} = 0.43$, $\text{HR}_{\text{Winter}} = 0.27$).

Common guillemots core isotopic niches in winter were in all three years positioned above autumn in the bivariate stable isotope plots (Fig. 4 – upper panels). However, the species SEAC , were overall slightly larger in autumn than the following winter (Appendix, Table 2). Despite the small difference, there was a 98%, 100% and 81% probability that the Bayesian standard ellipse area (SEAB) display respectively similar pattern as SEAC . Based on Bayesian iterations. In neither of the years, overlap between Common guillemots seasonal core isotopic niches were found. The intraspecific separation between core isotopic niches were overall driven by Common guillemots higher $\delta^{15}\text{N}$ values in winter, and the lower $\delta^{13}\text{C}$ values in autumn 2014 and 2015.

The widest range in $\delta^{13}\text{C}$ were found in autumn 2014 and 2015, while the widest range in $\delta^{15}\text{N}$ were found in winter 2015 and 2017 (Appendix, Table 2). Statistical multivariate significant differences were found between Common guillemot in autumnal and winter all three years (Wilks MANOVA_{2014/15}: $F_{2,53} = 95.41$, $p < 0.0001$; Wilks MANOVA_{2015/16}: $F_{2,84} = 81.77$, $p < 0.0001$; Wilks MANOVA_{2016/17}: $F_{2,120} = 69.34$, $p < 0.0001$). Univariately, both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in winter were significantly higher than autumn in 2014/15 (Welch ANOVA: $\delta^{13}\text{C}$, $F_{1,41} = 133$, $p < 0.0001$; $\delta^{15}\text{N}$, $F_{1,54} = 108$, $p < 0.0001$). The same applies for in

2015/16, although $\delta^{15}\text{N}$ more than $\delta^{13}\text{C}$ (ANOVA: $\delta^{13}\text{C}$, $F_{1,85} = 49.7$, $p < 0.0001$; $\delta^{15}\text{N}$, $F_{1,85} = 145$, $p < 0.0001$). Whereas only $\delta^{15}\text{N}$ were found significantly higher in winter during 2016/17 (Welch ANOVA: $\delta^{13}\text{C}$, $F_{1,107} = 0.04$, $p > 0.05$; $\delta^{15}\text{N}$, $F_{1,114} = 138$, $p < 0.0001$).

Brünnich guillemot

Although Brünnich guillemot utilized two distinct areas during autumn, the autumnal distributions were overall located further away from colony, more north-easter, than the distribution in winters (Fig. 5 – lower panels). In all three years, the species were also more widely distributed in autumn compared to winter (Appendix, Table 1). However, seasonal overlap between kernel UDs fluctuated: from medium in 2014/15 ($\bar{x} = 34\%$, $\text{HR}_{\text{Autumn}} = 0.18$, $\text{HR}_{\text{Winter}} = 0.50$), to small in 2015/16 ($\bar{x} = 7\%$, $\text{HR}_{\text{Autumn}} = 0.05$, $\text{HR}_{\text{Winter}} = 0.09$), and back to medium in 2016/17 ($\bar{x} = 35\%$, $\text{HR}_{\text{Autumn}} = 0.26$, $\text{HR}_{\text{Winter}} = 0.44$).

In all three years, Brünnich guillemots core isotopic niche in winter were positioned above autumn in the bivariate stable isotope plots (Fig. 5 – upper panels). However, the species SEAC , were overall larger in autumn than the following winter (Appendix, Table 2). Based on Bayesian iterations, there was a 99%, 100% and 100% probability that the Bayesian standard ellipse area (SEAB) display respectively similar pattern as SEAC . In neither of the years, Brünnich guillemots seasonal core isotopic niches were found overlapping. The intraspecific separation between core isotopic niches were overall driven by Brünnich guillemots higher $\delta^{15}\text{N}$ values in winter, and the lower $\delta^{13}\text{C}$ values in autumn 2014 and 2015.

In all years, Brünnich guillemots widest range both in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were found in autumn (Appendix, Table 2). Furthermore, statistical multivariate significant differences were found between Brünnich guillemot in autumn and winter, throughout the entire study period (Pillai's $\text{MANOVA}_{2014/15}$: $F_{2,35} = 36.63$, $p < 0.001$; Wilks $\text{MANOVA}_{2015/16}$: $F_{2,33} = 64.113$, $p < 0.001$; Wilks $\text{MANOVA}_{2016/17}$: $F_{2,34} = 65.945$, $p < 0.001$). Univariately, both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was found significantly higher in winter 2014/15 and 2015/16, although $\delta^{15}\text{N}$ more than $\delta^{13}\text{C}$ in, whereas only $\delta^{15}\text{N}$ was higher in winter 2016/17 (ANOVA_{2014/15}: $\delta^{13}\text{C}$, $F_{1,36} = 5.14$, $p < 0.05$; $\delta^{15}\text{N}$, $F_{1,36} = 66.2$, $p < 0.0001$, Welch ANOVA_{2015/16}: $\delta^{13}\text{C}$, $F_{1,32} = 4.85$, $p < 0.05$; $\delta^{15}\text{N}$, $F_{1,31} = 135$, $p < 0.0001$, ANOVA_{2016/17}: $\delta^{13}\text{C}$, $F_{1,35} = 0.44$, $p > 0.05$; $\delta^{15}\text{N}$, $F_{1,35} = 58.9$, $p < 0.0001$).

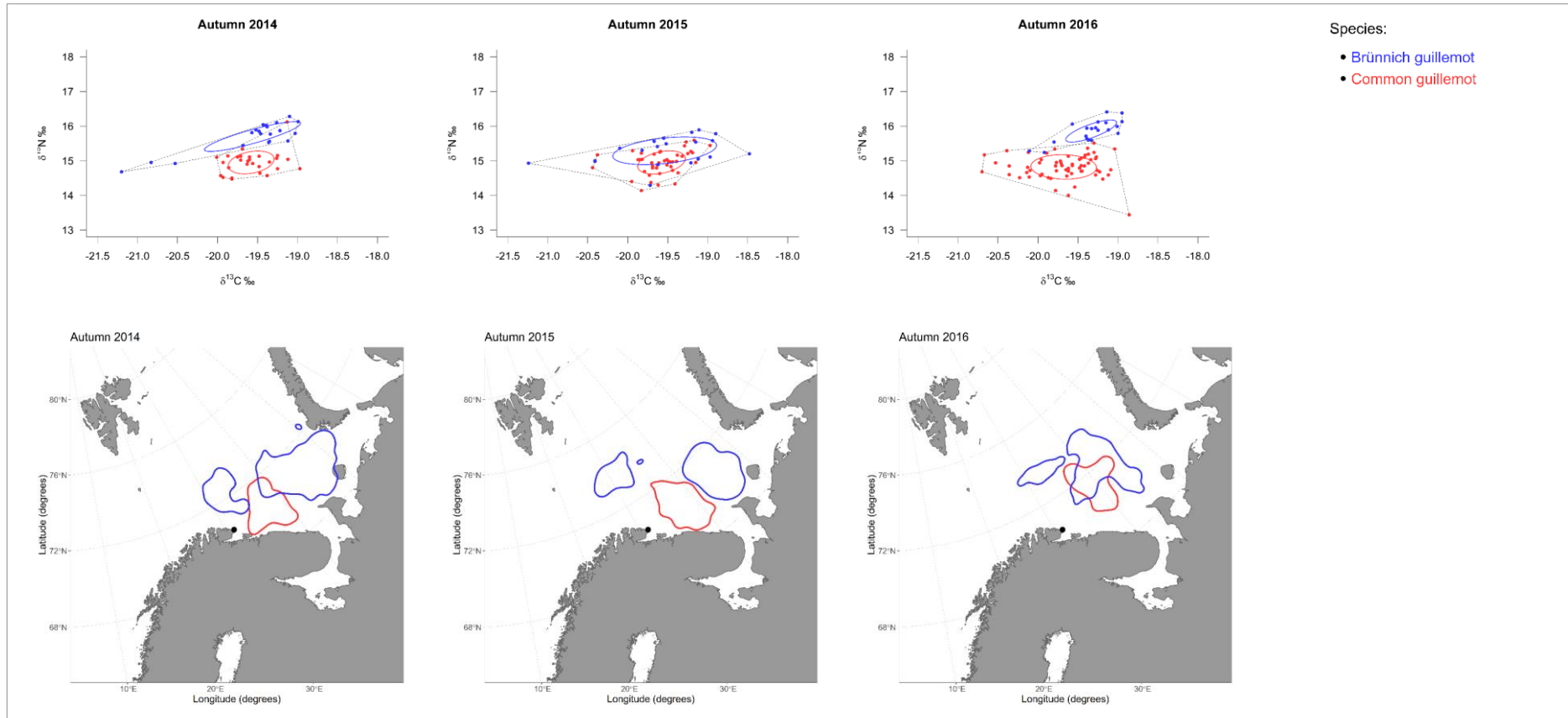


Figure 2. Common (Red) and Brünnich (blue) guillemots autumnal (August-September) isotopic niches (upper panels) and distribution (lower panels) in the years: 2014, 2015, and 2016. The bivariate stable isotope plots ($\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$) in the upper panels, with coloured standard ellipses corrected for sample size (SEAc , solid line) and associated convex hulls (TA, dashed lines), represent the birds autumnal core isotopic niches (includes approximately 40% of the data). The coloured contours in the lower panels represent the birds kernel Utilization Distribution (50% kernel contours), and black dot represent the birds' breeding colony, Hornøya.

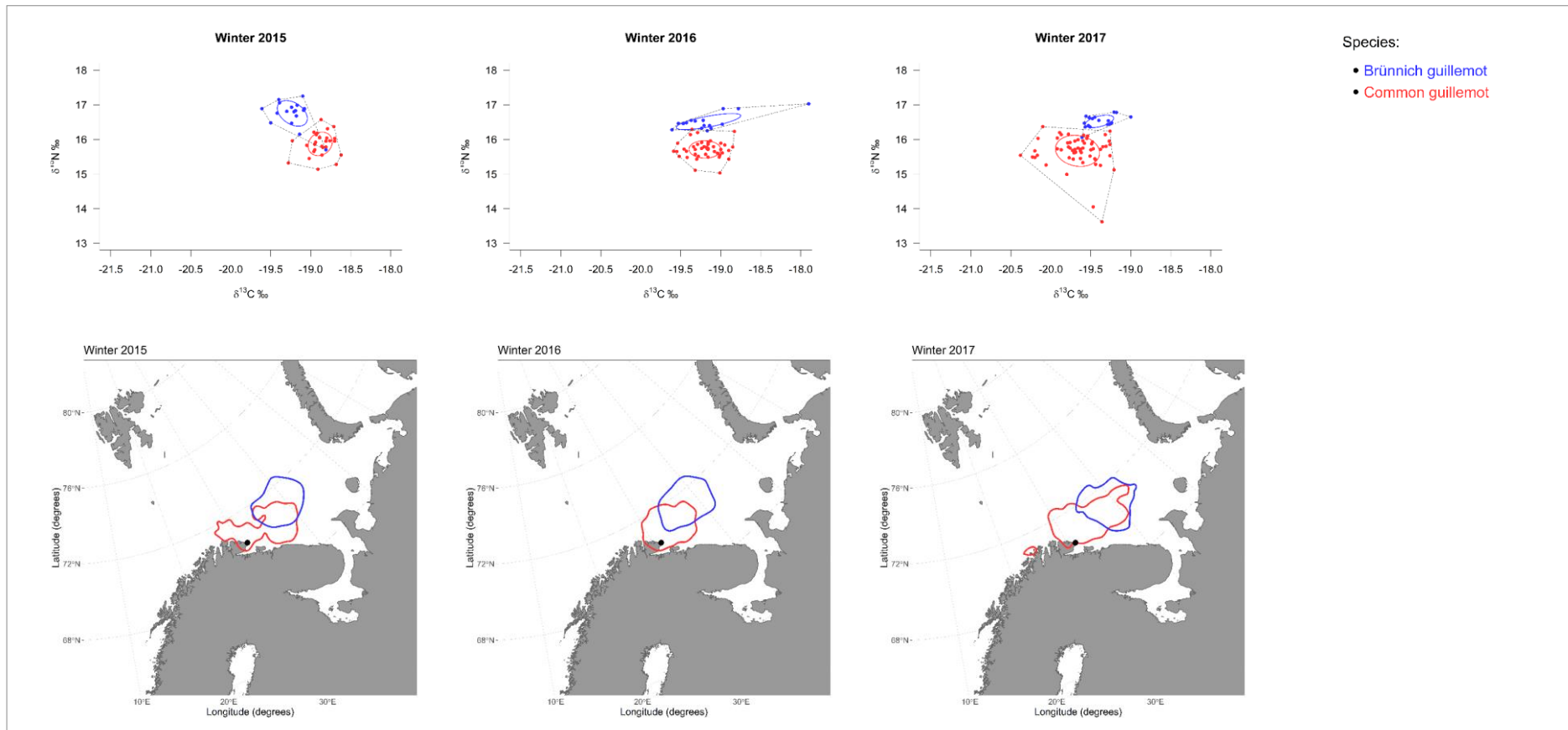


Figure 3. Common (Red) and Brünnich (blue) guillemots winter (January) isotopic niches (upper panels) and foraging distribution (lower panels) in the years: 2015, 2016, and 2017. The bivariate stable isotope plots ($\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$) in the upper panels, with coloured standard ellipses corrected for sample size (SEAC , solid line) and associated convex hulls (TA, dashed lines), represent the birds winter core isotopic niches (includes approximately 40% of the data). The coloured contours in the lower panels represent the birds kernel Utilization Distribution (50% kernel contours), and black dot represent the birds' breeding colony, Hornøya.

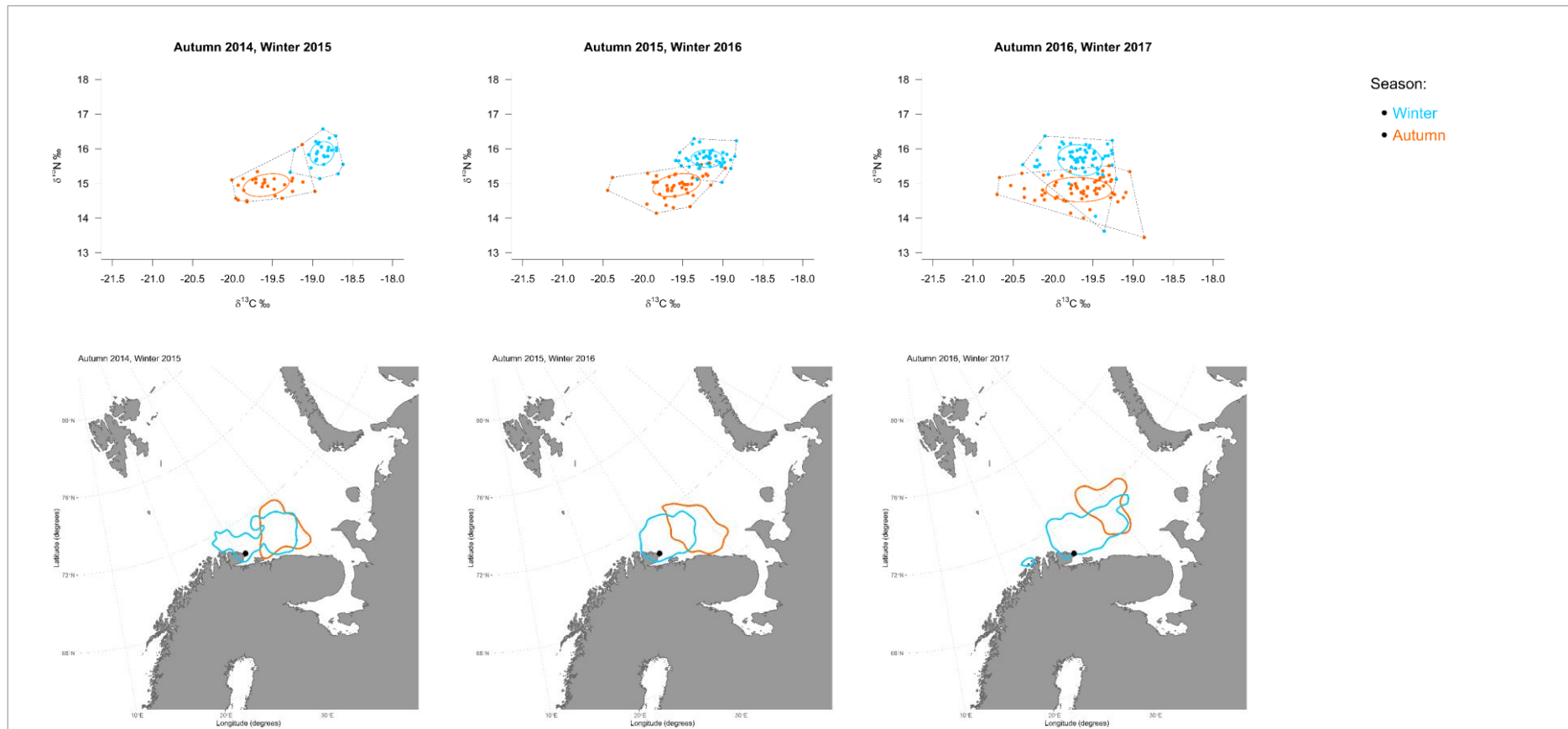


Figure 4. Common guillemots autumnal (August-September, orange) and winter (January, blue) isotopic niches (upper panels) and foraging distribution (lower panels) in first-, second-, and third non-breeding period, 2014/15, 2015/16, 2016/17 respectively. The bivariate stable isotope plots ($\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$) in the upper panels, with coloured standard ellipses corrected for sample size (SEAc, solid line) and associated convex hulls (TA, dashed lines), represent Common guillemots' seasonal core isotopic niches (includes approximately 40% of the data). The coloured contours in the lower panels represent Common guillemots seasonal kernel Utilization Distribution (50% kernel contours), and black dot represent the birds' breeding colony, Hornøya.

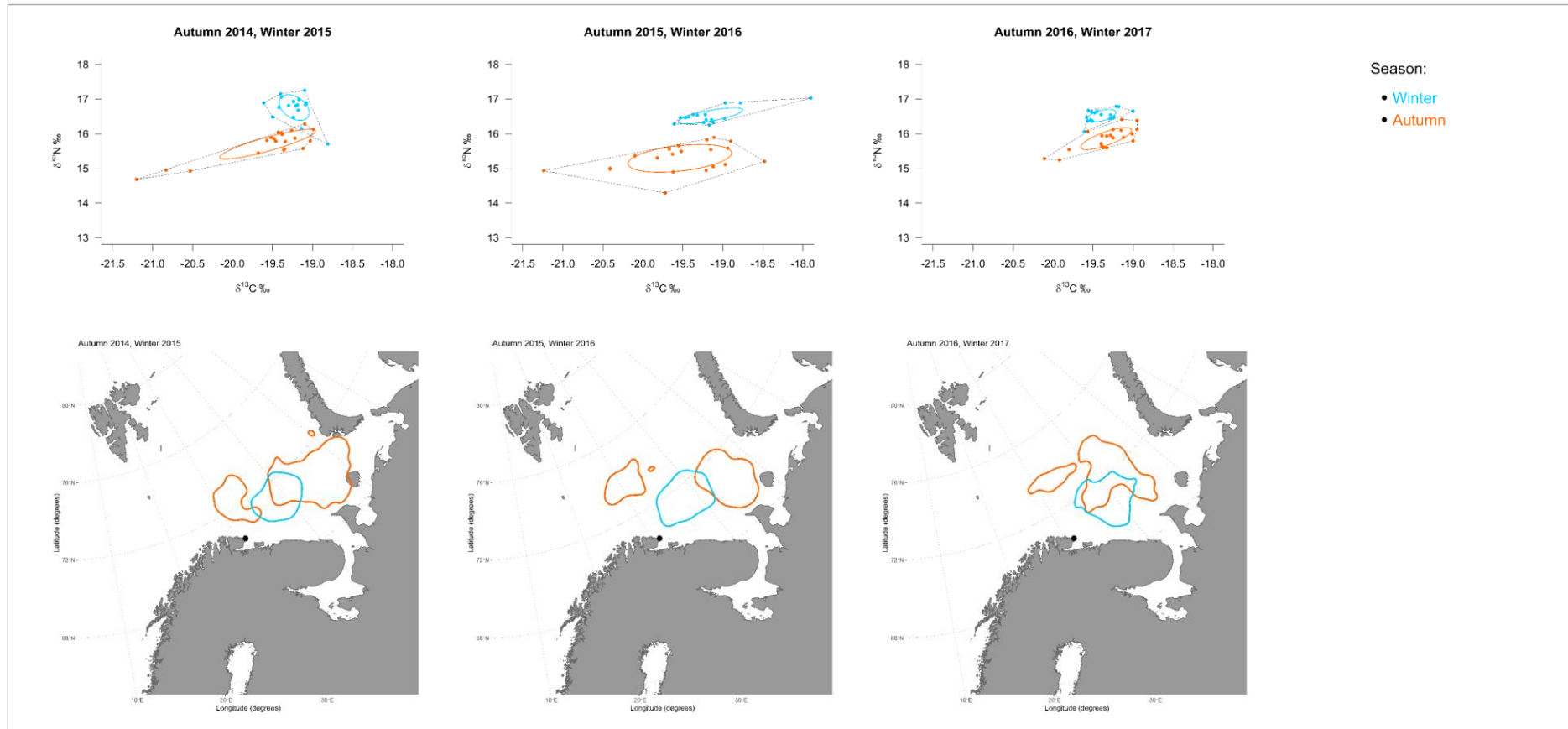


Figure 5. Brünnich guillemots autumnal (August-September, orange) and winter (January, blue) isotopic niches (upper panels) and foraging distribution (lower panels) in first-, second-, and third non-breeding period, 2014/15, 2015/16, 2016/17 respectively. The bivariate stable isotope plots ($\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$) in the upper panels, with coloured standard ellipses corrected for sample size (SEAC, solid line) and associated convex hulls (TA, dashed lines), represent Brünnich guillemots' seasonal core isotopic niches (includes approximately 40% of the data). The coloured contours in the lower panels represent Brünnich guillemots seasonal kernel Utilization Distribution (50% kernel contours), and black dot represent the birds' breeding colony, Hornøya.

4 DISCUSSION

This study found that when Common and Brünnich guillemots overlapped in distribution, they showed no overlap in isotopic niches, indicating that they segregate in feeding niches when utilizing the same areas. Additionally, both species isotopic niches reduced from autumn to winter, indicating that they feed on a less diverse diet. This may be either due to increased specialization in diet or because of reduced diversity in prey species in winter. The range of the distributional area of the two species differed from autumn to winter, showing an overall increase for the Common guillemots, while a reduction for the Brünnich guillemots. The increased distribution seen in Common guillemot, in combination with reduced isotopic niche might indicate a specialized habitat utilization during winter, a dynamic predicted to be seen in pursuing predators. Brünnich guillemots overall large foraging distribution and isotopic niche seen in autumn, might indicate a more generalized foraging strategy in autumn compared to the Common guillemots, while the reduction in both foraging distributions and isotopic niches from autumn to winter, might indicate a more specialized foraging strategy in winter. An alternative explanation for the change in pattern seen in the Brünnich guillemot is that they loose in competition for the same diet to the Common guillemots.

4.1 Competitive avoidance mechanisms?

During the three non-breeding years included in this study, both Common and Brünnich guillemots utilized central to eastern parts of the Barents Sea. However, the Brünnich guillemots were distributed further away from the breeding colony, more north-easterly compared to the Common guillemots (Fig. 2 and 3 – lower panel). This result support other studies that have also found that Brünnich guillemots migrate further away from the breeding colony compared the Common guillemots (Steen et al. 2013).

However, when Common and Brünnich guillemots overlapped in distribution, they showed no overlap in isotopic niches, indicating that they segregate in feeding niches when utilizing the same areas. These findings might in first-hand indicate interspecific competition or competitive avoidance for equal resource utilization through spatial segregation as stated as a hypothesis, but also that the species prefer to segregate their isotopic niches, thus their resources, over foraging distribution during the non-breeding season.

The strong isotopic niche segregation appears to be overall driven by differences in $\delta^{15}\text{N}$, as Brünnich guillemots had significantly higher $\delta^{15}\text{N}$ values than Common guillemot. However, the isotopic differences (ca. 0.70‰ in autumn and 0.80‰ in winter) seem to be of small ecological importance, as $\delta^{15}\text{N}$ vary with 3-4‰ between trophic levels. Nevertheless, significant differences may indicate different diet, although standardized values in Common and Brünnich guillemot in this ecosystem is not available to neither confirm nor deny general differences. However, such differences might also originate from spatial variations in the ecosystems baseline values (Casey and Post 2011). This may be likely in years where distributional overlap is small or absent (e.g., Autumn 2014 and 2015), while less likely when interspecific overlap is medium to high (e.g., Autumn 2016, Winter 2015, 2016, and 2017).

Moreover, $\delta^{13}\text{C}$, were only differing significantly in years where interspecific distributional overlap was great (Fig. 2 and 3, autumn 2016, and winter 2015 and 2017). $\delta^{13}\text{C}$ have in several ecological studies been found increasing with decreasing latitudes (Graham et al. 2010). However, this seems to be an unlikely reason for significant $\delta^{13}\text{C}$ between species in the respective periods, as distributional overlap was medium to high, and Brünnich guillemot were overall more northerly distributed, while having significantly higher $\delta^{13}\text{C}$ values than Common guillemot, in two of three periods where $\delta^{13}\text{C}$ were found being significantly different. During pre-breeding season, Common and Brünnich guillemot have been found partitioning their foraging habitat vertically, in addition to size of their prey items, when foraging in mixed flocks (Erikstad 1989). More specifically, both species were mainly found feeding on capelin, however, Common guillemots were exclusively feeding maturing females in the upper water masses, while Brünnich guillemot dove deeper, foraging on mature and spent males and females. As benthic food webs tend to be more enriched than pelagic food webs (Peterson and Fry 1987, Post 2002, Inger and Bearhop 2008, St. John Glew et al., 2018), differences in $\delta^{13}\text{C}$ might thus indicate that the species are segregating more vertically (benthic or pelagic) when overlap is great, while utilizing equal foraging habitat (coastal-benthic/pelagic, or offshore-benthic/pelagic) when distributional overlap is low, and either way differentiate in their dietary items.

Anatomical comparisons and underwater observations have described Common guillemots as having better manoeuvring abilities than Brünnich guillemots, while Brünnich guillemots better swimming capacity than Common guillemots (Spring 1971). Their different underwater

abilities have been attributed as possible explanations to different utilization of the water column, where Common guillemots exploit the pelagic water masses more effectively than Brünnich guillemots, while Brünnich guillemots utilizes the deeper water masses better than Common guillemots. However, as Common guillemots $\delta^{13}\text{C}$ values in winter 2015 were significantly greater than Brünnich guillemots', while opposite in autumn 2016 and winter 2017, might indicate that this vertical segregation is neither due to competitive avoidance mechanisms nor adaptive differences, but simply because of different prey preference, and their horizontal and vertical distribution in the water column. Of course, one cannot rule out the possibility that one species utilizes some area of the water column better than the other. This may have been an important mechanism for niche differentiation into co-existence, which today is displayed by i.e., different prey preferences during the non-breeding season. Hence, Common and Brünnich guillemots non-breeding foraging distribution and isotopic niches might overall be influenced by their preferred prey species abundance, distribution, and competition with other species.

4.2 Responses to seasonal variations in prey availability

The non-breeding season is regarded as a critical period, especially in winter, as climate conditions may be harsh and prey availability rather limited (Frederiksen et al. 2008, Smith and Gaston 2012). Both Common and Brünnich guillemot seems to respond to such conditions by shrinking their isotopic niche from autumn to winter, although Brünnich guillemot responded with a markedly different range compared to Common guillemot, who only displayed a slightly decrease. In general, one can assume that a reduction in niche happens due to good foraging conditions, though enabling them to specialize on preferred diet (Optimal foraging theory, MacArthur and Pianka 1966), or as a consequence of competition forcing them to limit their diet or a lesser prey diversity. However, as winter conditions in the Barents Sea are expected to be poor, it seems reasonable to believe that competition plays a role.

Interspecific overlap between distributions were annually stronger in autumn compared to winter, as medium degree overlap was found in all three study years. Under the assumption that climate condition is more extreme in winter, while prey availability limited (Frederiksen et al. 2008, Smith and Gaston 2012), one might assume that such distributional overlap would

be a driver to interspecific competition. However, as the species isotopic niches seems to become more segregated in winter compared to autumn, niche differentiation appears to exist.

Both Common and Brünnich guillemots' isotopic niches were found shrinking from autumn to winter, while only Brünnich guillemots foraging distributions displayed similar pattern. The exhibited isotopic niche reduction corresponds well with niche variation hypothesis, where it is predicted that species should reduce their intraspecific variation and become more specialized, when facing competition (van Valen 1965). However, the competitive aspect seems to have a greater effect on Brünnich guillemot compared to Common guillemot, who's isotopic niches only differed slightly between seasons. A decrease in both C- and N-ratio were seen from autumn to winter in Brünnich guillemot, while only the C-ratio reduced in Common guillemot (Appendix, Table 2). Brünnich guillemots foraging distributions and isotopic niches, which overall were greater than Common guillemot in autumn, became closer to Common guillemots in size (Appendix, Table 1 and 2). Thus, Brünnich guillemot seemingly change from having a generalized foraging strategy in autumn, to become more specialized in winter.

But, what are causing the substantial greater changes seen Brünnich guillemots foraging distribution and isotopic niches?

As Common guillemot is described as the expert in the pelagic water masses, while Brünnich guillemot demersally (Spring 1971), one possibility might be that Common guillemot indirectly outcompetes Brünnich guillemot by being the effective exploiter. However, this seems less likely, as important prey species usually goes further down in the water masses during winter, and thus Brünnich guillemot might be assumed to have the advantage.

The isotopic niche between autumn and winter segregated in both species. The segregation seems to be overall driven by differences in $\delta^{15}\text{N}$, as $\delta^{15}\text{N}$ was significantly higher in winter compared to autumn in all years. However, $\delta^{13}\text{C}$ in both species were significantly higher in winter 2014/15 and 2015/16 – where Common guillemots autumnal and winter distributions overlapped the most, and Brünnich guillemot the least. The significant $\delta^{13}\text{C}$ might thus indicate that both species change their foraging habitat during winter; Common guillemot more vertically – as distributional overlap was medium to high, while Brünnich guillemot more horizontally – as distributional overlap was small to medium. These findings seem to

match the assumption of more demersal foraging in winter, as Brünnich guillemot were overall found having a significantly higher $\delta^{13}\text{C}$ value in winter compared to Common guillemot, while both seems to become more carbon enriched from autumn to winter, although with different degree of distributional overlap between seasons.

The isotopic differences in $\delta^{15}\text{N}$ from autumn to winter (ca. 0.84‰ in Common guillemot and 0.98‰ in Brünnich guillemot), on the other hand, seem to be of small ecological importance, as $\delta^{15}\text{N}$ vary with 3-4‰ between trophic levels. Nevertheless, significant differences may indicate alteration in diet to larger/older species from autumn to winter, although standardized values in Common and Brünnich guillemot in this ecosystem is not available to neither confirm nor deny general differences. Capelin is considered to be an important food source for several seabird species in the Barents Sea, both inside and outside their breeding season (Barrett 1979, Furness and Barrett 1985, Erikstad and Vader 1989; Erikstad 1990). Common and Brünnich guillemots from Hornøya have in earlier studies been suggested following the migrational itinerary of capelin during non-breeding season (e.g., Barrett 1979, Brown 1985; Erikstad 1989, Steen et al. 2013), where the birds swims with the Atlantic water current, north-east, along the coast of Finnmark and Murmansk, into central parts of the Barents Sea, feeding on drifting capelin larvae, when leaving the colony in late summer/early autumn, while following the spawning migration of mature capelin from the northern Barents Sea, back to the Norwegian coast and Murmansk, in winter. Current study seems to have found such corresponding patterns in Common and Brünnich guillemots seasonal foraging areas, as both species autumnal distributions were located further away from colony, more east to northerly than in winter. These findings, in relation to both species significantly higher $\delta^{15}\text{N}$ values in winter, might thus be explained by a dietary alteration from fish larvae in autumn, to larger species in winter, near bottom. However, seasonal differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ might originate from both spatial and temporal variations in the ecosystems baseline values, as the species utilized different areas in varying degree between seasons (Casey and Post 2011). Indeed, both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ have been seen varying in time and space, due to several biotic and abiotic factors, such as primary production, plankton bloom, temperature, depth, salinity, upwellings, among other.

Climate warming and borealization of the Barents Sea might be another reason. Brünnich guillemots is characterized as a more Arctic species, due its abundance increases with the

northern latitudes. Consequently, it is also expected that Brünnich guillemot is more adapted for harsh and colder climate and will respond poorer to a warmer Barents Sea compared to Common guillemot. Whether these responses should display in as seen in winter in this study is hard to say, as the results are not seen in relation to environmental change. However, Brünnich guillemots from Hornøya is the southernmost Brünnich guillemot population in the Barents Sea. These individuals might be expected to live on the edge of its natural habitat, and thus the overall findings in this study might be more extreme compared to what more northerly populations would display.

Individuals facing high population density and increased resource competition are expected to migrate or distribute themselves more widely, in order to avoid resource depletion affecting their overall fitness (Svanbäck and Bolnik 2005, Kobler et al. 2009, Begon et al. 2014). During all three years of this study, Brünnich guillemots foraging distributions shrunk from autumn to winter. Superficially, a reduction in distribution in addition to niche seems to be likely in a situation where a highly preferred prey species aggregates in high densities. However, tracking data detected several Brünnich guillemot individuals outside the Barents Sea in the winter season (Appendix, Table A3). These individuals were found emigrating soon after autumnal feather regrowth and may thus indicate that prey conditions were constrained even before the winter set. Brünnich guillemots autumnal foraging distributions may further amplify these assumptions, as great and segregated area utilization is associated with low prey density (Svanbäck and Bolnik 2005, Kobler et al. 2009, Begon et al. 2014). This might be the reason why some Brünnich guillemot individuals emigrated the Barents Sea seen later-on in the non-breeding season. However, the withdrawn might have enabled better foraging conditions for the remaining population, as both isotopic niches and foraging distributions shrunk from autumn to winter, - findings which might indicate that the remaining population's density correspond with prey density. Common guillemot, on the other hand, seems to be more or less unaffected by the seasonal changes in the Barents Sea, as size of foraging distributions fluctuated annually; from winter being greatest in 2014/15 and 2016/17, to being smallest in 2015/16, while isotopic niches were only slightly larger in autumn. However, an increased foraging distribution in combination with niche reduction, may also indicate a more specialized habitat utilization, expected to be seen in a pursuing predator (MacArthur and Pianka 1966).

The migrating Brünnich guillemot individuals exhibited ca. 14-22% of the winter sample size in the GLS-data, and 10-16% in the stable isotope data (Appendix, Table A3 and A4). Thus, it may seem reasonable to assume that the number of migrating individuals makes up a large proportion of the total Brünnich guillemot population, and that emigration likely will lead to better conditions for the remaining individuals (although this was not tested). The way sampling was conducted in this study may therefore be problematic, as most individuals were opportunistically captured, usually at the edge of the flock. Thus, the trends we see here might not include the whole intra-variety of the Hornøya population, especially in the Brünnich guillemots, as they were captured from the bottom up.

4.3 Future implications

The different responses shown in Common and Brünnich guillemots' isotopic niches and foraging distributions in this study, suggest a three-dimensional avoidance mechanism for equal resource (i.e., utilization of foraging distribution, foraging habitat and diet). In years where distributional overlap is low or absence, the species segregate their diet, but not foraging habitat (i.e., either coastal -benthic/pelagic or offshore-benthic/pelagic). While in years with great distributional overlap, the species tend to segregate their foraging habitat, in addition to diet. Fluctuations in vertical habitat segregations, suggests that one species is not banned to be more benthic or pelagic than the other, but rather that the species follow their preferred prey species, which seems to differ between species. The species foraging distribution and resource utilization (i.e., isotopic niche), seems therefore to be overall affected by their prey species distribution, abundance, and dynamics with other species (e.g., competition).

The species responses to limitations in food conditions in the Barents Sea, under the assumption that food conditions are poorer during winter, compared to autumn, seems not to be interspecifically equal. While both species reduce their isotopic niches from autumn to winter, only Brünnich guillemot displayed similar pattern in its foraging distribution. Small size differences and fluctuations were seen between season in Common guillemots foraging distribution, however, the overall trends seem to be an increase from autumn to winter. Small size differences were also seen between seasons in Common guillemots isotopic niches. Thus, the overall findings suggest that Common guillemot exhibit small degree of seasonal change but might be characterized as more of a pursuing predator in winter. Brünnich guillemot, on

the other hand, seems to change from having a generalized foraging strategy in winter, to become more specialized. This specialization might exhibit due to several reasons, however, as Brünnich guillemot is characterized as more of an arctic species, winter conditions in the Barents Sea seems to suit the species well, and the bottoming of prey species seems also suitable regarding the species adaptations to the demersal habitat. The emigration conducted by some individuals prior to the winter season, possibly enabled better foraging conditions for the remaining individuals. On the other hand, it might also indicate that the autumnal conditions in the Barents Sea is less favourable. Brünnich guillemots generalized foraging strategy during autumn (i.e., great foraging distribution and isotopic niches), may reinforce the assumptions, as species facing low prey availability and poor conditions should respond by increasing the niches, according to optimal foraging theory.

Prey species abundance and distribution seems to affect both inter- and intraspecific dynamics in the species non-breeding distribution and niche. In relation to climate warming and the mass-distributional change seen in the Barents Sea ecosystem, might therefore cause inter-and intra-dynamical changes in the species non-breeding ecology. However, due to few years of data to detect any fluctuating trends, low sample size (Especially in Brünnich guillemot), and high interspecific differences in sample size (especially in the third non-breeding period), such findings are certainly not any certainty, and cautions need to be taken. Further studies should therefore focus on linking the relation to distributional data and isotopic niche data with resource and environmental data, in addition to year-round diving activity.

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APPENDIX

Table A1. Common and Brünnich guillemots kernel Utilization Distribution (km²), distance to colony (km) and number of IDs tracked during autumn and winter in the respective non-breeding periods: 2014/15, 2015/16, and 2016/17.

Tracking cycle	Period	Species	No. IDs tracked (n)	Kernel Utilization Distribution (km ²)	Distance to colony (km)
1					
Autumn 2014		Common guillemot	23	61 500	241
		Brünnich guillemot	34	175 800	430
Winter 2015		Common guillemot	23	76 600	137
		Brünnich guillemot	26	61 200	302
2					
Autumn 2015		Common guillemot	31	71 600	254
		Brünnich guillemot	30	123 000	396
Winter 2016		Common guillemot	29	69 900	111
		Brünnich guillemot	21	73 600	275
3					
Autumn 2016		Common guillemot	28	61 600	330
		Brünnich guillemot	35	127 200	397
Winter 2017		Common guillemot	28	97 500	155
		Brünnich guillemot	29	74 000	299

Table A2. Common and Brünnich guillemots stable isotope value range, with mean and standard deviation (2SD), total isotopic niche area (TA), standard ellipse area corrected for small sample size (SEAC), Bayesian standard ellipse area (SEAB), 50% Bayesian credible interval (50% CrI SEAB), and sample size (n) during autumn and winter in three non-breeding periods: 2014/15, 2015/16, and 2016/17. SEAB is a Bayesian point estimate of posterior distribution most plausible standard ellipse area (SEA, i.e., the posterior distributions most likely mode), while the credible interval represents the 50% most plausible value range of SEAB. The width of the credible interval indicates how confident we are in the point estimate (SEAB), and thus a narrow credible interval indicates more confidence than a wide. Stable isotope ratios, mean and standard deviation are expressed in per mille (‰), while TA, SEAC, SEAB and credible intervals are all in units of per mille squared (‰²).

Tracking cycle	Period	Species	n	$\delta^{13}\text{C}$ -range (mean \pm 2SD)	$\delta^{15}\text{N}$ -range (mean \pm 2SD)	TA (‰ ²)	SEAC (‰ ²)	SEAB (‰ ²)	50% CrI SEAB (‰ ²)
1									
Autumn 2014	Common guillemot	28	-20.01 – -18.97 (-19.58 \pm 0.56)	14.47 – 16.12 (14.95 \pm 0.66)	1.03	0.29	0.27	0.24 – 0.31	
	Brünnich guillemot	20	-21.20 – -18.99 (-19.56 \pm 1.18)	14.68 – 16.28 (15.70 \pm 0.86)	0.84	0.40	0.43	0.36– 0.49	
Winter 2015	Common guillemot	28	-19.28 – -18.62 (-18.88 \pm 0.30)	15.14 – 16.57 (15.87 \pm 0.68)	0.65	0.16	0.15	0.13 – 0.17	
	Brünnich guillemot	18	-19.61 – -18.81 (-19.23 \pm 0.38)	15.70 – 17.25 (16.75 \pm 0.74)	0.57	0.21	0.19	0.16 – 0.22	
2									
Autumn 2015	Common guillemot	44	-20.44 – -18.97 (-19.58 \pm 0.58)	14.14 – 15.59 (14.95 \pm 0.66)	1.27	0.30	0.29	0.26 – 0.32	
	Brünnich guillemot	20	-21.24 – -18.48 (-19.54 \pm 1.28)	14.29 – 15.89 (15.29 \pm 0.80)	2.16	0.78	0.72	0.61 – 0.84	
Winter 2016	Common guillemot	43	-19.59 – -18.83 (-19.20 \pm 0.40)	15.03 – 16.29 (15.71 \pm 0.50)	0.70	0.16	0.15	0.14 – 0.17	
	Brünnich guillemot	16	-19.61 – -17.90 (-19.15 \pm 0.80)	16.25 – 17.03 (16.52 \pm 0.46)	0.51	0.21	0.20	0.17 – 0.24	
3									
Autumn 2016	Common guillemot	62	-20.70 – -18.86 (-19.68 \pm 0.42)	13.44 – 15.51 (14.82 \pm 0.70)	2.23	0.45	0.44	0.40 – 0.48	
	Brünnich guillemot	20	-20.11 – -18.95 (-19.34 \pm 0.62)	15.24 – 16.41 (15.86 \pm 0.64)	0.59	0.21	0.20	0.18 – 0.24	
Winter 2017	Common guillemot	61	-20.38 – -19.21 (-19.67 \pm 0.54)	13.62 – 16.37 (15.67 \pm 0.90)	1.92	0.39	0.37	0.34 – 0.41	
	Brünnich guillemot	17	-19.61 – -19.00 (-19.39 \pm 0.36)	16.06 – 16.79 (16.52 \pm 0.36)	0.21	0.09	0.08	0.07 – 0.10	

Table A3. Number of individuals detected outside the Barents Sea during non-breeding season in the GLS-data

Season	Year	CG	BG
Fall			
	2014	0	0
	2015	0	0
	2016	0	0
Winter			
	2015	0	7
	2016	1	6
	2017	0	5

Table A4. Number of individuals detected outside the Barents Sea during non-breeding season in the stable isotope data

Season	Year	CG	BG
Fall			
	2014	0	0
	2015	0	0
	2016	0	0
Winter			
	2015	0	2
	2016	0	3
	2017	0	3

