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Repeatability in isotopic signatures is linked to consistent individual migration strategies and individual specialization in a long-distance migratory seabird

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Abstract

Animal populations can consist of specialized individuals with different foraging strategies. There could be several advantages for specialized individuals, such as higher foraging efficiency, breeding success and survival. Individuals may follow the same foraging strategies over several years, showing a high foraging consistency. In this seven-year study, we investigated the variation of foraging ecology in individuals of the Arctic skua (*Stercorarius parasiticus*) wintering in six different areas. We analyzed stable isotopes of nitrogen and carbon ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) in feathers to define their isotopic niche during winter which indicates their ecological niche. Combining stable isotope analyses with migration tracks from light-level loggers (Global Location Sensing loggers) of 58 individuals in three breeding colonies in Svalbard and Northern Norway from 2010 to 2016, we describe variation in foraging ecology between wintering areas, among individuals and within individuals among years. The core of the study design is therefore repeated sampling of feathers and tracking of the same individuals across several years. Individuals wintered in one of six areas; Benguela current, Caribbean, Canary current, Falkland current, Gulf of Guinea and Mediterranean, and displayed consistent migration strategies across years. Isotopic niche differed among the six wintering areas and differed also among individuals within wintering areas. The high individual repeatability for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, after controlling for wintering area, indicates consistent individual foraging strategies and a high level of specialization. This study is one of few that shows consistency in the winter foraging ecology in seabirds. The individual consistency in foraging ecology of Arctic skuas raises the question if birds are able to adapt their feeding behavior to changes in forage distribution due to climate change.

KEY WORDS: Individual consistency · Stable isotopes · *Stercorarius parasiticus* · Foraging specialization · Niche variation · ICC · Isotopic niche

Sammendrag

Dyrepopulasjoner kan bestå av spesialiserte individ med forskjellige fôringsstrategier. Det kan være flere fordeler for spesialisering, blant annet høyere fôringseffektivitet, reproduksjonssuksess og økt overlevelse. Individ kan følge de samme fôringsstrategiene over flere år, og vil dermed ha en høy grad av fôringskonsistens. I dette sjuårige studiet har vi undersøkt variasjonen i fôringsøkologien hos individ av tyvjo (*Stercorarius parasiticus*) som overvintret i seks forskjellige områder. Vi har analysert stabile isotoper av nitrogen og karbon ($\delta^{15}\text{N}$ og $\delta^{13}\text{C}$) i fjær for å bestemme fuglenes isotopiske nisje om vinteren, som er en indikasjon på deres økologiske nisje. Ved å kombinere analyser av stabile isotoper med migrasjonsruter fra lysloggere ('Global Location Sensing loggers') hos 58 individ fra tre forskjellige hekkekolonier på Svalbard og i Nord-Norge mellom 2010 til 2016, beskriver vi variasjon i fôringsøkologi mellom vinterområder, mellom individ og innad individ mellom år. Kjernen i dette studiet er dermed gjentakende prøvetakninger av fjær og sporing av de samme individene over flere år. Individ overvintret i et av seks områder; Benguelastrømmen, Karibien, Kanaristrømmen, Falklandstrømmen, Guineabukta og Middelhavet, og viste konsistente migrasjonsstrategier over år. Isotopisk nisje varierte mellom de seks vinterområdene, og det var i tillegg variasjoner mellom individ i samme vinterområder. Den høye individuelle repeterbarheten for både $\delta^{15}\text{N}$ og $\delta^{13}\text{C}$, etter å ha kontrollert for effekter av vinterområdene, indikerer konsistente individuelle fôringsstrategier om vinteren og et høyt nivå av spesialisering. Dette studiet er et av få som viser konsistens i fôringsøkologien på vinteren hos sjøfugl. Den høye graden av spesialisering vist i fuglene reiser spørsmål om deres evne til å tilpasse seg fremtidige miljøforandringer.

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Introduction

According to optimal foraging theory, animals will maximize energy intake while minimizing time spent foraging and thus energy output (Schoener 1971; Zach 1979). To optimize foraging strategies, several species have evolved individual foraging specializations resulting in individuals exploiting different niches. Many populations are composed of individuals using different subsets of the available resources (Roughgarden 1972). When these differences are seen among individuals of the same sex or age class, the individual-level variation is called “individual specialization” (Bolnick et al. 2003; Araujo et al. 2007). Individual specialization in communities can be a mean to avoid competition and may also increase foraging efficiency for specialized individuals (Bolnick et al. 2003). To detect individual specialization, it is common to compare the amount of variation within and among individuals. The ratio between these two sources of variation, also known as intraclass correlation coefficient (ICC), is a measure of individual repeatability. A high ICC value means low within-individual variance compared to the among-individual variance (Nakagawa & Schielzeth 2010; Wolak et al. 2012; Carneiro et al. 2017).

Animals can show consistency in foraging strategies, following the same strategies over several years. By analyzing stable isotope ratios in tissue collected over years, it is possible to provide information of animals’ long-term foraging ecology (Dalerum & Angerbjörn 2005). Variation in isotope ratios among individuals or over years can thus be interpreted as diet variation (Araujo et al. 2007). The isotopic data can be used to calculate the isotopic niche which is closely correlated with the ecological niche of animals (Newsome et al. 2007). Stable isotope analyses can therefore yield quantitative information on resource use and width, since consumers feeding on resources with greater differences in isotopic values will have a broader isotopic niche. The term ‘niche width’ refers to the variety of resources a population exploit (Roughgarden 1972).

Stable isotopes of nitrogen and carbon from consumer tissue can be used to detect trophic level and foraging habitat of consumers during tissue formation (Hobson 1990; Hobson et al. 1994; Cherel et al. 2000; Phillips et al. 2009). For birds, this can be used to investigate their foraging ecology while molting of feathers occur (Mizutani et al. 1990). Stable isotope ratios of nitrogen indicate trophic level while stable isotope ratios of carbon indicate primary source in the food web (Hobson & Clark 1992; Bearhop et al. 2004). In addition, the carbon and

nitrogen stable isotope ratios can vary spatially at the base of food webs, in so called isoscapes, and can thus give an indication of geographical foraging areas (Graham et al. 2010).

Understanding the spatial and temporal variation in abundance of animals is an important factor in ecology. Many seabirds experience a shift in food resources and travel long distances to more productive areas between seasons to take advantage of the abundance in resources (Dingle 1996). Pelagic seabirds perform some of the world's most extensive journeys among species, where longer travels are more common in seabirds breeding at higher latitudes (Egevang et al. 2010; Newton 2010). Migration can be interpreted as an adaptation to seasonal changes in habitat quality, where individuals or populations move between areas as resources become available (Dingle & Drake 2007).

Traditionally, information about the spatial movements and foraging ecology of seabirds in wintering areas were based on ship-based observations and ringing recoveries, which have substantial drawbacks and biases due to variability in reporting rates (Wernham et al. 2002). In the last years, more sophisticated methods have become available, with the use of tracking devices (e.g. geolocators) and environmental tracers ('biomarkers', such as stable isotopes) (Cherel et al. 2000). The use of geolocators (Global Location Sensing or GLS loggers) have increased the insight of migratory routes and wintering areas of several species (Phillips et al. 2004; Lisovski et al. 2012). This method also allows monitoring of consistency or flexibility in migration routes taken by individual birds, because individual differences in movement patterns within populations can be detected (Phillips et al. 2005).

Information of the spatial movement and foraging ecology of seabirds can reflect environmental conditions. Seabirds are top marine predators, and therefore good ecological indicators of changes in the marine ecosystems (Furness & Monaghan 1987; Furness & Camphuysen 1997; Gremillet & Boulinier 2009). Consequently, monitoring of seabirds is important to understand the rapid changes in the environment due to climate change and disappearance of prey due to pollution, habitat destruction and over-exploiting of resources (Grémillet & Boulinier 2009), as changes in diet and spatial distribution can be an indicator of change in environment (Montevecchi 1988). Highly specialized individuals may face challenges in a changing environment, as their feeding behavior may be less adaptable to changes in food resources. Data collected repeatedly over time, give the possibility to assess the flexibility of individuals of long-lived species, and if, and how, these individuals can modify their feeding strategies to cope with the environmental changes (Camprasse et al.

2017). This can give important insights into the ecology of the species and help taking management decisions (Wakefield et al. 2015; Carneiro et al. 2017).

Many studies of seabirds have been undertaken during the breeding season when the birds are commuting between feeding grounds and the nest, behaving as central place foragers (Barrett et al. 2007). However, far less is known about their foraging ecology in the wintering areas. This period is critical for birds to regain their body condition before the next breeding season (Barbraud & Weimerskirch 2003) as different phases in migratory species are codependent and may have carry-over effects important for the ecology, evolution and conservation of the species (Fretwell 1972; Gill et al. 2001; Bogdanova et al. 2017).

Few studies of the foraging ecology of seabirds comprise repeated sampling of the same individuals over several years. In this study, we combine data from geolocators with stable isotopes analyzed from feathers collected over a period of seven years with several individuals repeatedly sampled. This provides the possibility to detect where the birds are wintering and gathers information about their foraging ecology in the wintering areas. We investigate differences in the isotopic niche between individuals of Arctic skuas (*Stercorarius parasiticus*) wintering in six different areas, and how the foraging ecology varies among individuals within the same region. We also test whether individuals show a consistent or flexible foraging strategy over years, and if this might be linked to individual consistency in migration strategies.

Methods

Study species

The Arctic Skua (*Stercorarius parasiticus*) is a migratory seabird that weighs 350-600 grams and has a reversed sexual-size dimorphism where females are slightly larger than males (Furness 1987). They are monogamous and both sexes incubate and defend the nest and chicks. They rely on kleptoparasitism to obtain their food, but can also show a predatory and self-foraging behavior (Furness 1987). The Arctic skua are polymorphic, with pale, dark and intermediate phenotypes. They have a circumpolar breeding distribution (Furness 1987). After breeding, they migrate to various areas in the Atlantic Ocean and the Mediterranean Sea (figure 1). They show a high site-fidelity, where individuals are shown to return to the same

breeding territories and wintering areas year after year (Skottene 2015). The breeding populations migrate to several wintering areas, where individuals of the same population, and even of the same breeding pair, can over-winter in different regions.

Study Sites and Sample Collection

We captured adult Arctic Skuas in June and July during the breeding season, from 2010 to 2016 in Kongsfjorden, Svalbard (78° 94' N, 12° 26' E), from 2011 to 2016 at Brensholmen, Norway (69° 60' N, 18° 04' E), and 2014 to 2016 in Slettnes, Norway (71° 08' N, 28° 21' E) (figure 1), as a part of an ongoing study by Norwegian Institute for Nature Research (NINA).

We captured birds of both sexes on the nest while incubating using a remote-controlled bownet or snare trap, or in the air with a handheld net gun. We ringed all birds with a plastic and metal leg ring engraved with a unique code. We weighed birds to the nearest 1g using a hand-held scale and we measured tarsus length and head-bill length with a caliper to the nearest mm. We measured wing length and inner and outer central tail feathers with a metal ruler to the nearest 5mm. We sampled one to six back feathers which were kept dry in sealed plastic bags after sampling. We also sampled 1-2 mL blood from the branchial vein. The blood samples were preserved in ethanol upon returning from the field each day. We sexed all individuals by molecular methods as described in Fridolfsson & Ellegren (1999).

We collected geolocator data-loggers from birds equipped between 2010 and 2015 and deployed new geolocators on both previously captured and new individuals by mounting the geolocators with cable ties and glue on a plastic leg ring. Five different geolocator models were used, dependent on sampling year (Mk18h, Mk9 and Mk15, British Antarctic Survey, Cambridge, UK; Mk3006, Biotrack, Cambridge, UK; c250, Migrate Technology, Cambridge, UK). The geolocators weighted 2.5 gram. With the cable ties and the plastic rings the weight in total was 5 g, corresponding to 0.8 to 1.4% of the birds' body mass, which is well below the recommended threshold of 3% of body mass (Phillips et al. 2003; Wakefield et al. 2009).

We collected data from a total of 58 individuals during the years at all three locations, of which 37 individuals were sampled more than one year during the period 2010-2016 (1 year: N = 21, 2 years: N = 18, 3 years: N = 11, 4 years: N = 7, 5 years: N = 1) (table A-5). Total

number of samples were $N = 123$ (with $N = 77$ from Kongsfjorden, $N = 23$ from Brensholmen and $N = 23$ from Slettnes).

Stable Isotope Analyses

The stable isotope ratio in feathers represents the birds foraging ecology at the time the feathers are grown, since keratin is metabolically inert after synthesis (Hobson 1999; Bearhop et al. 2004; Camprasse et al. 2017). Molting of back feathers in the Arctic Skua is proved to happen in the wintering area before spring migration (van Bemmelen, unpublished data), and will thus reflect the foraging ecology of the bird in this period. The ratio of ^{15}N to ^{14}N ($\delta^{15}\text{N}$) generally increase with 2.5‰ to 5‰ for each trophic level (Hobson & Clark 1992; Bearhop et al. 2004). There is also an increase in the ratio of ^{13}C to ^{12}C ($\delta^{13}\text{C}$) with trophic levels, but only in the order of 1‰ (Hobson & Clark 1992).

We cleaned feathers prior to analyses in a solution of 2:1 chloroform:methanol, and then rinsed them twice in a methanol solution. The feathers were dried in a heating cabinet at 45°C for 48 hours before we homogenized one to three feathers from each individual with stainless steel scissors. We then loaded ~0.5 mg subsamples into tin cups for analyses in an elemental analyzer (Flash EA 1112, Thermo Fisher) coupled in continuous flow mode to an isotope ratio mass spectrometer (Delta V Advantage, Thermo Fisher, Bremen, Germany). Analyses were performed at the Littoral Environnement et Sociétés laboratory (LIENSs, La Rochelle, France). Isotope ratios are expressed in δ values in ppt (‰) according to the following equation:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000 \quad (1)$$

where X is ^{13}C or ^{15}N and R are the corresponding ratios of $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. R_{standard} values for ^{15}N are based on atmospheric N_2 , and R_{standard} values for ^{13}C are based on the Vienna Pee Dee Belemnite (VPDB). To ensure accuracy of measurements, an internal laboratory standard (acetanilide) was run every 10 samples.

Spatial Analyses

Migration data from geolocators were analyzed by Rob van Bemmelen at the University of Wageningen, The Netherlands, following methods outlined in van Bemmelen et al. (2017). Geolocators record ambient light, and locations are estimated by time of sunrise and sunset, where longitude is estimated by time of midday and midnight with respect to Greenwich Mean Time and Julian day, and latitude are estimated by day- and night-length. The accuracy of the estimated position is about 185 km (Phillips et al. 2004), and is therefore ideal for large-scale movement monitoring. For the 58 individuals, 113 migration tracks were obtained (figure 1). Of these, 9 tracks were incomplete. The data were downloaded from the geolocators and decompressed using BASTrack (British Antarctic Survey) or IntigeoIF software (Migrate technology), and analyzed in R 3.4.0 (R Development Core Team 2017), using the R package ‘GeoLight’ (Lisovski et al. 2012). Sunset and sunrise were calculated from light measurements using the function ‘twilightCalc’ with specific light threshold values for each logger model. Unlikely twilight events were removed. Locations at noon and midnight were calculated for each day. Positions within 14 days from either side of the equinoxes (20 March and 22 September) were removed due to large errors in the estimation of the latitude at this time. Remaining positions were estimated using a 3-day smoothing equation from Gilg et al. (2013), giving one averaged position per day.

A Lambert azimuthal equal-area projection was used to determine the 75% utilization kernel density distribution of the wintering home area, based on position estimates from January. Based on the centroid of positions in January, individuals were categorized into one of the following areas: Caribbean (Ca), Falkland Current (FC), Benguela Current (BC), Gulf of Guinea (GG), Canary Current (CC) or Mediterranean (Me) (table A-6). As Arctic skuas show a high site fidelity by returning to the same wintering area every year (Skottene 2015), tracking data from one year are enough to determine wintering area for each individual.

Statistical analyses

To investigate how stable isotope ratios vary between wintering areas, we used linear mixed effects models (LMMs) with the R package “lmer” (Bates et al. 2014). To control for pseudo-replication issues due to the resampling of some birds in multiple years, we included bird ID as a random effect. The global model included the following fixed effects: wintering area, breeding colony, sex and wing length. Wintering area were included to test for the effect of

area on stable isotope ratios, because they are expected to vary between regions due to differences in stable isotope baseline. Breeding colony was included to test for possible effects of breeding area because colonies in Svalbard and mainland Norway show slightly different territorial and feeding behavior, which could have possible carry-over effects for the feeding ecology in the wintering area. Sex was included to test for possible differences between sexes, while wing length was included as an index of body size, because larger birds could feed on a larger diversity of prey sizes which would affect stable isotope ratios. Model selection was performed using the Akaike's information criterion corrected for small sample size (AICc) based on the models' maximum likelihood (Burnham and Anderson 2002). We refitted the selected models with REML to estimate the model parameters (Zuur et al. 2009) and evaluated residuals for deviations from normality.

To determine birds isotopic niche width within wintering areas, we used the package 'Stable Isotope Bayesian Ellipses' (SIBER) in R (Jackson et al. 2011). The standard ellipse area after correcting for small sample size (SEAc) is an estimated ellipse encompassing 40% of the data regardless of sample size, which we calculated to compare estimated isotopic niche width among populations in the six different wintering areas.

We estimated repeatability, or ICC, (R) of the isotope ratios of individuals over years as:

$$R = \frac{\sigma_{\alpha}^2}{(\sigma_{\alpha}^2 + \sigma_{\epsilon}^2)}, \quad (2)$$

where σ_{α}^2 is the variance between individuals within region, and σ_{ϵ}^2 is the variance within individuals (Nakagawa & Schielzeth 2010; Wolak et al. 2012). The variance components were extracted from the mixed effect models.

To test how well wintering areas of Arctic skuas can be predicted based on stable isotope ratios of nitrogen and carbon, a linear discriminant analysis (LDA) with jackknife procedure was used with the R package 'Mass' (Venables & Ripley 2002).

All statistical analyses were conducted in R version 3.4.0 (R Development Core Team 2017) and statistical significance was assumed at $p < 0.05$.

Results

We observed differences in the birds' foraging ecology between wintering areas as revealed by the statistically significant differences in values of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (figure 2). The best models explaining variation in stable isotope ratios only included wintering area as a predictor variable (Table A-3a and A-3b). One alternative model including wintering area and wing length had $\Delta\text{AICc} < 2$, however the parameter estimates of the effect of wing length had no statistically significant effect on the variation of stable isotope ratios ($t=-0.85$, $p=0.41$). There was no statistically significant effect of sex, breeding colony, wing length or body mass on the stable isotope ratios.

Individuals from the Benguela Current and the Canary Current had similar mean values of $\delta^{15}\text{N}$, but differed more in $\delta^{13}\text{C}$ values (table 1, figure 2). Individuals wintering in the Canary Current, had higher mean values of $\delta^{13}\text{C}$ than individuals from other areas, while individuals wintering in the Mediterranean had lower mean values of $\delta^{13}\text{C}$. Individuals wintering in the Falkland current had the highest mean values of $\delta^{15}\text{N}$, while individuals wintering in Caribbean had lower mean values of $\delta^{15}\text{N}$ than individuals from other areas. Individuals wintering in Caribbean, the Benguela Current, Gulf of Guinea and Falkland Current had similar values of $\delta^{13}\text{C}$. All mean values \pm SE are shown in table 1. The isotopic niche width was largest for individuals wintering in Caribbean and lowest for those wintering in the Mediterranean area (table 1, figure 3).

Variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were high between individuals but low within individuals from year to year (figure 4). The repeatability of isotope ratios within wintering area was high; for $\delta^{15}\text{N}$ $R=0.823$ ($\text{SE} \pm 0.044$, $\text{CI} = 0.717, 0.897$) and for $\delta^{13}\text{C}$ $R= 0.685$ ($\text{SE} \pm 0.072$, $\text{CI} = 0.54, 0.819$).

The accuracy of the predictions of wintering area from the linear discriminant analysis was high for Canary current (87.50%), Falkland current (92.59%) and Mediterranean (85.71%), intermediate for Caribbean (70.73%) and Gulf of Guinea (57.89%), and lowest for Benguela current (20.00%) (figure A-1).

Discussion

This study demonstrates a strong link between stable isotope ratios of nitrogen and carbon and wintering areas of Arctic skuas. Furthermore, a high individual repeatability in isotope ratios within wintering areas indicates a high individual consistency in foraging ecology. Migration movements were also consistent within individuals between years, thus the repeatability in isotopic signatures is linked to consistent individual migration strategies.

Among region variation

Stable isotope ratios of nitrogen and carbon in feathers of Arctic skuas differed between individuals wintering in the different areas, which may be due to different baseline of isotopes in different geographical areas, so called isoscapes. As described in Graham et al. (2010), $\delta^{15}\text{N}$ in zooplankton have a lower baseline value around the Caribbean ($\sim 1\text{‰}$), and higher values around Argentina and South Africa ($\sim 6.5\text{‰}$). This would probably explain most of the large difference in stable isotope ratios between individuals in Caribbean and Falkland current (table 1). Thus, variation in trophic relations between individuals can only be compared among individuals wintering within the same region.

Values of $\delta^{13}\text{C}$ reflect the primary productivity found in the area, hence differences in $\delta^{13}\text{C}$ values indicate differences in foraging habitat (Hobson 1990). The baseline of $\delta^{13}\text{C}$ is less varying than $\delta^{15}\text{N}$ between the regions (Graham et al. 2010). This could explain the lower variation seen in $\delta^{13}\text{C}$ values compared to the $\delta^{15}\text{N}$ values between individuals wintering in the different areas.

To determine the correct trophic niche of Arctic skuas, and to be able to compare this between regions, it would be necessary to take samples from possible prey species and compare these stable isotope ratios with those of Arctic skuas in the respective regions, as done in other studies (Ceia et al. 2014a; Ehrich et al. 2015; Leal et al. 2017 and others). Concerning the wide distribution of the Arctic skua during winter, it would prove difficult to obtain tissue samples from prey species in all wintering areas.

The prediction of accuracy of wintering area demonstrated by the linear discriminant analysis, showed a high accuracy in most areas, except Benguela current and to some extent Gulf of Guinea. The accuracy predictions correspond with the estimated isotopic niches of individuals in the different areas. Individuals wintering in Benguela current and Gulf of Guinea reflect

intermediate values of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, and are less distinct from individuals wintering in the other areas. Individuals wintering in the other areas show more extreme values, either in $\delta^{15}\text{N}$ (as in Caribbean and Falkland current) or $\delta^{13}\text{C}$ (Mediterranean and Canary Current) (table 1, figure 2). For the areas with high accuracy, the combination of stable isotope ratios of nitrogen and carbon can be used to detect the wintering area with high precision without the use of geolocators. The accuracy prediction of Benguela current and Gulf of Guinea is however lower, and underlines the importance of using geolocators to determine the accurate wintering area of Arctic skuas. Studies that have shown even greater segregation in isotopic signatures, have determined wintering areas of birds with high accuracy without the use of geolocators (Cherel et al. 2000; Leat et al. 2013). The Arctic skua are migrating to several areas, and thus the segregation between the stable isotope ratios in individuals wintering in the different areas may be less distinct.

Variation among individuals within region

A large variation in stable isotope ratios of nitrogen was found among individuals within Caribbean, Canary current and in Falkland current (figure 3), indicating that individuals within these areas reflect different foraging strategies. The birds wintering in Caribbean had a high variation among individuals, with $\delta^{15}\text{N}$ values ranging from 7.69‰ to 15.44‰. Individuals within Falkland current and Canary current also showed values of $\delta^{15}\text{N}$ with variation greater than 5‰. As the stable isotope ratio of nitrogen has a stepwise enrichment between 2.5‰ to 5‰ for each trophic level (Hobson & Clark 1992), this variation indicates therefore that individuals are feeding at different trophic levels within these areas. Some of the difference observed could be due to different species targeted for kleptoparasitism, such as surface-feeders or diving species, as the Arctic skua gather most of its food by stealing from other birds. This would then be reflected in the stable isotope ratios of Arctic skuas.

The large variation in stable isotope ratios of carbon in individuals wintering in Caribbean can be due to variation in the baseline for inshore and offshore areas. $\delta^{13}\text{C}$ values are higher in areas with high primary productivity, such as areas along the coast, while it is lower offshore (Hobson and Clark 1992). The difference seen in $\delta^{13}\text{C}$ in individuals wintering in the Benguela Current, could likewise be due to the fact that some birds have their main foraging areas near the Agulhas rings where the Indian Ocean and Atlantic Ocean meets. This area has a lower degree of primary productivity due to higher temperatures and limited light (Dower

and Lucas 1993). Birds feeding closer to the shore, benefiting from upwellings along the coast, will therefore reflect a higher value of $\delta^{13}\text{C}$. Individuals within Mediterranean and Gulf of Guinea show less variation of stable isotope ratios, indicating that birds within these areas share a similar foraging habitat.

Spatial studies of stable isotope ratios of nitrogen and carbon in zooplankton, suggests that there can be a high variation in the baseline within smaller areas (Schell et al. 1998). Some of the variation seen in individuals within one region can thus also be due to variation in baseline within the defined areas. Fine spatial sampling of plankton would be necessary to test for this effect.

No differences were detected in stable isotope ratios between sexes. However, trophic or spatial segregation may occur, but not be detected by stable isotope analyses if seabirds feed on different prey species with similar $\delta^{15}\text{N}$ values, or in areas with similar values of $\delta^{13}\text{C}$ (Graham et al. 2010). Other studies have as well found that males and females share the same foraging niche (Cherel et al. 2008; Weimerskirch et al. 2009; Mancini et al. 2013; Mancini & Bugoni 2015), indicating that there's no sexual segregation in resource partitioning in many seabird species.

Isotopic niche width

Individuals wintering in Caribbean were estimated to have the widest isotopic niche width compared with the other areas, as reflected by the SEAc values. In this study, the Caribbean category covers a large area, spanning from the Gulf of Mexico to the north of Brazil (figure 1b). A positive relationship between isotopic niche width and variation in spatial distribution among individuals in seabird populations has been found in previous studies (Bearhop et al. 2005; Ceia et al. 2014b). Their studies suggest that populations with more variability in spatial distribution have a wider isotopic niche. Other factors resulting in the wide isotopic niche width of the Caribbean winter population could be higher prey diversity due to the large area. Additionally, high intra- and inter-specific competition could increase the foraging diversity within a population (Mancini et al. 2014). This, included with the fact that Caribbean reflects a more geographically diverse region than the other wintering areas, would explain the wide isotopic niche width for the individuals wintering here.

On the other hand, areas reflecting a smaller niche width might experience less competition and a limited availability of prey species and foraging habitat (Ceia et al. 2014b). Mean values of $\delta^{13}\text{C}$ in Arctic skuas wintering in Canary current are similar to those seen in wing feathers of Cory's shearwater *Calonectris diomedea borealis* breeding in the same area (Roscales et al. 2011). It is suggested that this region only have a few types of prey that are very abundant, which decrease competition and results in a narrow isotopic niche width for populations here. Likewise, low prey diversity could explain the narrower niche widths in other areas, as Mediterranean and Gulf of Guinea.

Winter populations of Arctic skua in all wintering areas reflect a wide isotopic niche width compared with other foraging studies of seabirds (Ceia et al. 2014b; Mancini & Bugoni 2014; Ramirez et al. 2015). Flaherty and Ben-David (2010) found that populations of foraging specialists have a broader isotopic niche than populations composed of foraging generalists, likely because generalist consumers sample a wider range of resources and therefore average their diets. This indicates that winter populations of Arctic skua consists of specialists rather than generalists.

Individual consistency

The variation between individuals within the different wintering areas, and the within-individual consistency in stable isotope ratios of nitrogen and carbon from one year to another (figure 4), suggest consistency in diet and foraging habitat, and support the hypothesis of individual specialization. Ramirez et al. (2015) found a high repeatability in Desertas petrels *Pterodroma deserta* wintering in five different regions in the Atlantic Ocean during a five-year study. This indicates that other seabirds may also follow a fixed strategy, and may hence be a widespread trait among pelagic seabirds.

Individuals may specialize on one foraging strategy, such as kleptoparasitism on one particular species, due to advantages of learning and memorizing a feeding strategy. This may increase foraging efficiency, and optimize energy gain (Bolnick et al. 2003). Several advantages have been found to be associated with specialization in seabirds. Specialization increase reproductive success in western gull *Larus occidentalis* compared to non-specialized individuals (Spear 1993). Similarly, specialized Great skuas *Stercorarius skua* spent less time foraging and had a slightly higher breeding success than generalists (Votier et al. 2004).

With a fixed strategy, it may be more challenging for birds to modify their feeding behavior to cope with changes in the environment. Global warming will have a bottom-up impact on marine top-predators (Grémillet and Boulinier 2009). Combined with human impact such as over fishing and harvest, this threatens seabirds. Barbraud and Weimerskirch (2003) found increased winter mortality in a marine top predator, the blue petrel *Halobaena caerulea*, during warmer years and at high population densities. Food resources will in warmer years become less available due to the negative effects of warm sea-surface temperatures on zooplankton communities, and is suggested to be the main reason for the increased winter mortality. This demonstrates that seabirds are vulnerable to warming of ocean temperatures that can lead to shortage of resources and highlights the importance of the non-breeding season for recovery of body condition between breeding seasons.

Concluding remarks

This study demonstrates a wide winter distribution of the Arctic skua, where individuals show a high spatial and trophic consistency for a time frame for up to seven years. The high repeatability for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ indicates that some Arctic skuas have been feeding on similar food items and in the same foraging areas throughout this study. This trend is apparent in all wintering areas and could indicate that the environment, and hence food availability, has been relatively stable during the study period. By pursuing long-term monitoring of individuals, it would eventually be possible to monitor changes or consistency in the foraging ecology of seabirds, which would serve as an indication for ongoing changes in the environment.

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Tables

Table 1: Number of feather samples from each colony wintering in the different areas, with mean values (in ‰) of $\delta^{15}\text{N}$ and $\delta^{13}\text{C} \pm \text{SE}$. SEAc estimates isotopic niche width.

Wintering area	n_{tot}	n_{ind}	n_K	n_B	n_S	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	SEAc (‰ ²)
Benguela Current	5	4	-	-	5	15.57 ± 0.94	-15.85 ± 0.43	2.61
Caribbean	41	16	39	-	2	10.82 ± 0.41	-15.51 ± 0.18	4.82
Canary Current	24	11	20	2	2	15.36 ± 0.64	-14.34 ± 0.29	2.34
Falkland Current	27	15	-	15	12	18.81 ± 0.59	-16.11 ± 0.27	2.88
Gulf of Guinea	19	9	15	3	1	12.49 ± 0.68	-15.78 ± 0.31	1.75
Mediterranean	7	3	3	3	1	13.05 ± 1.03	-17.17 ± 0.46	1.32

n_{tot} = total samples, n_{ind} = individuals sampled, n_K = samples from Kongsfjorden, n_B = samples from Brensholmen, n_S = samples from Slettnes.

Figures

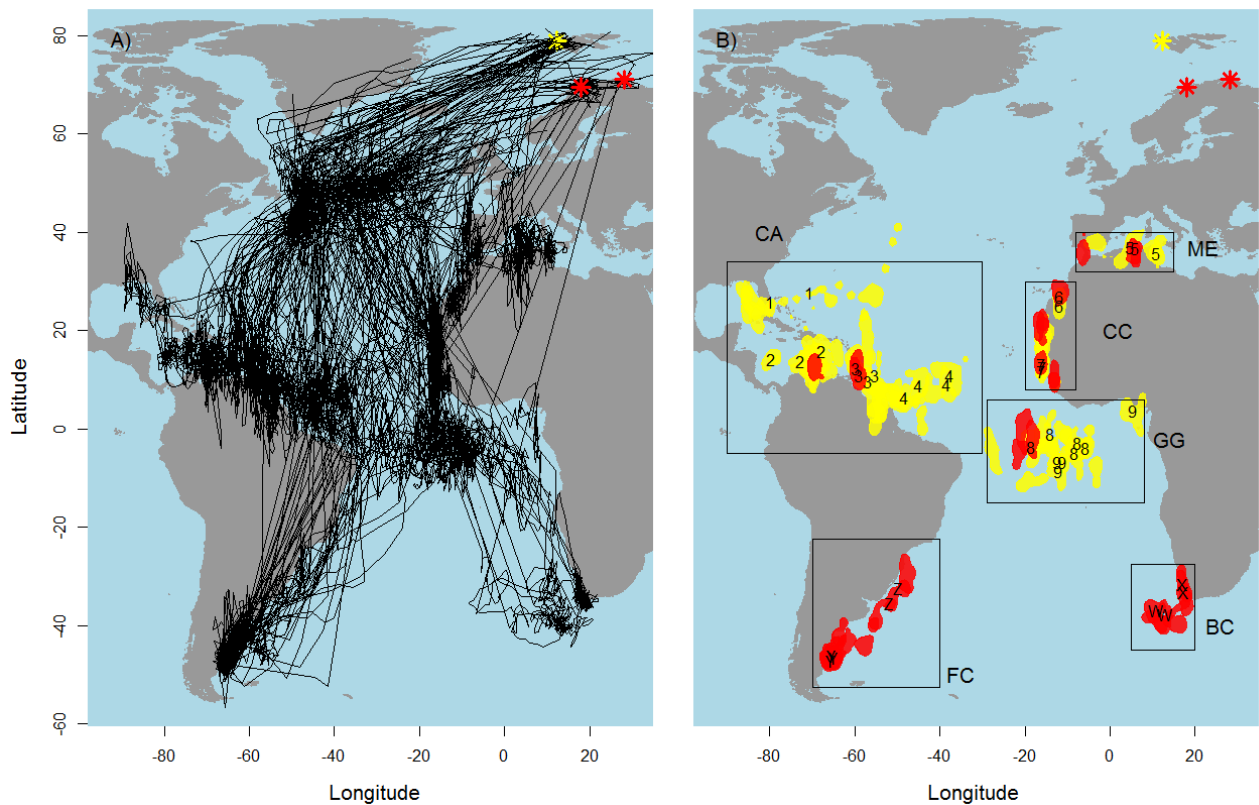


Figure 1a: Map of tracks from geolocators of each Arctic skua ($N_{ind}=58$, $N_{tracks}=113$) sampled during the period 2009-2017. Asterisks indicate breeding colonies in Kongsfjorden, Svalbard (yellow), and Brensholmen and Slettnes, Norway (red). During a period of four weeks around equinoxes, tracks are drawn as straight lines from the last position before to the first position after the period as latitude location is unreliable in this period (van Bemmelen et al. 2017). Mean error is ~ 185 km). b) 75% kernel density polygons for birds from Kongsfjorden (yellow) and Slettnes and Brensholmen (red). Individual consistency in wintering areas are demonstrated by January centroids for 13 individuals (labelled 1-9, W, X, Y and Z) tracked for 2-4 years. All tracked birds show the same consistency, here are only eleven individuals represented for readability. All birds were categorized into one of the following wintering areas: CA=Caribbean, FC=Falkland Current, BC=Benguela Current, GG=Gulf of Guinea, CC=Canary Current and ME=Mediterranean.

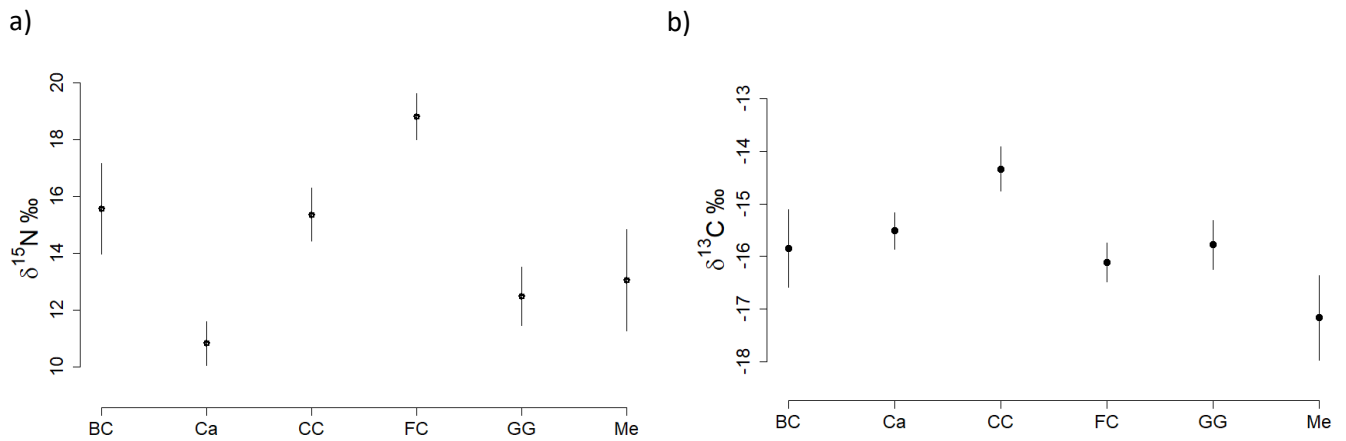


Figure 2: Mean values of $\delta^{15}\text{N}$ (a) and $\delta^{13}\text{C}$ (b) in wintering areas with 95 % confidence intervals based on linear mixed models. BC=Benguela Current, Ca=Caribbean, CC=Canary Current, FC=Falkland Current, GG=Gulf of Guinea and Me=Mediterranean.

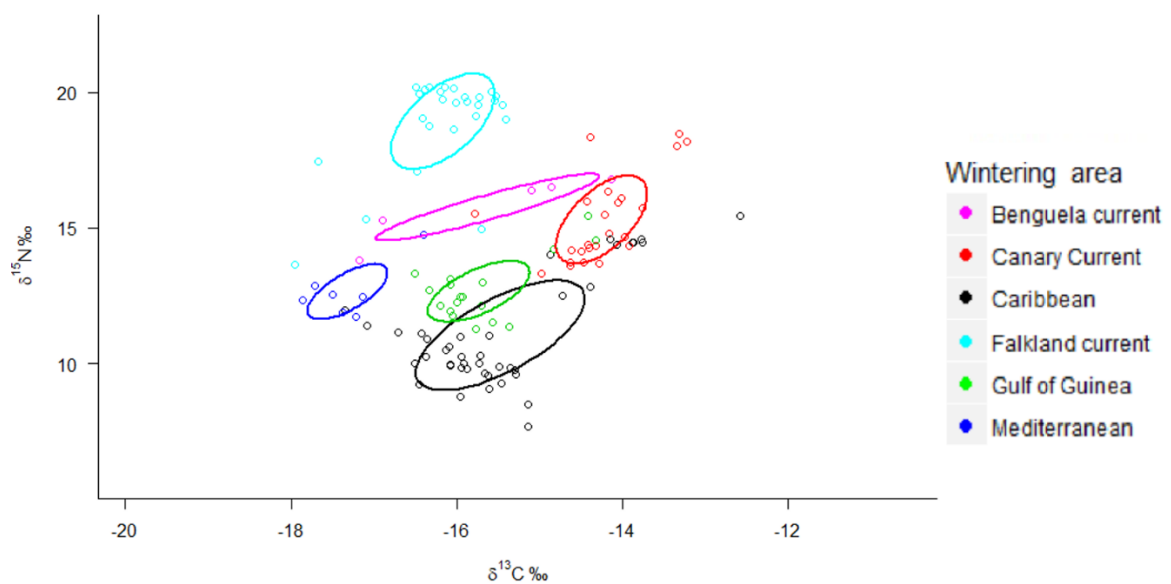


Figure 3: Isotopic niche space estimated from body feathers of Arctic skuas. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values and standard ellipse areas corrected for small sample sizes (SEAc) using stable isotope Bayesian ellipses in R (SIBER). Ellipses are covering 40% of the stable isotope data.

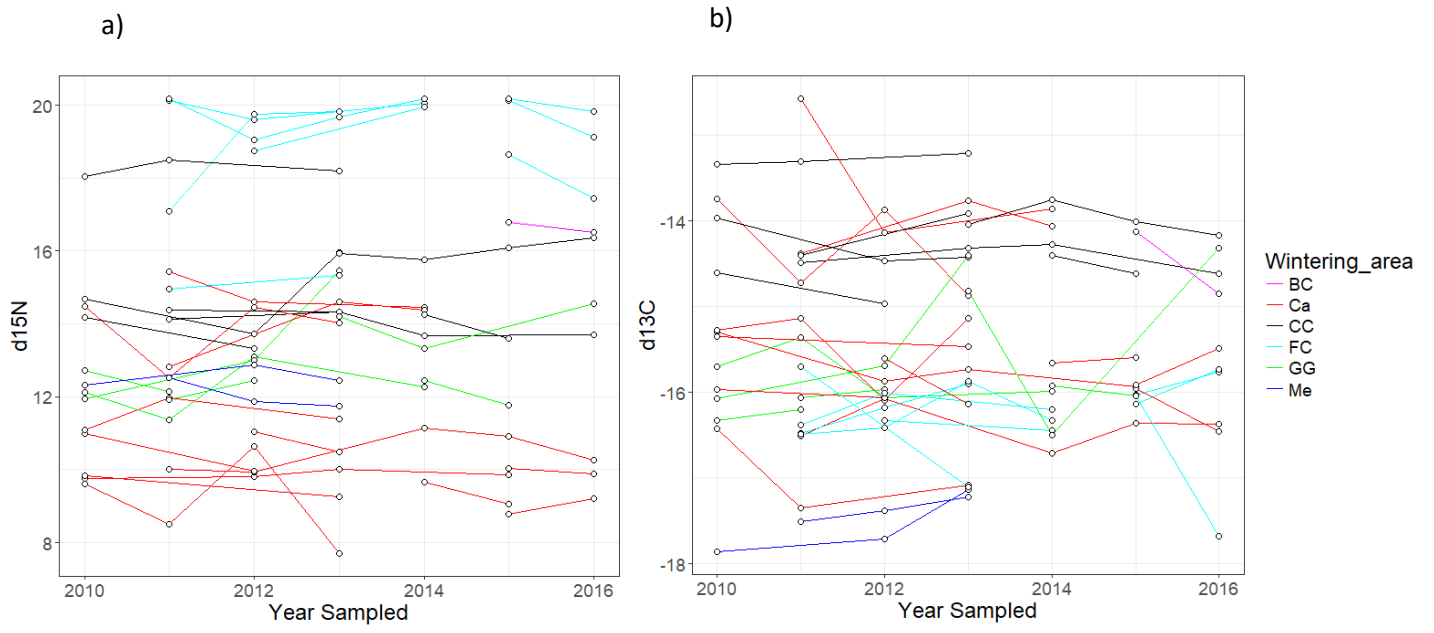


Figure 4: Individual variation in $\delta^{15}\text{N}$ (a) and $\delta^{13}\text{C}$ (b) between years. Each line represents one individual. Only individuals sampled more than one year are included (n=37 individuals).

Appendix

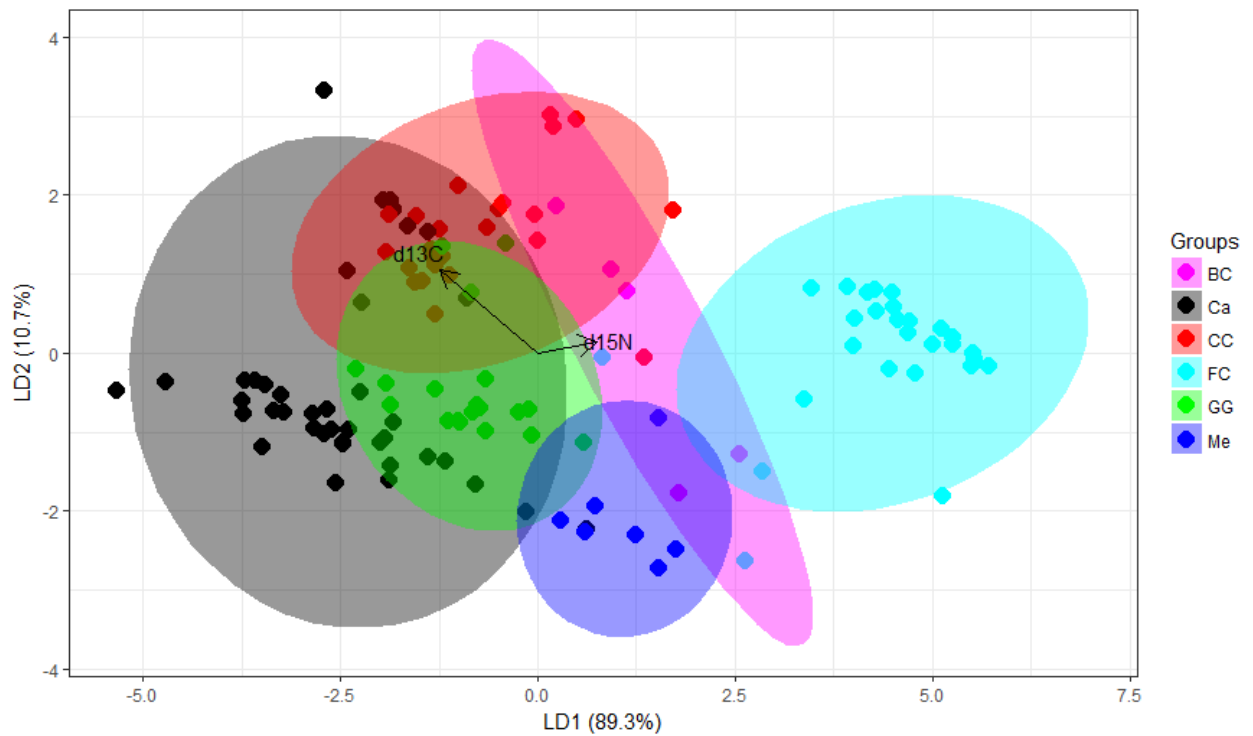


Figure A-1: Linear discriminant analysis based on stable isotope ratios of nitrogen and carbon in wintering populations of the Arctic skua. Ellipses of 95% confidence are shown. 89.3% of the variance is explained by the first axis (LD1), on which $\delta^{13}\text{C}$ is the highest contributor visualized by the vectors. The second axis (LD2) explain 10.7% of the variance. BC=Benguela Current, Ca=Caribbean, CC=Canary Current, FC=Falkland Current, GG=Gulf of Guinea and Me=Mediterranean.

Table A-1a: P-values from pairwise comparisons of wintering areas from the linear mixed model with $\delta^{15}\text{N}$ as the response variable, wintering area as explanatory variable and individual as random factor.

	Caribbean	Benguela Current	Canary Current	Falkland Current	Gulf of Guinea
Benguela Current	<0.0001				
Canary Current	<0.0001	0.84			
Falkland Current	<0.0001	0.0012	<0.0001		
Gulf of Guinea	0.019	0.0035	<0.0001	<0.0001	
Mediterranean	0.035	0.053	0.035	<0.0001	0.61

Table A-1b: P-values from pairwise comparisons of wintering areas from the linear mixed model with $\delta^{13}\text{C}$ as the response variable, wintering area as explanatory variable and individual as random factor.

	Caribbean	Benguela Current	Canary Current	Falkland Current	Gulf of Guinea
Benguela Current	0.45				
Canary Current	<0.0001	0.0013			
Falkland Current	0.033	0.55	<0.0001		
Gulf of Guinea	0.35	0.88	<0.0001	0.3	
Mediterranean	0.0014	0.025	<0.0001	0.027	0.0066

Table A-2: Estimated isotopic niche widths for wintering populations of the Arctic skua. Convex hull area (TA), Standard ellipse area (SEA) and Standard ellipse area with correction for small sample size (SEAc) (numbers in $\%o^2$).

	Benguela Current	Canary Current	Caribbean	Falkland Current	Gulf of Guinea	Mediterranean
TA	2.013	7.658	15.937	11.149	4.485	1.423
SEA	1.955	2.238	4.696	2.768	1.654	1.103
SEAc	2.606	2.340	4.816	2.879	1.752	1.323

Table A-3a: Model selection for the effects on $\delta^{15}\text{N}$ values in Arctic Skuas. AIC_c is the Aikake information criterion corrected for small sample size, ΔAIC_c is the difference in AIC_c compared with the model with lowest AIC_c . 'X' indicates if a variable was included in the model. All models included individual as random factor.

Model rank	Wintering area	Breeding colony	Sex	Wing length	AIC_c	ΔAIC_c
1	x				375.42	0
2	x			x	377.24	1.82
3	x	x			377.91	2.49
4	x		x		380.07	4.65
5	x		x	x	381.79	6.37

Table A-3b: AIC_c and ΔAIC_c for the five best models for the analysis of $\delta^{13}\text{C}$ values in Arctic Skuas. 'X' indicates if a variable was included in the model. All models included individual as random factor.

Model rank	Wintering area	Breeding colony	Sex	Wing length	AIC_c	ΔAIC_c
1	x				235.3	0
2	x			x	237.51	2.21
3	x	x			238.23	2.93
4	x		x		239.85	4.55
5	x		x	x	242.02	6.72

Table A-4: Mean timing of migration of Arctic skuas in the different breeding colonies. Autumn departure were decided by the date birds start to move away from the breeding area. Arrival in wintering area was decided by the date birds switched from fast migration to slower movements, and departure from wintering areas was decided by when birds started fast movements towards the north. Arrival at breeding area was estimated by adding four days to the last position obtained after the geolocators lost the night signal due to midnight sun. Lay date was estimated by identifying the start of incubation-pattern from the light-data.

Breeding colony	Breeding area			Wintering area		
	spring arrival	lay date	autumn departure	autumn arrival	spring departure	time spent
Kongsfjorden	25th May	17th June	23rd Sept	29th Oct	11th May	195
Brensholmen	7th May	3rd June	19th Aug	27th Sept	7th April	193
Slettnes	11th May	31st May	21st Aug	2nd Oct	30th March	179

Table A-5: Isotopic data for each individual for the respective years. K=Kongsfjorden, B=Brensholmen and S=Slettnes.

Ring number	Breeding area	Wintering area	Sex	Year Sampled	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Bodymass (g)
6217924	K	CC	F	2010	-13.97	14.68	527
6217924	K	CC	F	2012	-14.47	13.72	542
6217924	K	CC	F	2013	-14.43	15.97	530
6217923	K	CC	M	2010	-14.15	14.79	522
6217919	K	Ca	M	2010	-15.30	9.76	477
6217919	K	Ca	M	2012	-15.87	9.81	508
6217919	K	Ca	M	2013	-15.73	10.01	468
6217919	K	Ca	M	2015	-15.94	9.86	477
6217936	K	GG	M	2010	-15.70	12.12	460
6217936	K	GG	M	2011	-15.36	11.37	458
6217936	K	GG	M	2012	-16.07	13.10	462
6217936	K	GG	M	2014	-15.99	12.27	472
6217935	K	GG	F	2010	-16.33	12.72	482
6217935	K	GG	F	2011	-16.20	12.15	481
5184802	K	GG	F	2010	-15.56	11.53	532
6217933	K	CC	M	2010	-14.39	18.34	442
6217934	K	Ca	F	2011	-16.51	10.00	516
6217934	K	Ca	F	2012	-16.08	9.94	490
6217934	K	Ca	F	2014	-16.71	11.15	497
6217934	K	Ca	F	2015	-16.36	10.92	476
6217934	K	Ca	F	2016	-16.37	10.26	500
6217938	K	Ca	M	2011	-12.57	15.44	416
6217938	K	Ca	M	2012	-14.14	14.59	427
6217938	K	Ca	M	2014	-13.86	14.46	425
6217940	K	CC	M	2010	-14.61	14.18	444
6217940	K	CC	M	2012	-14.97	13.33	436
5184803	K	GG	F	2010	-16.07	11.94	487
5184803	K	GG	F	2012	-15.69	13.00	577
5184803	K	GG	F	2013	-14.41	15.46	490
6217941	K	Ca	F	2010	-15.28	9.61	490
6217941	K	Ca	F	2011	-15.14	8.50	555
6217941	K	Ca	F	2012	-16.09	10.63	543
6217941	K	Ca	F	2013	-15.14	7.69	485
6217942	K	Ca	M	2010	-15.96	11.00	430
6217942	K	Ca	M	2012	-16.07	9.96	456
6179829	K	Ca	F	2010	-13.75	14.48	475
6179829	K	Ca	F	2011	-14.72	12.51	497
6179829	K	Ca	F	2012	-13.87	14.46	493
6179829	K	Ca	F	2013	-14.87	14.03	455
6218054	K	Ca	M	2010	-15.35	9.84	472
6218054	K	Ca	M	2013	-15.46	9.26	468
6218055	K	Me	F	2010	-17.86	12.32	507
6218055	K	Me	F	2012	-17.71	12.86	593
6218055	K	Me	F	2013	-17.14	12.45	533
5184801	K	CC	F	2010	-13.34	18.04	522
5184801	K	CC	F	2011	-13.31	18.49	527
5184801	K	CC	F	2013	-13.22	18.20	535
6218058	K	Ca	M	2010	-16.42	11.10	432
6218058	K	Ca	M	2011	-17.35	11.97	443
6218058	K	Ca	M	2013	-17.08	11.38	420
5184806	K	GG	M	2011	-16.07	11.92	428

5184806	K	GG	M	2012	-15.96	12.44	447
5184807	K	CC	F	2011	-14.49	14.14	517
5184807	K	CC	F	2013	-14.32	14.33	515
5184807	K	CC	F	2014	-14.27	13.68	515
5184807	K	CC	F	2016	-14.62	13.71	516
5184808	K	Ca	M	2011	-14.39	12.81	444
5184808	K	Ca	M	2013	-13.77	14.59	425
5184808	K	Ca	M	2014	-14.06	14.38	442
6223841	K	Ca	M	2013	-15.71	10.28	457
6223846	K	Ca	F	2012	-15.60	11.04	557
6223846	K	Ca	F	2013	-16.13	10.49	500
6223849	K	CC	F	2013	-14.05	15.94	489
6223849	K	CC	F	2014	-13.75	15.75	491
6223849	K	CC	F	2015	-14.01	16.08	499
6223849	K	CC	F	2016	-14.17	16.35	484
6228571	K	CC	M	2014	-14.40	14.25	447
6228571	K	CC	M	2015	-14.62	13.60	439
6228574	K	Ca	M	2014	-15.66	9.65	472
6228574	K	Ca	M	2015	-15.60	9.06	396
6228552	K	GG	M	2014	-15.93	12.45	417
6228552	K	GG	M	2015	-16.05	11.77	399
6228553	K	Ca	M	2015	-15.95	8.78	429
6228553	K	Ca	M	2016	-16.45	9.21	341
6228558	K	Ca	F	2015	-15.91	10.02	484
6228558	K	Ca	F	2016	-15.48	9.88	488
6228576	K	GG	NA	2016	-15.77	11.26	518
6218801	B	FC	F	2011	-16.48	17.08	
6218801	B	FC	F	2012	-16.17	19.75	438
6218801	B	FC	F	2013	-15.90	19.82	435
6218802	B	Me	F	2011	-17.50	12.53	
6218802	B	Me	F	2012	-17.38	11.88	480
6218802	B	Me	F	2013	-17.22	11.73	435
6218805	B	FC	F	2011	-16.38	20.12	
6218805	B	FC	F	2012	-16.01	19.60	425
6218805	B	FC	F	2014	-16.20	20.04	445
6218807	B	CC	M	2011	-14.41	14.39	
6218807	B	CC	M	2013	-13.92	14.32	400
6218808	B	FC	M	2011	-16.49	20.18	
6218808	B	FC	M	2012	-16.41	19.06	405
6218808	B	FC	M	2013	-15.87	19.67	382
6218808	B	FC	M	2014	-16.33	20.18	390
6218809	B	FC	F	2011	-15.70	14.96	
6218809	B	FC	F	2013	-17.10	15.34	415
6218810	B	FC	M	2012	-16.33	18.75	
6218810	B	FC	M	2014	-16.45	19.95	400
6218811	B	GG	F	2013	-14.82	14.20	435
6218811	B	GG	F	2014	-16.50	13.32	525
6218811	B	GG	F	2016	-14.31	14.56	
6218813	B	FC	M	2014	-17.95	13.63	375
6218773	S	FC	NA	2015	-16.03	20.13	389
6218773	S	FC	NA	2016	-15.77	19.12	455
6218934	S	FC	M	2015	-15.52	19.86	378
6218776	S	FC	F	2015	-16.14	20.17	475
6218776	S	FC	F	2016	-15.73	19.83	414
6218927	S	FC	M	2015	-16.04	18.65	391
6218927	S	FC	M	2016	-17.67	17.44	425
6218922	S	BC	M	2015	-14.13	16.78	387

6218922	S	BC	M	2016	-14.85	16.50	383
6218910	S	BC	M	2016	-15.09	16.39	402
6179066	S	FC	F	2016	-15.45	19.53	485
6218926	S	FC	F	2016	-15.74	19.52	472
6218907	S	Ca	F	2016	-15.62	9.54	404
6218766	S	CC	F	2016	-15.78	15.54	430
6218906	S	BC	F	2016	-16.89	15.30	435
6218918	S	FC	F	2016	-15.54	19.69	440
6218769	S	GG	F	2016	-16.08	12.91	383
6218768	S	FC	M	2016	-15.40	18.99	424
6218767	S	Me	M	2016	-16.40	14.76	391
6218928	S	BC	F	2016	-17.17	13.82	455
6218932	S	CC	F	2016	-14.21	15.47	485
6218765	S	FC	F	2016	-15.58	20.04	445
6218770	S	Ca	M	2016	-15.94	10.25	397

Table A-6: Years of tracking data for each individual. Y1=first year tracked, Y2=second year tracked, Y3=third year tracked, Y4=fourth year tracked, and Y5=fifth year tracked. K=Kongsfjorden, B=Brensholmen and S=Slettnes.

Ring number	Y1	Y2	Y3	Y4	Y5	Breeding area	Wintering area
6217924	2009/10	2010/11	2011/12			K	CC
6217923	2009/10					K	CC
6217919	2009/10	2012/13	2013/14	2014/15		K	Ca
6217936	2009/10	2010/11	2011/12	2012/13	2013/14	K	GG
6217935	2009/10	2010/11				K	GG
5184802	2009/10					K	GG
6217933	2009/10					K	CC
6217934	2009/10	2010/11	2011/12	2015/16		K	Ca
6217938	2009/10	2010/11	2011/12	2012/13	2013/14	K	Ca
6217940	2009/10	2010/11				K	CC
5184803	2009/10	2010/11	2011/12	2012/13		K	GG
6217941	2009/10	2010/11	2011/12	2012/13		K	Ca
6217942	2009/10	2010/11	2011/12			K	Ca
6179829	2010/11	2011/12				K	Ca
6218054	2011/12	2012/13				K	Ca
6218055	2010/11	2011/12	2012/13			K	Me
5184801	2010/11	2011/12	2012/13			K	CC
6218058	2010/11	2011/12				K	Ca
5184806	2011/12					K	GG
5184807	2011/12	2012/13	2013/14			K	CC
5184808	2011/12	2012/13				K	Ca
6223841	2011/12	2012/13				K	Ca
6223846	2012/13					K	Ca
6223849	2014/15					K	CC
6228571	2014/15					K	CC
6228574	2014/15					K	Ca
6228552	2014/15					K	GG
6228553	2015/16					K	Ca
6228558	2015/16					K	Ca

6228576	2016/17			K	GG
6218801	2011/12	2012/13		B	FC
6218802	2011/12	2012/13		B	Me
6218805	2011/12	2012/13	2013/14	B	FC
6218807	2011/12	2012/13		B	CC
6218808	2011/12	2012/13	2013/14	B	FC
6218809	2011/12	2012/13		B	FC
6218810	2012/13			B	FC
6218811	2013/14	2014/15	2015/16	B	GG
6218813	2014/15			B	FC
6218773	2015/16			S	FC
6218934	2014/15			S	FC
6218776	2015/16			S	FC
6218927	2015/16			S	FC
6218922	2015/16			S	BC
6218910	2014/15	2015/16		S	BC
6179066	2014/15	2015/16		S	FC
6218926	2014/15	2015/16		S	FC
6218907	2014/15	2015/16		S	Ca
6218766	2015/16			S	CC
6218906	2014/15	2015/16		S	BC
6218918	2014/15	2015/16		S	FC
6218769	2015/16			S	GG
6218768	2015/16			S	FC
6218767	2015/16			S	Me
6218928	2014/15	2015/16		S	BC
6218932	2014/15	2015/16		S	CC
6218765	2015/16			S	FC
6218770	2015/16			S	Ca
