Moult location and diet of auks in the North Sea, inferred from coupled light-based and isotope-based geolocation

Running page head: **Foraging behaviour of North Sea auks**

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Abstract:

Many pelagic seabirds moult their feathers while at sea, which is an energetically costly behaviour. Mortality rates during moult can be high, so spatial and trophic ecology during this critical period is important for understanding demographic patterns. Unfortunately, individual foraging behaviours specifically linked to at-sea moult are commonly unclear. This paper combines two different approaches to geolocation: data from bird-borne geolocation loggers and stable-isotope assignment using carbon and nitrogen isotope maps (isoscapes). Coupling two geolocation processes allows some uncertainties associated with isotope-based assignment to be constrained. We applied this approach to quantify species-specific foraging locations and individual trophic variability during feather regrowth in three sympatric auk populations breeding on the Isle of May, Scotland (common guillemot (*Uria aalge*), razorbill (*Alca torda*) and Atlantic puffin (*Fratercula arctica*)). Inferred foraging areas during moult differed between species and feather types. Guillemots likely underwent moult within the southern North Sea, razorbills along the east coast of England and into the southern North Sea and puffins off the east coast of Scotland. Estimates of individual trophic position varied considerably within feather types (up to 1 trophic level difference between individuals), among feather types grown during different time periods, and across the three species, with guillemots consistently foraging at higher trophic positions than razorbills and puffins. Used in combination, these methods better constrain foraging areas during moult, as well as providing a technique to explore individual differences and flexibility in foraging strategy, which is valuable information for both seabird conservation and marine spatial planning.

Key words: Isoscape, trophic ecology, foraging, moult, Atlantic puffin, common guillemot, razorbill

Introduction:

The widespread use of miniaturised, ring-mounted data loggers that use light levels in conjunction with a time base to provide positional data, has greatly increased our knowledge of important foraging grounds for pelagic seabirds. Tag-based geolocation data are particularly useful in time periods when birds are away from the breeding colonies, for example by identifying migration routes and locations of wintering hot spots (Guilford et al. 2009, Jessopp et al. 2013, Frederiksen et al. 2016). Birds must replenish feathers to maintain feather function. In marine birds, feather moult typically occurs outside the breeding season and potentially has major fitness consequences because flight feathers are crucial for long distance migration while body feathers play an important role in thermoregulation, particularly for diving species (Daunt et al. 2006). In most alcid species, there is typically one period of the non-breeding season lasting a few weeks when moult of flight feathers is focused, known as the main feather moult. At this time individuals have fewer foraging options making them less able to cope with adverse environmental conditions or reduced prey availability (Sandvik et al. 2005, Harris et al. 2014). Environmental sensitivity during feather moult is particularly acute in species such as auks and ducks that are flightless while replacing their remiges. Given the increasing pressures on the marine environment from multiple anthropogenic activities, quantification of foraging location and diet whilst birds are moulting is urgently required for effective conservation and marine spatial planning (Grecian et al. 2010, Lewison et al. 2012, JNCC 2015, MMO 2015).

74 Geolocator derived data alone cannot identify specific foraging locations during moult as
75 individual moult timing is unconstrained therefore location and foraging behaviours during
76 winter feather moult are relatively poorly known (Sandvik et al. 2005, Harris & Wanless
77 2011, Breton & Diamond 2014). The stable isotope compositions of animal tissues provide a
78 complimentary approach for geolocating animals, particularly when combined with isoscapes
79 (spatially explicit predictive maps of isotope ratios derived from process level models of
80 isotope fractionation or distribution (Royle & Rubenstein 2004, Hobson et al. 2010)).
81
82 Stable-isotope-based geolocation has been widely used for migratory terrestrial birds utilising
83 well-established hydrogen isoscapes (Wunder & Norris 2008, Wunder 2010, Hobson et al.
84 2012, Hobson et al. 2014). In the marine environment, the ocean is spatially homogenous
85 with regard to hydrogen isotope ratios, so $\delta^{2}H$ values cannot be used to assign marine
86 animals to a likely geographic origin (Trueman et al. 2012). The isotopic composition of
87 carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) in phytoplankton varies spatially, largely reflecting
88 differences in the isotopic composition of nutrients and phytoplankton taxonomic
89 composition. Spatial variations in the isotopic compositions of phytoplankton are passed
90 through the food chain to higher trophic level organisms (Jennings & Warr 2003, Somes et al.
91 2010, McMahon et al. 2013) and can be used to infer animal movement patterns across
92 marine isotopic gradients (Quillfeldt et al. 2005, Cherel & Hobson 2007, Cherel et al. 2008,
93 MacKenzie et al. 2011). In the context of feather moult in seabirds, the isotopic composition
94 of a regrown feather provides a chemical record of the area from which resources used in
95 feather growth are derived.
96
97 To date, the limited number of detailed and spatially explicit, regional and *in situ* sample
98 based marine isoscapes (Jaeger et al. 2010, MacKenzie et al. 2014, Radabaugh & Peebles

99 2014, Vander Zanden et al. 2015) has limited the application of these techniques in the
100 marine environment. Geolocation using $\delta^{13}C$ and $\delta^{15}N$ ratios of animal tissues is further
101 complicated as the isotopic composition of a consumer's diet reflects both the spatial origin
102 of the prey items and their trophic level. Here we address this limitation by combining light-
103 and stable-isotope-based geolocation approaches.
104
105 Bird-borne data loggers can indicate the general location of an animal at known points in
106 time (with an error on the order of ±200km (Phillips et al. 2004, Lisovski et al. 2012)),
107 whereas $\delta^{13}C$ and $\delta^{15}N$ measurements depict the most likely origin of the resources
108 assimilated during tissue growth and are influenced by both the location of foraging and
109 composition of the diet. Isotope-based geolocation is generally performed by comparing the
110 isotopic composition of a consumer's tissue to a spatial model (isoscape). If the reference
111 isoscape is created using tissues from species other than the species to be assigned, then some
112 form of isotopic offset or calibration is needed (e.g. Bowen et al. (2014) and Trueman et al.
113 (2017)). Consumer tissues are typically enriched in ^{15}N by 3.4‰ and in ^{13}C by 1‰, relative
114 to their prey (Kelly 2000, Cherel & Hobson 2007, Ramos & Gonzalez-Solis 2012). Hence,
115 accurate geolocation using $\delta^{13}C$ and $\delta^{15}N$ ratios requires prior knowledge of the isotopic
116 difference between the reference isoscape and the measured tissue attributed to differences in
117 tissue composition, trophic level and individual physiology. Individual differences in trophic
118 geography (the location and composition of a consumer's diet (Bird et al. 2018)) may,
119 however, complicate the use of a single calibration value applied to all individuals within a
120 population. Population-level isotopic calibration-offsets between reference isoscapes and
121 tissues of interest can be estimated if the region of foraging is known *a priori*. Population
122 average tissue isotopic compositions can be compared to spatially averaged isotope
123 compositions across the known foraging area extracted from isoscapes (Fig. 1). This

approach assumes that individual differences in isotopic calibration effects are normally distributed.

Here we studied individual variation in location and diet during winter moult in three species of auks: common guillemot (*Uria aalge*, hereafter guillemot), razorbill (*Alca torda*) and Atlantic puffin (*Fratercula arctica*, hereafter puffin) from the Isle of May (Fig. 1), a major colony in the western North Sea. We draw on light-based geolocator data from breeding individuals for which we also had stable isotope data for flight and body feathers. We interpreted isotope data with reference to recently developed $\delta^{13}C$ and $\delta^{15}N$ isoscapes for the North Sea (MacKenzie et al. 2014, Trueman et al. 2017). Our primary aims were to determine population-level foraging locations and quantify individual diet variability during annual moult by combining two complimentary geolocation techniques.

Methods:

Study area and species:

Fieldwork for this study was carried out on the Isle of May National Nature Reserve, southeast Scotland (56°11'N, 2°34'W)(Fig. 1) which is a major breeding colony for puffins (*c.*40,000 pairs), guillemots (*c.*16,000 pairs) and razorbills (*c.*3,000 pairs) in the western North Sea. Data from ringing recoveries of all three species indicate that most individuals from the Isle of May winter and moult (shed and replace their feathers) within the North Sea (Wernham et al. 2002). However, information from geolocators deployed in the Isle of May colonies indicates that some puffins travel around the north of Scotland into the northeast Atlantic and a single, probably atypical, guillemot had replaced its wing feathers while in the

148 Barents Sea in three consecutive winters while all other guillemots appear to have moulted in
149 the North Sea (Harris et al. 2010, Harris et al. 2015b).
150
151 Evidence from beached birds and observations at sea suggest that timing of moult differs
152 somewhat between the species although information at the colony level is largely lacking
153 (Gaston & Jones 1998). Guillemots undergo a complete post-breeding moult soon after they
154 leave the colony in July, emerging into the winter plumage when birds have white cheek and
155 neck feathers. The primary wing feathers are shed first followed soon by the secondaries
156 resulting in birds becoming flightless for between 25 and 80 days (Thompson et al. 1998) and
157 regrowth is complete by the end of September. In October birds from the Isle of May
158 immediately start a partial pre-breeding moult back into summer plumage when the white
159 feathers of the head and cheek are replaced by dark ones; this moult is completed by the end
160 of December (Harris & Wanless 1990). Body feathers are not replaced during the pre-
161 breeding moult (Gaston & Jones 1998). Razorbill moult is similar except that the post-
162 breeding moult starts slightly earlier and pre-breeding moult starts later so that cheek and
163 neck feathers are not replaced until late winter/early spring, meaning that adults spend several
164 months longer in winter plumage compared to guillemots (Harris & Wanless 1990, Wernham
165 et al. 2002). Puffins undergo a complete moult of the feathers of the body and head (when the
166 white cheek feathers are replaced by black ones) soon after leaving the colony in mid- to late
167 July. The timing of the replacement of the flight feathers, and hence the flightless period,
168 appears to be much more variable compared to guillemots and razorbills and can occur any
169 time between September and March, with peaks in October and March (Harris et al. 2014).
170 The partial pre-breeding moult during which the black feathers of the winter face are replaced
171 by white ones occurs immediately prior to the birds returning to the colony in March (Harris
172 & Wanless 2011).

Small fish, mainly sandeels (Ammodytidae), juvenile herring (*Clupea harengus*) and sprat (*Sprattus*) and various species of juvenile Gadidae, make up the bulk of the diet of all three auks during winter. Some crustacea, polycheate worms and other pelagic invertebrates are also eaten, the proportion of invertebrates in the diet appearing to be higher in the puffin (45% by biomass) than in the guillemot (<5%) (Blake 1984, Blake et al. 1985, Sonntag & Hüppop 2005, Harris et al. 2015a). The limited data available describing winter diet for razorbills in the North Sea suggest that few invertebrates are eaten but elsewhere crustacea can dominate the winter diet (Hipfner & Chapdelaine 2002, Lilliendahl 2009).

Data Loggers:

In June and July 2014 breeding birds were caught and each was equipped, under British Trust for Ornithology licence, with a data logger (Migrate Technology, UK: model C250 on guillemots, model C65 on razorbills, model W65 on puffins) attached to a plastic leg ring (combined mass of logger and ring < 0.4 % the mass of the adults on which they were deployed). Birds were recaught in June and July 2015, the data loggers removed and the data downloaded. Details of the field protocols for guillemots and puffins are given in Harris et al. (2010) and Harris et al. (2015b). The methods for razorbills were the same as those for guillemots.

The data loggers measured light intensity at 60 second intervals and recorded the maximum value in each 10 minute interval. This allowed the determination of dawn and dusk which when linked to a time base enabled the determination of latitude from the duration of night and day, and longitude from timing of local midnight or mid-day. Details of data-handling and processing are given in Hanssen et al. (2016). Latitudes are unreliable around the

198 equinoxes so locations during the periods 10 September to 18 October, and 20 February to 5
199 April were excluded, as were latitudes that were clearly unreliable on visual inspection. The
200 average error of locations has been estimated to be ±200 km (Phillips et al. 2004) so for birds
201 with coastal distributions many positions occurred over land but such positions were not
202 filtered out.
203
204 To assess usage of the North Sea by each species, temporally specific kernel density maps
205 were produced in R 3.1.2 (R Core Development Team 2016). Kernel density data were subset
206 for each population for the known moulting periods of each feather type (Fig. 2). As
207 secondary feather moult timing of puffins is extremely variable, in this case a kernel density
208 area over the entire winter period was produced. Temporally specific kernel density maps
209 provide a visual representation of the likely location of populations of birds at broadly known
210 moulting seasons throughout the winter, but locations are not necessarily specific to the
211 individual short term feather moult and/or regrowth periods. Utilization distributions were
212 estimated using Kernel density distribution with the 'bkde2d' function in the 'KernSmooth'
213 package (Wand & Jones 1995). All grid cells (0.1 decimal degrees square) with a population
214 density value greater than 0.01 were interpreted as a possible location, and each cell within
215 this area was given a value of 1. This was done in order to compare geolocation results with
216 isotopic assignment areas, which represents all likely moulting areas within the isoscape.
217 Individuals with inferred kernel density areas outside the North Sea (1 guillemot secondary
218 feather out of 20 samples, and 1 razorbill cheek feather out of 8 samples) were excluded from
219 the population kernel density areas and the rest of the study, as the isoscape range is currently
220 limited to within this region.
221
222 **Stable isotope data collection and analysis:**

On recapture of each data logger-equipped bird, samples of feathers were collected, under UK Home Office licence. The distal two-thirds of a central secondary wing feather was snipped off each individual. Secondary feathers moult synchronously in the study species, therefore the specific secondary feather sampled was not specified. In addition 2-5 ventral body feathers and 2-5 head feathers were taken from the sides of the neck (guillemot) or cheeks (puffin and razorbill) (Table 1). Feathers were stored in paper envelopes and deep-frozen until needed.

Feathers were cleaned of surface contaminants using 0.25M NaOH and rinsed with milliQ water, dried in a 60°C oven for 12 hours, then cut into small fragments avoiding the quill and shaft. For secondary, body and neck feathers only one feather sample was analysed per individual; however, cheek feathers were pooled to obtain enough material for analysis. A 0.5-0.7mg sample was weighed into a tin capsule and bulk $\delta^{13}C$ and $\delta^{15}N$ values were measured by Elemtex Laboratories, Cornwall, UK.

Population Level Assignment:

The carbon and nitrogen isoscapes for the North Sea produced by Trueman et al. (2017) were used to assign seabirds to likely foraging areas. Although these isoscapes were produced from samples collected in summer 2015, the spatial distribution of $\delta^{13}C$ and $\delta^{15}N$ values in consumers within the North Sea are relatively stable over time (MacKenzie et al. 2014, Trueman et al. 2017). Seasonal variations in isotopic compositions of primary producers and low trophic level consumers are probable (Kürten et al. 2013) but are likely attenuated during successive predator-prey interactions so that higher trophic level consumers (such as the

248 jellyfish used to construct the isoscape and seabirds) inherit isotopic compositions that reflect
249 a seasonal average value. Therefore we assume that the time difference between isoscape
250 construction and collection of bird samples is unlikely to significantly influence geographic
251 assignments at the broad spatial scales considered here. Isotope values for each species and
252 feather type were used to identify a most likely spatial origin within the North Sea using
253 continuous assignment methods following Trueman et al. (2017) and Vander Zanden et al.
254 (2015). Assignments were made by estimating the likelihood that each raster cell of the North
255 Sea carbon and nitrogen isoscapes represented the foraging area of each individual, using the
256 bivariate normal probability function (Vander Zanden et al. 2015, Trueman et al. 2017).
257 Assignment results indicate the likely origin of food resources the birds utilised during the
258 period of feather growth. As auks are flightless during flight feather moult, these locations
259 were determined as the likely location of shedding and regrowth of secondaries.
260
261 The North Sea isoscape models were derived from jellyfish bell tissues, therefore a
262 calibration was required to refer the isotope values to bird feathers, accounting for systematic
263 isotopic offsets arising from differences in the amino acid compositions of tissues, and
264 combined effects of trophic level and physiology. Data loggers provided an independent
265 estimate of location from which a population-average calibration-offset value was derived for
266 each species and feather type. The calibration-offset value combines any isotopic offset
267 between jellyfish tissue and feather keratin associated with differences in amino acid
268 composition, which is assumed to be consistent across all species and feather types (however
269 specific alcid offset values have yet to be explicitly determined), and isotopic offsets
270 associated with differences in trophic level between jellyfish and seabirds. Any trophic offset
271 (trophic enrichment factor) may vary among individuals, species and feather types due to
272 differences in diet compositions and diet quality during different time periods. To estimate

calibration-offset values, the most likely spatial location of birds at the population level was estimated from light-based geolocation data as the average temporally specific kernel density areas for the population. Population-level likely locations were then overlaid on the carbon and nitrogen isoscapes and spatial average (median and standard deviation) isotope values were extracted at the corresponding coordinates (Fig. 1). Median extracted values represent the $\delta^{13}C$ and $\delta^{15}N$ composition the birds would display foraging within these estimated regions during moult, if tissue and diet correction factors were not required. By comparing the population median expected values in regions prescribed by light-based geolocation, to the population median measured isotope values, population level calibration-offset values can be estimated (Fig. 1);

$$Calibration\text{-}Offset_{(C,N)} = Median\ Measured\ Value_{(C,N)} - Median\ Extracted\ Value_{(C.N)}\ (+/-\ error\ terms)$$

Combined variance values were calculated by summing the isoscape-extracted isotope variance value and the measured isotope variance value from each feather type and species;

$$\sigma^2_{(Combined)} = \sigma^2_{(isoscape\ extracted\ values)} + \sigma^2_{(feather\ measured\ values)}$$

Population level calibration-offset values were applied to each individual within a population and of the same feather type to compare feather and jellyfish isotopic compositions. Individual birds were then assigned to likely foraging areas as per Trueman et al. (2017), using assignment conditions summarised in Table 2. A threshold odds ratio was set at 1.42 (representing approximately 70% of the probability values and 70% of the isoscape area), meaning any grid cells with a probability value greater than this threshold (the highest 30%)

were classed as likely, and all other grid cells were classed as unlikely (Trueman et al. 2017). The total number of individual birds assigned to each grid cell was summed for each species and feather type, to depict the most likely population-level foraging locations.

Isotope-based likely foraging locations during moult, and light based kernel density areas, representing possible locations visited during the assumed seasonal feather moult period, were mapped together. The resulting overlapping locations were inferred as the most likely predicted moult locations based on two alternative geolocation techniques.

Isotopic variation among individuals:

Individual differences in foraging behaviour within a population were then investigated to determine the extent of deviation from an average population diet. It was assumed that any isotopic differences associated with the difference in protein compositions between jellyfish and feather proteins are consistent within species and feather types. Thus, individual variability between feather isotopic values within a population moulting in the same region at the same time are assumed to largely represent isotopic differences associated with diet. To assess individual-level foraging behaviour, a similar approach was adopted as used to determine population calibration-offset values (Fig. 1).

Individual-level light-based logger kernel density areas (rather than population kernel density areas) were overlaid on the carbon and nitrogen isoscapes, and the corresponding spatial median and variance isotope values were extracted (Fig. 1). To calculate the expected feather isotope values, the population-level isotopic calibration estimate was applied to each individual. If the individual was foraging at the same trophic position as the average value for

the population, the expected and extracted isotope values would match. Individual differences in isotopic compositions associated with diet were therefore quantified as:

$$Ind.\ Expected\ value_{(C,N)} = Median\ Extracted\ Ind.\ value_{(C,N)} + Pop.\ Calibration\text{-}Offset_{(C,N)}$$

$$Residual\ Ind.\ Variability_{(C,N)} = Ind.\ Expected\ value_{(C,N)} - Ind.\ Measured\ Value_{(C,N)}$$

Residual individual variability measures indicate the deviation of each individual from the average population calibration-offset value, reflecting the range of trophic levels that individuals from the same population are feeding over and any individual variability in isotopic fractionation due to differences in diet quality and physiological stress (McMahon et al. 2015). The extent of residual individual isotopic variability associated with diet within species and feather types were displayed graphically using density histogram plots produced in R 3.1.2 (R Core Development Team 2016).

Results:

Population Moult Location:

In all species and feather types the population median isotope-based assignment areas overlapped light-based estimates of likely location during the moulting period, indicating consistency of methods and allowing refinement of the most likely foraging areas during moult (Fig. 3). The refined most likely foraging area, determined from the coupled geolocation approach, shows greater precision in comparison to either geolocation method used alone, as depicted by the reduced surface area (Fig. 3). The guillemots most likely grew their secondary and neck feathers while in the mid to southern North Sea (Fig. 3A-B).

Razorbills also most likely grew cheek feathers in the southern North Sea (Fig 3C), whereas body and secondary feather moult likely occurred off east England or north of the Firth of Forth (Fig. 3D-E). For puffins, the most likely location of foraging prior to feather moult was off northeast Scotland or east England across all feather types (Fig. 3F-H).

Population and individual level offsets:

Isotopic offsets between jellyfish and feather tissues for carbon ($\delta^{13}C_{f\text{-}j}$) were relatively similar across all species and feather types, with specific species and feather type calibration-offset values falling within 2‰ and ranging between -0.77 and 0.91‰ (Table 3, Fig. 4). Guillemot feather isotope values had consistently higher $\delta^{13}C$ values than jellyfish tissue whereas puffins had lower $\delta^{13}C$ values and razorbill feathers showed mixed results (Table 3, Fig. 4). Isotopic offsets between feather keratin and jellyfish bell tissues for nitrogen ($\delta^{15}N_{f\text{-}j}$) ranged from 4.53-7.23‰. $\delta^{15}N_{f\text{-}j}$ values were highest for guillemots, followed by razorbill cheek feathers. Razorbill body and secondary feathers and all puffin feather types had similar $\delta^{15}N_{f\text{-}j}$ values (Table 3, Fig. 4).

A large degree of residual individual variability in diet-related isotopic compositions was observed within species and feather types (individual $\delta^{13}C$ values ranged from 0.74-3.13‰ and $\delta^{15}N$ values ranged from 0.92-3.73‰), likely representing up to 1 trophic level difference between individuals within a population (Fig. 4). In general, guillemots showed the greatest among individual residual isotopic variability in both feather types, with greater variability observed in $\delta^{15}N$ values. Razorbill and puffin body feathers also displayed greater among-individual residual variation in $\delta^{15}N$ values, compared to $\delta^{13}C$ values, whereas the opposite

372 was observed within secondary feathers (Fig. 4). The small number of individual puffin
373 cheek feather samples prevents reliable interpretation of results.
374
375 **Discussion:**
376
377 Both bird-borne data loggers and isoscape assignment geolocation methods produce
378 relatively accurate location and resource origin information with quantifiable degrees of error
379 (Phillips et al. 2004, Trueman et al. 2017), but both methods currently lack precision.
380 Combining the two techniques begins to address some of complications surrounding isoscape
381 assignment, particularly calibration-offsets when the species of interest is different to the
382 organism used to define the isoscape. Combining geolocation approaches may improve
383 assignment precision whilst maintaining accuracy and provides additional information on
384 individual dietary variation during the annual moult. Here we combined light-based and
385 stable-isotope based geolocation methods to compare foraging location and trophic position
386 in three species of auk while they were growing wing and body feathers, but the approach
387 could readily be applied to other populations of seabird that winter in the North Sea and can
388 be fitted with data loggers.
389
390 **Feeding locations during moult:**
391
392 The most likely foraging region of Isle of May guillemots during post-breeding secondary
393 feather growth and pre-breeding neck feather growth in guillemots was in the southern North
394 Sea. This area has previously been identified as a major wintering area for guillemots
395 including those from the Isle of May (Stone et al. 1995, Harris et al. 2015b), but our results
396 emphasise its importance for moult. To our knowledge, the light based data logger results

presented here are the first for razorbills from a North Sea colony. Taken together with the stable isotope data they indicate that foraging during the post-breeding body and secondary feather growth most likely occurred in waters off the east coast of England, whereas pre-breeding cheek feather growth primarily occurred in the southern North Sea suggesting a shift in foraging location during different feather moults. Individual puffin overwintering areas vary greatly, with locations of birds from the Isle of May sometimes extending beyond the North Sea into the northeast Atlantic (Harris et al. 2010, Harris et al. 2013). In our study, puffin foraging areas during moult of individuals that remained in the North Sea were relatively consistent across the three feather types, with the most likely foraging areas during autumn and spring restricted to waters off the east coast of Scotland and northeast England.

Body feathers of pelagic species are not always grown outside the breeding season (Graña Grilli & Cherel 2016), which could affect interpretation of the results. However, neck and cheek feather moult of these auk species definitely occurs outside the breeding season as indicated by the change in feather colour between the summer and winter plumage. Isotope-based geolocation is currently only possible within the North Sea; a more extensive isoscape is required to investigate foraging location during moult of populations with winter distributions that extend beyond the North Sea into the east Atlantic.

Diet during moult:

In the absence of a dataset of tissue samples from animals from known spatial origins, accurate spatial assignment to an isoscape relies on determining trophic level and tissue offset estimates for each individual and species (e.g. (Trueman et al. 2017)). In our study, locations of individual auks estimated via light-based data loggers were used to calibrate isotopic

offsets between the reference isoscape and feather tissues, and therefore derive population level (combined tissue and trophic) calibration-offset values. By then assuming that the isotopic contrast associated with differing protein composition of jellyfish bell tissue and species and feather specific keratin is constant, between-individual residual variations in isotopic composition should reflect differences in individual dietary effects.

In general, inferred trophic positions were in line with previous studies of winter diet, i.e. with guillemots feeding at a higher trophic level than razorbills (Blake 1984, Blake et al. 1985). The trophic niche of puffins has been found to decrease from a highly specialised high trophic level diet in summer to a more generalized lower trophic level diet, consisting of more invertebrate prey items, in winter (Hedd et al. 2010, Harris et al. 2015a). Our results add to this picture and suggest that within the North Sea auk community guillemot, razorbill and puffin populations have different winter diets during different feather moult periods and trophic level segregation could be a mechanism to reduce interspecific competition outside the breeding season.

The high degree of residual individual variability (Table 3, Fig. 4) between and within feather types and species indicates flexible and generalist diets during the moulting periods. Such flexibility in winter diet has been found in many other species, with individuals also displaying as much as one trophic level difference between diets (Phillips et al. 2009, Young et al. 2010, Grecian 2011, Phillips et al. 2017). Guillemots were observed to have the greatest residual individual variability, potentially representing a flexible and adaptive winter diet (Blake et al. 1985, Smout et al. 2013). Both puffin and razorbill individuals displayed reduced isotopic residual variability for nitrogen during secondary feather moult, indicating a more uniform population behavioural response during flight feather regrowth. Isotopic

residual variability differed between feather types and between species, suggesting different population and individual scale foraging strategies, during different feather moult time periods. Whilst observed differences in residual isotopic variability seem biologically plausible in terms of dietary differences, variability could also be a result of spatially diverse foraging locations, different body conditions or potentially different melanin content across the different feather types (Michalik et al. 2010, McMahon et al. 2015, Phillips et al. 2017). Further work is needed to clarify these sources of variation.

Method constraints:

Our approach of combining light based and isotope-based geolocation methods has some limitations. In the absence of sampling constraints, the calibration-offset values for each population and feather type would be calculated from an additional training data set covering the range of all possible locations. However, the volume of data required is beyond the scope of many tracking studies. We appreciate that there is circularity in our approach: we use the estimated population-level calibration-offset values to infer location and individual level diet within the same individuals. In addition, although we have demonstrated an increase in method precision by combining two techniques we are currently unable to explicitly quantify the cost in terms of accuracy. Without a further third, independent measure of individual seabird location such as satellite or immersion tags (e.g. (Cherel et al. 2016), we are unable to quantify the proportion of birds truly undertaking moult within the inferred most likely foraging region, or how this differs to the accuracy achieved for each method alone. As satellite tags get smaller and less expensive to deploy, we suggest further research quantifying the relative cost of accuracy corresponding to the increased precision identified by this technique.

Conclusions:

Both bird-borne data loggers and isoscape assignment geolocation techniques have their limitations and associated errors. However, used in combination they provide a powerful approach to better constrain foraging areas and diet, as well as facilitating exploration of individual differences and flexibility in foraging behaviour during moult. Such information is urgently needed for the North Sea both to inform marine spatial planning decisions, for example the positioning of offshore renewable energy developments, and to develop effective conservation strategies by assessing regions of importance and therefore vulnerability to anthropogenic activities, such as increased fishing efforts.

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675

676 Table 1. Sample sizes of feathers collected from data logger-equipped birds known to spend

677 the winter within the North Sea.

678
679

	Guillemot		**Razorbill**			**Puffin**		
Feather Type	**Neck**	**Secondary**	**Cheek**	**Body**	**Secondary**	**Cheek**	**Body**	**Secondary**
Sample size (Birds)	18	19	7	9	9	3	12	12

680 Table 2. Assignment conditions adopted for stable isotope-based location of guillemots,

681 razorbills and puffins against isoscapes derived from jellyfish tissue.

682

Variable	**Isoscape**	**Seabird Assignment**		
	Jellyfish	**Guillemot**	**Razorbill**	**Puffin**
Measurement error (σ) (measured)(‰)	$\delta^{13}C$ & $\delta^{15}N$: 0.2	$\delta^{13}C$ & $\delta^{15}N$: 0.2		
Between individual variance (measured)(‰)	$\delta^{13}C$: 0.78, $\delta^{15}N$: 1.02	$\delta^{13}C$: 0.52, $\delta^{15}N$: 0.91	$\delta^{13}C$: 0.51, $\delta^{15}N$: 0.58	$\delta^{13}C$: 0.53, $\delta^{15}N$: 0.56
Calibration-Offset and variance values	NA	*Derived – see Results Table 3 below.*		
Threshold odds ratio	NA	1.42		

683 Table 3. Population calibration-offset values and combined variances calculated from the
684 difference between median extracted isotope values and median measured isotope values.
685 Individual isotope difference values are the difference between individual expected isotope
686 values (individual extracted + population offset) and individual measured values and
687 represent individual diet differences.

688
689

	Guillemot		**Razorbill**			**Puffin**		
Feather Type	**Neck**	**Secondary**	**Cheek**	**Body**	**Secondary**	**Cheek**	**Body**	**Secondary**
δ^{13}C Cal. Offset (‰)	0.75 ±1.68	0.47 ±1.33	0.91 ±1.02	-0.33 ±1.07	-0.08 ±1.18	-0.2 ±0.84	-0.65 ±0.98	-0.77 ±0.73
δ^{15}N Cal. Offset (‰)	7.23 ±2.81	6.74 ±2.20	6.30 ±2.70	4.64 ±1.11	4.86 ±0.74	5.87 ±1.02	4.53 ±0.97	5.21 ±0.93
δ^{13}C Ind. Diff. (‰)	-0.62 – 2.51	-0.65 – 0.91	-0.25 – 1.86	-0.33 – 1.00	-0.21 – 1.41	-0.15 – 0.59	-0.87 – 1.31	-1.47 – 0.83
δ^{15}N Ind. Diff. (‰)	-1.67 – 2.06	-1.70 – 1.20	-0.72 – 0.71	-1.18 – 0.76	-0.21 – 0.89	-0.84 - 0.08	-1.28 – 1.50	-0.75 – 0.75

690 **Fig. 1** Schematic depicting the location of the Isle of May within the Firth of Forth, SW
691 Scotland and the methodology used to determine the calibration-offset value between seabird
692 measured feather isotope values and isoscape isotope values within the over winter locations
693 indicated by light-based data loggers. This method was repeated for both $\delta^{15}N$ and $\delta^{13}C$
694 values for all species and feather types
695
696 **Fig. 2** Graphical representation of assumed moult timings used for subsetting data logger-
697 based geolocation data in guillemots, razorbills and puffins. The prolonged period for
698 secondary moult of puffins is due to the extreme inter-bird variability in the timing of this
699 moult
700
701 **Fig. 3** Population isoscape assignment areas (purple: darker colours indicate more individuals
702 consumed food resources from this area) and corresponding kernel density (green: where
703 density values were >0.01) areas for the months when moult of each feather type for each
704 species (guillemots, razorbills and puffins) is known to occur. Guillemot (a,b) secondary and
705 neck feathers, razorbill (c,d,e) body, secondary and cheek feathers and puffin (f,g,h) body,
706 secondary and cheek feathers. Overlap area, and therefore the highest likely foraging area
707 during feather moult is indicated in dark violet
708
709 **Fig. 4** Individual carbon and nitrogen isotope variability of guillemot, razorbill and puffin
710 feathers displayed in density histograms. Individual variability is calculated by determining
711 the difference between the individual expected and measured isotope values, where expected
712 values are individual extracted isotope values plus/minus the population calibration-offset.
713 Guillemot (a,b) secondary and neck feathers, razorbill (c,d,e) body, secondary and cheek
714 feathers and puffin (f,g,h) body, secondary and cheek feathers. Numbers in green ($\partial^{15}N$) and

715 purple ($\partial^{13}C$) are the isotope variability ranges for each feather type and species, n = number

716 of individuals.

Fig. 1

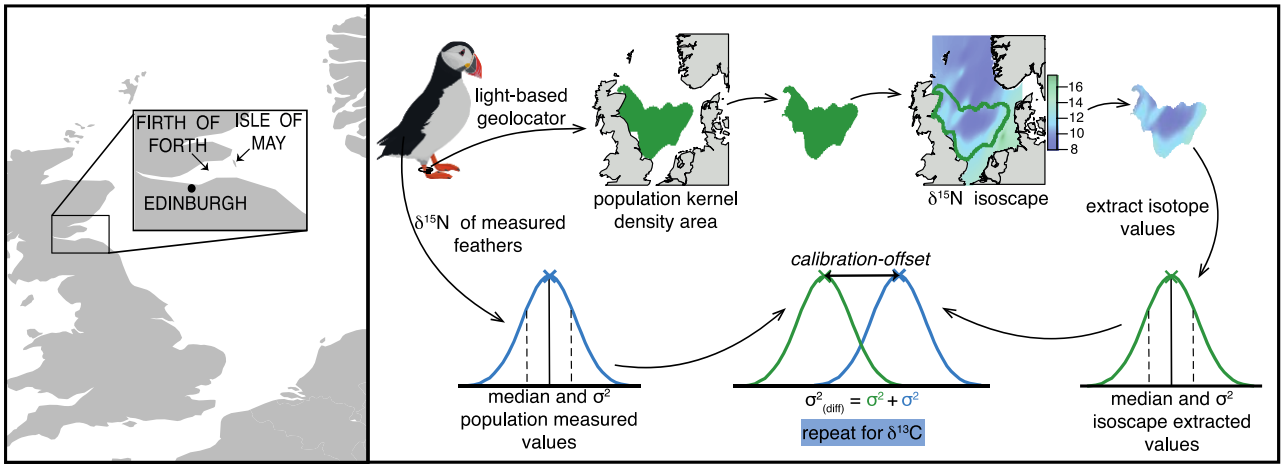
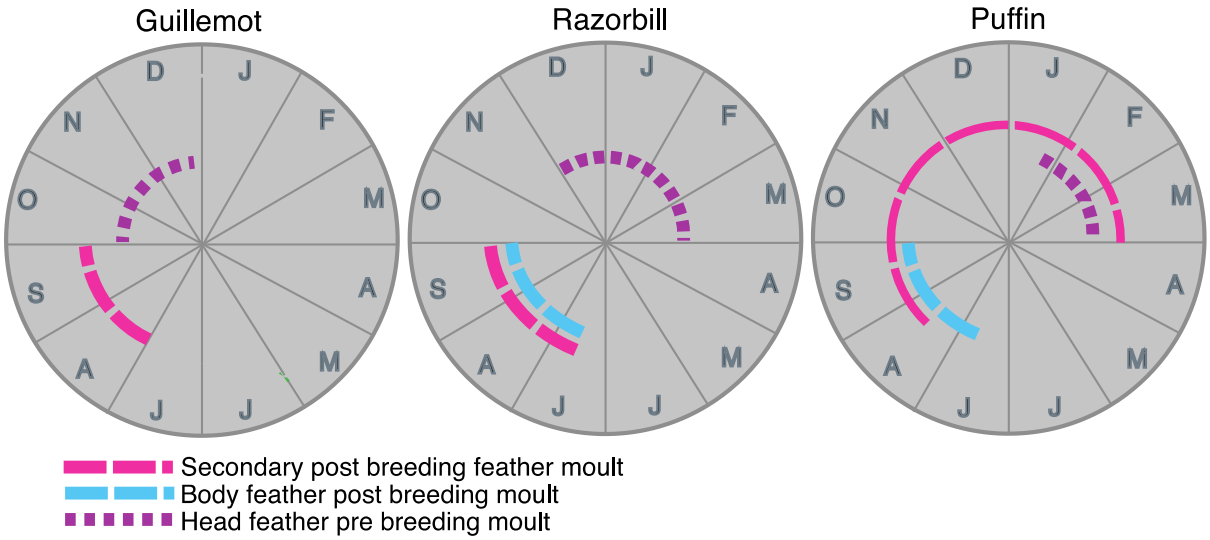

FIRTH OF FORTH
ISLE OF MAY
EDINBURGH
light-based geolocator
population kernel density area
δ15N isoscape
16
14
12
10
8
extract isotope values
δ15N of measured feathers
calibration-offset
median and σ2 population measured values
σ2(diff) = σ2 + σ2
repeat for δ13C
median and σ2 isoscape extracted values

Fig. 2


Guillemot
Razorbill
Puffin
D
J
F
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A
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S
O
N
Secondary post breeding feather moult
Body feather post breeding moult
Head feather pre breeding moult

Fig. 3

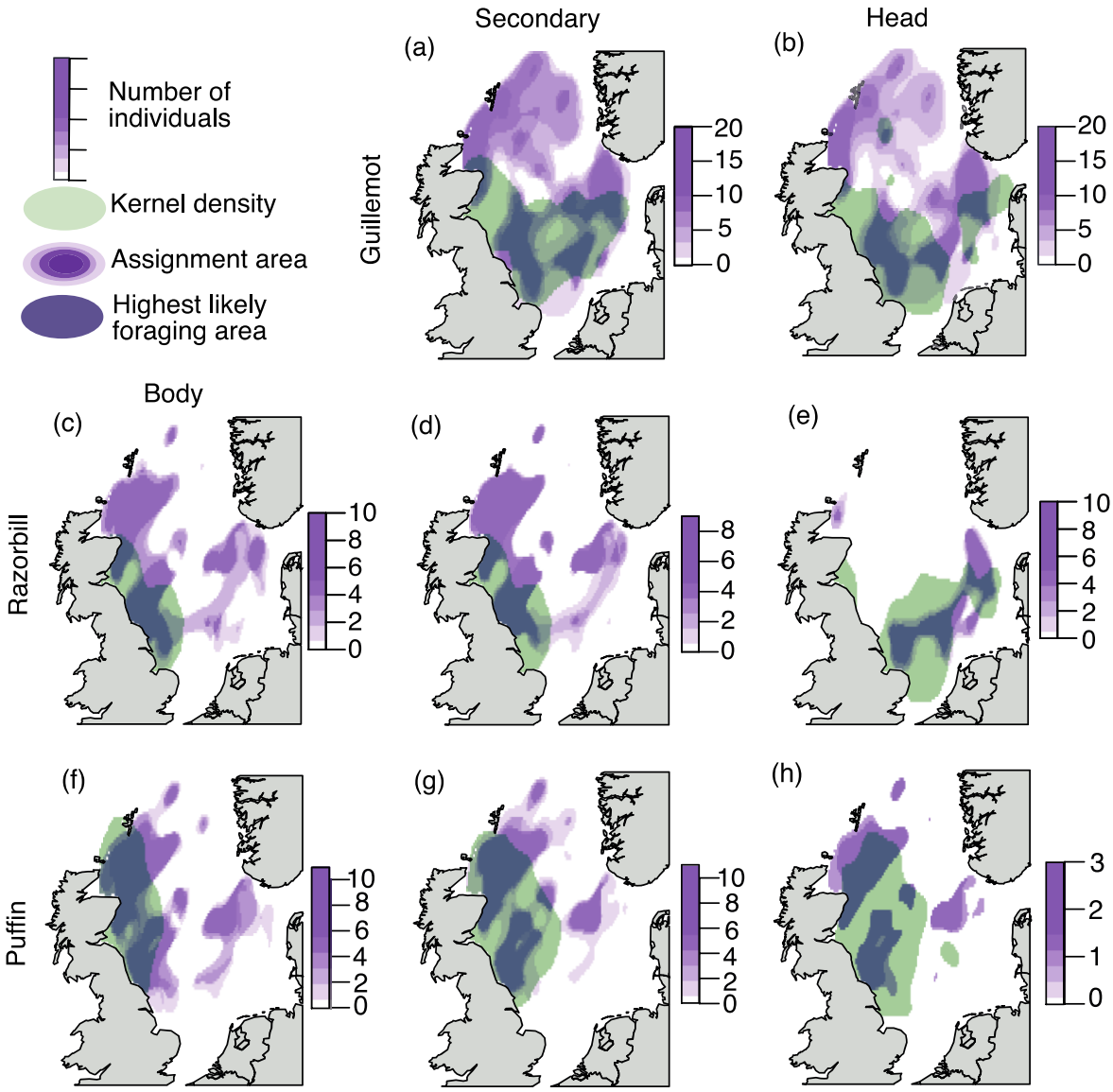
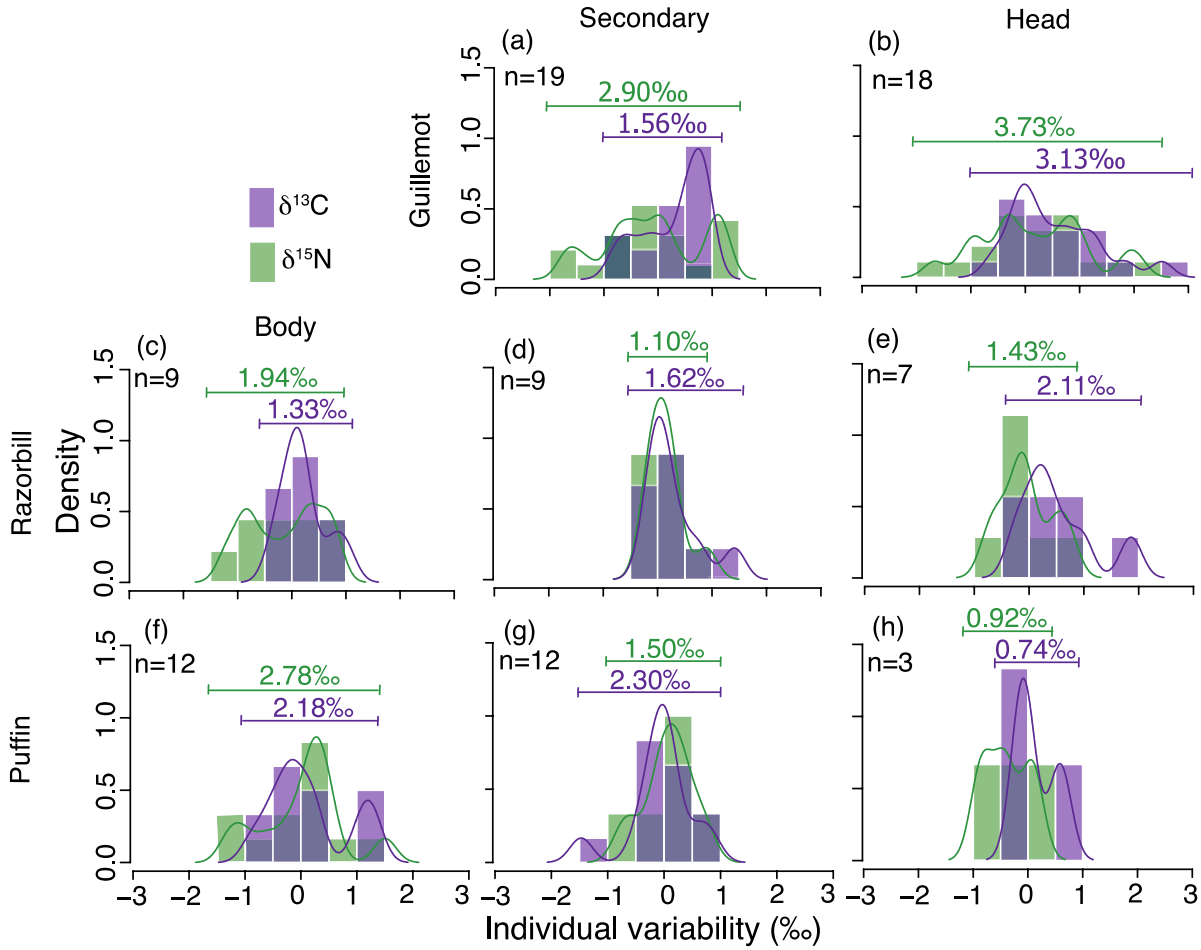

Number of individuals
Kernel density
Assignment area
Highest likely foraging area
Secondary
Head
Body
Guillemot
Razorbill
Puffin
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
20
15
10
5
0
8
6
4
2
3
1

Fig. 4


Secondary
Head
Body
(a)
n=19
2.90‰
1.56‰
(b)
n=18
3.73‰
3.13‰
(c)
n=9
1.94‰
1.33‰
(d)
n=9
1.10‰
1.62‰
(e)
n=7
1.43‰
2.11‰
(f)
n=12
2.78‰
2.18‰
(g)
n=12
1.50‰
2.30‰
(h)
n=3
0.92‰
0.74‰
δ13C
δ15N
Guillemot
Razorbill
Puffin
Density
Individual variability (‰)