



FEATURE ARTICLE



Sexual segregation of gannet foraging over 11 years: movements vary but isotopic differences remain stable

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ABSTRACT: Sex-specific niche differentiation is common in marine vertebrates, but how this varies long-term is poorly understood. Here we investigated interannual variation in sexual segregation among breeding northern gannets *Morus bassanus*, wide-ranging central-place foragers with slight sexual dimorphism. Over 11 breeding seasons, we used GPS tracking and/or stable isotopes to test for sex differences in foraging trip characteristics (range, duration and timing); spatial distribution; habitat selection; and carbon and nitrogen isotopes in blood. When combining data from all years, females foraged further and for longer than males, yet despite this, the foraging areas of the sexes almost completely overlapped. Males and females selected foraging habitats that differed in terms of oceanography but not fishing vessel density. We also detected temporal segregation: females were more likely to be at sea during the day than at night, while males were more likely to be at sea during the night. However, foraging behaviour quantified by all GPS analyses varied interannually, with sex differences detected in some years but not others. Finally, males had consistently higher red blood cell $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ than females across all years, which was not driven by size dimorphism, instead likely by prey choice or very fine-scale habitat selection. We conclude that environmental variation influenced short-term sex differences in movement, but sex differences in stable isotopes that integrate behaviour over longer periods reveal more consistent differences. Our results suggest that inferences drawn from single-year studies may not relate to general patterns, highlighting the importance of long-term studies and combining methods.



Northern gannet *Morus bassanus* female and male swap between foraging and guarding their chick on Grassholm, Wales, UK.

Photo: Bethany Clark

KEY WORDS: Sex-specific · Ecological niche · Stable isotopes · Biologging · Seabird · Central-place foraging · Northern gannet · *Morus bassanus*

1. INTRODUCTION

Male and female animals frequently occupy separate foraging niches (Myysterud 2000, Catry et al. 2005, Wearmouth & Sims 2008), hypothesised to be driven by a combination of competitive displacement

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and sex-specific specialisation (Catry et al. 2005). Sex-specific foraging plays a major role in structuring species distributions by reducing intraspecific competition (González-Solís et al. 2000, Catry et al. 2005) and allowing the sexes to differ in activity budgets or nutritional requirements related to their reproductive roles (Ruckstuhl & Neuhaus 2002). Sex-specific niches can manifest in different ways, including in space, time, habitat use, diet and parental roles (Selander 1966, Bernstein & Maxson 1984, Mysterud 2000, Fraser et al. 2002, Breed et al. 2006). The degree of sexual segregation can vary over time, both between breeding stages (Phillips et al. 2004) and across the annual cycle (Castillo-Guerrero & Mellink 2011, Besel et al. 2018), but few studies have examined this over long periods. Therefore, the persistence of such niche segregation is rarely known and needs to be addressed by multi-year studies during which environmental conditions are likely to vary, and by using multiple approaches to understand how the method chosen impacts our ability to detect differences.

Seabirds are a useful model for studying sexual segregation as they are socially monogamous and share parental duties (Lack 1968), restricting both sexes to the colony such that they compete during breeding. Moreover, their longevity and the large scale of their foraging trips allows us to explore segregation over a range of ecological conditions. Studies have revealed sex differences in broad-scale space use, fine-scale habitat use, activity patterns, diet and trophic position (Solís et al. 2000, Bearhop et al. 2006, González-Harris et al. 2013, De Pascalis et al. 2020). Such studies are generally conducted over 1–3 breeding seasons (e.g. Becker et al. 2007, Woo et al. 2008, Elliott et al. 2010, Burke et al. 2015), with few examining long-term variability (but see Paiva et al. 2017). Determining the extent to which sex differences are maintained over multiple years provides insight into the possible influence of extrinsic and intrinsic factors that underpin such differences.

Most studies of sexual segregation have focussed on size dimorphic species (Ruckstuhl & Clutton-Brock 2006, Phillips et al. 2011), and have demonstrated that size differences explain significant amounts of variation in habitat selection and foraging behaviour (Selander 1966, Ruckstuhl & Neuhaus 2002, Wearmouth & Sims 2008). However, monomorphic seabirds also segregate by sex (Thaxter et al. 2009, Hedd et al. 2014), and there is no evidence that the degree of size dimorphism is linked to the degree of dietary segregation (Mancini et al. 2013). The mechanisms for sex-specific foraging in species where the sexes are broadly similar in size are often

unclear, as males and females appear to have similar physical abilities to access prey and therefore potentially more flexibility in the extent to which their foraging niches overlap. Differences may instead be linked to distinct parental roles in which males prioritise nest defence and females prioritise chick provisioning (Burger 1981, Wojczulanis-Jakubas et al. 2009). As such, considering behavioural sex differences without clear morphological differences promotes a greater understanding of the processes underlying sex-specific foraging.

Here, we investigated long-term patterns in the sex-specific foraging behaviour of a slightly dimorphic species, the northern gannet *Morus bassanus* (hereafter 'gannet'). Previous research revealed sex differences over 1–3 breeding seasons in isotopic niche, departure direction, dive characteristics, foraging trip distance and duration, and habitat selection (Lewis et al. 2002, 2004, Stauss et al. 2012, Cleasby et al. 2015, Cox et al. 2016). We used GPS tracking and stable isotopes to test for sex differences in trophic (isotopic), spatial and temporal niches across 11 breeding seasons from 2006 to 2017. We aimed to measure the stability of foraging niche differentiation between the sexes to provide insights into the drivers of sexual segregation whilst highlighting methodological considerations for similar studies.

2. MATERIALS AND METHODS

2.1. Study site and sampling

Fieldwork took place on Grassholm Island, Wales, UK (51° 43' N, 05° 28' W), during the chick-rearing periods (late June to August) of 11 breeding seasons (2006 and 2008–2017, with GPS tracking in 2006 and 2010–2017, and stable isotope sampling in 2006, 2008–2014 and 2016). The colony held ~30 000 pairs during the study period (Murray et al. 2015, Deakin et al. 2019). Adult gannets were captured at the nest using a carbon fibre pole with a noose or crook during the changeover between partners so that chicks were not left unattended. We captured the outgoing parent to ensure that foraging trips began immediately after release. GPS loggers were attached to the lower back or central tail feathers with Tesa® 4651 cloth tape. In 2006, birds were equipped with Earth and Ocean Technology 'GPSlog' loggers (65 g) set to record fixes every 3 min. In 2010–2017, birds were equipped with Mobile Action Technology i-gotU GT-120 (18 g) or GT-600 (35 g) loggers set to record fixes every 1 or 2 min. In some years, a subset of birds was

equipped with additional loggers (time depth recorders, altimeters, accelerometers or video cameras) with a maximum total weight of 50.5 g, but their presence had no effect on the spatial foraging behaviours recorded here (M. Francis et al. unpubl.). Studies have shown no effects of loggers weighing 20, 30 or 70 g on the foraging trip duration or body mass of chick-rearing gannets (Lewis et al. 2002, Hamer et al. 2007, 2009, Cleasby et al. 2015). Individual consistency in the foraging trip destination and dive location of chick-rearing individuals means that tracking a single foraging trip is likely to be representative of that individual within years and, to a lesser extent, between years (Patrick et al. 2014, Wakefield et al. 2015, Votier et al. 2017). A 1–2 ml blood sample was taken from the tarsal vein using 23–25-gauge needles for stable isotope analysis and molecular sexing. We recorded mass to the nearest 50 g, flattened wing chord length to the nearest 1 cm and bill length to feathering to the nearest 0.1 mm. All procedures were carried out under licence from Natural Resources Wales (22478:OTH:SB:2010), the British Trust for Ornithology (BTO:A4257), the BTO Special Methods Panel and the UK Home Office (30/3065).

2.2. Foraging trip range and duration

We defined foraging trips as beginning and ending when individuals crossed a radius of 200 m from the centre of the colony (approximately the radius of the island) and excluded incomplete trips. We calculated foraging range (maximum Euclidean distance from the colony) using the R package ‘geosphere’ (Hijmans 2017). Range and trip duration were Box-Cox transformed, then modelled as functions of sex, year (treated as a factor), mass (as females are 6.8% heavier than males, with no difference in bill or tarsus length; Table S1 in the Supplement at www.int-res.com/articles/suppl/m661p001_supp.pdf) and a sex:mass interaction using linear mixed-effects models in the R package ‘lme4’ (Bates et al. 2014), with random intercepts for each individual. We present the models with the lowest value of Akaike’s information criterion corrected for sample sizes (AICc).

2.3. Spatial segregation

We used GPS locations to quantify the broad-scale spatial overlap of foraging trips between males and females for each year. We subsampled locations to the nearest 2 min interval and excluded loca-

tions within 6.8 km of the colony, as gannets from Grassholm rest on the water in this area (Carter et al. 2016). We projected locations onto a Lambert azimuthal equal-area projection centred around the colony and estimated 100% utilisation distributions (UDs) for each year and sex with kernel density estimation in the R package ‘adehabitatHR’ (Calenge 2006), using the bivariate normal kernel with a cell size of 500 m and a smoothing parameter of 11 km (chosen to reflect the mean area-restricted search scale for foraging gannets of 9.1 ± 1.9 km, Hamer et al. 2009). We measured UD overlap using Bhattacharyya’s affinity (BA), which uses the kernel density in 3D, as this is robust to outliers and considers the parts of the distributions that do not overlap as well as parts that do. BA ranges from 0 (no overlap) to 1 (total overlap) (Bhattacharyya 1943, Fieberg & Kochanny 2005). We tested for a significant difference between the observed BA and a null distribution generated from 1000 randomisations of sex using the observed sex ratio of each year. Significance is defined as when P , the proportion of randomised BAs that do not exceed the observed BA, is less than 0.05 (see Breed et al. 2006, Cleasby et al. 2015). As sample sizes varied between 29 (in 2006) and 203 trips, we repeated the procedure with 3 random samples of 29 trips for 2010–2017. Home range size was estimated in km^2 using the 95% UD (because home range size is more affected by outliers than BA overlap), and was then Box-Cox transformed and analysed using a linear model in R with sex and number of trips fitted as fixed effects. We calculated 25% UD to visualise core use areas.

2.4. Habitat selection

We tested whether foraging habitat use differed between the sexes as a function of 4 candidate covariates: sea surface temperature (SST), chlorophyll *a* (chl *a*), thermal fronts and fishing vessel density. We included SST and chl *a* given that male gannets from some colonies are more likely to use warmer areas with higher productivity than females (Cleasby et al. 2015). We included thermal fronts as gannets are more likely to perform area-restricted searching behaviour and dive in areas of seasonally persistent fronts (Scales et al. 2014, Cox et al. 2016), and the response to fronts can differ with sex (Cox et al. 2016). Fishing vessel locations were included because gannets scavenge at fishing boats (Votier et al. 2010, 2013, Bodey et al. 2014), with some evidence that males scavenge more than females (Stauss et al. 2012, Votier et al. 2013), al-

though other studies suggest no sex differences in terms of scavenging (Patrick et al. 2015). The Natural Environment Research Council Earth Observation Data Acquisition and Analysis Service (NEODAAS) supplied data for chl *a* concentration (Aqua-MODIS and Suomi-VIIRS, see Gohin et al. 2002), SST (AVHRR, see Miller et al. 1997) and thermal fronts (see Miller 2009) in a 1 × 1 km grid. Composite front maps for the month of July (when the majority of the data were collected) were used to provide sufficient cloud-free time and because persistent fronts are important as foraging habitat (Scales et al. 2014, Cox et al. 2016). To reduce noise from non-persistent transient features, front composites combined the gradient, persistence and proximity of fronts over this 1 mo period (see 'Fcomp' in Suberg et al. 2019). This combined front metric facilitated the analysis by reducing the number of variables included in the habitat models. Vessel monitoring system (VMS) data, on the density of vessels ≥ 15 m in length, was obtained for 3 years (2005–2007) in a 3 × 3 km grid for vessels travelling at speeds of 3–10 km h⁻¹, which indicates fishing activity (Witt & Godley 2007). Although we recognise that these data do not match our tracking period, Witt & Godley (2007) found that fisheries activity hotspots were consistent over a 5 yr period (2000–2004). To account for very high vessel densities near ports, we calculated the maximum vessel density in the study area more than 5 km from the coast, and then excluded values exceeding this maximum within 5 km of the coast (Witt & Godley 2007).

We modelled selection by comparing the habitat at foraging locations with the available habitat (Aarts et al. 2008). We first subsampled GPS data to 2 min intervals and extracted foraging locations based on speed, acceleration and tortuosity thresholds (see Wakefield et al. 2013, Bennison et al. 2018). For each foraging location, we generated 3 pseudo-absences from areas with complete environmental information within the 100% minimum convex polygon for all years (we did not use the 100% UD calculated from the kernel density, as this results in separated areas when gannets could forage in between). We first fitted binomial generalised linear models (GLMs; R package 'glmmTMB', Brooks et al. 2017) with a logit link to model the presence/pseudo-absence of foraging locations in relation to each of the habitat variables (SST, chlorophyll, thermal fronts, vessel density), sex and the interaction between habitat and sex. We did not include bird ID as a random term because all birds were given the same number of pseudo-absences per presence point, so all individuals have the same intercept (probability of any location being a presence or a pseudo-absence).

We did not include random slopes because individual responses did not appear to be linear, even though the population response is in aggregate. To account for spatial autocorrelation, we used residual autocovariate (RAC) models (Crase et al. 2012, 2014, Escalle et al. 2016). To do this, we extracted residuals from a fully fitted GLM to create a gridded raster of the spatial autocorrelation between neighbouring cells (based on a mean focal operation for a first-order neighbourhood) using the R package 'raster' (Hijmans 2018). We extracted the corresponding RAC value for each presence/pseudo-absence location and then re-fitted a GLM including the generated RAC as a linear term (Crase et al. 2012, 2014). We fitted a model for all years, and separate models for each year (2006 and 2010–2016) to investigate interannual variation. We did not have oceanographic variables for 2017. Models were assessed with and without the RAC term using Cohen's kappa, the area under the receiver operating characteristic curve (AUC), and the Boyce index (Boyce et al. 2002, Hirzel et al. 2006).

2.5. Diel segregation

To test whether male and female foraging trips differed with the time of day, we extracted the times of at-sea locations during foraging trips at a 30 min resolution. We analysed the timestamps using the R package 'overlap' designed for quantifying the overlap in diel cycles (Ridout & Linkie 2009). Using this package, we calculated kernel density estimates from the timestamps, with time of day treated as a circular variable such that 23:59 h is 1 min before 00:00 h. We used the recommended smoothing parameter based on simulations in Ridout & Linkie (2009). We tested the overlap between males and females by combining the data for all years, and separately for each year. We quantified the overlap using the $\hat{\Delta}_4$ coefficient of overlap (0 = no overlap, 1 = total overlap) and estimated 95% confidence intervals by bootstrapping with 10 000 resamples (Linkie & Ridout 2011).

2.6. Isotopic segregation

To test for sex differences in diet, we measured stable isotope ratios in red blood cells (which have a turnover of 4–6 wk; Rodnan et al. 1957, Hobson 2005). Blood samples collected in 9 years (2006, 2008–2014 and 2016) were centrifuged to separate red blood cells from plasma. Red blood cells were freeze-dried and homogenised into a fine powder, and 0.7 ± 0.1 mg

was weighed into tin capsules. Analysis took place at the National Environment Research Council National Environmental Isotope Facility in East Kilbride, or the University of Exeter facility at the Environment and Sustainability Institute in Penryn. Results for isotope ratios of carbon $^{13}\text{C}/^{12}\text{C}$ and nitrogen $^{15}\text{N}/^{14}\text{N}$ are expressed as delta (δ) units, as parts per thousand (‰) difference from international standards (Vienna Pee Dee belemnite for carbon and atmospheric N_2 for nitrogen). Using linear models, we modelled stable isotope values for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in response to sex, year (treated as a factor), mass and the interaction between sex and mass.

3. RESULTS

3.1. Foraging trip range and duration

We recorded 645 620 GPS locations during 634 complete foraging trips from 138 female and 159 male gannets across 9 breeding seasons. Females undertook trips with 21% greater foraging ranges and 20% longer trip durations, controlling for mass (Table 1). Mean \pm SE foraging trip range was 107 ± 4 km for males and 129 ± 5 km for females, with a mean trip duration of 20.1 ± 0.8 h for males and 24.2 ± 1.2 h for females (Fig. 1, Tables S2–S4). Heavier individuals of both sexes made shorter trips (Table S3). Foraging range and duration both varied with year, but there were no significant year:sex or year:mass interactions (Table 1, Fig. 1).

3.2. Spatial segregation

There was no difference in home range size across all years (linear model, $F_{2,15} = 1.54$, $p = 0.234$; Fig. 2), but the home range was slightly larger for females in some years and males in others (Fig. 3; Table S2), with a substantial difference in 2006 (223% larger for fe-

males). When the data from all years were combined, the 100% UD for males and females were not significantly different (BA overlap = 0.92, $p = 0.087$; Fig. 2). There was, however, interannual variation (Fig. 3), with significant segregation occurring in 2006 (BA = 0.432, $p = 0.004$) and 2013 (BA = 0.798, $p = 0.022$). As the sample size was smallest in 2006 (29 trips), we took 3 random sub-samples of 29 trips for the years 2010–2017. These produced lower BA values, but no significant segregation was detected (Table S5), indicating that the segregation detected in 2006 was not a result of the smaller number of recorded trips.

3.3. Habitat selection

Male and female gannets differed in their habitat selection, but this was highly variable between years (Fig. 4, Table S6). When combining all years, females made greater use of locations with lower SSTs and higher composite thermal front intensity (combined strength, persistence and proximity) than males. Sex-specific differences in response to SST occurred in 4 years, 5 years for chl *a* and 3 years for thermal fronts. Responses to chl *a* concentrations varied inter-annually in the direction of the effect. There was no sex-specific selection for the density of fishing vessel activity (number of VMS records at fishing speed) when considering all years, but small effects were detected in 3 years when considered individually. The models performed very well ($\kappa = 0.86$ – 0.95 , AUC = 0.98–0.997, Boyce index = 0.797–0.992), although this is partially explained by the residual auto-correlation term (Table S7).

3.4. Diel segregation

Male and female gannet at-sea locations broadly overlapped in their time of day, but the bootstrapped upper 95% confidence intervals (CIs) indicate tempo-

Table 1. Top candidate linear mixed models to explain northern gannet foraging trip range and duration as a function of sex, year and mass, with individual as a random intercept. Means, estimates and test statistics are provided in Tables S2–S4. AICc: Akaike's information criterion corrected for small sample size

Model	AICc	Δ AICc	AICc weights	Deviance	Resid. df	
Range	Sex + Year + Mass + Sex:Mass	1051.2	–	0.564	1022.4	497
	Sex + Year + Mass	1052.0	0.78	0.383	1025.2	498
	Sex + Year	1057.9	6.69	0.020	1033.3	499
Duration	Sex + Year + Mass	378.5	–	0.659	351.7	498
	Sex + Year + Mass + Sex:Mass	379.9	1.40	0.327	351.0	497
	Sex + Year	387.5	9.05	0.007	362.9	499

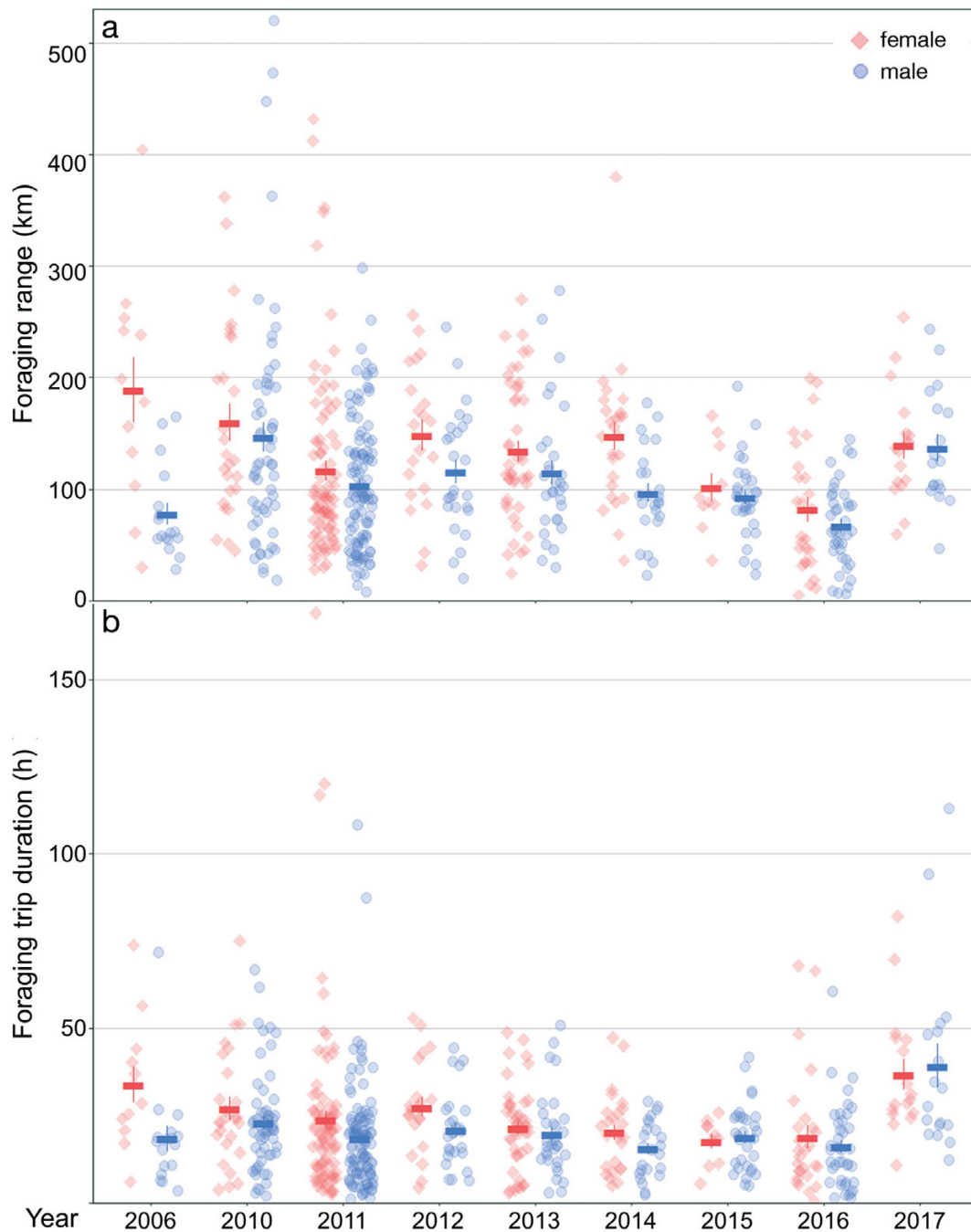


Fig. 1. Foraging trip (a) range (maximum distance from the colony) and (b) duration for 138 female (red diamonds, $n = 272$ trips) and 159 male (blue circles, $n = 362$ trips) chick-rearing northern gannets on Grassholm, Wales, UK. Bars show annual means \pm SE and jittered points show individual trips

ral segregation (across all years: $\hat{\Delta}_4$ coefficient of overlap = 0.970, 95% CI = 0.960–0.980). Males were more likely to have foraging trips that included an overnight component, while females were more likely to be away from the colony during the day (Fig. 5). This effect was detected within 6 of the 9 years studied.

3.5. Isotopic segregation

Stable isotope values for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were significantly different between the sexes and were also significantly associated with year and mass (Table 2). There was a sex:year interaction for $\delta^{13}\text{C}$, with over-

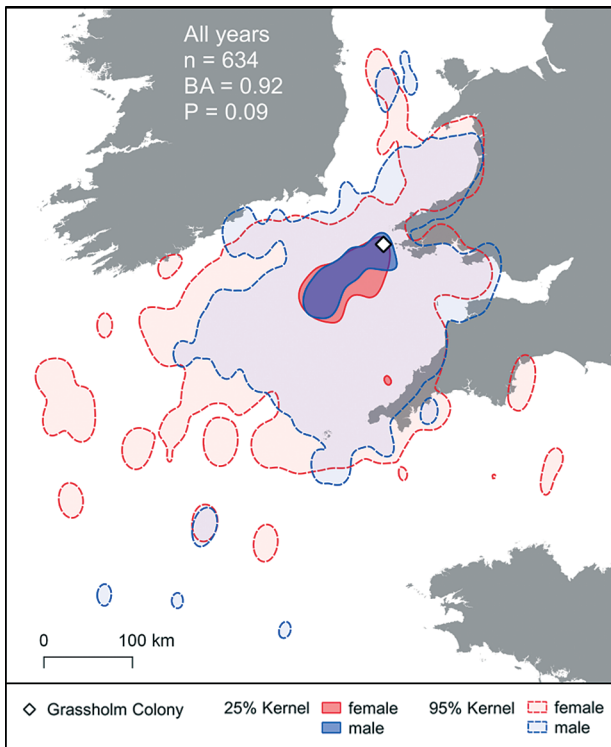


Fig. 2. Home ranges (95% utilisation distribution isopleth) and core areas (25% isopleth) for female (red) and male (blue) northern gannets GPS-tracked from Grassholm, UK, combined across 2006 and 2010–2017. Bhattacharyya's affinity (BA): estimated overlap between male and female 100% utilisation distributions; P: proportion of simulated BAs that did not exceed the observed BA; n: number of trips

lap in 2010 and 2013 (Table 2), but females still had lower mean $\delta^{13}\text{C}$ than males in all years of the study (Fig. 6, Tables S8–S10). There was no sex:year interaction for $\delta^{15}\text{N}$, and errors overlapped only in 2010 (Fig. 6). The best models for $\delta^{13}\text{C}$ ($r^2 = 0.478$) and $\delta^{15}\text{N}$ ($r^2 = 0.479$) also contained a sex:mass interaction, although this was within 2 ΔAICc units of the model without the interaction for $\delta^{15}\text{N}$ (Table 2, Fig. 7). Values for $\delta^{13}\text{C}$ were significantly lower for females than males, and values increased with mass for females (the heavier sex), but not for males (Table 2, Fig. 7).

4. DISCUSSION

By combining GPS and stable isotope analysis, we show that, despite overlap in broad-scale space use, breeding male and female gannets differed in terms of their foraging niche as characterised by foraging trip range, duration and timing, fine-scale

habitat selection and isotopic niche. Importantly, these sex differences varied over the 11 years studied in terms of trip range, duration, habitat selection, timing and space use, while isotopic niche remained consistent.

4.1. Foraging trip range and duration

Overall, females spent 20% more time on foraging trips and reached distances 21% further from the colony than males (Fig. 1). Seabirds of the larger sex generally make shorter foraging trips (Weimerskirch et al. 1997, González-Solís et al. 2000, Lewis et al. 2005). However, female gannets are slightly heavier than males (Table S1) but travelled further. Heavier gannets within each sex made shorter trips in distance and duration, showing that the differences related to sex are not due to size dimorphism (Table 1). Instead, sex differences may relate to competitive exclusion of females (Bodey et al. 2018), sex-specific dietary requirements (Machovsky-Capuska et al. 2016) leading to habitat selection (Cleasby et al. 2015), or males investing more time in nest defence (Burger 1981). A key finding was that sex differences varied among years (Fig. 1) as observed in other seabird species (Ishikawa & Watanuki 2002, Gladbach et al. 2009, Castillo-Guerrero & Mellink 2011, Paiva et al. 2017). This suggests a role for extrinsic factors such as variation in food availability, wind, oceanography or a combination of these things. For instance, breeding female Cory's shearwaters *Calonectris borealis* travelled relatively further than males during years when oceanographic conditions were 'poor' compared to 'good' years (Paiva et al. 2017), as did female Cape gannets *Morus capensis* (Botha et al. 2017). However, prey shortages may also decrease sex differences (Fraser et al. 2002), highlighting the need to better understand how environmental conditions may influence sex-specific foraging.

4.2. Spatial segregation

Male and female foraging areas overlapped extensively, and we only detected significant spatial segregation in 2006 and 2013 (Fig. 3). In contrast, gannets tracked from the much larger colony at Bass Rock, UK, had consistent sexual segregation over 3 breeding seasons (Cleasby et al. 2015). This may relate to a more predictable envi-

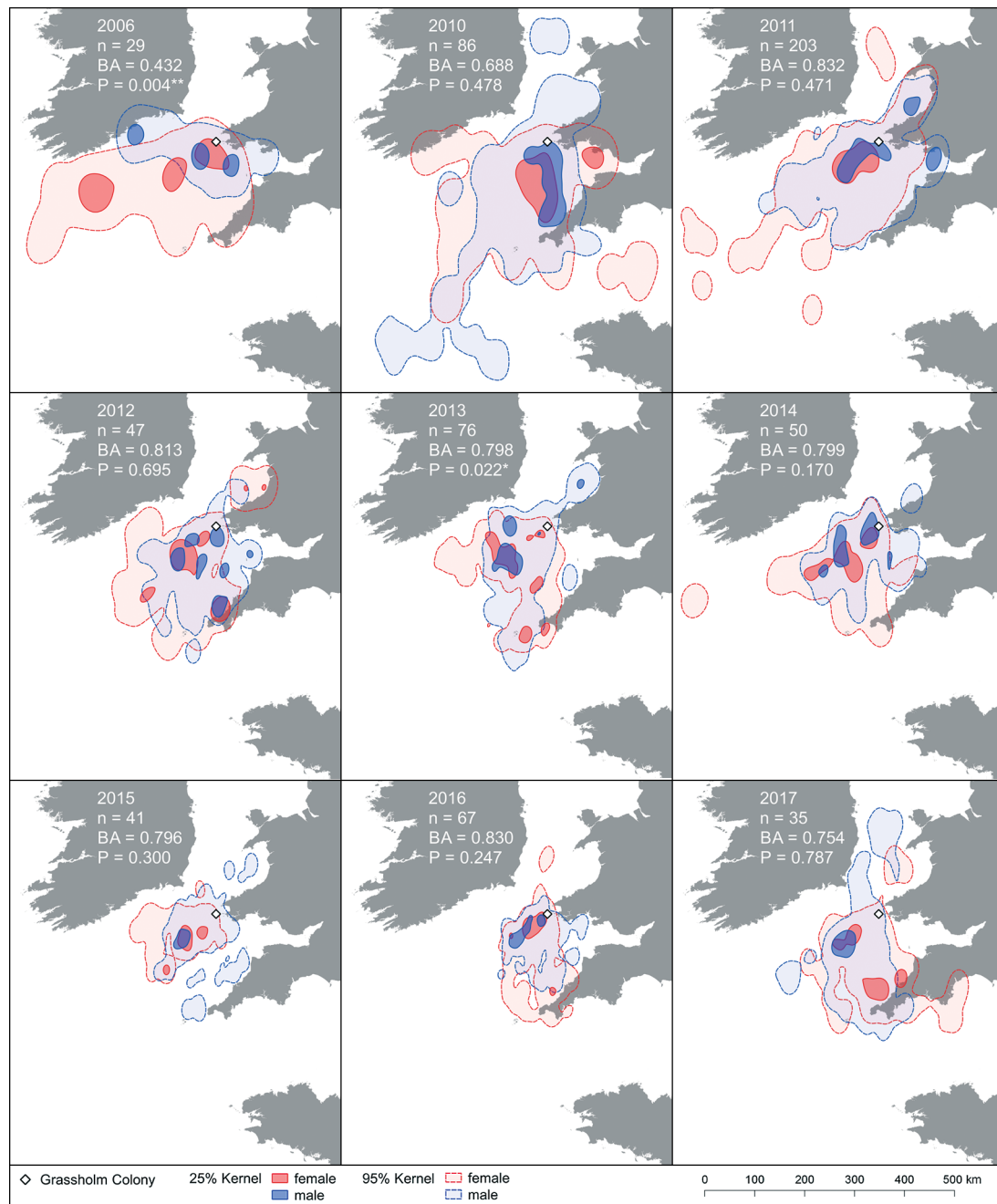


Fig. 3. Annual home ranges (95% utilisation distribution isopleths) and core areas (25% isopleths) for female (red) and male (blue) northern gannets GPS-tracked from Grassholm, UK. Bhattacharyya's affinity (BA): estimated overlap between male and female 100% utilisation distribution; P: proportion of simulated BAs that did not exceed the observed BA; n: number of trips; * $p < 0.05$, ** $p < 0.01$

ronment in the North Sea (Hamer et al. 2001), different coastal morphology creating fewer foraging areas (Cleasby et al. 2015) and/or the larger colony increasing intraspecific competition (Wakefield et al. 2013). Inter-colony variation in sex segregation has been observed for other seabirds, with wandering albatrosses *Diomedea exulans* exhibiting

broad-scale spatial sexual segregation at some sites (Weimerskirch et al. 2012, Åkesson & Weimerskirch 2014), but not others (Xavier et al. 2004, Pereira et al. 2018). These patterns indicate that the extent of spatial segregation is not fixed over time but instead may relate to sex differences in response to intrinsic and extrinsic factors.

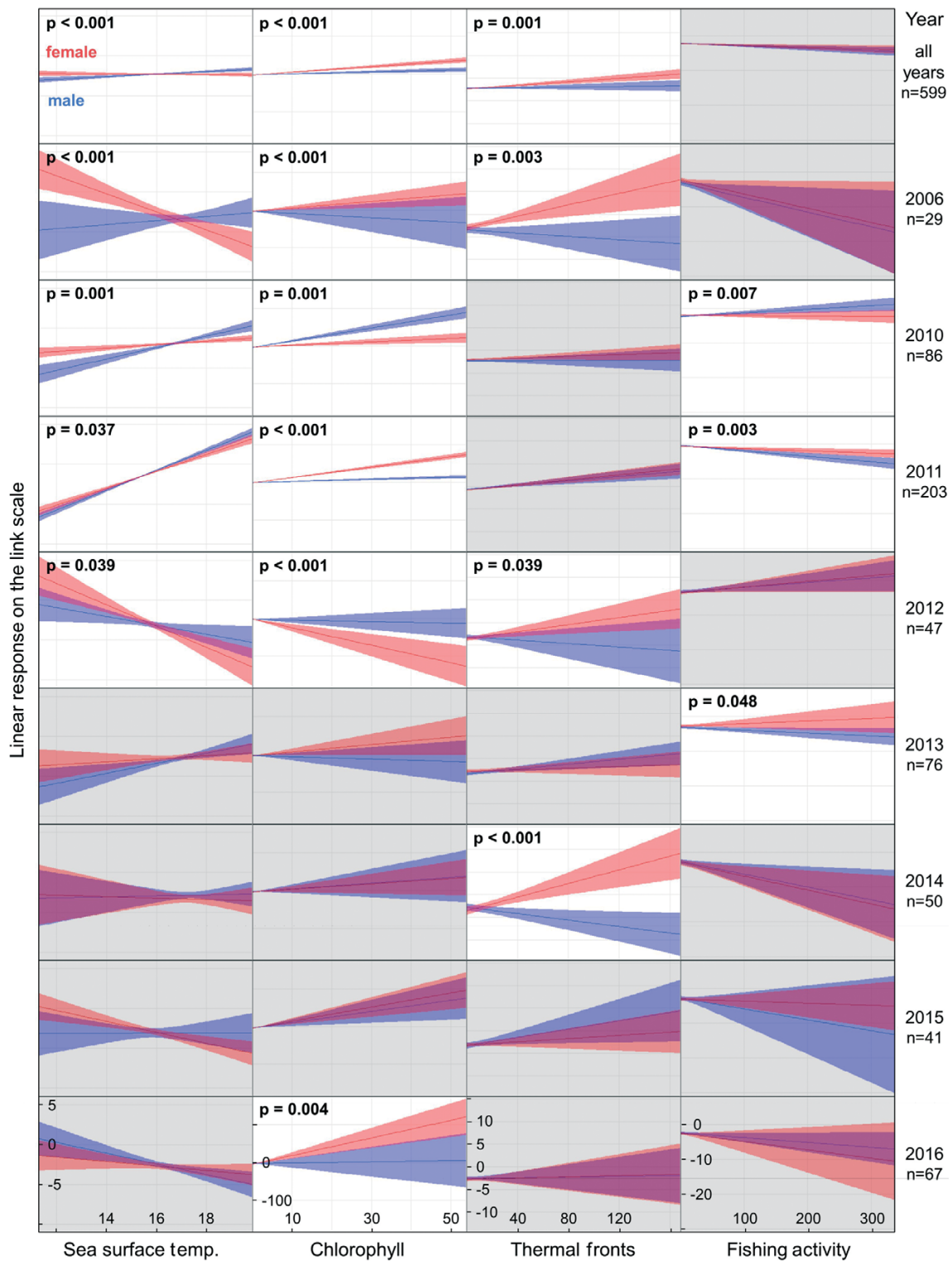


Fig. 4. Habitat selection for female (red) and male (blue) northern gannets GPS-tracked from Grassholm, UK, over 8 breeding seasons. Plots show the predicted linear response on the logit link scale for the probability of locations being a foraging event rather than a pseudo-absence in response to sea surface temperature ($^{\circ}\text{C}$), chlorophyll *a* concentration, thermal fronts (strength, persistence and proximity) and density of fishing vessels travelling at fishing speed. Ribbons represent 95% confidence intervals. Grey shading indicates that the sex:habitat interaction is not significant ($p > 0.05$). p : p -value of the sex:habitat interaction; n : number of trips

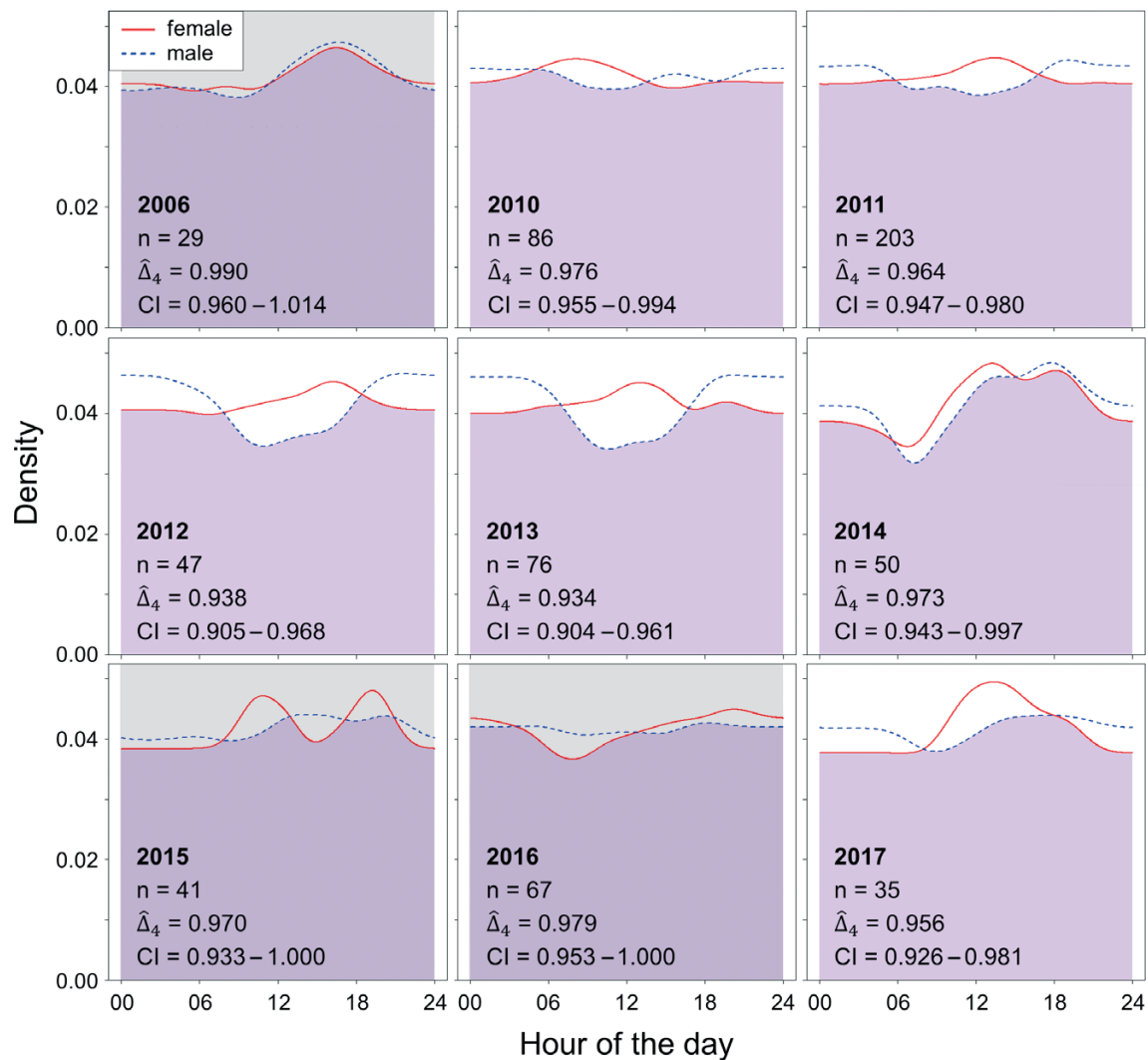


Fig. 5. Density of at-sea locations across the hours of the day for female (red) and male (blue) northern gannets GPS-tracked from Grassholm, UK, during the breeding seasons of 2006 and 2010–2017. Purple shading indicates the overlap between sexes. n: number of trips; $\hat{\Delta}_4$: coefficient of overlap; CI: bootstrapped 95% confidence interval (CIs crossing 1 indicate that no difference was detected; grey shading)

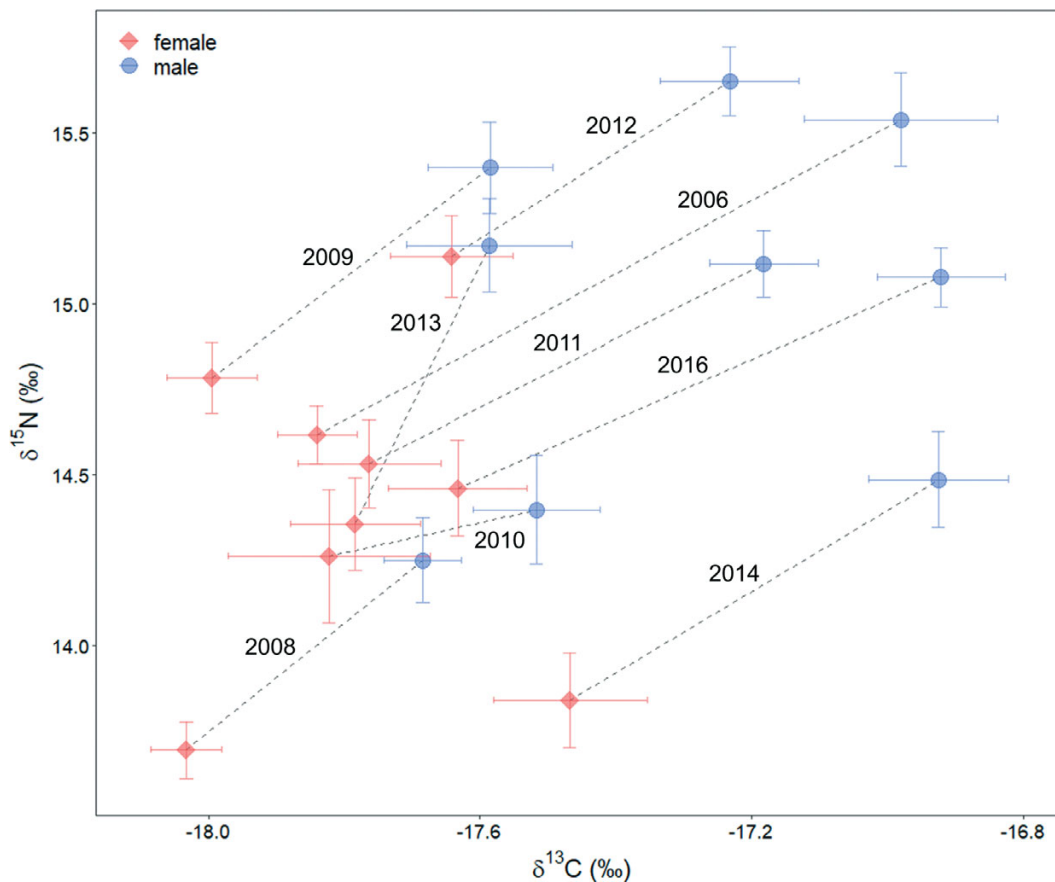
4.3. Habitat selection

We found evidence for sex-specific habitat selection despite large-scale spatial overlap (Figs. 2–4). When effects were detected, females preferred to forage in cooler waters with higher front intensity compared to males. There was no sex difference in response to fishing vessel density when data were aggregated across years. However, small differences were detected in 2010, 2011 and 2013 (Fig. 4), but this may be because the vessel data were not temporally matched to the gannet tracking data. There was much inter-annual variation in the effect size (SST and fronts) and direction (chl *a* and fishing density), indicating that sex differences in habitat choice were

not fixed. We detected a sex interaction with all oceanographic indices only in 2006 and 2012. Overall, responses to the habitat variables measured in our study were highly changeable, which may be explained by the sample of individuals tracked each year, individual flexibility in foraging strategy and/or by interannual variation in local conditions. Individual gannets may have specific habitat types or foraging specialisms (such as scavenging from fishing vessels; Votier et al. 2013), with competitive pressure leading to a diversity of strategies, where the likelihood of choosing a particular specialism may or may not relate to sex. Furthermore, most individual gannets repeatedly use the same foraging areas (Patrick et al. 2014, Wakefield et al. 2015, Votier et al. 2017), and so

Table 2. Top candidate linear models to explain $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope values in blood for northern gannets. Means, estimates and test statistics are provided in Tables S8–S10

Model	AICc	ΔAICc	AICc weights	Resid. deviance	Resid. df	Adj. r^2
$\delta^{13}\text{C}$ Sex + Year + Mass + Sex:Year + Sex:Mass	433.1	–	0.586	62.52	314	0.478
Sex + Year + Mass + Sex:Year	435.2	2.09	0.206	63.34	315	0.473
Sex + Year + Mass	436.8	3.66	0.094	67.11	323	0.477
$\delta^{15}\text{N}$ Sex + Year + Mass + Sex:Mass	577.3	–	0.393	101.54	322	0.479
Sex + Year + Mass	577.4	0.09	0.375	102.23	323	0.477
Sex + Year	579.6	2.31	0.124	103.58	324	0.472

Fig. 6. Mean \pm SE stable carbon and nitrogen isotope values derived from red blood cells for 168 female (red diamonds) and 193 male (blue circles) northern gannets from Grassholm, UK (2006, 2008–2014 and 2016). Dashed lines indicate that values are from the same year

differences in sex-specific behaviour may occur due to changes in the underlying habitat if individuals are more faithful to geographic space than habitat types.

4.4. Diel segregation

There were slight sex differences in the timing of foraging trips; males were more likely to be at sea overnight and females during the day (Fig. 5), as

observed in other sulids (Botha et al. 2017, Miller et al. 2018). This may occur if males invest more in defending the nest against diurnal conspecifics and predators (e.g. great black-backed gulls *Larus marinus*; Garthe & Huppopp 1996). Diel segregation reduces intraspecific competition (Bernstein & Maxson 1984), including between sexes (Elliott & Gaston 2015). However, sex-specific timing of foraging in imperial shags *Phalacrocorax atriceps* occurred only during the breeding season, suggesting that this was

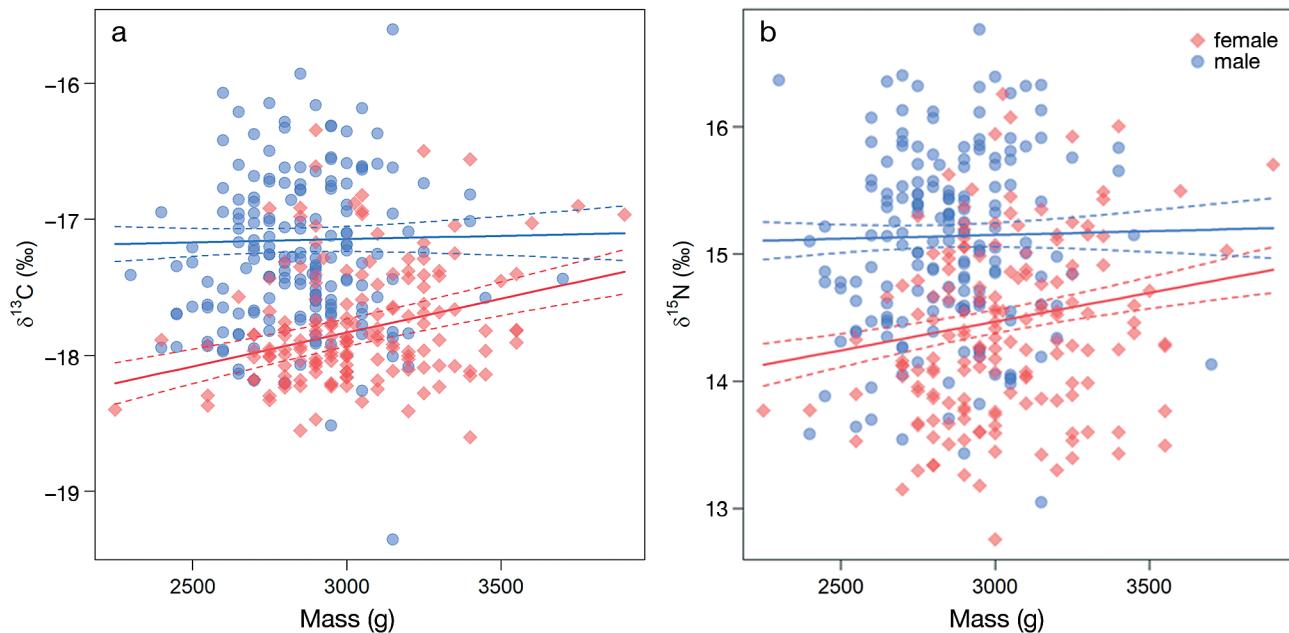


Fig. 7. Stable isotope values for (a) carbon ($\delta^{13}\text{C}$) and (b) nitrogen ($\delta^{15}\text{N}$) in relation to body mass derived from red blood cells for female (red diamonds) and male (blue circles) northern gannets from Grassholm, UK, collected during the breeding seasons of 2006, 2008–2014 and 2016. Solid lines: model predictions; dashed lines: SE

driven by the constraint of competition or attending the nest rather than foraging specialisation (Harris et al. 2013). Diel cycles could also impact gannet diet. Fish tend to inhabit deeper waters during daylight to avoid visual predators (Gliwicz 1986, Wilson et al. 1993), and so diel vertical migration can impact prey accessibility (Garthe et al. 2000, 2007). Male gannets perform overall shallower V-shaped dives than females when accounting for body size differences (Lewis et al. 2002, Cleasby et al. 2015, Cox et al. 2016). There were no sex differences in the depth of U-shaped 'pursuit' dives, but they were less likely at dusk and dawn (Cleasby et al. 2015), which may relate to visibility constraints.

4.5. Isotopic segregation

The strongest and most consistent sex difference was in terms of isotopic niche (Fig. 6). Males had higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than females across all years, although there was some interannual variation in the strength of the effect (Fig. 6). These differences may relate to differences in isotopic baselines (Kelly 2000), such as the tendency for coastal areas to have lower $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than offshore waters (Hobson et al. 1994, Cherel & Hobson 2007). These findings are consistent with more offshore foraging in females, but somewhat at odds with the consider-

able spatial overlap (Fig. 2). The largest difference in $\delta^{13}\text{C}$ occurred in 2006, which also had the greatest spatial segregation, but other years show very high overlap between the sexes. Isotopic differences in the absence of spatial segregation may be because red blood cells represent foraging over the previous 4–6 wk (Hobson 2005), so they are less susceptible to short-term environmental fluctuations that may influence movement behaviour. Alternatively, our results may reflect differences in fine-scale habitat use (Fig. 4), diel segregation (Fig. 5) or prey choice. While there were no sex differences in selection for fishing activity density (Fig. 4), this may be due to temporal mismatch with the vessel data, and so scavenging may still explain isotopic differences. Previous work from this colony suggested males fed more on discards (Stauss et al. 2012, Votier et al. 2013), which would create the observed isotopic differences (Votier et al. 2010). However, spatial analysis here (Fig. 4) and elsewhere (Bodey et al. 2014, Patrick et al. 2015) suggest no sex difference in fisheries overlap. It is unclear whether these inconsistencies are due to methodological differences (e.g. limitations in VMS, especially for illegal, unreported and unregulated fishing), environmental variation influencing scavenging tendency (Clark et al. 2020) or both.

Males and females may select different prey due to distinct nutritional requirements (Morehouse et al. 2010), leading to isotopic differences. For instance,

male Australasian gannets *M. serrator* feed on fish with a higher protein-to-lipid and water-to-lipid ratio and a higher trophic level than females (Machovsky-Capuska et al. 2016). Nutritional requirements can be linked to size dimorphism, but our results showed that the trophic niche was not driven by mass (Fig. 6). Sex differences in chick-rearing gannets are unlikely to be due to female investment in the egg since the single-egg clutch laid by gannets is one of the smallest compared to female mass at 3.3% (Perrins 1970, Western & Ssemakula 1982), with a very low energy and lipid content (Ricklefs & Montevecchi 1979).

4.6. Sexual segregation in gannets

For gannets nesting on Grassholm, we found consistent sexual segregation in isotopic values and more variable segregation in movement metrics. Our results are consistent with both competitive exclusion and niche specialisation as potential mechanisms (Catry et al. 2005). Overall, female gannets travelled further than males, which is unusual for the larger sex (Weimerskirch et al. 1997, González-Solís et al. 2000, Lewis et al. 2005). Females could be competitively excluded by males despite being larger if they are less aggressive (Nelson 1965), but we have no direct evidence for this. As such, it seems unlikely to be the only driver. The sexes may instead each prefer slightly different prey or select habitats at a scale that is finer than our methods could detect, or involving other factors such as wind (De Pascalis et al. 2020). A third explanation for consistent differences in trophic indicators could be that males invest more time in nest defence (Burger 1981), particularly during the day. As a consequence, males are unable to travel as far as females, and spend more time at-sea during the late evenings and early mornings when different prey may be available in the same location in the middle of the day. As such, differing diets may be in part a by-product of parental niche segregation rather than selection at sea. It is likely that a combination of mechanisms is involved, each with a different sensitivity to environmental conditions. Future work could examine the influence of inter-annual variation in food availability, or their proxies such as SST, primary production and wide scale climatic indices, such as the North Atlantic Oscillation (NAO) Index (Paiva et al. 2017). In addition to the NAO, progressive warming in the North Atlantic poses a challenge to gannets breeding at the southerly edges of their range, with warm years leading to reduced pro-

ductivity (Montevecchi et al. 2013). Data for further years or comparisons between colonies could provide a means to investigate how the degree of sexual segregation may relate to climatic conditions.

4.7. Methodological considerations

Our findings suggest that interpreting tracking data over small temporal windows could lead to spurious inference. This could relate to sex-specific responses to short-term variation in environmental conditions. More research into the impact of the spatial and temporal scale of remotely sensed variables required to reveal individual niches would be valuable, and technological developments are likely to facilitate this in coming years. Finally, we do not have a good understanding of the sample sizes required to characterise possible sex-specific behaviours (Soanes et al. 2013). We therefore encourage tracking over an extended period, careful consideration of statistical power and accounting for variation in environmental conditions. Our stable isotope results indicate more consistent sexual niche segregation across years, probably because they integrate foraging over the previous 4–6 wk (Hobson 2005). However, the significant year:sex interaction for $\delta^{13}\text{C}$ (Fig. 6) reveals variation in the degree of segregation, possibly relating to differences in habitat specialisation (because $\delta^{13}\text{C}$ has a strong spatial component; Cherel & Hobson 2007). We therefore recommend the use of stable isotopes and tracking in tandem to better understand the extent to which males and females segregate, along with other types of niche segregation.

4.8. Conclusion

Male and female gannets exhibited consistent isotopic differences among years, although the strength of segregation varied, possibly relating to habitat specialisations that are not driven by size dimorphism. However, the degree of spatial and temporal sex-specific segregation was more variable, possibly related to environmental conditions or the short temporal scale of GPS tracking. We also conclude that analysis based on data from 1 or 2 years may not reflect overall movement patterns, although stable isotopes tend to be less affected, emphasising the value of long-term studies and multiple methods for fully understanding sex differences in behaviour.

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