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1 **Sexual segregation in a wide-ranging marine predator is a**
2 **consequence of habitat selection**

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25
26 Running Head: Sexual segregation in northern gannets

27

28 **Abstract**

29 Sexual segregation, which is common in many species, is usually attributed to intra-specific
30 competition or habitat choice. However, while segregation in space has been widely reported,
31 few studies have simultaneously quantified sex-specific foraging behaviour and habitat use.
32 Here, we combine movement, diving, stable isotope and oceanographic data to test whether
33 sexual segregation in northern gannets *Morus bassanus* results from sex-specific habitat use.
34 Breeding birds, foraging in a seasonally stratified shelf sea, were tracked over three
35 consecutive breeding seasons (2010-2012). Females made longer trips, foraged further
36 offshore and had lower $\delta^{13}\text{C}$ values than males. Male and female foraging areas overlapped
37 only slightly. Males foraged more in mixed coastal waters, where net primary production
38 (NPP) was relatively high ($>3 \text{ mg C m}^{-2} \text{ day}^{-1}$) and sea-surface temperature (SST) was
39 relatively low ($< 10^\circ\text{C}$). Males also tended to use areas with higher SSTs ($> 15^\circ\text{C}$) more than
40 females, possibly as a consequence of foraging in productive mixed waters over offshore
41 banks. Females foraged most frequently in stratified offshore waters, of intermediate SST (12
42 - 15°C), but exhibited no consistent response to NPP. Sex-specific differences in diving
43 behaviour corresponded with differences in habitat use: males made more long and deep U-
44 shaped dives, which were characteristic of inshore foraging, whereas shorter and shallower
45 V-shaped dives occurred more often in offshore waters. Heavier birds attained greater depths
46 during V-shaped dives but even when controlling for body mass, females made deeper V-
47 shaped dives than males. Together these results indicate that sexual segregation in gannets is
48 driven largely by habitat segregation between mixed and stratified waters, which in turn
49 results in sex-specific foraging behaviour and dive depths.

50 Keywords: competition, foraging behaviour, sexual segregation, oceanography, wildlife
51 telemetry

52 **Introduction**

53 Segregation of males and females occurs in a wide range of animal species and over a wide
54 variety of spatiotemporal scales (Ruckstuhl & Neuhaus 2005, Wearmouth & Sims 2008,
55 Alves et al. 2013, Levin et al. 2013). It is particularly common in marine central-place
56 foragers during the breeding period, when foraging ranges are restricted by the need to return
57 repeatedly to the breeding site to care for offspring (Page et al. 2005, Weimerskirch et al.
58 2009). Segregation is thought to reflect niche specialisation or competitive exclusion by the
59 dominant sex (Phillips et al. 2004) but could, alternatively be a consequence of differing
60 parental roles (Thaxter et al. 2009, Elliot et al. 2010), or differences in the nutritional
61 requirements of males and females as proposed by Lewis et al. (2002).

62 In many species, between-sex differences in isotopic signatures suggest that males
63 and females exploit different prey species or habitats (Bearhop et al. 2006, Phillips et al.
64 2011). However, while sex-specific habitat use has been widely documented in terrestrial
65 species (Ruckstuhl & Neuhaus 2005), between-sex differences in habitat use in relation to
66 dynamic oceanographic features have rarely been quantified (but see Pinet et al. 2012).
67 Moreover, in the marine environment, sexual segregation may occur in the vertical as well as
68 horizontal dimension, especially in diving species (Kato et al. 2000, Lewis et al. 2002). Such
69 vertical niche segregation may result from between-sex differences in diving capabilities
70 mediated by morphology or physiology or as a consequence of habitat choice (Le Boeuf et al.
71 2000). Thus, a detailed understanding of sex-specific differences in foraging behaviour
72 requires a combination of horizontal tracking and dive data with environmental data
73 (Takahashi et al. 2008, Thaxter et al. 2009).

74 Many air-breathing diving species perform dives with two distinct profiles: V-shaped
75 and U-shaped. V-shaped dives tend to be shallower and of shorter duration than U-shaped
76 dives which typically involve underwater propulsion (Garthe et al. 2000, Ropert-Coudert et

77 al. 2009a). Both the dive type and depth attained may be influenced by intrinsic factors such
78 as an individual's mass as well as extrinsic factors, including the type of prey and its depth
79 distribution, which in turn may be influenced by the presence of other predators and the
80 structure of the water column (Elliott et al. 2008, Capuska et al. 2011). In addition, recent
81 work demonstrates that dive type is determined before birds enter the water (Capuska et al.
82 2013), suggesting that gannets use visual cues pre-dive in order to optimize their foraging
83 performance. Therefore, sex-specific differences in diving behaviour should arise as a
84 consequence of habitat segregation as individuals adjust their foraging technique for different
85 prey or habitats (Garthe et al. 2000).

86 Northern gannets (*Morus bassanus*, henceforth gannets) are medium-range foragers,
87 typically travelling tens to hundreds of kilometres from their colonies to obtain food for
88 themselves and their offspring (Hamer et al. 2000, Wakefield et al. 2013). Adults exploit a
89 wide range of prey but feed predominantly by plunge-diving for shoaling fish within the
90 upper 30 m of neritic waters (Garthe et al. 2000). In addition, gannets also scavenge for
91 discards from fishing vessels (Hamer et al. 2007, Votier et al. 2010, 2013). Gannets tracked
92 from a large colony at Grassholm (~40,000 breeding pairs) in the Celtic Sea showed marked
93 sexual divergence in spatial distribution and diet (Stauss et al. 2012). Males made greater use
94 of discards from fishing vessels and foraged closer inshore than females, although it was not
95 clear whether females fed in different areas from males as a consequence of habitat selection
96 or if they were displaced from fishing vessels by competition with males. In addition, time-
97 depth recorder (TDR) data from birds breeding at Bass Rock (~60,000 pairs) in the North Sea
98 showed that females dived to greater depths than males, suggesting that they may have been
99 selecting different prey than males or that heavier females were able to dive deeper (Lewis et
100 al. 2002). Gannets from both colonies forage in relatively shallow regimes (i.e. <200 m),
101 shelf regions in which the oceanography is dominated by tidal processes (Simpson et al.

102 1981). In the summer months, deeper waters become thermally stratified, while coastal
103 waters and those overlaying shallow banks remain mixed due to tidal stirring. These two
104 regimes are separated by tidal mixing fronts (Simpson et al. 1981, Barnes & Hughes 1988).
105 Birds from Bass Rock forage in association with one such front, located ~50 km offshore
106 (Skov et al. 2008, Hamer et al. 2009), which we term the East Scotland tidal mixing front.
107 The sex-specific behaviour of marine predators with respect to tidal mixing regimes has
108 rarely been investigated. However, the foraging behaviour of many marine predators,
109 including gannets, differs between mixed and stratified waters (Takahasi et al. 2008, Hamer
110 et al. 2009, Camphuysen et al. 2012). Consequently, sexual niche segregation across tidal
111 regimes may shape sex-specific differences in diving behaviour and optimal foraging
112 strategies.

113 Here, we aim to quantify sexual differences in the foraging behaviour and habitat use
114 of gannets foraging in the North Sea. We use a combination of horizontal and vertical
115 tracking, stable isotope and environmental data, collected over three consecutive breeding
116 seasons at Bass Rock, to address the hypotheses that during foraging: (1) sexual segregation
117 is driven by sex-specific habitat selection; (2) habitat segregation occurs across tidal mixing
118 regimes, and; (3) sex-specific foraging behaviour arises as a consequence of habitat
119 segregation as birds adapt their foraging behaviour to the local foraging environment.

120 **Methods**

121 **Study Site and Sampling**

122 Fieldwork took place on Bass Rock, UK (56° 6'N, 2° 36'W) between mid-June and mid-
123 August in 2010 to 2012. We caught adult gannets attending young chicks at the nest with a 6-
124 m telescopic pole fitted with a wire crook. Upon capture, we fitted birds with a metal British
125 Trust for Ornithology ring and an individually numbered plastic colour ring. We then

126 recorded their body mass to the nearest 25g using a spring balance and took 1 ml of blood
127 from the tarsal vein. Shortly after sampling, blood samples were separated into red blood
128 cells (RBC) and serum by centrifuging and stored frozen prior to stable isotope analysis and
129 genetic sexing.

130 **Instrumentation**

131 A GPS logger (i-gotu 200 or 600; Mobile Action Technology, Taiwan) weighing 30g was
132 attached to the upper side of the three central tail feathers of each bird (n = 55 birds in total;
133 Table S1) using Tesa© tape. GPS loggers were programmed to record location data at 2
134 minute intervals. In addition, a subset of birds caught in 2011 and 2012 was fitted with a
135 TDR (Table S1), which was taped to the underside of the central tail feathers. TDR models
136 were either G5 (CEFAS Technology, UK) or MSR145 (MSR Electronics GmbH,
137 Switzerland), weighing 2.5g and 18g respectively). G5 loggers recorded pressure at 10 Hz
138 when the bird was submerged (> 1.5m depth), whilst MSR145 loggers recorded pressure
139 continuously at 1 Hz. Total handling time was ~15 minutes and after release, birds returned
140 almost immediately to their nest and resumed normal behaviour. Birds were tracked for 4-7
141 days, after which time they were recaptured and the loggers retrieved. The maximum weight
142 of loggers deployed on birds (48g) was <2% of body mass (3kg) and previous studies (Hamer
143 et al. 2007, 2009) recorded that such loggers had no discernible effects on trip durations or
144 body masses of birds. Similarly, we found that trips durations of instrumented birds in 2010
145 (mean = 23.9 hrs, n = 211 trips from 52 birds, SD = 12.6) were very similar to those of non-
146 instrumented birds observed via a remote radio link using a Mobotix© surveillance camera
147 installed in the same area of the colony (mean = 23.5 hrs, n = 636 trips from 27 birds, SD =
148 14.4).

149 **Trip metrics and spatial usage**

150 We modelled trip duration (hrs), total distance travelled during each trip (km) and time spent
151 at the colony between trips using Bayesian linear mixed effects models (BLMM) with the R
152 package MCMCglmm (Hadfield 2010, R Core Team 2012). All variables were log-
153 transformed prior to analysis to ensure normality. Sex and year, and their two-way
154 interactions, were included as explanatory covariates and a random intercept was specified
155 for each bird. Minimum adequate models were selected according to their Deviance
156 Information Criterion (DIC) scores (Lunn et al. 2013).

157 For each year and sex, we estimated 95% and 50% utilization distributions (UD)
158 using kernel analysis conducted with the R package adehabitatHR (Calenge 2006). The
159 extent of within-year overlap between male and female home-ranges was estimated using
160 Bhattacharyya's affinity (BA; Bhattacharyya 1943) which ranges from 0 (no overlap) to 1
161 (complete overlap). Using BA as our measure of spatial overlap, we used a randomization
162 procedure to test the null hypothesis that there was no difference in the spatial distribution of
163 males and females each year (see Appendix S1).

164 **Stable Isotope Analysis**

165 To examine sex-specific dietary niches during the breeding season, we analysed stable carbon
166 ($\delta^{13}\text{C}$) and nitrogen isotope ratios ($\delta^{15}\text{N}$) in red blood cells. Avian erythrocytes have a
167 lifespan of 28 to 45 days (Rodnan et al. 1957) and hence represent assimilated prey over the
168 previous 4-6 weeks. In general, $\delta^{15}\text{N}$ increases by 3 to 5 ‰ with each trophic level whereas
169 $\delta^{13}\text{C}$ typically reflects differences between water masses. Isotope analysis was conducted at
170 the Natural Environment Research Council (NERC) Life Science Mass Spectrometry
171 Facility, East Kilbride, UK. We modelled $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ as response variables in a Bayesian
172 multi-variate analysis including year and sex as well as their two-way interaction as

173 predictors; bird identity was included as a random intercept (further details in Supplementary
174 Material).

175 **Habitat Selection**

176 Environmental covariates

177 The distribution of forage fish in the North Sea cannot currently be measured simultaneously
178 over all scales at which we tracked gannets in this study (seconds to weeks and metres to
179 100s of km). However, foraging seabirds show marked associations with particular habitats
180 that concentrate prey in relatively large or predictable aggregations (Wakefield et al. 2009,
181 Wakefield et al. 2014). Previous studies have shown that northern gannets associate with
182 shelf sea fronts and areas of high primary production (Skov et al. 2008, Votier et al. 2010).
183 We therefore described gannet habitat using sea surface temperature (SST, °C, Figs. 1a, S1)
184 and net primary production (NPP, mg C m⁻² day⁻¹, Figs. 1b, S1). Monthly NPP data were
185 estimated on a 1 km² grid using data from the Aqua-MODIS sensor. Monthly mean SST data
186 were supplied on a 4 km² grid from the AVHRR sensor. All environmental data were
187 supplied by the Natural Environment Research Council Earth Observation Data Acquisition
188 and Analysis Service, Plymouth, UK.

189 Habitat Selection Functions

190

191 We used Habitat Selection Functions (HSF) to test whether males and females differed in
192 their habitat usage. HSFs compare habitat usage to availability using a logistic-regression
193 based approach with a case-control design (Aarts et al. 2008). The case-control design
194 generates a binomial response (\hat{u}_i) which takes the value 1 for the *i*th data point if it belongs
195 to the tracking dataset or 0 if belongs to the control dataset. Tracking locations ($\hat{u}_i = 1$) were
196 generated by selecting animal locations that were associated with putative foraging behaviour
197 defined on the basis of movement indices such as speed, acceleration and track tortuosity (see

198 Wakefield et al. 2013 for further details). The control dataset comprised five pseudo-absence
199 locations ($\hat{u}_i=0$) for each observed foraging location. Pseudo-absences were assigned to the
200 same month as the foraging location with which they were paired and were generated
201 randomly within the boundaries of the population's 95% UD (i.e. the UD for both sexes
202 combined, calculated separately for each year) using a uniform spatial Poisson process.

203 Foraging HSFs were modelled using a binomial generalised additive mixed model
204 (GAMM) in the mgcv R package (Wood 2006). To facilitate biological interpretation and to
205 keep computer running time within reasonable limits (~ 2 h to fit each model) we fitted
206 separate models for each study year. Environmental covariates were fitted either as
207 parametric variables, a single smoother for both sexes or as separate smoothers for each sex.
208 The inclusion of smoothers allows for the possibility of non-linear responses to
209 environmental covariates and fitting separate smoothers for each sex allowed the response of
210 males and females to differ. A random intercept was specified for each bird. In order to
211 account for residual spatial auto-correlation, we also included a thin-plate regression spline
212 based upon the spatial coordinates of each data point (further details in Supplementary
213 Material).

214 **Diving behaviour**

215 Using the TDR data, we categorised dives as either V-shaped (bottom time ≤ 2.7 s) or U-
216 shaped (bottom time > 2.7 s) (Garthe et al. 2000; see Supplementary Material for details).
217 Dive locations were estimated by combining TDR and GPS data. We used a binomial
218 GAMM to model the probability of dives being U-or V-shaped and a Gaussian GAMM to
219 model maximum depth attained during either V-shaped or U-shaped dives. The maximum
220 depth of U-shaped dives was log-transformed to increase normality (no transformation was
221 required for V-shaped dive depth). In each model, we considered sex, body mass and the
222 interaction between the two as explanatory variables. In addition, each model included a

223 smoother for time of day to explain diurnal variation in behaviour and a spatial smoother to
224 account for spatial auto-correlation. Random intercepts were specified for year and for trip
225 identity nested within bird identity. A continuous-time correlation structure was included to
226 account for temporal auto-correlation between dives. Throughout our analysis, minimum
227 adequate models for all GAMMs were selected by backwards selection, using K-folds cross-
228 validation (where $K = 5$ equal sized sub-samples of the data; More details in the
229 Supplementary Material).

230 **Results**

231 Female gannets were ~200g heavier than males on average (mean \pm SD; female: 3021 ± 315
232 g; male: 2810 ± 190 g; student t-test = 3.71, df= 47, $p \leq 0.001$).

233 **Spatial Distribution of Males and Females**

234 Males made significantly shorter trips than females, both in duration ($\beta_{\text{SEX}} = -0.14 \log(\text{hrs})$,
235 95% Bayesian Credible Interval (CRI) = $-0.24 - -0.041$, $p = 0.0081$, $n = 493$ trips from 55
236 birds; Table 1 & S2) and total distance travelled per trip ($\beta_{\text{SEX}} = -0.19 \log(\text{km})$, 95% CRI -
237 $0.34 - -0.035$ $p = 0.046$; Table 1). Thus, the duration of male trips was 13% (95% CRI = 4 -
238 21%) shorter than that of females and the distance males travelled was 17% (95% CRI = 3 -
239 28%) less than travelled by females. In general, females foraged more frequently in offshore
240 waters to the east of the colony, whereas males foraged most frequently in coastal waters to
241 the north-east and south-east of the colony (Fig. 1, Fig. S1). Consequently, the overlap
242 between male and female 50% and 95% utilization distributions was significantly lower than
243 the null expectation each year except for the 50% utilization distribution in 2011, which was
244 marginally significant ($p = 0.052$) and the 95% utilization distribution in 2012 ($p = 0.083$;
245 Table 2).

246 **Habitat Selection Functions**

247 In each year, the best fitting model contained a sex-specific smoother for SST and NPP
248 (Table S3 & S4). Both random intercepts for bird identity and spatial smoothers (Fig. S4)
249 were retained in the final models. Females foraged mainly over waters with a temperature
250 between 10°C and 15°C. In contrast, males foraged relatively little over such waters, tending
251 to forage in significantly cooler (8 – 12°C) or warmer waters (> 15°C, Fig. 2a). In addition,
252 males made greater use than females of areas with high NPP (> 3 mg C m⁻² day⁻¹; Fig. 2b).

253 **Stable isotope ratios**

254 Male RBCs had significantly higher $\delta^{13}\text{C}$ values than those of females in each study year and
255 significantly higher $\delta^{15}\text{N}$ values than females in 2010 and 2011, but not during 2012 (Fig. 3;
256 Table 3).

257 **Diving behaviour**

258 V-shaped dives were more frequent than U-shaped dives across both sexes (Total number of
259 V-dives = 4784; Total number of U-dives = 2151) but males were more likely than females to
260 make U-shaped dives (males = 38% of 3904 dives classed as U-shaped; females = 22% of
261 3031 dives classed as U-shaped; $\beta_{\text{SEX}} = 0.92$, 95% Confidence Interval (CI) = 0.35 – 1.48, p
262 = 0.0012, $n = 6310$ dives from 23 birds; Table S5). Body mass did not affect the probability
263 of a dive being U-shaped or V-shaped ($\beta_{\text{MASS}} = -0.024$, 95% CI = -0.29 – 0.25, $p = 0.90$).
264 Plots of dive locations and the spatial smoother from the dive type model indicate that in both
265 sexes, U-shaped dives were more likely to occur close to the colony and inshore of the East
266 Scotland tidal mixing front (Fig. 4). Dives at dawn or dusk were more likely to be V-shaped
267 than U-shaped (Fig. S5)

268 The maximum depth achieved during V-shaped dives was positively associated with
269 body mass ($\beta_{\text{MASS}} = 0.52$, 95% CI = 0.31 – 0.91, $p = 0.019$). In addition, after controlling for

270 body mass, the maximum depth attained during V-shaped dives was greater in females than
271 males (Table 1; $\beta_{\text{SEX}} = -0.81$, 95% CI = $-1.55 - 0.11$, $p = 0.021$, $n = 4272$, 23 birds; Table
272 S7). In both sexes, the deepest V-shaped dives tended to occur in offshore waters (Fig. 5a)
273 and V-shaped dives were shallowest at dawn and dusk (Fig. S6a). There was little difference
274 in the maximum depth reached by males and females during U-shaped dives ($\beta_{\text{SEX}} = 0.11$,
275 95% CI = $-0.086 - 0.31$, $p = 0.28$, $n = 2036$ dives/ 23 birds; Table 1 & Table S9), nor was
276 there a significant association between maximum depth and body mass ($\beta_{\text{MASS}} = 0.073$, 95%
277 CI = $-0.026 - 0.17$, $p = 0.16$). The maximum depth of U-shaped dives generally increased
278 closer to the colony (Fig. 5b) and U-shaped dives were also shallower at dawn and dusk (Fig.
279 S6b).

280 **Discussion**

281 This study provides clear evidence of sexual segregation in northern gannets in both
282 horizontal and vertical planes. We found that males and females differed in their usage of
283 mixed and stratified waters, providing evidence for sex-specific habitat segregation across
284 tidal mixing regimes. Moreover, our data highlight the association between sex-specific
285 foraging behaviour and spatial and habitat segregation.

286 **Differences in Habitat Usage**

287 Males foraged predominantly in mixed waters to the North-East of Bass Rock inshore of the
288 tidal mixing front, whereas females foraged predominantly in offshore stratified waters.
289 These results are consistent with previous work showing that chick-provisioning males from
290 Bass Rock departed on more North-easterly bearings than females (Lewis et al. 2004) and
291 that chick-provisioning females from Grassholm foraged further offshore than males in the
292 Celtic Sea (Stauss et al. 2012). In addition, RBC $\delta^{13}\text{C}$ values were lower in females than in
293 males at Bass Rock, which also indicates that females foraged further offshore than males,

294 because inshore habitats characteristically have higher $\delta^{13}\text{C}$ values (Hobson et al. 1994).
295 Lower blood $\delta^{13}\text{C}$ values in females has also been observed at other gannet colonies (Stauss
296 et al. 2012), suggesting that the pattern of sex-specific habitat segregation observed at Bass
297 Rock reflects a general feature in gannets. Males made greater use than females of areas with
298 high NPP as would be expected given that NPP is generally higher in mixed, coastal waters
299 where males foraged (Fig. S2). NPP is often used as a proxy for food availability further up
300 the food chain (Barnes & Hughes 1988, Wakefield et al. 2014) suggesting males foraged in a
301 more productive environment than females. However, potential mismatches between
302 productivity towards the bottom of the food web and at intermediate trophic levels (pelagic
303 fish) means that this interpretation should be treated with caution (Gremillet et al. 2008).

304 Male gannets from Bass Rock had higher $\delta^{15}\text{N}$ values than females in 2010 and 2011,
305 but not in 2012. Higher $\delta^{15}\text{N}$ in males from Grassholm may occur if males consume a higher
306 proportion of whitefish fishery discards than females (Stauss et al. 2012). However, at Bass
307 Rock the between-sex differences in $\delta^{15}\text{N}$ each year were small and could have arisen from
308 the observed habitat segregation between males and females (as a consequence of variation in
309 isotopic baselines in the areas where individuals foraged; Woodcock et al. 2012) or from
310 lower body condition among males (as a consequence of variation in physiological processes
311 affecting fractionation; Lee Cruz et al. 2012) or both.

312 Sex specific responses to SST were generally consistent across years, with males
313 foraging more in cold mixed waters and females foraging in seasonally stratified offshore
314 waters. As well as using colder waters more often than females, males also made greater use
315 of areas with high SSTs ($> 15^\circ\text{C}$). This was a consequence of males travelling south-east to
316 forage at the Dogger Bank, where SST was relatively high. The Dogger Bank is a productive
317 shallow offshore bank, which is also targeted by other wide-ranging higher predators (de
318 Boer 2010). Due to benthic-pelagic coupling, such features may lead to elevated prey

319 abundance in the epipelagic waters accessible to gannets (Wakefield et al. 2012). In 2011,
320 differences between male and female responses to SST were smaller (Figs. 1 and 2), probably
321 because the East Scotland tidal mixing front was located closer to shore and the extent of cold
322 mixed waters ($SST < 10^{\circ}\text{C}$) was relatively limited (Fig. 1a). Between 2010 and 2012 there
323 was also variation in climatic conditions in the North Atlantic as indicated by the North
324 Atlantic Oscillation (NAO) index which varied from -4.64 in 2010 to 3.17 in 2012
325 ([https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-](https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based)
326 [station-based](https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based)). Effects of climate on lower levels of the food web may, in turn, have
327 influenced both the locations where gannets foraged and the prey species they targeted. Thus,
328 our results highlight the importance of inter-annual variation in oceanic conditions and
329 climatic conditions in shaping the spatial and trophic ecology of marine predators (Garthe et
330 al. 2011).

331 Sex-specific Diving Behaviour

332 Males and females may adopt different diving tactics as a consequence of intrinsic
333 constraints, competition, habitat segregation or prey preferences (Le Boeuf et al. 2000,
334 Garthe et al. 2001, reviewed in Machovsky Capuska et al. 2011). Here, we found that male
335 gannets made a greater proportion of U-shaped dives than females. Moreover, U-shaped
336 dives were more common in coastal habitats, whilst V-shaped dives were more frequent
337 offshore. Therefore, the different dive types may represent tactics for foraging in different
338 environments, with males making more U-dives as a consequence of their inshore
339 distribution and the prey they encounter.

340 Why U-shaped dives were more frequent inshore of the mixing front is less clear. The
341 higher frequency of U-dives in the vicinity of Bass Rock, and the greater depth of U-dives
342 close to the colony, may arise due to the high density of gannets in these areas. In particular,
343 when large aggregations of gannets form during feeding events, prey may descend to deeper

344 depths to escape predation forcing gannets to dive deeper as a result (Elliott et al. 2008,
345 Capuska et al. 2011). However, this would not explain why U-shaped dives are also more
346 frequent in coastal areas further from the colony, where the density of conspecifics is
347 relatively low (Camphuysen et al. 2012). Instead, diving behaviour may reflect the
348 environment and prey encountered (Garthe et al. 2000, Garthe et al. 2011) as observed in
349 other marine predators which dived deeper in mixed waters than in stratified waters
350 (Takahashi et al. 2008). In particular, the location of the deepest U-shaped dives corresponds
351 with the location of sandeel (*Ammodytes* spp.) habitat within the Firth of Forth (Wanless et al.
352 1998), suggesting that deeper U-shaped dives could result from birds feeding on sandeels.
353 Alternatively, the shallower waters in coastal areas may prevent prey escaping to deeper
354 depths, enhancing prey capture and making longer U-shaped dives more profitable than in
355 deeper waters.

356 Females attained greater depths than males during V-shaped dives, which supports
357 similar findings in gannets and other Sulidae (Lewis et al. 2002, Zavalaga et al. 2007,
358 Weimerskirch et al. 2009). Gannets initially attain depth by plunge-diving from height,
359 therefore the greater mass of females may give them greater dive momentum and allow to
360 dive deeper (Kato et al. 2000). However, even when holding body mass constant in our
361 models, females were still predicted to reach deeper depths during V-shaped dives than
362 males. Such a difference may reflect the vertical distribution of prey that males and females
363 target when foraging or assessing prey densities (Wilson 2003, Machovsky Capuska et al.
364 2011, Machovsky Capuska et al. 2013). For example, because females tend to forage more in
365 offshore stratified waters than males, deeper V-shaped dives may be required to reach the
366 thermocline, which influences the distribution of biomass in the water column (Mann &
367 Lazier 2006) and may play a role in shaping dive profiles (Takahashi et al. 2008, Ropert-
368 Coudert et al. 2009b).

369 In contrast to V-shaped dives, body mass had no effect on the depth of U-shaped
370 dives, probably because extra depth can be achieved during the latter by underwater
371 swimming after the initial momentum phase (Ropert-Coudert et al. 2009a).

372 Factors underlying segregation

373 Sex-specific differences in foraging behaviour are usually ascribed to the influence of body
374 size on foraging efficiency and intra-specific competition (Shaffer et al. 2001, Wearmouth &
375 Sims 2008, Phillips et al. 2011). Competition may play a greater role in segregating birds
376 from the same colony than it does in between-colony segregation (Wakefield et al. 2013)
377 because the rate at which indirect competition varies with colony distance will be equal for
378 all individuals at the colony. Because males made shorter trips than females it is possible that
379 females were excluded from areas close to the colony via indirect competition and were
380 pushed into offshore, stratified waters as a result. However, this would not explain why
381 females did not appear to be pushed into inshore sites further from the colony in a similar
382 fashion. Moreover, when the tidal mixing front was less well-defined and occurred closer to
383 the coast-line in 2011 the 50% utilization distribution of females shifted inshore suggesting
384 females are not excluded from this area. Similarly, even when males ventured offshore they
385 still foraged in more mixed, productive waters such as those over the Dogger Bank.

386 Alternatively, the greater mass of females may make them more efficient at foraging in
387 offshore environments because they can reach deeper prey. Greater mass appears to be
388 advantageous when performing V-dives and as the deepest V-dives occurred in stratified
389 waters this may give females an advantage in this environment. Nevertheless, the slight
390 sexual size dimorphism (~5-10%) seen in gannets suggest differences in body mass alone
391 will not create large asymmetries in either competitive ability or foraging efficiency.
392 Therefore, other aspects of morphology not measured here, such as wing loading and agility
393 (Weimerskirch et al. 2006), may also be important. Finally, the fact that in addition to Bass

394 Rock, females breeding at Grassholm also foraged further offshore than males (Stauss et al.
395 2012), despite differences between regions in the arrangement of mixed and stratified waters
396 suggests that sexual segregation is driven primarily by habitat selection.

397 Sex-specific niche divergence and habitat segregation can also arise from a difference
398 between sexes in parental roles (Thaxter et al. 2009) but the roles of male and female gannets
399 do not appear to differ during chick-rearing (Nelson 2002, Redman et al. 2002). However,
400 males and females could forage in different areas in order to ensure their chicks receive the
401 optimum blend of prey species (Elliot et al. 2010). Sex-specific differences in nutritional
402 requirements related to egg production, incubation costs or feather moult could also result in
403 sexual segregation (Carey 1996, Lewis et al. 2002), particularly if key prey items are found in
404 specific habitats. Gannets lay only a single small egg which seems unlikely to result in
405 temporary sex differences in dietary need. However, although it is not known whether there
406 are sex-specific differences in moult in gannets such differences do occur in other seabirds
407 (Weimerskirch 1991) and could potentially create temporary sex differences in dietary needs
408 and/or foraging abilities (Lewis et al. 2002).

409 Overall, our results suggest that sexual segregation in gannets is mediated by habitat
410 segregation across tidal mixing regimes. Males foraged more in mixed coastal waters inshore
411 of the tidal mixing front whereas females foraged more offshore. Hence, while tidal mixing
412 regimes have been identified as important habitat features for marine predators (Skov et al.
413 2008), our results highlight that males and females may respond differently to such features.
414 In addition, sex-specific diving behaviour may result from males and females adapting their
415 behaviour to suit the differing habitats in which they forage, particularly in relation to
416 whether they are foraging in mixed or stratified waters.

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578

579 **Tables and Figures**

580 **Table 1.** Summary of foraging trip and dive metrics.

Variable		Mean (SD)	Range	n
Trip Duration (hrs)	Males	21.40 (12.02)	0.91 – 69.76	493 trips
	Females	24.14 (12.77)	3.71 – 95.11	
Trip Length (km)	Males	454.63 (277.79)	27.32 – 1265.72	493 trips
	Females	512.56 (262.74)	69.64 – 1461.62	
Time at Colony Between Trips (hrs)	Males	10.31 (8.53)	1.07 – 24.76	379 trips
	Females	10.11 (8.59)	1.07 – 48.51	
Maximum V-dive depth (m)	Males	4.40 (1.92)	1.52 – 11.03	4274 dives
	Females	6.69 (2.01)	1.52 – 9.25	
Maximum U-dive depth (m)	Males	7.23 (4.06)	1.64 – 27.75	2036 dives
	Females	7.59 (3.78)	1.70 – 25.96	

581

582

583

584 **Table 2.** Estimated overlap (Bhattacharyya's Affinity, BA) between male and female
585 utilisation distributions (UD). p represents the proportion of randomised overlaps that were
586 smaller than the observed overlap

587

UD	Year	BA	p
50%	2010	0.22	0.046
	2011	0.25	0.052
	2012	0.22	0.022
95%	2010	0.75	0.011
	2011	0.65	0.027
	2012	0.76	0.083

588 **Table 3.** Bayesian multi-variate mixed effects model of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in gannets from Bass

589 Rock (n = 138 observations/66 birds.)

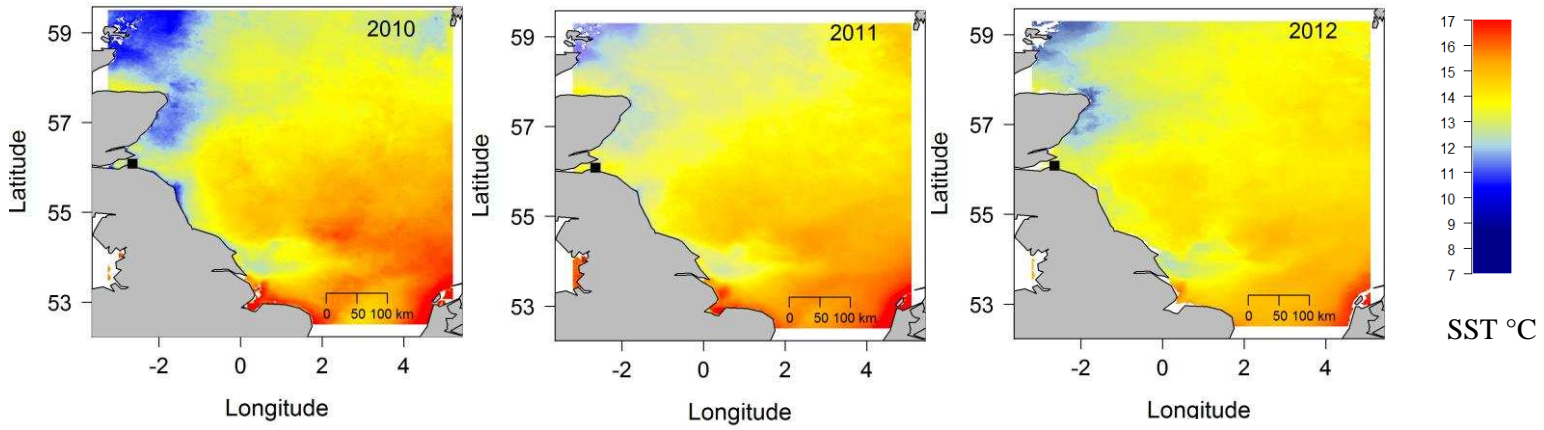
Variable	Isotope							
	$\delta^{15}\text{N}$				$\delta^{13}\text{C}$			
	β	Lower 95% CI	Upper 95% CI	p	β	Lower 95% CI	Upper 95% CI	p
Intercept	13.55	13.40	13.67	<0.001	-18.04	-18.11	-17.95	< 0.001
Sex	0.27	0.09	0.46	0.007	0.19	0.08	0.31	0.001
Year 2011	0.48	0.29	0.68	<0.001	0.38	0.24	0.52	<0.001
Year 2012	0.90	0.72	1.09	<0.001	0.11	-0.02	0.24	0.100
Sex \times Year 2011	-0.10	-0.36	0.17	0.480	0.20	0.02	0.48	0.022
Sex \times Year 2012	-0.31	-0.59	-0.02	0.022	0.21	0.03	0.41	0.036

590 **Figures**

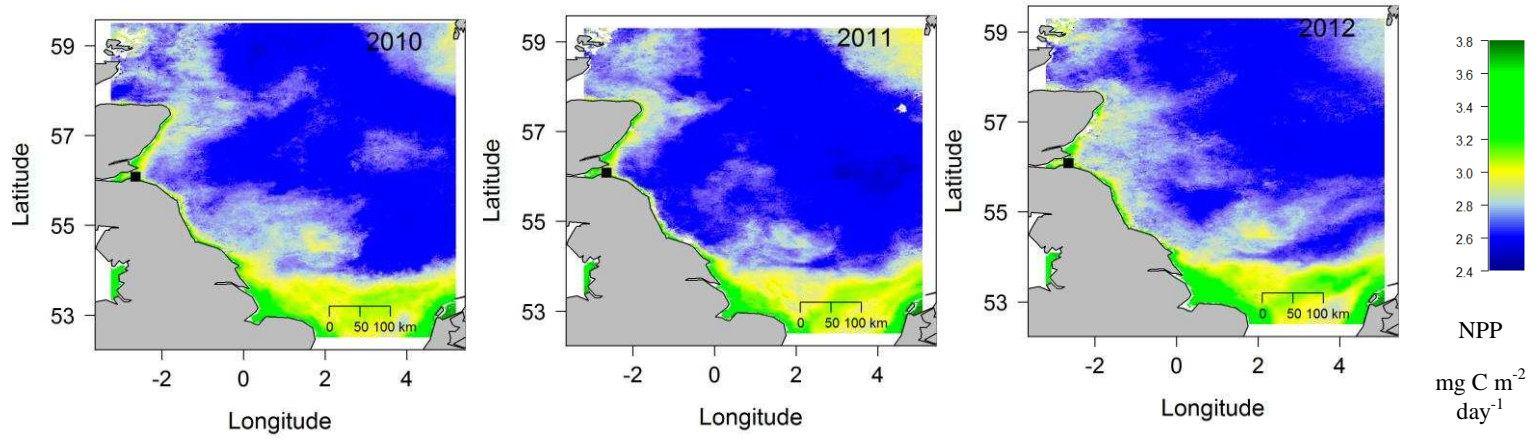
591 **Fig. 1.** Plots of the average a) SST and b) NPP recorded during the breeding season in the
592 foraging range of gannets from Bass Rock (denoted as a black square) for each study year.

593

a)



b)



596 **Fig. 2.** Foraging ranges of male (blue) and female (red) gannets during the breeding season.

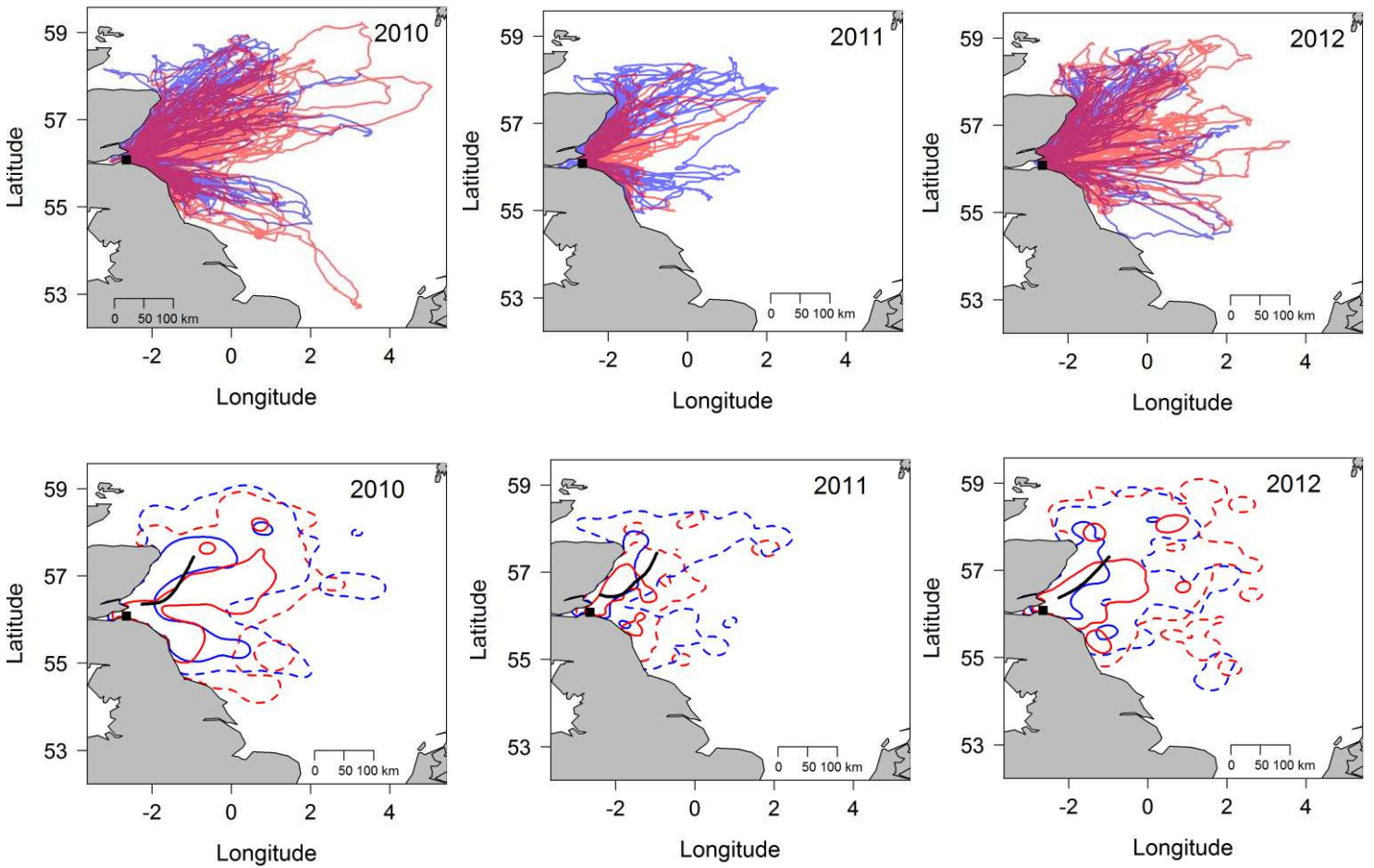
597 a) Raw location data; b) kernel density based utilization distributions at 95% (dotted lines)

598 and 50% (solid lines). Bass Rock is shown as a square and the approximate position of the

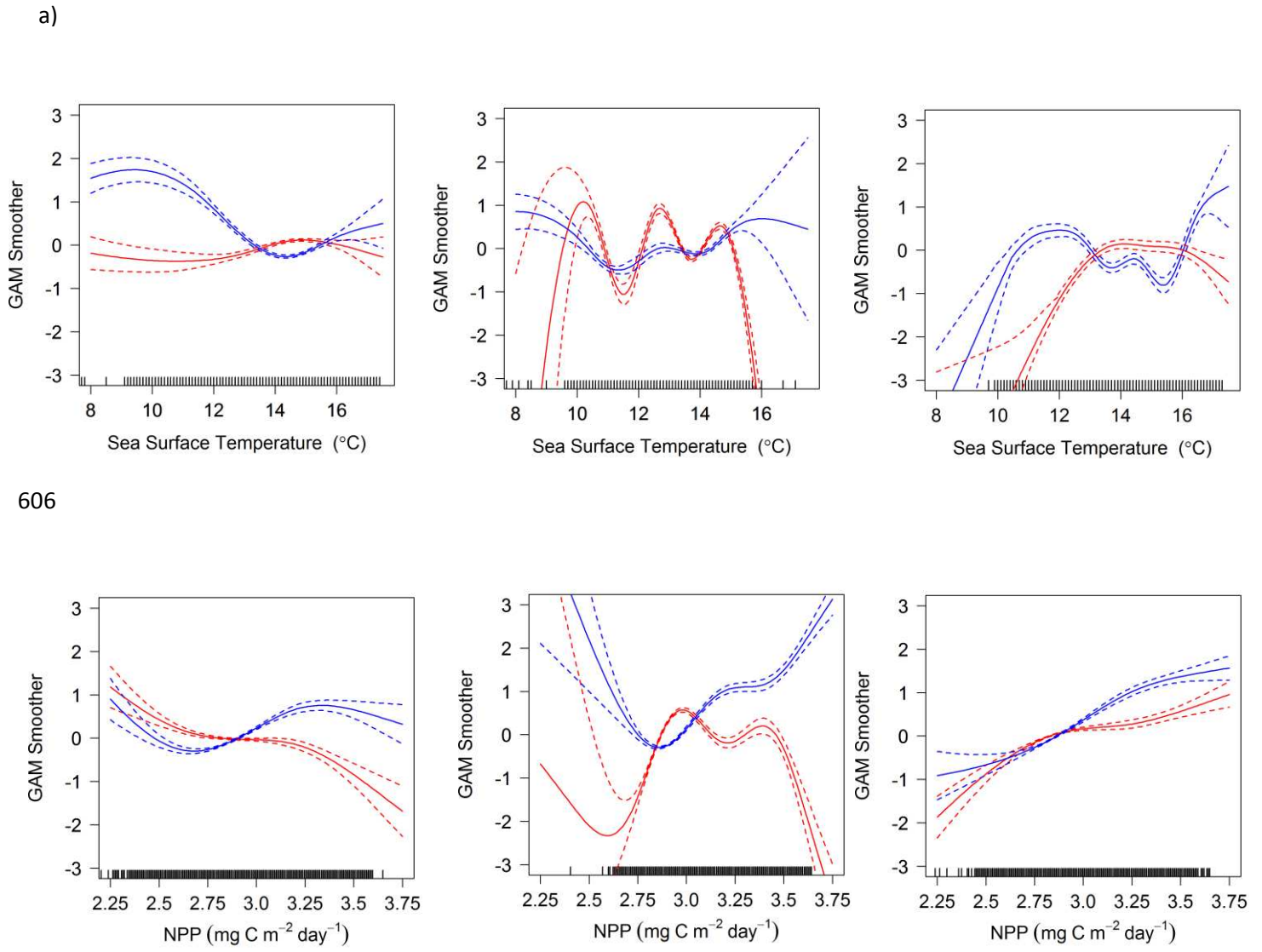
599 tidal mixing front each year is shown as a solid black line in (b).

600

a)
601



602 **Fig. 3.** Habitat selection functions for SST, NPP and front density for a) SST & b) NPP. Plots
 603 show the predicted curve from the model (solid line) and 95% confidence intervals (dashed
 604 line) for males (blue) and females (red) when the sexes differed and for both sexes combined
 605 (black) when they did not differ.



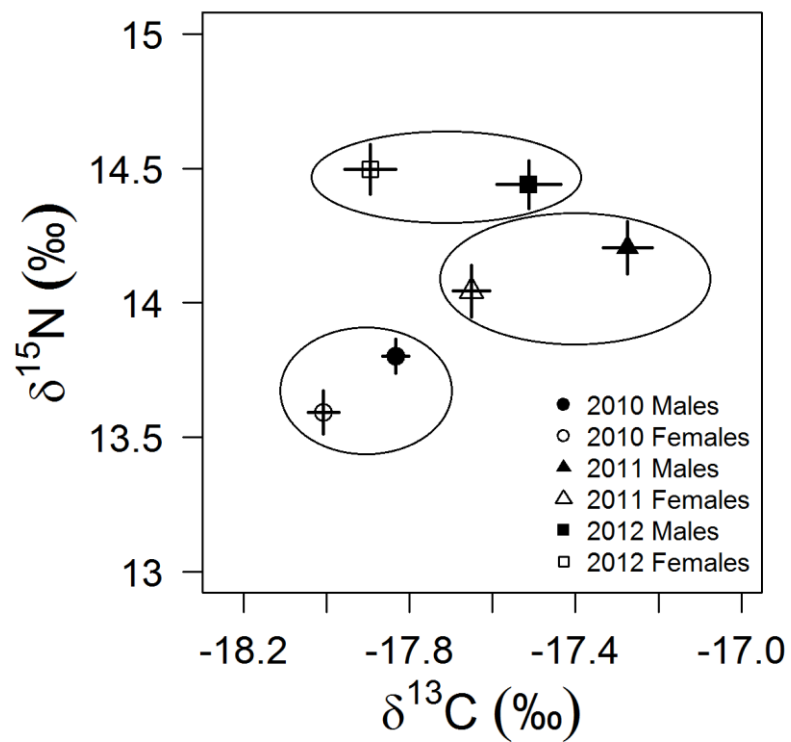
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611 **Fig. 4.** Mean \pm SE $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in red blood cells of breeding northern gannets.

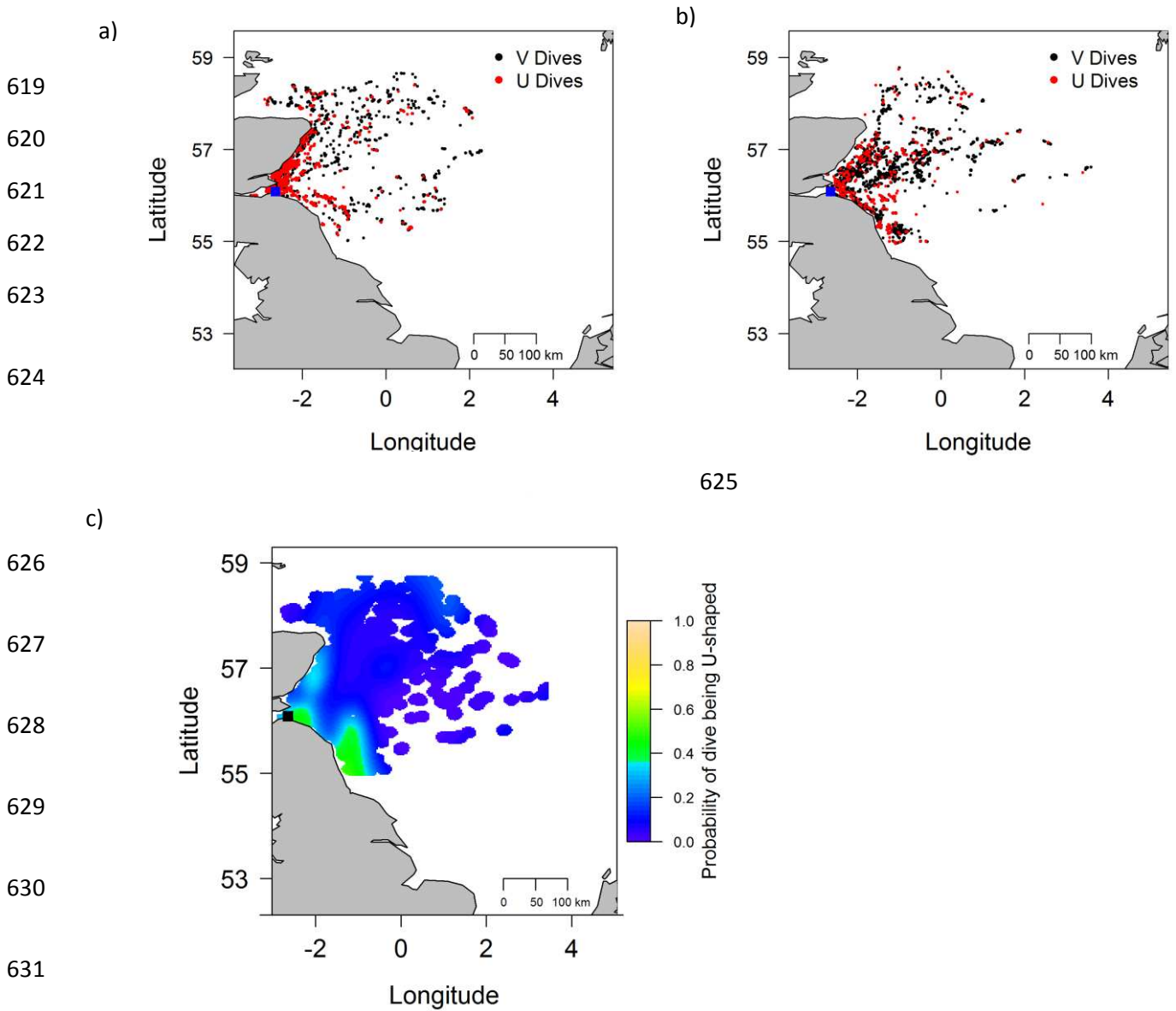
612 Values from the same year are circled.

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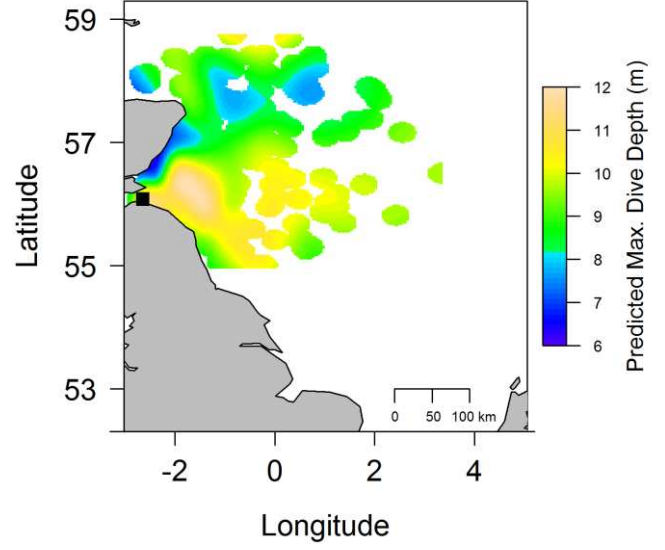
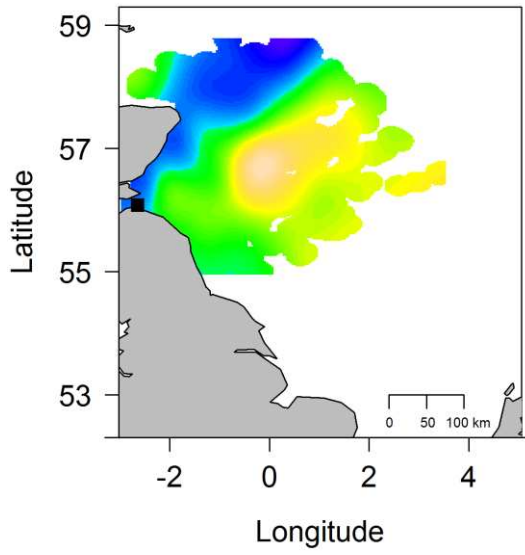
615 **Fig. 5.** The locations of U-shaped (red) and V-shaped (black) dives by (a) males and (b)
616 females. A plot of the spatial smoother from the GAMM dive-type analysis showing the
617 predicted probability that a dive will be classed as U-shaped (c). The square denotes the
618 position of Bass Rock.



634 **Fig. 6.** Spatial smoothers from the models of dive depth for (a) V-shaped dives and (b) U-
635 shaped dives. The location of Bass Rock is shown as a black square.

636 a)

b)



637