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Running head: Trends in year round shag diet

1 Pronounced long-term trends in year-round diet composition of the European shag

2 *Phalacrocorax aristotelis*

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13 Abstract (Word Count: 249)

14 Populations of marine top predators are exhibiting pronounced demographic changes due to
15 alterations in prey availability and quality. Changes in diet composition is a key potential
16 mechanism whereby alterations in prey availability can affect predator demography. Studies
17 of long-term trends in diet have focused on the breeding season. However, long-term changes
18 in non-breeding season diet is an important knowledge gap, since this is generally the most
19 critical period of the year for the demography of marine top predators. In this study, we
20 analysed 495,239 otoliths from 5888 regurgitated pellets collected throughout the annual
21 cycle over three decades (1985–2014) from European shags *Phalacrocorax aristotelis* on the
22 Isle of May, Scotland (56°11'N, 02°33'W). We identified dramatic reductions in the frequency
23 of lesser sandeel *Ammodytes marinus* occurrence over the study, which was more
24 pronounced during the non-breeding period (96% in 1988 to 45% in 2014), than the breeding
25 period (91% to 67%). The relative numerical abundance of sandeel per pellet also reduced
26 markedly (100% to 13%), with similar trends apparent during breeding and non-breeding
27 periods. In contrast, the frequencies of Gadidae, Cottidae, Pleuronectidae and Gobiidae all
28 increased, resulting in a doubling in annual prey richness from 6 prey types per year in 1988
29 to 12 in 2014. Our study demonstrates that the declining importance of the previously most
30 prominent prey and marked increase in diet diversity is apparent throughout the annual cycle,
31 suggesting that substantial temporal changes in prey populations have occurred, which may
32 have important implications for seabird population dynamics.

33 **Key words:** seabird; long-term study; North Sea; winter diet; non-breeding diet; pellet
34 analysis; lesser sandeel *Ammodytes marinus*.

35 Introduction

36 Marine environments are changing rapidly across the globe due to a range of anthropogenic
37 activities, including pollution, overfishing and climate change (Halpern 2009, Poloczanska et
38 al. 2013). These effects have altered the abundance and distribution of lower trophic
39 organisms such as plankton, with consequences for mid-trophic level fish which are the
40 principal prey for a guild of marine top predators (Cury et al. 2000, Frederiksen et al. 2006).
41 Many marine top predator populations are declining markedly in association with these
42 changes in prey availability and quality (Paleczny et al. 2015, Sydeman et al. 2015). Altered
43 diet composition is a key potential mechanism whereby changes in prey availability can affect
44 marine top predators (Reid & Croxall 2001, Cury et al. 2011). Several studies have
45 demonstrated long-term changes in marine top predator diet, in particular seabirds (Miller &
46 Sydeman 2004, Gaston & Elliott 2014). However, these studies have mainly been undertaken
47 during restricted periods of the annual cycle, because of logistical challenges of obtaining diet
48 data throughout the year. In seabirds, diet studies are usually conducted during the breeding
49 season, from samples delivered by adults to offspring (Barrett et al. 2007). However, the non-
50 breeding period is critically important for the population dynamics of seabirds, since most
51 mortality occurs at this time (Weimerskirch 2002, Frederiksen et al. 2008). Thus, a key
52 question in understanding the link between changes in prey availability and seabird
53 population dynamics is the extent to which there have been long-term changes in non-
54 breeding season diet, and whether these differ from those during the breeding season.

55 Our understanding of seabird diet outside the breeding period is largely based on indirect
56 methods such as stable isotopes and fatty acid analysis (Owen et al. 2013, Kowalczyk et al.
57 2014) or samples from shot/dead birds (Blake 1984, Harris et al. 2015). Such studies have
58 produced valuable insights into non-breeding diet, demonstrating marked differences from

59 the breeding season, owing to a combination of altered prey availability (Kowalczyk et al.
60 2015), energetic constraints (Markones et al. 2010), habitat association (Ainley et al. 1996)
61 and, in migratory species, altered locations (Ronconi et al. 2010). However, there is very
62 limited information on long-term changes in non-breeding diet. Green et al. (2015) examined
63 differences in breeding and non-breeding season diet in Cape gannets *Morus capensis* over a
64 thirty-year period. However, due to sporadic sampling, their trends analysis was restricted to
65 the breeding period only. To our knowledge, no published studies have quantified long-term
66 trends in non-breeding season diet composition in seabirds, and compared these with trends
67 in breeding season diet from the same population.

68 In this paper, we analysed three decades of year-round diet in the European shag
69 *Phalacrocorax aristotelis* (hereafter shag) collected on the Isle of May, south-east Scotland.
70 The shag is a coastally distributed seabird that spends a large proportion of the day and every
71 night on land (Wanless & Harris 1997). Full-grown shags regularly regurgitate pellets
72 containing prey remains, which can be collected at accessible roosts, offering a rare
73 opportunity to quantify year-round diet (Barrett et al. 2007). Shags show a flexible foraging
74 strategy such that diet varies substantially across the species range. Lesser sandeel
75 *Ammodytes marinus* (hereafter sandeel) is the dominant prey in many populations (Harris &
76 Wanless 1993, Velando & Freire 1999, Lilliendahl & Solmundsson 2006), but at others,
77 Gadoids (Gadidae), in particular saithe *Pollachius virens*, are the principal prey (Swann et al.
78 2008, Lorentsen et al. 2018). Seasonal variation in diet composition has been recorded in
79 some populations in response to changes in prey availability (Velando & Freire 1999,
80 Lilliendahl & Solmundsson 2006). Previous studies of the Isle of May population
81 demonstrated that, in the late 1980s and early 1990s, the diet of shags consisted mainly of
82 sandeels, with limited evidence of seasonal differences in diet composition (Harris and

83 Wanless 1991, 1993). However, the North Sea has warmed substantially over the past three
84 decades (Høyer & Karagali 2016), which has resulted in changes in the distribution,
85 abundance and diversity of many fish populations, including sandeel (Perry et al. 2005, Deurs,
86 Van et al. 2009, ter Hofstede et al. 2010). A recent analysis of diet based on prey delivered to
87 shag chicks on the Isle of May demonstrated a marked decline in the proportion of sandeel,
88 from 0.99 (1985) to 0.51 (2014), over this period, along with a concurrent dietary
89 diversification (Howells et al. 2017). The authors attributed this dietary change to climate-
90 mediated alterations in the availability of sandeels and alternative prey. Similarly, a
91 community-scale analysis of seabird breeding diet at this colony demonstrated a decline in
92 the importance of sandeels over the past three decades (Wanless et al. 2018). As local sandeel
93 populations are resident (Boulcott et al. 2007), it is probable that any effect of environmental
94 change on abundance or quality of these populations will affect both breeding and non-
95 breeding diet of shags which over-winter on the Isle of May. Thus, we might predict a decline
96 in the importance of sandeel in the diet throughout the annual cycle. However, sandeel
97 availability varies among seasons since they are present in the water column during the spring
98 and summer, but are buried in the sand during the winter, apart from a brief period when
99 they emerge to spawn (Wright & Bailey 1993). Furthermore, environmental conditions,
100 habitat use and energetic costs also vary between seasons (Daunt et al. 2014, Michelot et al.
101 2017). Thus, any changes in overall prey abundance or availability during the study might have
102 different effects on diet composition at different times of the year. However, whether long-
103 term changes in diet composition outside the breeding season has matched trends observed
104 in diet during the breeding season (Howells et al 2017) is untested. Therefore, our specific
105 aims were to: a) quantify year round diet composition of shags over three decades; and b)
106 test whether dietary trends differ between the non-breeding and breeding period.

107 Methods

108 Quantifying diet

109 The study was conducted between 1985 and 2014 at a European shag *Phalacrocorax*
110 *aristotelis* (hereafter shag) colony on the Isle of May National Nature Reserve, Firth of Forth,
111 south-east Scotland (56°11'N, 02°33'W). Shags are present on the island throughout the year,
112 with a resident proportion of the breeding population joined in winter by migrants from other
113 locations (Grist et al. 2014), allowing for the collection of pellets throughout the year. Pellets
114 were collected opportunistically (mean number of sample days year⁻¹ ± SD: 23 ± 14; range: 3–
115 49) at roosts and breeding colonies using forceps, placed into a plastic bag and frozen. The
116 breeding status and age of individuals that produced pellets was unknown. However, as chicks
117 do not produce pellets, all samples were from full-grown (i.e. fledged) birds (Russell et al.
118 1995).

119 Samples were submerged in a saturated solution of biological washing powder (Biotex©) and
120 heated at 40–50°C, until all soft tissue and mucus was digested. Residual hard parts (e.g. fish
121 otoliths, vertebrae and mouth parts, cephalopod beaks, mollusc shells and crustacea
122 exoskeletons) were then identified to the lowest possible taxon using keys in Härkönen (1986)
123 and Watt et al. (1997), allowing the presence/absence of each prey type to be recorded in
124 each pellet. Sandeels *Ammodytes* spp. (principally, lesser sandeels *A. marinus*; Harris and
125 Wanless 1991), the most frequent prey type recorded, have previously been classified in
126 dietary studies on the basis of age (Harris and Wanless 1991, Howells et al. 2017). However,
127 differentiating between sandeel age classes is generally not possible from otoliths obtained
128 from pellets due to the effect of digestive erosion on otolith structure. Therefore, for the
129 purposes of this study, all sandeels were aggregated into a single prey category. The presence

130 of sand was also noted, since it may arise from accidental ingestion when foraging in sandy
131 habitats and therefore be an index of prey species that live in these habitats, notably sandeels
132 (Winslade 1974, Holland et al. 2005). The number of otoliths of each prey type in each pellet
133 was then counted. Each fish has two otoliths, but due to the large numbers that may be
134 encountered in a pellet and the potential for otoliths within a pair to undergo differential
135 digestion, it was not possible to accurately match otoliths from the same fish. Therefore, each
136 otolith was treated as an individual sample within each pellet.

137 Pellet analysis has been used to quantify diet in a range of seabirds, including shags,
138 cormorants, skuas and terns (reviewed in Barrett et al. 2007). In appropriate study systems,
139 large sample sizes may be obtained in a non-intrusive way throughout the year. However,
140 quantifying diet from pellets involves two well-established limitations that must be
141 considered when interpreting the data. First, due to differential rates of erosion, small or soft
142 prey may be completely absent or under-represented in pellets, with larger prey, or those
143 with more resilient body parts, more commonly retained (Barrett et al. 2007). For example,
144 Johnstone et al. (1990) showed that in captive shags the recovery of otoliths from Sprat
145 *Sprattus sprattus*, sandeel and Cod *Gadus morhua* was 17%, 20% and 52%, respectively.
146 Accordingly, the most robust diet metric used to quantify prey in pellets is frequency of
147 occurrence, in which items are scored on the basis of presence or absence. This method does
148 not capture prey types that are completely digested, but accounts for any differential in
149 digestion rates among prey types that are recorded by giving equal weighting to prey types
150 irrespective of abundance in the sample. We also considered a second diet measure that is
151 typically quantified from pellets, the numerical abundance of different prey types. This
152 measure is more informative, but must be interpreted with care because it is more sensitive
153 to the effects of differential digestion rates (Barrett et al. 2007).

154 A second limitation of quantifying diet from pellets is that the exact date when the prey were
155 ingested is not known. However, the vast majority of pellets were fresh when collected, and
156 they do not persist on rocks at our study colony because they disintegrate in rain or are
157 consumed by herring gulls *Larus argentatus*, so we consider that pellets will have been
158 produced within ca. two weeks of the sampling date.

159 Dietary response variables

160 For each pellet, we recorded the presence or absence of diagnostic remains (e.g. fish otolith,
161 vertebra, bone, mollusc shell, cephalopod beak) of each prey type. Frequency of occurrence
162 was then calculated as the percentage of pellets in which the prey type was found in each
163 period within each study year. We focused our analysis on frequency of occurrence of the top
164 five most abundant fish prey: sandeel *Ammodytes* spp., Gadidae (Cod Fishes), Cottidae
165 (Cottids), Pleuronectidae (Flatfish) and Gobiidae (Gobies). All other prey types occurred in \leq
166 10% of pellets and could thus not be analysed robustly, but due to their low prevalence in the
167 diet, we consider the omission of these prey unlikely to significantly affect our interpretation
168 of changes in diet composition.

169 Numerical abundance is typically quantified as the proportion of otoliths of a given fish prey
170 type relative to all otoliths in the pellet. However, where the diet is dominated by a small
171 number of prey types, as in this study (Sandeel 88% and Gadidae 7% of all otoliths), analysis
172 of relative proportions leads to problems of interpretation, since a change in one prey type
173 cannot be readily distinguished from a reciprocal change in the other. We therefore modelled
174 number of sandeel otoliths relative to all prey otoliths and number of Gadidae otoliths relative
175 to all non-sandeel prey otoliths. All other individual prey types occurred too infrequently for

176 their relative abundance to be analysed. However, their summed contribution was < 5% of all
177 otoliths.

178 Diet diversity was quantified by calculating sample-level prey richness, which was the number
179 of prey types recorded in each pellet. Due to the effects of digestion on prey items, it was not
180 generally possible to identify all body parts to species level, but to a higher taxonomic level
181 which varied with prey type (fish: family; Crustacea and Mollusca: subphylum; Polychaeta:
182 class). As prey richness is a count, the aggregate, annual prey richness (pooling all pellets in
183 each year) was systematically higher than the sample average (sample-level prey richness:
184 median: 5; range: 0–9; annual prey richness: median: 12; range: 6–14). However, as annual
185 prey richness is a measure of the total number of prey types exploited each year, we included
186 it in our analysis.

187 Defining breeding and non-breeding periods

188 For the purpose of this study, a study year commenced at the onset of breeding in one
189 calendar year and ended at the commencement of breeding in the subsequent calendar year.
190 To determine the timing of onset of breeding in each study year we calculated the month in
191 which the population median egg laying date occurred, estimated from weekly observations
192 at long-term monitoring plots (1985–2014: median day of year: range: 101–181; Newell et al.
193 2015; updated). In shags, average incubation duration of a clutch of three eggs, the modal
194 clutch size in this population, is 36 days (Potts et al. 1980), with fledging occurring at a mean
195 of 53 days after hatching (range: 48–58, n = 35; Potts et al. 1980). Therefore, we defined each
196 breeding season as the month of median egg laying date plus the following three months.
197 This four month period was longer than the breeding period of individual pairs (~3 months),
198 but was designed to capture the spread of laying that occurs in each year (Daunt et al. 2007).

199 We found that 97% of all observations of breeding activity (defined as observations of
200 incubating eggs or brooding chicks; $n = 29,075$) at our long-term monitoring plots occurred in
201 this four month time window, confirming that it was a robust representation of the breeding
202 period. The non-breeding period commenced in the first month after the breeding period
203 until the last month before the month of median laying date in the following year (range of
204 months: breeding: April–September; non-breeding: August–May; Supplementary Material
205 Table S1).

206 Statistical analysis

207 All statistical analyses were conducted using the R programming software (version 3.4.0, R
208 Development Core Team 2016). To test for temporal trends and effects of period (breeding
209 vs non-breeding) on sample-level presence, relative numerical abundance and prey richness,
210 we fitted Generalised Linear Mixed Models (hereafter GLMMs), using the ‘glmer’ function in
211 the ‘lme4’ package (Bates et al. 2015). Binomial models with a logit-link function were fitted
212 for presence and relative numerical abundance, and Poisson models with a log-link function
213 for sample-level prey richness. For each of the sample-level dietary components we fitted a
214 global model containing fixed effects of year, period and a year by period interaction. This
215 framework allowed us to test for temporal trends, the differences between periods, and
216 differing temporal trends between breeding and non-breeding periods in each of the dietary
217 components. Within each model, we also included random effects for month, year and month
218 nested within year, to account for residual temporal autocorrelation. To account for
219 overdispersion, we also included an individual, sample-level random effect in models of
220 sandeel otoliths relative to all prey and Gadidae relative to non-sandeel prey (Harrison 2015).
221 We did not consider sample date as an explanatory variable, since this variable had no clear

222 biological relevance, due to the variable time elapsed between pellet production and
223 collection.

224 To identify trends in annual prey richness, where there was just a single value per year, we
225 fitted a Poisson GLMM with a log-link function. We subtracted 6 (the minimum annual prey
226 richness value over the study) from each value, so that the data are consistent with the
227 distributional properties of the Poisson distribution. However, we present the results and
228 plots on the original, unadjusted scale. This step was not necessary with the sample-level prey
229 richness data, as the minimum value was zero i.e. pellets where no species were identified.

230 Visual inspection indicated that the annual prey richness may be exhibiting non-linear trends.

231 To test this, a global model containing both a linear and quadratic numeric fixed effect of year
232 was fitted, along with a categorical, annual level random effect of year to account for
233 overdispersion (Harrison 2015). We weighted each annual prey richness value by the number
234 of pellets per year and included a fixed (offset) effect of $\log(\text{number of pellets year}^{-1})$ to
235 account for any systematic change in annual prey richness with annual sample size.

236 In order to compare models with different fixed effects but the same random structure we
237 used maximum likelihood in all models (Zuur et al. 2009). In each analysis, the fixed effect of
238 year was centred on zero (by subtracting mean year from each value) and rescaled (by dividing
239 the centred value by the standard deviation of year). The inclusion of all years in the analysis
240 led to difficulties with model convergence. Preliminary analyses confirmed that this was
241 caused by the inclusion of years where samples were not collected in both the breeding and
242 non-breeding periods, so these were excluded from the modelling process (707 samples in 7
243 years; 1985–87, 1994, 1998–99, 2008).

244 Model selection was performed on the four models (null, year, period, and year by period
245 interaction) for each variable using Akaike's Information Criterion corrected for small sample
246 sizes (AICc), where the best-supported model was considered to have the lowest AICc value
247 compared to alternative models. Models within two AICc ($\Delta AICc < 2$) of the top model were
248 deemed as having similar levels of support (Burnham & Anderson 2002), unless they
249 contained an additional parameter, in which case they were considered uninformative
250 (Arnold 2010). Analysis was conducted according to an established protocol (Zuur et al. 2010),
251 with the 'MuMIn' (Bartoń 2016) package used to obtain model selection outputs (see
252 Supplementary Material for full details of model selection). Due to the large number of
253 models, we only report those within 10 AICc points of the best model in the main text.

254 For figures and tables, annual means were calculated by pooling all samples in each period
255 within a year. For presence, each mean value was calculated as the frequency of occurrence
256 i.e. the percentage of samples in which the prey class was present. For numerical abundance,
257 each mean value was calculated as the proportion of all otoliths of a given prey type relative
258 to all otoliths. To aid comparison with frequency of occurrence, we converted numerical
259 abundance proportions into percentages. Study years commenced at the onset of breeding,
260 so each spanned two calendar years. All study years were retained in figures of annual mean
261 data (1985–2014), with model plots presented over the range of years included in the analysis
262 (1988–2014).

263 Results

264 Pellet composition

265 A total of 5888 pellets were collected between 1985 and 2014 ($n = 23$ years; mean \pm SD pellets
266 year⁻¹: 256 ± 212 ; range: 31–973), with 5,668 (96%) containing at least one identifiable prey

267 type. The data set comprised 3140 pellets from the breeding period (mean \pm SD pellets year⁻¹: 136 \pm 112; range: 0–342) and 2748 from the non-breeding period (mean \pm SD pellets year⁻¹: 119 \pm 132; range: 0–538; Supplementary Material Table S2).

270 Fifteen individual prey types were identified using all prey remains (Table 1). Fish were the
271 dominant prey, with sandeel the most frequently encountered, occurring in 79% of pellets
272 (Table 1; Figure 1a). The next most frequently encountered prey was Gadidae (Cod Fishes)
273 occurring in 41% of pellets (Figure 1b), followed by Cottidae (Cottids; 20%; Figure 1c),
274 Pleuronectidae (Rigthead Flounders; 19%; Figure 1d) and Gobiidae (Gobies; 19%; Figure 1e).
275 All other prey occurred in \leq 10% of pellets (Table 1). Sand occurred in 52% of pellets (Figure
276 1e; Table 1). The median sample-level and annual prey richness was 5 (range: 0–9) and 12
277 (range: 6–14), respectively.

278 We recorded 495,239 otoliths belonging to 11 fish prey types, with 4913 (83%) pellets
279 containing at least one identifiable otolith (Table 2; mean \pm SD otoliths pellet⁻¹: 84 \pm 117;
280 range 0–1,048). Otoliths were dominated by sandeel (88%; mean \pm SD relative numerical
281 abundance per sample: 70 \pm 40%). Gadidae were the second most common (7%; mean \pm SD:
282 46 \pm 41% numerical abundance relative to all non-sandeel otoliths). All other fish prey
283 comprised $<$ 5% of otoliths (Table 2).

284 Temporal and seasonal changes in pellet composition

285 The best-supported model for sandeel presence contained an effect of year, period and a year
286 by period interaction (Table 3; full model selection table presented in Supplementary Material
287 Table S3). Overall, sandeel frequency of occurrence decreased markedly in both the breeding
288 and non-breeding periods. However, the decline was more pronounced during the non-
289 breeding period, from 96% in 1988 to 45% in 2014, compared to 91% to 67% during the

290 breeding season (data values: Figure 1a; predicted values from model: Figure 2a). The best-
291 supported model for both Gadidae and Cottidae presence contained an effect of year only
292 (Table 3; Table S3). Gadidae frequency of occurrence increased from 22% in 1988 to 66% in
293 2014 (data values: Figure 1b; predicted values from model: Figure 2b), whereas Cottidae
294 frequency of occurrence increased from 5% in 1988 to 45% in 2014 (data values: Figure 1c;
295 predicted values from model: Figure 2c; Table 3; Table S3). Overall, there was an increase in
296 Pleuronectidae presence over the study, driven predominantly by the breeding period, when
297 frequency of occurrence increased from 7% (1988) to 23% (2014), with frequency during the
298 non-breeding period remaining relatively constant at 15% in 1988 and 14% in 2014 (data
299 values: Figure 1d; predicted values from model: Figure 2d; Table 3; Table S3). Gobiidae
300 presence increased overall between 1988 and 2014, but there was a significant interaction
301 between year and period such that presence was higher during the non-breeding period at
302 the start of the study (breeding 2%; non-breeding 6%), while by the end of the study the
303 frequency was the same in both periods (breeding 21%; non-breeding 21%; data values:
304 Figure 1e; predicted values from model: Figure 2e; Table 3; Table S3). Presence of sand
305 displayed a substantial decline over the study, with a significant year by period interaction
306 such that frequency reduced from 44% to 19% during breeding and 92% to 16% in the non-
307 breeding period (data values: Figure 1f; predicted values from model: Figure 2f; Table 3; Table
308 S3).

309 Sandeel numerical abundance relative to all otoliths decreased from 100% in 1988 to 13% in
310 2014, but there was no evidence of a difference between the breeding and non-breeding
311 periods (data values: Figure 3a; predicted values from model: Figure 4a; Table 4; full model
312 selection table presented in Supplementary Material Table S4). The decline was less marked
313 at the start of the study, but accelerated from the early 2000s. Gadidae numerical abundance

314 relative to all non-sandeel otoliths reduced overall, but was consistently higher during
315 breeding (data values: Figure 3b; predicted values from model: Figure 4b; Table 4; Table S4).
316 The magnitude of change was similar in the two seasons, from 68% (1988) to 48% (2014) in
317 the breeding period, and from 54% (1988) to 34% (2014) in the non-breeding period.

318 Sample-level prey richness increased over the study, but with a more marked increase during
319 breeding (from 1.16 prey types pellet⁻¹ in 1988 to 3.36 in 2014) than non-breeding (1.67 prey
320 types pellet⁻¹ in 1988 to 2.69 in 2014; data values: Figure 5a; predicted values from model:
321 Figure 6a; Table 5; full model selection table presented in Supplementary Material Table S5).
322 Annual prey richness displayed a quadratic trend over the study, increasing from 6.27 prey
323 types year⁻¹ in 1988 to 12.31 in 2014, with a peak of 15.80 in 2007 (data values: Figure 5b;
324 predicted values from model: Figure 6b; Table 5; Table S5). However, a model containing a
325 linear effect of year received similar support, providing strong evidence for an increasing
326 trend in annual prey richness.

327 Discussion

328 We identified dramatic changes in the diet composition of full-grown European shags
329 *Phalacrocorax aristotelis* (hereafter shag) on the Isle of May over the past three decades both
330 during and outside the breeding season. The dominance of lesser sandeels *Ammodytes*
331 *marinus* (hereafter sandeel) decreased, with the decline in sandeel occurrence more marked
332 during the non-breeding period. In contrast, the frequency of Gadidae, Cottidae,
333 Pleuronectidae and Gobiidae increased. Prey richness also increased over the course of the
334 study, in particular during the breeding period. These marked changes highlight the
335 importance of monitoring changes in diet composition throughout the annual cycle.

336 Dietary change

337 Our findings of an overall decline in the dietary contribution of sandeel throughout the annual
338 cycle, support our general prediction that changes in the importance of sandeels over time
339 would be similar in breeding and non-breeding diets, since local sandeel populations are
340 resident (Boulcott et al. 2007). One explanation for this year-round reduction is climate-
341 mediated alterations in the abundance, availability or profitability of sandeels associated with
342 rising temperatures in the North Sea (Arnott & Ruxton 2002, Deurs, Van et al. 2009). Similar
343 dietary changes have been observed in other seabird populations in response to changes in
344 prey availability (Miller & Sydeman 2004, Gaston & Elliott 2014, Green et al. 2015). Howells
345 et al. (2017) also recorded a reduction in the length of sandeels fed to nestling shags at this
346 colony over the past three decades, which, due to the negative, non-linear relationship
347 between calorific content and sandeel size (Hislop et al. 1991, Wanless et al. 2005), may be
348 linked to the decreasing prevalence in shag diet. However, due to substantial digestive
349 erosion of sandeel otoliths in pellets (Johnstone et al. 1990), it was not possible to use otolith
350 length-fish length relationships to infer changes in sandeel length in this study. With flexible
351 foraging behaviours, as evidenced by the wide range of prey types exploited throughout their
352 range, shags may be able to adjust their diet in response to availability and quality of
353 alternative prey. Such flexibility may be a key mechanism underpinning the dietary trends
354 observed in this study, such that sandeel may have become scarcer or lessened in profitability
355 compared to alternative prey, which may themselves have become more abundant or
356 profitable. Data suggests that the energy density of alternative prey is similar to sandeels
357 (Spitz et al. 2010). However, in the absence of estimates of prey availability or capture rates,
358 it is not possible to fully establish the causes underpinning these temporal patterns in diet
359 composition. Industrial fisheries may also reduce the availability of sandeels, with knock-on

360 effects on seabird diet composition. However, the sandeel fishery off eastern Scotland did not
361 overlap spatially with the foraging distribution of this shag population (Bogdanova et al.
362 2014). Furthermore, the fishery was only operational between 1990 and 1999 (Daunt et al.
363 2008). As such, we would have expected a stepped reduction in sandeel occurrence in the
364 diet over this period, which was not what we found. Similarly, Wanless et al. (2018) did not
365 record a reduction in sandeel occurrence in the diet of the seabird community breeding at
366 the colony during the 1990s. We therefore consider it unlikely that top-down fishing pressure
367 was driving the observed trends in sandeel dietary contribution.

368 The steeper decline in sandeel frequency of occurrence during the non-breeding period may
369 be linked to reduced foraging capacity at this time of the year, as a result of shortened day
370 length, adverse weather and absence of sandeels in the water column, apart from a brief
371 period during spawning (Wright & Bailey 1993, Frederiksen et al. 2008, Daunt et al. 2014).
372 Accordingly, any changes in overall prey availability over the course of the study might have
373 had a more pronounced effect on diet composition at this time of year than during the
374 breeding season. However, no seasonal difference in the rate of change was apparent in
375 sandeel numerical abundance. This disparity with sandeel occurrence may arise because
376 numerical abundance is quantified as the proportion relative to other prey, which themselves
377 may have shown seasonal differences in trends. However, we could not test this since we
378 could not distinguish changes in sandeels from reciprocal changes in other prey. Whatever
379 the mechanism, the lack of difference between breeding and non-breeding periods in the
380 trend in numerical abundance of sandeels relative to other prey suggests that this species has
381 shown similar declines throughout the year in terms of biomass consumed. The overall
382 reduction in frequency of sand is in line with these conclusions. Sand ingestion likely reflects
383 accidental ingestion when foraging for sandeels, since shags generally extract sandeels

384 directly from within the sand sediment (Watanuki et al. 2008), whereas other prey species
385 that live in these habitats, such as Pleuronectidae and Callionymidae, are more likely captured
386 on the sea floor.

387 The increase in dietary frequency of Gadidae accords with recent evidence of a distributional
388 shift into Scottish waters of some Gadiformes in recent years (Cormon et al. 2014), including
389 saithe *Pollachius virens*, the principle prey of shags in some populations. Pleuronectidae
390 frequency also increased in the diet over the last thirty years, so shags may have continued
391 to forage in sandy areas through the course of the study, but increasingly targeted
392 Pleuronectidae, and other prey associated with sandeel habitats, such as Callionymidae,
393 rather than sandeels. Gobiidae also increased, but this prey class is predominantly associated
394 with rocky areas, which accords with past work on this population demonstrating the use of
395 multiple habitats (Watanuki et al. 2008). Gadidae otoliths relative to other non-sandeel prey
396 reduced over the study, suggesting that other non-sandeel prey have increased more rapidly
397 than Gadidae. However, there was strong evidence that Gadidae numerical abundance
398 relative to other non-sandeel prey was consistently higher during breeding. This is in contrast
399 to Lilliendahl and Solmundsson (2006) who observed a higher prevalence of Gadidae in
400 Icelandic shag pellets during winter. One possible explanation is that many Gadidae species
401 use inshore waters as nursery grounds, with immatures moving into shallow, coastal feeding
402 areas in the Firth of Forth during summer (Bergstad et al. 1987, Heessen et al. 2015).

403 One consequence of these dietary changes is that both sample-level and annual prey richness
404 increased over the study, with the latter peaking in 2007. Long-term dietary diversification
405 has also been observed in other seabird species in response to changes in prey availability
406 (Gaston & Elliott 2014). The parallel increase in diversity at the single pellet and whole year

407 scale suggests that, on average, the population is now exhibiting an individual
408 generalist/population generalist structure of resource use (Bolnick et al. 2003). Seasonal
409 patterns of sample-level prey richness changed over the study, such that the increase was
410 more pronounced during breeding, in line with seasonal differences in the pattern of change
411 among Pleuronectidae and Gobiidae frequency of occurrence. Climate-mediated changes in
412 fish populations have been widely reported in the North Sea, including changes in the
413 abundance and distribution of many species (Perry et al. 2005, Dulvy et al. 2008). Thus, the
414 dietary trends observed in our study population may be indicative of reductions in the
415 abundance and availability of sandeel, increases in non-sandeel prey or a combination of
416 both. These changes may vary among seasons, but without independent data on any
417 abundance of these prey types it is currently not possible to distinguish these alternatives.

418 Limitations

419 It is important to recognise the limitations of estimating year-round diet from pellets when
420 interpreting our results. The most important limitation of pellet analysis is the potential for
421 underrepresentation of soft-bodied or easily digestible prey (Barrett et al. 2007). For example,
422 Pholidae and Callionymidae (the otoliths of which are poorly sampled by pellet analysis) can
423 form a substantial proportion of chick diet in this population (Howells et al. 2017), but were
424 recorded infrequently in pellets. One important consequence of this is patterns of long-term
425 change over time might have been different had we been able to detect all prey types. In
426 particular, the increase in diversity over the course of the study may be greater than we could
427 demonstrate if more digestible prey than sandeels have become more common in the diet
428 throughout the year, as indicated from our diet data obtained from regurgitates (Howells et
429 al. 2017). A further limitation of our study is that we had to pool all sandeel age-classes. As a

430 result, we could not examine temporal and seasonal patterns in the relative contribution of
431 different age classes, in contrast to our recent analysis of diet from regurgitations (Howells et
432 al. 2017). Another consideration is that due to substantial differences in detection rates with
433 sandeel size (i.e. larger fish are better represented in pellets; Johnstone et al. 1990), some of
434 the observed reduction in sandeel relative numerical abundance may have been exacerbated
435 by changes in detectability, since average sandeel length declined over the course of the study
436 (Howells et al. 2017). However, given the dramatic trends observed in this study and the
437 comparatively small decrease in sandeel size observed in chick diet (from in 104.5 mm 1988
438 to 92.0 in 2014), we consider our observation of a decline in sandeel abundance to be robust
439 to this limitation. Finally, uncertainty in the date of pellet production could also have affected
440 our results, for example by assigning pellets to the wrong period. However, given the length
441 of non-breeding and breeding periods (several months) compared with the maximum likely
442 duration between pellet production and collection (ca. two weeks), and the fitting of month
443 as a random term in our models, we do not consider that this error would have had a strong
444 impact on our results.

445 Demographic and conservation implications

446 The year-round reduction in the importance of sandeels in shag diet and associated dietary
447 diversification may have important demographic consequences. In shags, the majority of
448 mortality occurs in winter (Aebischer 1986, Harris & Wanless 1996, Frederiksen et al. 2008),
449 linked to foraging capacity in more challenging environmental conditions (Daunt et al. 2006,
450 2014, Lewis et al. 2015). Such changes may also be important during pre-breeding, when diet
451 composition can be a key determinant of subsequent reproductive success (Sorensen et al.
452 2009). Prey availability during the breeding season is also a key determinant of breeding

453 success (Daunt et al. 2001, Frederiksen et al. 2007). Crucially, effects on fitness are likely to
454 depend on the relative profitability of different prey types throughout the annual cycle (Hislop
455 et al. 1991, Litzow et al. 2004). Due to the difference in habitat associations between prey
456 types, the dietary change observed may also have important implications for shag foraging
457 distributions (Bogdanova et al. 2014, Michelot et al. 2017). The increase in proportion of non-
458 sandeels in the diet could alter interactions with anthropogenic activities, such as offshore
459 renewable developments or recreation. Shags in this population are partial migrants,
460 whereby a proportion of individuals remain resident throughout the year while the remainder
461 migrate (Grist et al. 2014). Studies that estimate diet composition during the non-breeding
462 period throughout the population range would deliver a more complete picture of the
463 potential implications for population dynamics and conservation management.

464 In summary, we identified substantial alterations in diet composition of a population of shags
465 throughout the annual cycle over a thirty-year period. Our results accord with recent climate-
466 mediated changes in the distribution and abundance of many ecologically and commercially
467 important fish species in the North Sea, most notably sandeel. To our knowledge, this study
468 is the first to have quantified long-term trends in seabird diet outside the breeding season.
469 The similarities and differences observed in these long-term trends compared with those
470 during the breeding season highlight the importance of considering the diet of seabirds
471 throughout the annual cycle in assessments of long-term dietary change. That the decline in
472 sandeel frequency and abundance is apparent both during and outside the breeding season
473 suggests that substantial temporal changes in prey populations have occurred, and may have
474 important implications for seabird population dynamics in the region.

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491 References

- 492 Aebischer NJ (1986) Retrospective Investigation of an Ecological Disaster in the Shag,
493 Phalacrocorax aristotelis: A General Method Based on Long-Term Marking. *J Anim Ecol*
494 55:613–629
- 495 Ainley DG, Spear LB, Allen SG, Ribic CA (1996) Temporal and spatial patterns in the diet of the
496 common murre in California waters. *Condor* 98:691–705
- 497 Arnold TW (2010) Uninformative parameters and model selection using Akaike’s information
498 criterion. *J Wildl Manage* 74:1175–1178
- 499 Arnott SA, Ruxton GD (2002) Sandeel recruitment in the North Sea: Demographic, climatic
500 and trophic effects. *Mar Ecol Prog Ser* 238:199–210
- 501 Barrett RT, Camphuysen K, Anker-Nilssen T, Chardine JW, Furness RW, Garthe S, Hüppop O,
502 Leopold MF, Montevecchi WA, Veit RR (2007) Diet studies of seabirds: A review and
503 recommendations. *ICES J Mar Sci* 64:1675–1691
- 504 Bartoń K (2016) Multi-Model Inference “MuMIn.”
- 505 Bates D, Mächler M, Bolker BM, Walker SC (2015) Fitting linear mixed-effects models using
506 lme4. *J Stat Softw* 67:1–48
- 507 Bergstad OA, Jørgensen T, Dragesund O (1987) Life history and ecology of the gadoid
508 resources of the Barents Sea. *Fish Res* 5:119–161
- 509 Blake BF (1984) Diet and fish stock availability as possible factors in the mass death of auks in
510 the North Sea. *J Exp Mar Bio Ecol* 76:89–103
- 511 Bogdanova MI, Wanless S, Harris MP, Lindström J, Butler A, Newell MA, Sato K, Watanuki Y,
512 Parsons M, Daunt F (2014) Among-year and within-population variation in foraging
513 distribution of European shags *Phalacrocorax aristotelis* over two decades: Implications
514 for marine spatial planning. *Biol Conserv* 170:292–299
- 515 Boulcott P, Wright PJ, Gibb FM, Jensen H, Gibb IM (2007) Regional variation in maturation of
516 sandeels in the North Sea. *ICES J Mar Sci* 64:369–376
- 517 Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical

- 518 information-theoretic approach (KP Burnham and DR Anderson, Eds.), 2nd edn. Springer-
519 Verlag, New York
- 520 Cormon X, Loots C, Vaz S, Vermard Y, Marchal P (2014) Spatial interactions between saithe
521 (*Pollachius virens*) and hake (*Merluccius merluccius*) in the North Sea. ICES J Mar Sci
522 71:1342–1355
- 523 Cury P, Bakun A, Crawford RJM, Jarre A, Quiñones RA, Shannon L, Verheye HM (2000) Small
524 pelagics in upwelling systems: patterns of interaction and structural changes in “wasp-
525 waist” ecosystems. ICES J Mar Sci 57:603–618
- 526 Cury PM, Boyd IL, Bonhommeau S, Anker-Nilssen T, Crawford RJM, Furness RW, Mills JA,
527 Murphy EJ, Österblom H, Paleczny M, Piatt JF, Roux J-P, Shannon L, Sydeman WJ
528 (2011) Global Seabird Response to Forage Fish Depletion—One-Third for the Birds.
529 Science 334:1703–1706
- 530 Daunt F, Afanasyev V, Silk JRD, Wanless S (2006) Extrinsic and intrinsic determinants of winter
531 foraging and breeding phenology in a temperate seabird. Behav Ecol Sociobiol 59:381–
532 388
- 533 Daunt F, Monaghan P, Wanless S, Harris MP, Griffiths R (2001) Sons and daughters: Age-
534 specific differences in parental rearing capacities. Funct Ecol 15:211–216
- 535 Daunt F, Reed TE, Newell M, Burthe S, Phillips RA, Lewis S, Wanless S (2014) Longitudinal bio-
536 logging reveals interplay between extrinsic and intrinsic carry-over effects in a long-lived
537 vertebrate. Ecology 95:2077–2083
- 538 Daunt F, Wanless S, Greenstreet SPR, Jensen H, Hamer KC, Harris MP (2008) The impact of
539 the sandeel fishery closure in the northwestern North Sea on seabird food consumption,
540 distribution and productivity. Can J Fish Aquat Sci 65:362–381
- 541 Daunt F, Wanless S, Harris MP, Money L, Monaghan P (2007) Older and wiser: Improvements
542 in breeding success are linked to better foraging performance in European shags. Funct
543 Ecol 21:561–567
- 544 Deurs, Van M, VanHal R, Tomczak MT, Jónasdóttir SH (2009) Recruitment of lesser sandeel
545 *Ammodytes marinus* in relation to density dependence and zooplankton composition.

- 546 Mar Ecol Prog Ser 381:249–258
- 547 Dulvy NK, Rogers SI, Jennings S, Stelzenmüller V, Dye SR, Skjoldal HR (2008) Climate change
548 and deepening of the North Sea fish assemblage: A biotic indicator of warming seas. J
549 Appl Ecol 45:1029–1039
- 550 Frederiksen M, Daunt F, Harris MP, Wanless S (2008) The demographic impact of extreme
551 events: Stochastic weather drives survival and population dynamics in a long-lived
552 seabird. J Anim Ecol 77:1020–1029
- 553 Frederiksen M, Edwards M, Richardson AJ, Halliday NC, Wanless S (2006) From plankton to
554 top predators: Bottom-up control of a marine food web across four trophic levels. J Anim
555 Ecol 75:1259–1268
- 556 Frederiksen M, Mavor RA, Wanless S (2007) Seabirds as environmental indicators: The
557 advantages of combining data sets. Mar Ecol Prog Ser 352:205–211
- 558 Gaston A, Elliott K (2014) Seabird diet changes in northern Hudson Bay, 1981-2013, reflect
559 the availability of schooling prey. Mar Ecol Prog Ser 513:211–223
- 560 Green DB, Klages NTW, Crawford RJM, Coetzee JC, Dyer BM, Rishworth GM, Pistorius PA
561 (2015) Dietary change in Cape gannets reflects distributional and demographic shifts in
562 two South African commercial fish stocks. ICES J Mar Sci 72:771–781
- 563 Grist H, Daunt F, Wanless S, Nelson EJ, Harris MP, Newell M, Burthe S, Reid JM (2014) Site
564 fidelity and individual variation in winter location in partially migratory European shags.
565 PLoS One 9:e98562
- 566 Halpern BS (2009) A Global Map of Human Impact on Marine Ecosystems. Science 319:948–
567 952
- 568 Härkönen T (1986) Guide to the otoliths of the bony fishes of the northeast Atlantic. Danbiu
569 ApS., Hellerup, Denmark
- 570 Harris MP, Leopold MF, Jensen JK, Meesters EH, Wanless S (2015) The winter diet of the
571 Atlantic Puffin *Fratercula arctica* around the Faroe Islands. Ibis 157:468–479
- 572 Harris MP, Wanless S (1991) The importance of the lesser sandeel *Ammodytes marinus* in the
573 diet of the shag *Phalacrocorax aristotelis*. Ornis Scand 22:375–382

- 574 Harris MP, Wanless S (1993) The diet of shags *Phalacrocorax aristotelis* during the chick-
575 rearing period assessed by three methods. *Bird Study* 40:135–139
- 576 Harris MP, Wanless S (1996) Differential responses of guillemot *Uria aalge* and shag
577 *Phalacrocorax aristotelis* to a late winter wreck. *Bird Study* 43:37–41
- 578 Harrison XA (2015) A comparison of observation-level random effect and Beta-Binomial
579 models for modelling overdispersion in Binomial data in ecology & evolution. *PeerJ*
580 3:e1114
- 581 Heessen HJL, Daan N, Ellis JR (2015) *Fish atlas of the Celtic Sea, North Sea, and Baltic Sea*, 1st
582 edn. KNNV Publishing; Wageningen Academic Publishers, The Netherlands
- 583 Hislop JRG, Harris MP, Smith JGM (1991) Variation in the calorific value and total energy
584 content of the lesser sandeel (*Ammodytes marinus*) and other fish preyed on by seabirds.
585 *J Zool* 224:501–517
- 586 Hofstede R ter, Hiddink J, Rijnsdorp A (2010) Regional warming changes fish species richness
587 in the eastern North Atlantic Ocean. *Mar Ecol Prog Ser* 414:1–9
- 588 Holland GJ, Greenstreet SPR, Gibb IM, Fraser HM, Robertson MR (2005) Identifying sandeel
589 *Ammodytes marinus* sediment habitat preferences in the marine environment. *Mar Ecol*
590 *Prog Ser* 303:269–282
- 591 Howells R, Burthe S, Green J, Harris M, Newell M, Butler A, Johns D, Carnell E, Wanless S,
592 Daunt F (2017) From days to decades: short- and long-term variation in environmental
593 conditions affect offspring diet composition of a marine top predator. *Mar Ecol Prog Ser*
594 583:227–242
- 595 Høyer JL, Karagali I (2016) Sea Surface Temperature climate data record for the North Sea and
596 Baltic Sea. *J Clim* 29:2529–2541
- 597 Johnstone IG, Harris MP, Wanless S, Graves JA (1990) The usefulness of pellets for assessing
598 the diet of adult shags *Phalacrocorax aristotelis*. *Bird Study* 37:37–41
- 599 Kowalczyk ND, Chiaradia A, Preston TJ, Reina RD (2014) Linking dietary shifts and reproductive
600 failure in seabirds: A stable isotope approach. *Funct Ecol* 28:755–765
- 601 Kowalczyk ND, Chiaradia A, Preston TJ, Reina RD (2015) Fine-scale dietary changes between

- 602 the breeding and non-breeding diet of a resident seabird. *R Soc Open Sci* 2:1–17
- 603 Lewis S, Phillips RA, Burthe SJ, Wanless S, Daunt F (2015) Contrasting responses of male and
604 female foraging effort to year-round wind conditions. *J Anim Ecol* 84:1490–1496
- 605 Lilliendahl K, Solmundsson J (2006) Feeding ecology of sympatric European shags
606 *Phalacrocorax aristotelis* and great cormorants *P. carbo* in Iceland. *Mar Biol* 149:979–
607 990
- 608 Litzow MA, Piatt JF, Abookire AA, Robards MD (2004) Energy density and variability in
609 abundance of pigeon guillemot prey: Support for the quality-variability trade-off
610 hypothesis. *J Anim Ecol* 73:1149–1156
- 611 Lorentsen S-H, Anker-Nilssen T, Erikstad KE (2018) Seabirds as guides for fisheries
612 management: European shag *Phalacrocorax aristotelis* diet as indicator of saithe
613 *Pollachius virens* recruitment. *Mar Ecol Prog Ser* 586:193–201
- 614 Markones N, Dierschke V, Garthe S (2010) Seasonal differences in at-sea activity of seabirds
615 underline high energetic demands during the breeding period. *J Ornithol* 151:329–336
- 616 Michelot C, Pinaud D, Fortin M, Maes P, Callard B, Leicher M, Barbraud C (2017) Seasonal
617 variation in coastal marine habitat use by the European shag: Insights from fine scale
618 habitat selection modeling and diet. *Deep Sea Res Part II Top Stud Oceanogr* 141:224–
619 236
- 620 Miller AK, Sydeman WJ (2004) Rockfish response to low-frequency ocean climate change as
621 revealed by the diet of a marine bird over multiple time scales. *Mar Ecol Prog Ser*
622 281:207–216
- 623 Newell M, Wanless S, Harris M, Daunt F (2015) Effects of an extreme weather event on seabird
624 breeding success at a North Sea colony. *Mar Ecol Prog Ser* 532:257–268
- 625 Owen E, Daunt F, Moffat C, Elston DA, Wanless S, Thompson P (2013) Analysis of fatty acids
626 and fatty alcohols reveals seasonal and sex-specific changes in the diets of seabirds. *Mar*
627 *Biol* 160:987–999
- 628 Paleczny M, Hammill E, Karpouzi V, Pauly D (2015) Population Trend of the World's Monitored
629 Seabirds, 1950-2010. *PLoS One* 10:e0129342

- 630 Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine
631 fishes. *Science* 308:1912–1915
- 632 Poloczanska ES, Brown CJ, Sydeman WJ, Kiessling W, Schoeman DS, Moore PJ, Brander K,
633 Bruno JF, Buckley LB, Burrows MT, Duarte CM, Halpern BS, Holding J, Kappel C V,
634 O'Connor MI, Pandolfi JM, Parmesan C, Schwing F, Thompson SA, Richardson AJ (2013)
635 Global imprint of climate change on marine life. *Nat Clim Chang* 3:919–925
- 636 Potts G, Coulson J, Deans I (1980) Population dynamics and breeding success of the shag,
637 *Phalacrocorax aristotelis*, on the Farne Islands, Northumberland. *J Anim Ecol* 49:465–484
- 638 R Development Core Team R (2016) R: A language and environment for statistical computing.
639 R Found Stat Comput
- 640 Reid K, Croxall JP (2001) Environmental response of upper trophic-level predators reveals a
641 system change in an Antarctic marine ecosystem. *Proc Biol Sci* 268:377–384
- 642 Ronconi RA, Koopman HN, McKinstry CAE, Wong SNP, Westgate AJ (2010) Inter-annual
643 variability in diet of non-breeding pelagic seabirds *Puffinus* spp. at migratory staging
644 areas: Evidence from stable isotopes and fatty acids. *Mar Ecol Prog Ser* 419:267–282
- 645 Russell AF, Wanless S, Harris MP (1995) Factors affecting the production of pellets by Shags
646 *Phalacrocorax aristotelis*. *Seabird* 17:44–49
- 647 Sorensen MC, Hipfner JM, Kyser TK, Norris DR (2009) Carry-over effects in a Pacific seabird:
648 stable isotope evidence that pre-breeding diet quality influences reproductive success. *J*
649 *Anim Ecol* 78:460–7
- 650 Swann RL, Harris MP, Aiton DG (2008) The diet of European shag *Phalacrocorax aristotelis*,
651 black-legged kittiwake *Rissa tridactyla* and common guillemot *Uria aalge* on Canna
652 during the chick-rearing period 1981-2007. *Seabird* 21:44–54
- 653 Sydeman WJ, Poloczanska ES, Reed TE, Thompson SA (2015) Climate change and marine
654 vertebrates. *Science* 350:772–777
- 655 Velando A, Freire J (1999) Intercolony and seasonal differences in the breeding diet of
656 European shags on the Galician coast (NW Spain). *Mar Ecol Prog Ser* 188:225–236
- 657 Wanless S, Harris MP (1997) *Phalacrocorax aristotelis* Shag. In: BWP Update. Oxford

- 658 University Press, Oxford, p 3–13
- 659 Wanless S, Harris MP, Newell MA, Speakman JR, Daunt F (2018) A community wide decline in
660 the importance of lesser sandeels *Ammodytes marinus* in seabird chick diet at a North
661 Sea colony. *Mar Ecol Prog Ser*
- 662 Wanless S, Harris MP, Redman P, Speakman JR (2005) Low energy values of fish as a probable
663 cause of a major seabird breeding failure in the North Sea. *Mar Ecol Prog Ser* 294:1–8
- 664 Watanuki Y, Daunt F, Takahashi A, Newell M, Wanless S, Sato K, Miyazaki N (2008)
665 Microhabitat use and prey capture of a bottom-feeding top predator, the European shag,
666 shown by camera loggers. *Mar Ecol Prog Ser* 356:283–293
- 667 Watt J, Pierce GJ, Boyle PR (1997) Guide to the Identification of North Sea Fish Using
668 Prernaxillae and Vertebrae. Copenhagen, Denmark
- 669 Weimerskirch H (2002) Seabird Demography and Its Relationship with the Marine
670 Environment. In: Schreiber EA, Burger J (eds) *The Biology of Marine Birds*. CRC Press,
671 Boca Raton, FL, p 115–137
- 672 Winslade P (1974) Behavioural studies on the lesser sandeel *Ammodytes marinus* (Raitt) III .
673 The effect of temperature on activity and the environmental control of the annual cycle
674 of activity. *J Fish Biol* 6:587–599
- 675 Wright P, Bailey M (1993) *Biology of sandeels in the vicinity of seabird colonies at Shetland*.
676 Aberdeen Scotland
- 677 Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) *Mixed effects models and*
678 *extensions in ecology with R*. New York
- 679

30

Running head: Trends in year round shag diet

680 Tables

681

682 Table 1 Summary table of frequency of occurrence of each prey type and sand between 1985-
 683 86 and 2014-15, including the % for all pellets combined, mean of annual % and range of
 684 annual %. Prey that could not be identified to any taxonomic level are referred to as
 685 Unidentified.

Prey	Pellets (%)	Annual Mean \pm SD	Annual Range
Sandeel	4668 (79%)	77% \pm 17	47–96%
Gadidae	2409 (41%)	46% \pm 17	22–75%
Cottidae	1149 (20%)	21% \pm 16	2–47%
Pleuronectidae	1145 (19%)	19% \pm 9	4–33%
Gobiidae	1126 (19%)	22% \pm 16	2–56%
Crustacea	585 (10%)	13% \pm 7	2–27%
Callionymidae	414 (7%)	9% \pm 9	0–25%
Pholidae	364 (6%)	7% \pm 10	0–32%
Mollusca	354 (6%)	7% \pm 8	0–26%
Zoarcidae	346 (6%)	8% \pm 9	0–40%
Labridae	210 (4%)	5% \pm 5	0–16%
Polychaeta	181 (3%)	4% \pm 3	0–7%
Syngnathinae	50 (1%)	1% \pm 3	0–15%
Clupeidae	23 (< 1%)	< 1% \pm < 1	0–2%
Agonidae	7 (< 1%)	< 1% \pm < 1	0–2%
Unidentified	366 (6%)	6% \pm 7	0–30%
Sand	3070 (52%)	48% \pm 22	12–84%

687 Table 2 Summary table of otolith numerical abundance for each fish prey type between 1985-86 and 2014-15, including total number of otoliths
 688 (and %), annual mean \pm SD number of otoliths pellet⁻¹, and range of annual number of otoliths.

Prey	Otolith	Annual Mean \pm SD	Annual Range
Sandeel	434,629 (88%)	62.63 \pm 36.8	1081–97,665
Gadidae	33,897 (7%)	6.93 \pm 5.60	139–5044
Gobiidae	9830 (2%)	1.17 \pm 1.24	3–1098
Cottidae	6558 (1%)	2.05 \pm 1.80	11–1500
Pleuronectidae	6,291 (1%)	1.11 \pm 0.86	2–737
Pholidae	1787 (< 1%)	0.29 \pm 0.56	0–691
Zoarcidae	1031 (< 1%)	0.25 \pm 0.40	0–262
Callionymidae	805 (< 1%)	0.17 \pm 0.30	0–214
Labridae	335 (< 1%)	0.08 \pm 0.09	0–64
Clupeidae	64 (< 1%)	0.01 \pm 0.05	0–25
Agonidae	12 (< 1%)	< 0.01 \pm < 0.01	0–5

689

690 Table 3 Model selection table for Generalised Linear Mixed Models testing for effects of year, period and a year by period interaction (*) on
691 presence of each prey type. Periods are reported as non-breeding (NB) relative to breeding. Table shows model rank compared to other models,
692 model structure, fixed effect estimates, standard errors, z ratios, number of parameters (k), difference in AICc between top model and selected
693 model (Δ AICc) and Akaike weight relative to other models (ω_i). Due to the large number of prey types and models, we only report those models
694 within 10 AICc points of the top model, which is shown in bold (for full model selection tables see Table S3).

Response	Rank	Model	Estimate	SE	z value	k	$\Delta AICc$	ω_i
Sandeel	1	<i>i + year + period + year*period</i>				4	0	1.00
		<i>year</i>	-0.54	0.22	-2.42			
		<i>period (NB)</i>	0.24	0.16	1.52			
		<i>year*period (NB)</i>	-0.64	0.15	-4.35			
Gadidae	1	<i>i + year</i>				2	0	0.43
		<i>year</i>	0.67	0.11	6.35			
Gadidae	2	<i>i + year + period + year*period</i>				4	0.12	0.41
		<i>year</i>	0.83	0.13	6.36			
		<i>period (NB)</i>	0.02	0.18	0.1			
		<i>year*period (NB)</i>	-0.28	0.14	-1.99			
Gadidae	3	<i>i + year + period (NB)</i>				3	1.95	0.16
		<i>year</i>	0.67	0.11	6.27			
		<i>period (NB)</i>	0.04	0.19	0.24			
Gobiidae	1	<i>i + year + period + year*period</i>				4	0	0.78
		<i>year</i>	0.91	0.19	4.75			
		<i>period (NB)</i>	0.7	0.26	2.69			
		<i>year*period (NB)</i>	-0.41	0.19	-2.16			
Gobiidae	2	<i>i + year + period (NB)</i>				3	2.57	0.22
		<i>year</i>	0.72	0.16	4.45			
		<i>period (NB)</i>	0.84	0.25	3.33			
Pleuronectidae	1	<i>i + year + period + year*period</i>				4	0	0.98
		<i>year</i>	0.46	0.12	3.96			
		<i>period (NB)</i>	0.23	0.21	1.1			
		<i>year*period (NB)</i>	-0.47	0.14	-3.33			
Pleuronectidae	2	<i>i + year + period (NB)</i>				3	8.96	0.01
		<i>year</i>	0.23	0.1	2.36			
		<i>period (NB)</i>	0.37	0.2	1.84			
Cottidae	1	<i>i + year</i>				2	0	0.64

Running head: Trends in year round shag diet

		year	0.92	0.14	6.62			
Cottidae	2	<i>i + year + period</i>				3	2	0.24
		<i>year</i>	0.92	0.14	6.62			
		<i>period (NB)</i>	-0.01	0.19	-0.06			
Cottidae	3	<i>i + year + period + year*period</i>				4	3.3	0.12
		<i>year</i>	0.98	0.16	6.27			
		<i>period (NB)</i>	0	0.19	-0.01			
		<i>year*period (NB)</i>	-0.11	0.14	-0.84			
Sand	1	<i>i + year + period + year*period</i>				4	0	1.00
		<i>year</i>	-0.41	0.25	-1.66			
		<i>period (NB)</i>	1.62	0.32	5.1			
		<i>year*period (NB)</i>	-1.01	0.25	-4.04			

696 Table 4 Model selection table for Generalised Linear Mixed Models testing for effects of year, period and a year by period interaction (*) on
 697 numerical abundance of sandeel (relative to all otoliths) and Gadidae (relative to all non-sandeel otoliths). Periods are reported as non-breeding
 698 (NB) relative to breeding. Table shows model rank compared to other models, model structure, fixed effect estimates, standard errors, z ratios,
 699 number of parameters (k), difference in AICc between top model and top model (ΔAICc) and Akaike weight relative to other models (ω_i). Due to
 700 the large number of prey types and models, we only report those models within 10 AICc points of the top model, which is shown in bold (for full
 701 model selection tables see Table S4).

Response	Rank	Model	Estimate	SE	z value	k	ΔAICc	ω_i
Sandeel	1	<i>i + year</i>				2	0	0.65
		<i>year</i>	-2.84	0.31	-9.03			
Sandeel	2	<i>i + year + period (NB)</i>				3	1.89	0.25
		<i>year</i>	-2.83	0.32	-8.87			
		<i>period (NB)</i>	-0.14	0.39	-0.35			
Gadidae	1	<i>i + year + period</i>				3	0	0.92
		<i>year</i>	2.07	0.12	16.61			
		<i>period (NB)</i>	-0.65	0.23	-2.79			

703 Table 5 Model selection table for Generalised Linear Mixed Models testing for effects of year, period and a year by period interaction (*) on
 704 sample-level prey richness, and linear and quadratic trends in annual prey richness. Periods are reported as non-breeding (NB) relative to
 705 breeding. Table shows model rank compared to other models, model structure, fixed effect estimates, standard errors, z ratios, number of
 706 parameters (k), difference in AICc between top model and top model (ΔAICc) and Akaike weight relative to other models (ω_i). Due to the large
 707 number of prey types and models, we only report those models within 10 AICc points of the top model, which is shown in bold (for full model
 708 selection tables see Table S5). Models with similar levels of support as the top model indicated with †.

Response	Rank	Model	Estimate	SE	z value	k	ΔAICc	ω_i
Sample-level prey richness	1	<i>i + year + season (NB) + year*period (NB)</i>				4	0	1.00
		<i>year</i>	0.37	0.04	8.95			
		<i>period (NB)</i>	0.14	0.06	2.31			
		<i>year*period (NB)</i>	-0.2	0.04	-5.23			
Annual prey richness	1	<i>i + year + year²</i>				3	0	0.66
		<i>year</i>	0.93	0.26	3.62			
		<i>year²</i>	-0.86	0.37	-2.31			
	2 [†]	<i>i + year</i>				2	1.33	0.34
		<i>year</i>	1.23	0.27	4.63			

710 Figures

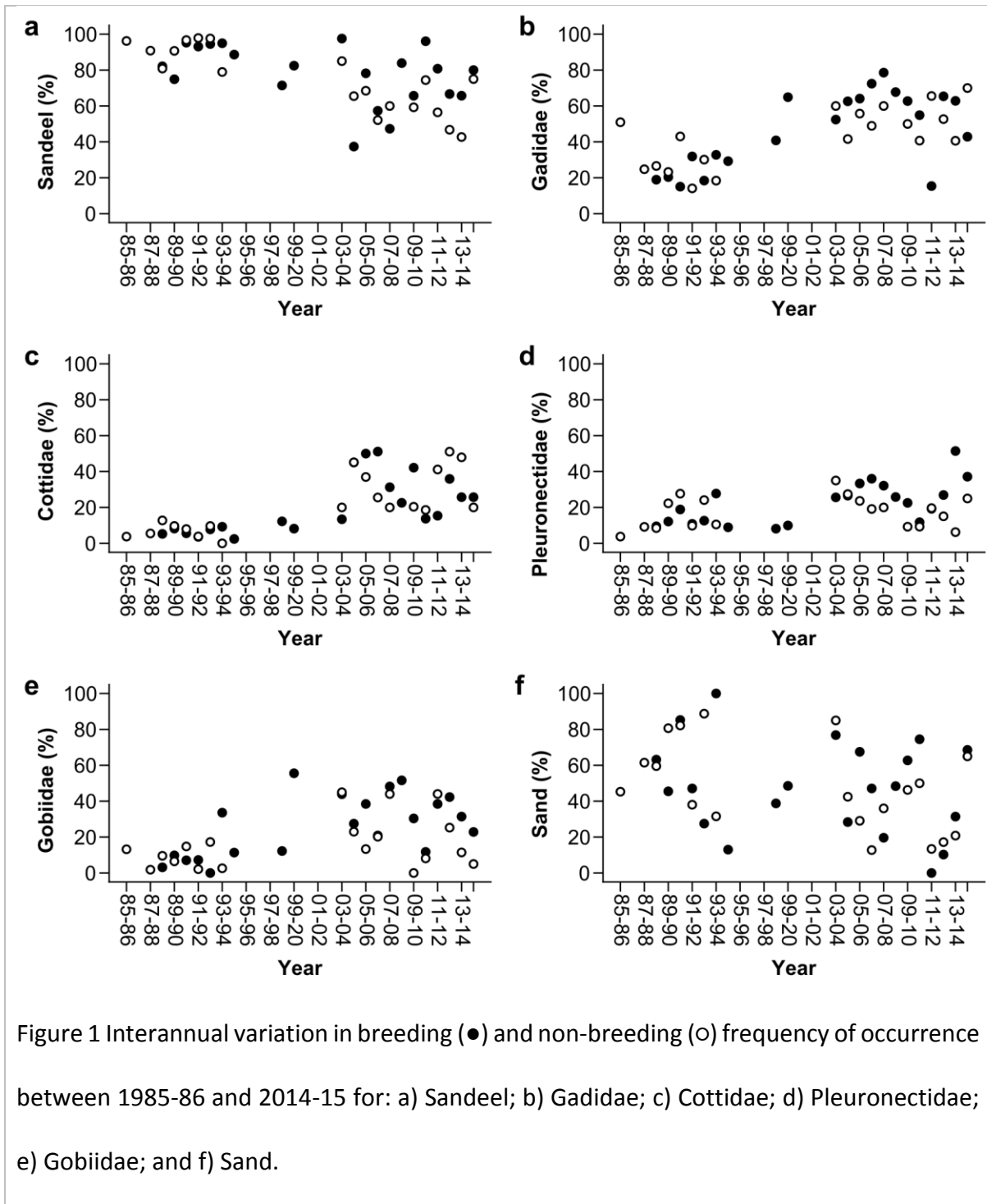
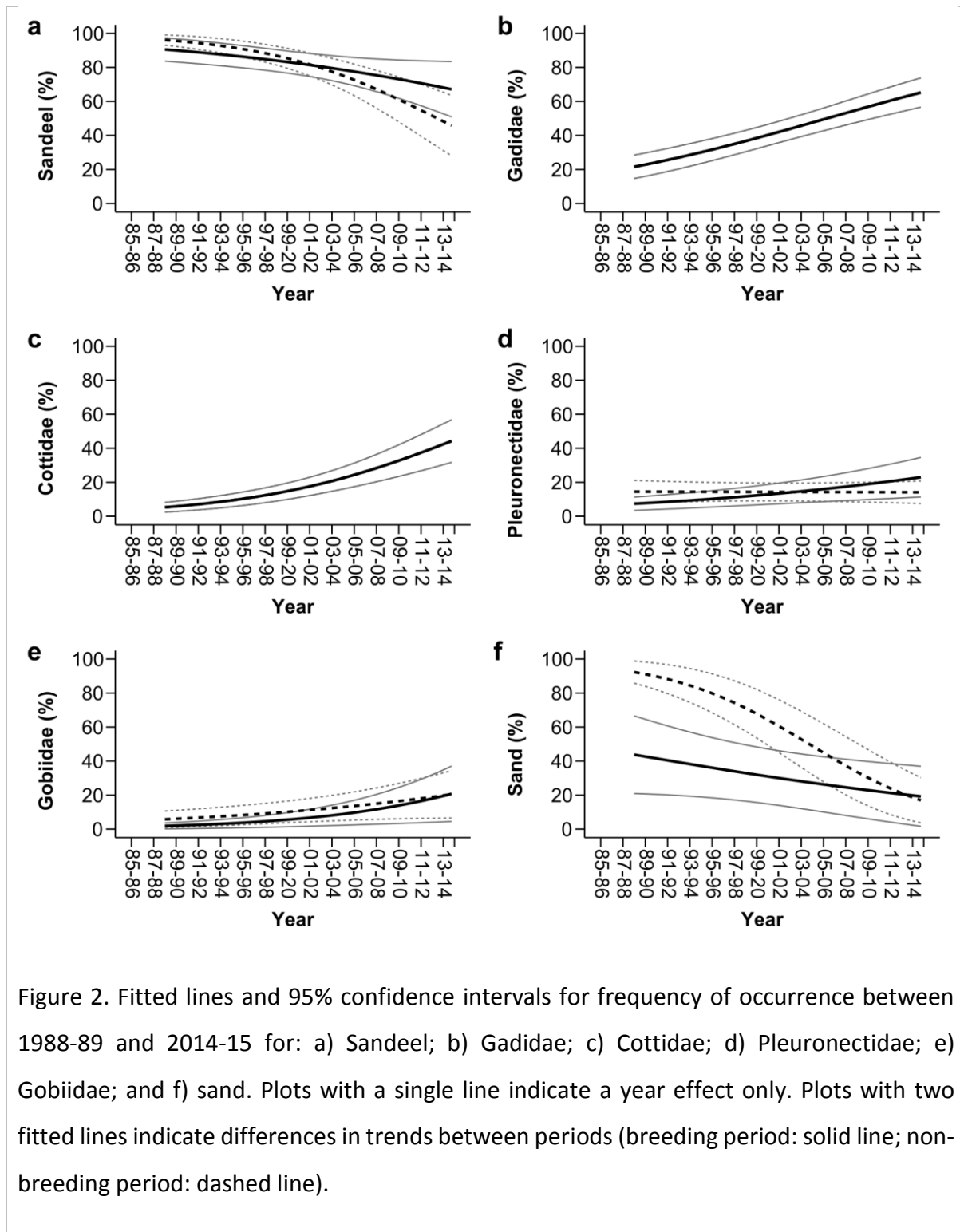


Figure 1 Interannual variation in breeding (●) and non-breeding (○) frequency of occurrence between 1985-86 and 2014-15 for: a) Sandeel; b) Gadidae; c) Cottidae; d) Pleuronectidae; e) Gobiidae; and f) Sand.



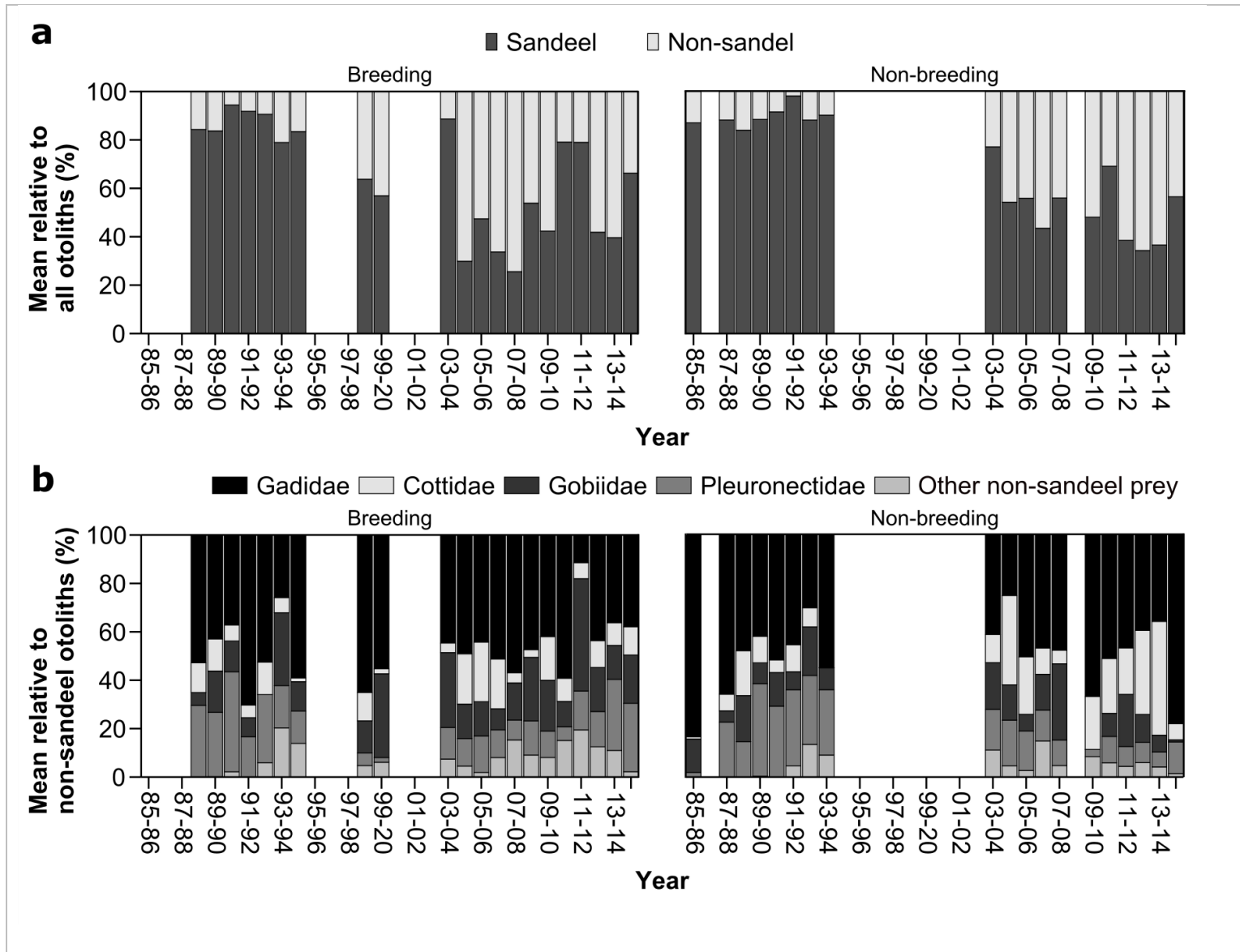
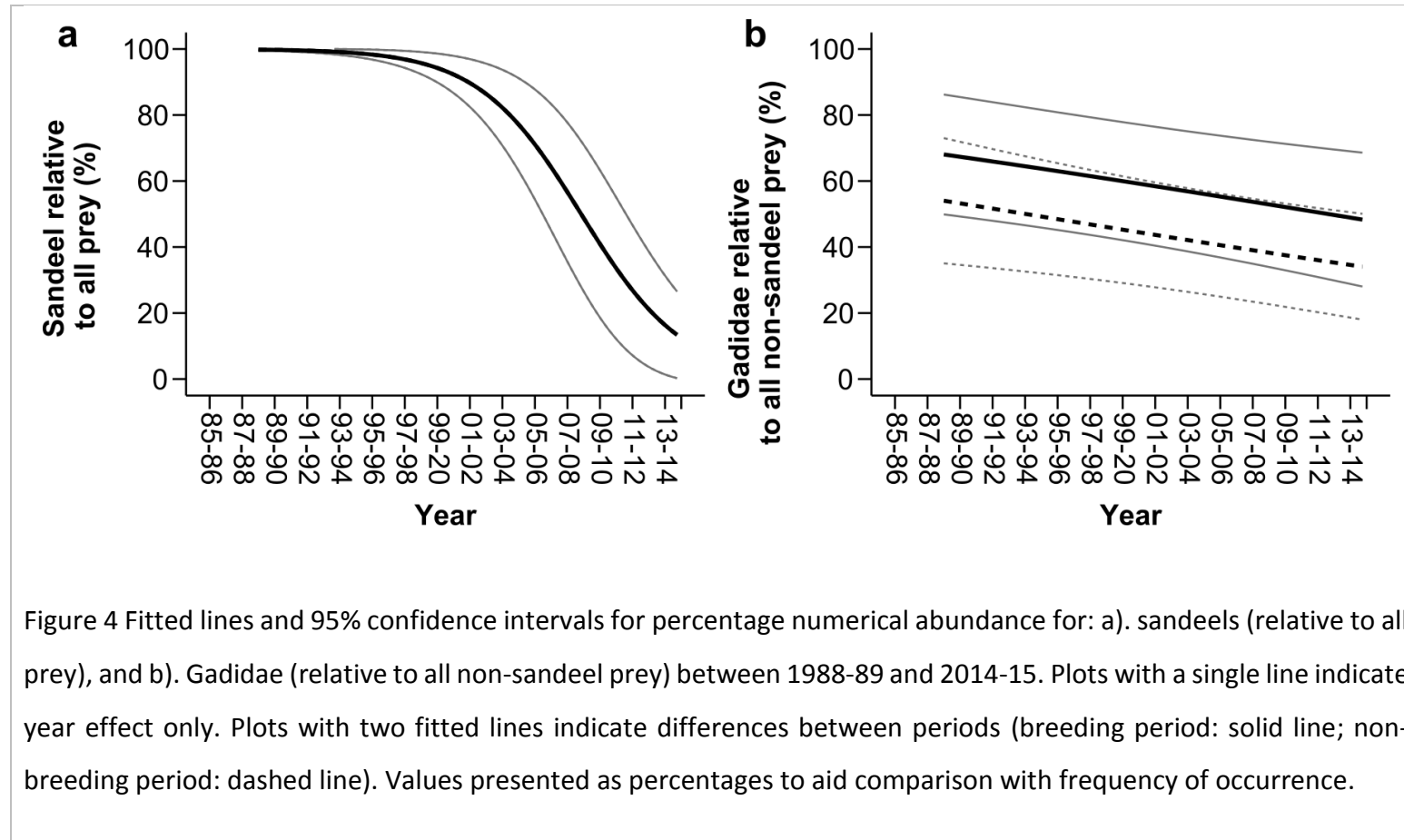
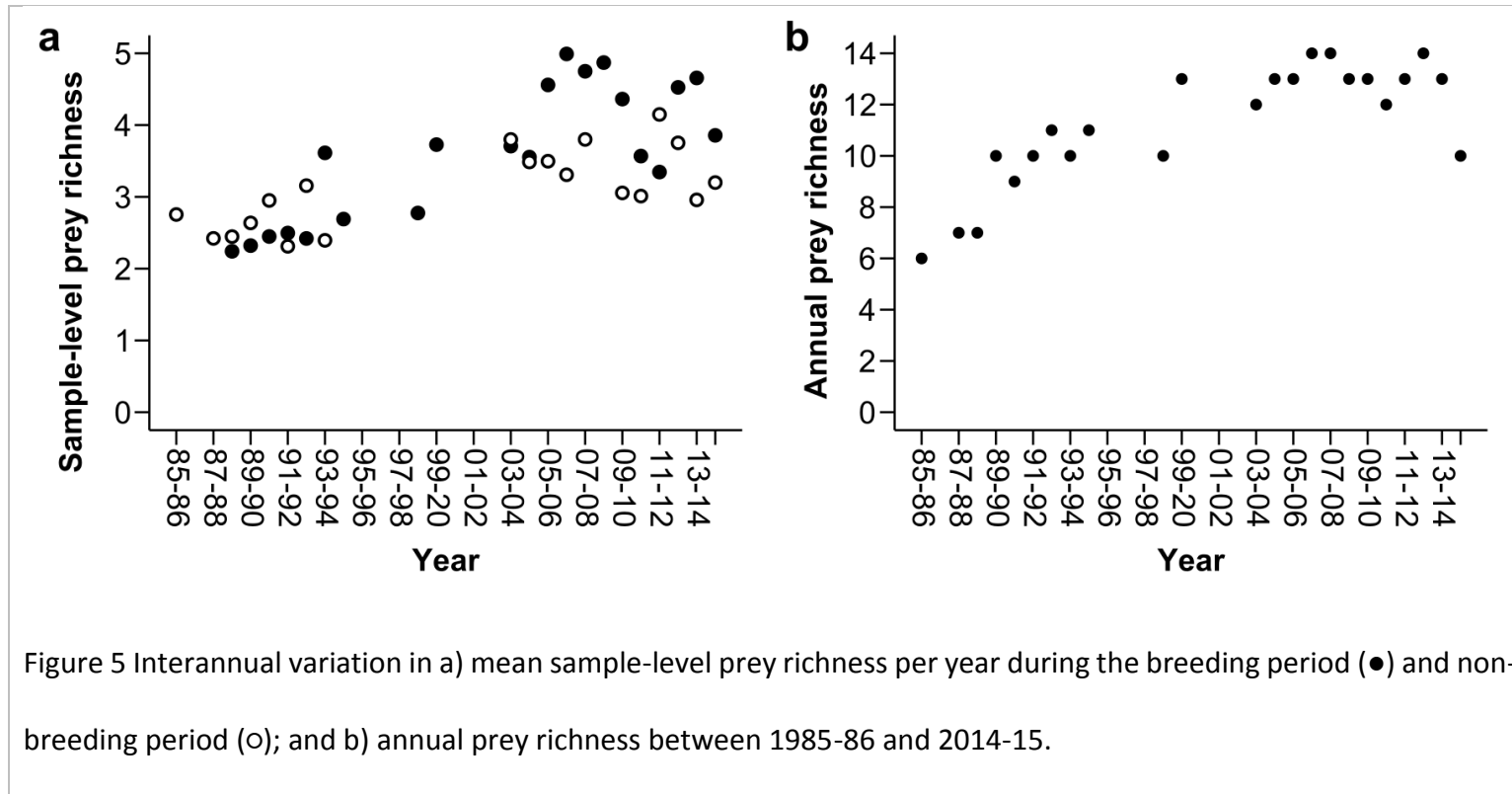


Figure 3 Interannual variation in breeding and non-breeding percentage numerical abundance, expressed as the mean across pellets between 1985-86 and 2014-15, for: a) sandeels (relative to all prey), and b) non-sandeels (relative to all non-sandeel prey). Blank years are those in which no pellets were collected. Values presented as percentages to aid comparison with frequency of occurrence.





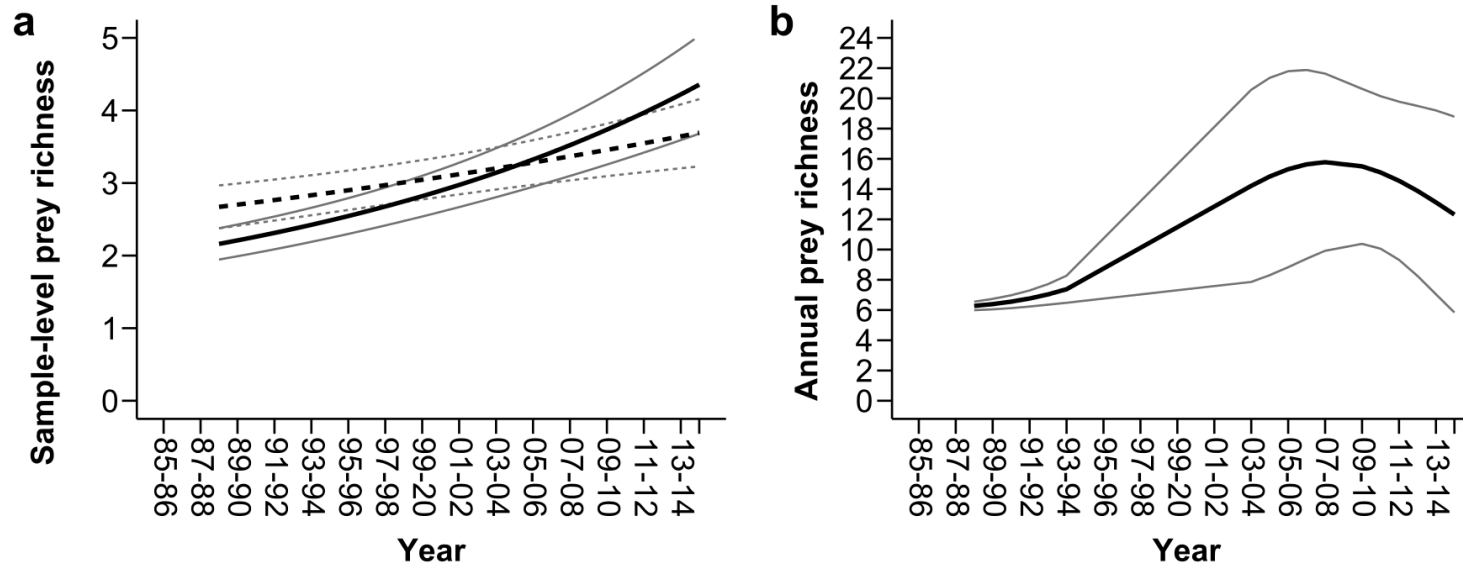


Figure 6 Fitted lines and 95% confidence intervals for modelled a) sample-level prey richness and b) annual prey richness between 1988-89 and 2014-15. Plots with two fitted lines indicate differences in trends between periods (breeding period: solid line; non-breeding period: dashed line). The linear and quadratic terms in the sample and annual prey richness plots appear as quadratic and cubic terms, respectively, due to the Poisson distribution of the data.

712 Supplementary Material

713 Pronounced long-term trends in year-round diet composition of the European shag

714 *Phalacrocorax aristotelis*

715

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724 Table S1 Start month, end month and length (in months) of breeding and non-breeding
 725 periods in each study year, together with the total number of months contributing to each
 726 study year.

Year	Breeding			Non-breeding			Total Length
	Start	End	Length (months)	Start	End	Length (months)	
1985-86	May	August	4	September	March	7	11
1987-88	April	July	4	August	March	8	12
1988-89	April	July	4	September	April	8	12
1989-90	May	August	4	September	April	8	13
1990-91	June	September	4	October	May	8	12
1991-92	June	September	4	October	April	7	11
1992-93	May	August	4	September	May	9	13
1993-94	June	September	4	October	April	7	11
1994-95	May	August	4	September	March	7	12
1998-99	May	August	4	September	April	8	12
1999-00	May	August	4	September	April	8	12
2003-04	April	July	4	August	April	9	13
2004-05	May	August	4	September	April	8	12
2005-06	May	August	4	September	April	8	12
2006-07	May	August	4	September	April	8	12
2007-08	May	August	4	September	April	8	12
2008-09	May	August	4	September	April	8	12
2009-10	April	July	4	August	March	8	12
2010-11	April	July	4	August	March	8	12
2011-12	April	July	4	August	March	8	12
2012-13	April	July	4	August	March	8	12
2013-14	May	August	4	September	April	8	12
2014-15	April	July	4	August	March	8	12

Running head: Trends in year round shag diet

Table S2 Sample size of pellets in each month between 1985-86 and 2014-15. Bold values indicate breeding period in each year. The non-breeding period in each year starts in the month after the breeding period and ends in the month preceding the commencement of the breeding period in the following calendar year.

Table S3 Full model selection table for Generalised Linear Mixed Models testing for effects of year, period and a year by period interaction (*) on presence of each prey type. Periods are reported as non-breeding (NB) relative to breeding. Table shows model rank compared to other models, model structure, number of parameters (k), difference in AICc between top model and top model ($\Delta AICc$) and Akaike weight relative to other models (ω_i). Top models are shown in bold.

Response	Rank	Model	k	$\Delta AICc$	ω_i
Sandeel	1	<i>i + year + period + year*period</i>	4	0	1.00
	2	<i>i + year</i>	2	15.38	<0.01
	3	<i>i + year + period</i>	3	16.76	<0.01
	4	<i>i</i>	1	25.75	<0.01
	5	<i>i + period</i>	2	27.12	<0.01
Gadidae	1	<i>i + year</i>	2	0	0.43
	2	<i>i + year + period + year*period</i>	4	0.12	0.41
	3	<i>i + year + period</i>	3	1.95	0.16
	4	<i>i</i>	1	17.44	<0.01
	5	<i>i + period</i>	2	18.9	<0.01
Gobiidae	1	<i>i + year + period + year*period</i>	4	0	0.78
	2	<i>i + year + period</i>	3	2.57	0.22
	3	<i>i + year</i>	2	12.35	<0.01
	4	<i>i + period</i>	2	12.63	<0.01
	5	<i>i</i>	1	22.66	<0.01
Pleuronectidae	1	<i>i + year + period + year*period</i>	4	0	0.98
	2	<i>i + year + period</i>	3	8.96	0.01
	3	<i>i + year</i>	2	10.34	0.01
	4	<i>i + period</i>	2	11.82	<0.01
	5	<i>i</i>	1	13.37	<0.01
Cottidae	1	<i>i + year</i>	2	0	0.64
	2	<i>i + year + period</i>	3	2	0.24
	3	<i>i + year + period + year*period</i>	4	3.3	0.12
	4	<i>i</i>	1	19.1	<0.01
	5	<i>i + period</i>	2	21.07	<0.01
Sand	1	<i>i + year + period + year*period</i>	4	0	1.00
	2	<i>i + year + period</i>	3	13.44	<0.01
	3	<i>i + period</i>	2	23.41	<0.01
	4	<i>i + year</i>	2	93.67	<0.01
	5	<i>i</i>	1	102.36	<0.01

Table S4 Full model selection table for Generalised Linear Mixed Models testing for effects of year, period and a year by period interaction (*) on numerical abundance of sandeel (relative to all otoliths) and Gadidae (relative to all non-sandeel otoliths). Periods are reported as non-breeding (NB) relative to breeding. Table shows model rank compared to other models, model structure, number of parameters (k), difference in AICc between top model and top model ($\Delta AICc$) and Akaike weight relative to other models (ω_i). Top models are shown in bold.

Response	Rank	Model	k	$\Delta AICc$	ω_i
Sandeel	1	<i>i + year</i>	2	0	0.65
	2	<i>i + year + period</i>	3	1.89	0.25
	3	<i>i + year + period + year*period</i>	4	3.89	0.09
	4	<i>i</i>	1	25.24	<0.01
	5	<i>i + period</i>	2	26.5	<0.01
Gadidae	1	<i>i + year + period</i>	3	0	0.92
	2	<i>i + year</i>	2	5.21	0.07
	3	<i>i + year + period + year*period</i>	4	8.84	0.01
	4	<i>i</i>	1	79.63	<0.01
	5	<i>i + period</i>	2	81.67	<0.01

Table S5 Full model selection table for Generalised Linear Mixed Models testing for effects of year, period and a year by period interaction (*) on sample-level prey richness, and linear and quadratic trends in annual prey richness. Periods are reported as non-breeding (NB) relative to breeding. Table shows model rank compared to other models, model structure, number of parameters (k), difference in AICc between top model and top model ($\Delta AICc$) and Akaike weight relative to other models (ω_i). Top models are shown in bold. Models with similar levels of support indicated with [†]

Response	Rank	Model	k	$\Delta AICc$	ω_i
Sample prey richness	1	<i>i + year + period + year*period</i>	4	0	1
	2	<i>i + year + period</i>	3	23.84	<0.01
	3	<i>i + year</i>	2	32.04	<0.01
	4	<i>i + period</i>	2	45.01	<0.01
	5	<i>i</i>	1	54.95	<0.01
Annual prey richness	1	<i>i + year + year²</i>	3	0	0.66
	2 [†]	<i>i + year</i>	2	1.33	0.34
	3	<i>i</i>	1	12.14	<0.01