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1           **A community wide decline in the importance of lesser sandeels *Ammodytes***  
2                           ***marinus* in seabird chick diet at a North Sea colony**

3  
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16 Running head: Decline of sandeels in seabird diet  
17

18 **ABSTRACT:** Many pelagic marine ecosystems have a wasp-waist trophic structure  
19 characterised by low diversity of mid-trophic species, typically small, shoaling forage fish  
20 that are eaten by a wide range of top predators. In the North Sea this mid-trophic position is  
21 occupied by the lesser sandeel *Ammodytes marinus*. Over the last 30-40 yr, the abundance  
22 and length-at-age of sandeels have declined but information on concurrent changes in the diet  
23 of seabird communities is scarce. We used data on chick diet composition, sandeel length-at-

24 age and energy density collected at a colony in the western North Sea from 1973–2015, to  
25 test for dietary shifts in this seabird community during a period when a local sandeel fishery  
26 opened, operated and was closed. We found a long-term decline in the overall importance of  
27 sandeels, particularly 1+ group fish. However, there were species-specific differences such  
28 that the overall decline in sandeels was strongest in common guillemots *Uria aalge*, while the  
29 shift from 1+ group to 0 group sandeels was apparent in all species except European shags  
30 *Phalacrocorax aristotelis*. Community level differences were also apparent in the alternative  
31 prey to sandeels with auk and black-legged kittiwake *Rissa tridactyla* chicks being fed  
32 clupeids, predominantly sprat *Sprattus sprattus* while shag chicks received a wide range of  
33 benthic fish species. There was also evidence for a decline in the quality of sandeels fed to  
34 chicks with significant decreases in length-at-age of 0 group and 1+ group. However, there  
35 was no significant annual variation in the energy density of sandeels except for 2004 when  
36 values were exceptionally low. Neither the opening nor the closing of the sandeel fishery had  
37 any detectable effect on chick diet composition, sandeel length or sandeel energy density.  
38 Overall, our results suggest marked community level changes in seabird diet composition  
39 over the last three decades that may reflect long-term declines in the abundance and quality  
40 of their principal prey.

41

42 KEY WORDS: Dietary shifts □ Fishery closure □ Forage fish □ Industrial fisheries □  
43 Predator-based diet sampling □ Sand lance □ Snake pipefish □ Trophic interactions

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## INTRODUCTION

49

50

51 Many pelagic marine ecosystems are characterised by a “wasp-waist” trophic structure  
52 with high species diversity at upper and lower trophic levels and low diversity of mid-trophic  
53 species (Cury et al. 2000). Typically, this mid-trophic position is occupied by an abundant  
54 forage fish that forms a major prey item for a wide range of higher predators. However,  
55 changing conditions, in particular rising sea temperatures, are thought to be causing changes in  
56 the distribution, abundance and energetic quality of mid-trophic forage fish and in some regions  
57 the situation has been further exacerbated by pressure from industrial fisheries (Sydeman et al.  
58 2017a). Given the importance of these forage fish species to marine predators, a decline in their  
59 availability and/or quality might be reflected in changes in predator diet with potentially  
60 important demographic consequences if the alternative prey are less available and/or  
61 energetically profitable. Furthermore, sympatric species are expected to vary in their dietary  
62 responses, for example in avian predators because of different foraging strategies such as  
63 surface-feeding versus diving species, and during the breeding season, because of different  
64 prey delivery methods such as whole fish transported in the bill versus regurgitation of semi-  
65 digested prey (Furness & Tasker 2000). However, although dietary shifts in particular species  
66 of avian predator have been identified in wasp-waist systems (Miller & Sydeman 2004, Gaston  
67 & Elliott 2014), community-level predator responses remain poorly known (Sydeman et al.  
68 2017b)-.

69 In the North Sea, the principal pelagic mid-trophic species is the lesser sandeel  
70 *Ammodytes marinus* (hereafter sandeel), a small, lipid-rich, shoaling fish with a complex life  
71 cycle after metamorphosis that alternates periods buried in sandy substrates with periods of  
72 activity in the water column (Winslade 1974, Wright & Bailey 1993). Sandeels make up a

73 major component of the diet of many marine mammals, fish and birds in the North Sea and are  
74 also the main target species for a large industrial fishery (Gislasson & Kirkegard 1998,  
75 Engelhard et al. 2014). The species is considered to be particularly at risk from rising sea  
76 temperatures due to its specialised habitat requirements and limited capacity to shift  
77 distribution in response to changing hydrographic conditions and prey distributions (Heath et  
78 al. 2012a, Frederiksen et al. 2013). Sandeels have also become smaller over the past four  
79 decades with significant declines in mean lengths-at-age being most marked in the  
80 northwestern North Sea (Wanless et al. 2004, Frederiksen et al. 2011, Rindorf et al. 2016).  
81 Mass/length relationships in sandeels are non-linear and thus mass and energy value have  
82 decreased disproportionately meaning that particularly in the northwestern North Sea,  
83 predators now need to catch more individual sandeels to meet their own and their offspring's  
84 energetic requirements (Rindorf et al. 2016). Analyses of sandeel body composition have also  
85 highlighted that in 2004, the mean energy density of sandeels in the northwestern North Sea  
86 was drastically lower than values in the previous 30 yr (Wanless et al. 2005). Concurrent with  
87 these changes, poor breeding success of seabirds at colonies along the west coast of the North  
88 Sea has repeatedly been attributed to declines in sandeel availability and quality (Mitchell et  
89 al. 2004, Daunt et al. 2017). However, for the most part direct information on chick diet for a  
90 range of seabird species has been lacking, precluding a systematic evaluation of the evidence  
91 for community level dietary shifts.

92        Much of what is known about changes in seabird diet in the North Sea in recent decades  
93 has come from long-term studies on the Isle of May, a major seabird colony off the coast of  
94 southeast Scotland. Here, standardised monitoring of prey brought in for chicks over the last  
95 30-40 yr has documented marked changes in diet composition, notably a decline in the relative  
96 importance of sandeels. However, to date the emphasis has been on single species assessments  
97 such as for common guillemots *Uria aalge* (Smout et al. 2013, Anderson et al. 2014) and

98 European shags *Phalacrocorax aristotelis* (Howells et al. 2017), rather than comparing  
99 responses at a community scale. Here, we use chick diet data from three pursuit-divers (Atlantic  
100 puffin *Fratercula arctica*, razorbill *Alca torda* and common guillemot) that carry back intact  
101 fish held in the beak for the chick, and one surface-feeder (black-legged kittiwake *Rissa*  
102 *tridactyla*) and one pursuit-diver (European shag) that regurgitate semi-digested food to their  
103 offspring, to quantify dietary trends in a seabird community over a 30 yr period. Together these  
104 five species account for >90% of the biomass of seabirds on the Isle of May that feed on marine  
105 prey during the breeding season (Daunt et al. 2008). All five have traditionally been viewed as  
106 relying on sandeels (both 0 group (fish of the year) and 1+ group (older fish)) as food for their  
107 chicks (Pearson 1968, Furness & Tasker 2000). Conditions for sandeels in the waters around  
108 the Isle of May have changed substantially over the period during which seabird diet data have  
109 been collected. Sea temperatures have risen and the thermal environment for the copepod  
110 *Calanus finmarchicus*, a major prey of sandeels, has deteriorated (Burthe et al. 2012,  
111 Frederiksen et al. 2013). In addition, between 1990 and 1999 sandeels were the target of a large  
112 industrial fishery that operated within 30–50 km of the Isle of May (Rindorf et al. 2000). Since  
113 2000, an area down the east coast of Britain, including the areas used for feeding by many Isle  
114 of May seabirds, has been closed to commercial sandeel fishing with the aim of conserving  
115 prey stocks for predators including seabirds (Daunt et al. 2008). A condition of the closure was  
116 that there should be an evaluation of whether the removal of sandeels by the fishery had a  
117 measurable effect on sandeel predators such as seabirds, and whether the establishment of a  
118 closed area could ameliorate any deleterious effects. Assessments based on seabird breeding  
119 success indicated that there was indeed evidence of a negative effect of the fishery and a  
120 positive effect of the closure in black-legged kittiwakes whereas the other species were  
121 unaffected (Daunt et al. 2008, Frederiksen et al. 2008). However, the focus of these analyses  
122 was on reproductive output rather than changes in diet composition or sandeel quality *per se*.

123 Our specific aims were therefore to test (1) for trends in the overall mean annual proportion of  
124 sandeel in chick diets of the five seabird species; (2) for changes in the relative importance of  
125 different age classes of sandeels in chick diets; (3) whether the downward trend in sandeel  
126 length had continued and (4) if the energy density of sandeels had been exceptionally low in  
127 any year since 2004. For each of these measures we also assessed whether there was evidence  
128 for step changes associated with the commencement of the local sandeel fishery in 1990 and/or  
129 its closure in 2000.

130

## 131 **MATERIALS AND METHODS**

132

133 Fieldwork was carried out on the Isle of May National Nature Reserve, Firth of Forth,  
134 southeast Scotland (56°11'N, 2°33'W) with diet samples collected throughout the chick-  
135 rearing periods of all species. Full details of the species-specific sampling periods and annual  
136 sample sizes are presented in Table S1.

137

### 138 **Diet sampling**

139

#### 140 Atlantic puffin

141

142 Atlantic puffins (hereafter puffins) carrying bill loads of fish destined for chicks were  
143 caught in mist-nets each year 1973-2015. Most loads were obtained in the early morning  
144 (04:00–07:00 h, all times given as GMT) or evening (18:00–21:00 h) but some additional loads



145 were collected throughout the day. When caught, puffins dropped their fish and a thorough  
146 search was made of the ground around the net to ensure that the complete load was collected.  
147 Each fish load (diet sample) was taken back to the laboratory where prey items were identified  
148 and the length of each intact fish was measured from the tip of the snout to the tip of the tail.  
149 Sandeels (*Ammodytidae*) were classified as 0 group or 1+ group. In 2000–2015 ageing was  
150 based on otolith macrostructure (ICES 1995). Prior to this we used year-specific discriminant  
151 analysis of fish length distributions (Wanless et al. 2004). Checks of the discriminant method  
152 against otolith macrostructure for 4169 otoliths from 3yr showed that classification of 0 group  
153 and 1+ group was 99.8% reliable. The occurrence of 0 group and 1+ group sandeels was not  
154 recorded at the sample level so annual measures of frequencies of these groups correspond to  
155 the proportions in the pooled sample of fish in a given year.

156

157

#### Razorbill

158

159 Visual observations of fish brought back to the colony by adult razorbills were made  
160 each year 1982–2015. Data were collected on many days during the chick period and covered  
161 the period from dawn to dusk (02:30–21:30 h). The species and size of fish in each load were  
162 recorded with the latter assessed qualitatively in relation to the size of the adult's bill and scored  
163 as minute, small, medium or large. For sandeels, these size classes were assumed to correspond  
164 to body lengths of 40 mm, 50 mm, 70 mm and 80 mm, respectively, for clupeids to correspond  
165 to lengths of 50 mm, 60 mm, 80 mm and 90 mm respectively, and for rockling (*Lotidae*) to  
166 correspond to an average fish length of 35 mm (Thaxter et al. 2013). Minute and small sandeels  
167 were assumed to be 0 group and longer fish to be 1+ group.

168

169

### Common guillemot

170

171         Diet of common guillemot chicks (hereafter guillemot) was assessed visually from  
172 observations of fish brought by adults and subsequently fed to chicks. Data were collected  
173 between dawn and dusk (02:30–21:30 h) on most days throughout each chick-rearing period  
174 1982–2015. The species and size of each fish were recorded with the latter classed as minute,  
175 small, medium or large relative to the size of the adult’s bill (Anderson et al. 2014). These size  
176 classes were converted to fish length using fish found dropped in the colony each year. Minute  
177 sandeels were assumed to be 0 group and all others to be 1+ group. Examination of otoliths of  
178 475 sandeels collected in the colony supported these assumptions of fish age.

179

180

### European shag and black-legged kittiwake

181

182         Diet was sampled using regurgitates from chicks or adults with chicks collected each  
183 year 1985–2015 (European shag, hereafter shag) and 1986–2015 (black-legged kittiwake,  
184 hereafter kittiwake). Previous work has shown that food regurgitated by adults at the nest is  
185 predominantly destined for the brood (Wanless et al. 1993), so samples from chicks and adults  
186 with chicks were pooled for analysis. Regurgitates were taken back to the laboratory and  
187 weighed and the approximate contributions of the main prey groups (see later) present were  
188 assessed visually. Each regurgitate was dissolved in a warmed, saturated solution of biological  
189 washing powder (Biotex©) until all the soft tissue had been digested (Lewis et al. 2001,  
190 Howells et al. 2017). The hard items, predominantly otoliths and large fish bones, were  
191 extracted and identified to the lowest possible taxon using keys in Härkönen (1986) and Watt  
192 et al. (1997). Otoliths were counted and measured under a binocular microscope. Sandeels were

193 classed as 0 group or 1+ group using otolith macrostructure (ICES 1995). Where no otoliths or  
194 hard items were present following digestion, the initial visual assessments of prey biomass  
195 proportions were used since there was very close accordance between these two methods in  
196 samples where both were available ( $r^2$  of arcsine transformed proportions of sandeels to non-  
197 sandeels = 0.96; n = 185; Howells et al. 2017).

198

### 199 **Diet composition**

200

201 Irrespective of the method used to sample diet, it was not always possible to identify  
202 all items to species level. Since the primary aim of this study was to assess temporal changes  
203 in the importance of sandeels during chick-rearing in this seabird community, for analysis prey  
204 were grouped as 0 group and 1+ group sandeels (all those identified to species were *Ammodytes*  
205 *marinus*), Clupeidae (sprat *Sprattus sprattus* and herring *Clupea harengus*, separated where  
206 possible, by examination of otoliths or counts of vertebrae) and other species (mainly cod-  
207 fishes Gadidae, rockling Lotidae and gunnel or rock butterfish Pholidae, depending on the  
208 seabird species). For each seabird species and year diet was expressed as (1) the frequency of  
209 samples (bill loads or regurgitates) containing each of these prey groups except for the puffin  
210 where the relative proportions of 0 group and 1+ group sandeels were based on the total  
211 sandeels examined that year and (2) the proportion by mass of each prey group in the diet after  
212 pooling all the samples for the year, using species-specific otolith length to fish length and fish  
213 length to mass relationships (Harris & Hislop 1978, Lewis et al. 2003, Howells et al. 2017).  
214 The number and length of fish in a razorbill load typically show an inverse relationship so  
215 where there was uncertainty about the numbers of prey items we followed Thaxter et al. (2013)  
216 and assumed that loads of minute, small, medium and large fish contained 16, 6, 4 and 2 items,

217 respectively. Frequency estimates derived from occurrence and biomass proportions were  
218 highly correlated e.g. for sandeels (puffin  $r = 0.741$ ,  $n = 43$ ,  $p < 0.001$ ; razorbill  $r = 0.948$ ,  $n =$   
219  $34$ ,  $p < 0.001$ ; guillemot  $r = 0.977$ ,  $n = 34$ ,  $p < 0.001$ ; shag  $r = 0.942$ ,  $n = 31$ ,  $p < 0.001$ ;  
220 kittiwake  $r = 0.821$ ,  $n = 30$ ,  $p < 0.001$ ) so unless otherwise stated, results relating to diet  
221 composition refer to the annual proportions based on biomass.

222

### 223 **Changes in energy value of sandeels**

224

225 Samples of intact sandeels collected from puffins (988 0 group, 123 1+ group) and  
226 guillemots (10 1+ group) in 19 yr were retained for analysis to determine energy content. Those  
227 collected between 1973 and 1987 were analysed using freeze-drying techniques and adiabatic  
228 bomb-calorimetry (Harris & Hislop 1978, Hislop et al. 1991). Details of methods used to  
229 analyse samples collected between 1988 and 2015 are given in Wanless et al. (2005). Each fish  
230 was dried to constant weight at 60°C and the fat extracted using diethyl ether in a soxhlet  
231 apparatus (Reynolds & Kunz 2001). The remaining material was dried, re-weighed and put into  
232 a muffle furnace at 600°C for 10 h to incinerate the protein. The resulting ash was then weighed  
233 to determine the mineral content. All measurements were made to 0.0001 g accuracy. The  
234 energy value of each fish was then obtained from the body composition using energy  
235 equivalents of 39.6 kJ g<sup>-1</sup> for fat and 23.7 kJ g<sup>-1</sup> for protein (Crisp 1971). All energy values  
236 were expressed on a dry weight basis.

237

### 238 **Statistical analysis**

239

240 Annual- rather than sample-level biomass proportions were analysed since this  
241 allowed us to include data from puffins where sandeels were not aged within individual  
242 samples. Generalized Linear Models (GLM) with a logit link function, with year, species and  
243 a year by species interaction as fixed effects were used to test trends in annual biomass  
244 proportions of different prey types. Following Wanless et al. (2004) and Frederiksen et al.  
245 (2008), we also fitted presence (1990-1999) or absence (all other years) of the industrial  
246 sandeel fishery as a fixed effect, to test for evidence of a step change in diet composition  
247 when the fishery was operating. In analyses of biomass proportions, a change in one prey  
248 type cannot be distinguished from an opposing change in the other prey types (Howells et al.  
249 2017). To allow for this we used a hierarchical approach sequentially testing for changes in  
250 (1) the proportion of sandeels relative to all prey, (2) the proportion of 1+ group sandeels  
251 relative 0 group sandeels and (3) the proportion of clupeids relative to other non-sandeel  
252 prey.

253 Temporal trends in lengths of 0 group and 1+ group sandeels were analysed by fitting  
254 linear mixed models using residual maximum likelihood (REML, Patterson & Thompson  
255 1971). Year, date (June 1st = 1) and fishery presence were fitted as covariates, and categorical  
256 sampling day, categorical year, and date by categorical year as random effects. A full  
257 description of the model is given in Wanless et al. (2004). The model was used to obtain annual  
258 estimates of the length standardised to 1 July (for 0 group sandeels) and 1 June (for 1+ group  
259 sandeels).

260 Trends in energy density ( $\text{kJ g}^{-1}$ ) were investigated by fitting linear mixed models using  
261 residual maximum likelihood (REML). Year, age (0 group and 1+ group) and fishery presence  
262 were fitted as fixed effects and a categorical variable for year was fitted as a random effect.  
263 However, data were only available for 7 sandeels during the fishery years, limiting the power  
264 of the test for fishery presence.

265

266

## RESULTS

267

268

### Diet composition

269

270 The number of chick diet samples (food loads brought in by puffins, razorbills and  
271 guillemots and regurgitates from shags and kittiwakes) collected during the study are  
272 summarized in Table 1 along with the total biomass of these samples. Species-specific  
273 estimates of the frequency of occurrence of sandeels, overall and for 0 group and 1+ group  
274 separately, and for the proportion of the biomass made up of sandeel both overall and by age  
275 group are also shown. These summaries indicate that, with the exception of guillemots,  
276 sandeels dominated the diet of chicks of all species both in terms of frequency of samples  
277 containing sandeels and as a proportion of the total biomass. Overall, the frequency of  
278 occurrence of 0 group sandeels was higher than that of 1+ group sandeels in puffin, razorbill  
279 and kittiwake with the reverse being the case in shag and particularly in guillemot where 0  
280 group sandeels made up a trivial proportion of chick diet.

281

282

### Puffin

283

284 Except for 1974-78 and 1993, sandeels always made up >50% of the biomass, and only  
285 in 1979 and 1982-87 did 1+ group sandeels comprise more of the biomass than 0 group  
286 sandeels (Figure 1a, Table S1a). The main alternative prey to sandeels was clupeids  
287 (Clupeidae). In 33 of the 42 yr the bulk of these were sprat and only in 1980-1982, 1984 and  
288 1988 did herring constitute >10% of the diet. In terms of other prey species, juvenile gadids

289 (Gadidae) were the most important group but only in 1990–92 and 2004 did the proportion of  
290 gadids exceed that of clupeids. In 2008, rockling (Lotidae) were the dominant other prey type.

291

### 292 **Razorbill**

293

294 Sandeel was the most important species in razorbill chick diet but its contribution varied  
295 markedly over short time periods, for example making up 100% of the biomass in 2005 and  
296 2006 but only 9% in 2004 (Figure 1b, Table S1b). Clupeids, probably mainly sprat, were the  
297 main alternative prey. Gadids were recorded in very small numbers and in only 3 yr (1999,  
298 2013, 2014 respectively) did they contribute >1% of chick diet.

299

### 300 **Guillemot**

301

302 Prior to the late 1990s, sandeels typically accounted for >60% of guillemot chick diet  
303 but after this 2009 was the only year in which they made up >20% of the biomass (Figure 1c,  
304 Table S1c). Almost all of the sandeels were 1+ group and only in 1 yr (1990) did 0 group  
305 constitute >2% of chick diet. The principal alternative prey was clupeids and based on 167 fish  
306 collected from breeding ledges, most (93%) were sprat, the remainder (7%) being herring.  
307 Gadids were recorded in very small numbers and only in 2006 did they account for >5% of the  
308 biomass.

309

### 310 **Shag**

311

312 The proportion of sandeel in the diet of shag chicks was >60% except in 2004–09  
313 and 2013 (Figure 1d, Table S1d). Except for 1989-91, 1994, 1999, 2005 and 2006, the  
314 predominant age class of sandeel taken was 1+ group. Clupeids were unimportant, only  
315 making up >5% of chick diet in 1994, 1995 and 1999. A variety of benthic fish species were  
316 the main alternative prey, the commonest being gunnel which made up >10% of the biomass  
317 in 7 yr between 2004 and 2014. Sygnathidae (all identified were snake pipefish *Entelurus*  
318 *aequoreus*) occurred in 2006 and 2007 but made up only 0.5% and 0.2% of the biomass,  
319 respectively.

320

321

### **Kittiwake**

322

323 The importance of sandeel in kittiwake chick diet varied markedly accounting for >90%  
324 between 1986 and 1989 but <50% in 1991, 2008 and 2010 (Figure 1e, Table S1e). In some  
325 years in the 1980s and early 1990s, 1+ group sandeels made up >50% of the sandeel biomass  
326 in chick diet but from the mid-1990s onwards 0 group were the dominant age class. The main  
327 alternative prey to sandeels were clupeids but juvenile gadids were also taken, particularly in  
328 years when the sandeel component in the diet was low. In addition, discards from fishing boats  
329 were recorded between 1990 and 1994. Sygnathidae (all identified were snake pipefish)  
330 occurred between 2005 and 2010 with numbers peaking in 2007 when they made up 10.5% of  
331 the biomass.

332

333

### **Temporal trends in diet composition**

334



335 The proportion of sandeel in the diet of chicks decreased significantly overall during  
336 the study period (Table 2a). There was a significant interaction between species and year in  
337 the model, whereby sandeels declined in all species except puffins (as evidenced by the  
338 significant interaction with year only apparent in puffins in relation to the reference species,  
339 kittiwakes; Table 2a). The proportion of 1+ group relative to 0 group sandeels also decreased  
340 over the study period (Table 2b). A species by year interaction was apparent, such that the  
341 decline was apparent in all species except shag (significant interaction with year in shags in  
342 relation to the reference species, kittiwakes). The proportion of clupeids relative to other non-  
343 sandeel prey increased over the course of the study (Table 2c). Again, there was a significant  
344 interaction between species and year such that this increase was not apparent in puffins or shags  
345 (significant interaction with year in these two species in relation to the reference species,  
346 kittiwakes). There was no effect of the presence of the sandeel fishery on any aspect of chick  
347 diet composition for any of the species (Table 2a-c).

348

349

350

#### **Temporal trends in sandeel length**

351

352 Between 1973 and 2015 there were highly significant declines in the mean annual  
353 lengths of 0 group and 1+ group sandeels in fish loads brought in by puffins, with no effect of  
354 the presence of a fishery (Figure 2a; REML on 0 group (mm): year =  $-0.451 \pm 0.081$ ,  $F = 30.77$ ,  
355  $p < 0.001$ ; date =  $0.245 \pm 0.050$ ,  $F = 24.28$ ,  $p < 0.001$ ; fishery =  $-0.618 \pm 2.336$ ,  $F = 0.07$ ,  $p =$   
356  $0.791$ ; REML on 1+ group (mm): year =  $-0.426 \pm 0.137$ ,  $F = 9.61$ ,  $p = 0.004$ ; date =  $0.449 \pm$   
357  $0.064$ ,  $F = 48.84$ ,  $p < 0.001$ ; fishery =  $0.314 \pm 3.860$ ,  $F = 0.01$ ,  $p = 0.936$ ;  $n = 42$  yr). Thus, in  
358 the 1970s mean annual lengths of 0 group sandeels were typically between 70 and 80 mm but

359 by the mid-2000s mean lengths were only between 50 and 60 mm. Similarly, 1+ group sandeel  
360 lengths decreased from 110 – 120 mm to 100 – 105 mm.

361

### 362 **Temporal trends in sandeel energy values**

363

364 Energy densities of 0 group sandeels were significantly lower than those of 1+ group,  
365 but there was no significant time trend over the 19 yr for which data were available, and no  
366 effect of the fishery (Figure 2b, REML: age =  $1.654 \pm 0.159$ ,  $F = 108.94$ ,  $p < 0.001$ ; year =  
367  $0.051 \pm 0.088$ ,  $F = 0.34$ ,  $p = 0.568$ ; fishery =  $2.932 \pm 2.747$ ,  $F = 1.14$ ,  $p = 0.300$ ). The only  
368 year characterised by exceptionally low energy densities of both 0 group and 1+ group sandeels  
369 was 2004.

370

## 371 **DISCUSSION**

372

373 Our comparison of dietary trends within a North Sea seabird community provides  
374 support for (1) a long-term decline in the overall importance of sandeels in chick diet, (2) a  
375 decline in the importance of 1+ group sandeels relative to 0 group, and (3) an increase in the  
376 importance of clupeids, predominantly sprats, as the main non-sandeel prey. Superimposed on  
377 these community level trends were species-specific differences in the strength of all these  
378 dietary shifts. There was also evidence for changes in sandeel quality with a long-term decline  
379 in mean annual lengths of 0 group and 1+ group sandeels although no marked change in energy  
380 density of sandeels, except for the exceptionally low value in 2004. Crucially we found no  
381 evidence that any of these changes were associated with the local sandeel fishery which

382 targeted predominantly 1+ group fish and which operated during the seabird breeding season  
383 (May – July) 1990-1999 (Rindorf et al. 2000).

384

### 385 **Diet composition and dietary trends**

386

387 Sandeels have traditionally been viewed as the main prey of most seabirds in the North  
388 Sea during the breeding season (Pearson 1968, Furness & Tasker 2000). Sampling of puffin  
389 chick diet on the Isle of May started in the early 1970s, 10-15 yr before the other species and  
390 it is noteworthy that clupeids rather than sandeels were the predominant prey at this time  
391 (Figure 1a). The lack of diet data for the other auks, kittiwake and shag at this time precludes  
392 any assessment of whether this was a community level phenomenon on the Isle of May while  
393 the lack of data from other puffin colonies in the North Sea precludes knowing whether it was  
394 a wide-scale effect. However, the importance of sandeels in puffin chick diet subsequently  
395 increased and by the mid-1980s when diet sampling for the other species started, sandeels were  
396 indeed the main prey species across the whole community, albeit with differences in the age  
397 class taken with guillemot and shag chicks being fed predominantly 1+ group and puffin,  
398 razorbill and kittiwake chicks receiving a mixture of 0 group and 1+ group. These initial species  
399 differences were apparent in subsequent trends such that the decline in overall importance of  
400 sandeels was most pronounced in shags and particularly guillemots. In razorbills and kittiwakes  
401 the decline in overall importance was less marked, and in puffins no decline was apparent.  
402 Furthermore, for all three species sandeels largely remained the dominant prey but the  
403 contribution of 0 group relative to 1+ group increased. Community level differences were also  
404 apparent in the alternative prey to sandeels. Thus in the auks and kittiwake the shift was  
405 relatively simple with clupeids, predominantly sprats, being the main alternative with reliance

406 relative to other non-sandeel species increasing over time in all the species except puffin. In  
407 contrast, clupeids were of minor importance for shags with sandeels being replaced by a wide  
408 range of benthic fish species resulting in a significant increase in dietary diversity (Howells et  
409 al. 2017).

410 Taken as a whole the changes in seabird chick diet recorded on the Isle of May are  
411 consistent with declines in the local availability of sandeels, particularly 1+ group and/or an  
412 increase in availability of clupeids, particularly sprats. Concurrent, independent time series data  
413 on prey abundance at a spatial scale relevant to seabird foraging ranges during the breeding  
414 season (mainly within 50 km; Thaxter et al. 2012, Wakefield et al. 2017) are lacking. However,  
415 the available data for both sandeels and sprats are broadly in line with the observed changes in  
416 seabird chick diet. Thus sandeel abundance declined significantly during the 1990s when the  
417 commercial sandeel fishery was operating on the Wee Bankie and Marr Bank, 30-50 km from  
418 the Isle of May, and apart from a brief recovery immediately after closure of the fishery in  
419 2000, abundance remained low until the early 2010s (Greenstreet et al. 2006, Frederiksen et al.  
420 2008, Heath et al. 2012b). Furthermore, monitoring of the age structure of the stock after the  
421 closure of the fishery highlighted sharply contrasting trends for 0 group and 1+ group with  
422 abundance of the former maintained whilst the latter was greatly reduced (Heath et al. 2012b).  
423 In the case of sprats, a fishery prosecuted by small boats based at ports on the Fife coast, started  
424 in the late 1960s (Jennings et al. 2012). The stock collapsed in the early 1980s and fishing  
425 ceased in 1985. It is notable that the 1980s was the only period when juvenile herring was the  
426 main prey taken by puffins consistent with sprat stocks being depressed at this time. However,  
427 sprat stocks recovered by the late 1990s (Jennings et al. 2012) and sprat has subsequently been  
428 the dominant clupeid in chick diet across the Isle of May seabird community.

429 Declines in sandeel abundance and increases in sprat abundance are both consistent  
430 with expected contrasting trends given rising sea surface temperatures (SST) in the North Sea

431 (Heath et al. 2012a). The shift from a boreal to a temperate regime could also enable warm-  
432 water forage fish species to colonise and increase in the region. However, as yet there have  
433 been no cases of species such as sardine *Sardina pilchardus* or anchovy *Engraulis encrasicolus*  
434 that are increasing in the southern North Sea and spreading northwards, being recorded in chick  
435 diet samples from the Isle of May (Heessen et al. 2015). The most dramatic example of the  
436 appearance of a new prey species during our study was the population explosion in the mid-  
437 2000s of snake pipefish that had previously been considered rare in the region (Harris et al.  
438 2007, van Damme & Couperus 2008, Kirby et al. 2006). Snake pipefish were very numerous  
439 in the waters around the Isle of May between 2005 and 2007 but the species was only recorded  
440 in any numbers in the diet of kittiwake chicks although there were a few records from shags  
441 and opportunistic sightings from puffins (Harris & Wanless 2011). The pipefish explosion  
442 coincided with the nadir in sandeel abundance suggesting that some change in the marine  
443 environment had occurred around this time that was beneficial to snake pipefish but detrimental  
444 to sandeels (Heath et al. 2012b, van Damme & Couperus 2008, Kirby et al 2006). However,  
445 pipefish numbers subsequently crashed as spectacularly as they increased and since 2010 the  
446 species has again become rare and has not been recorded in chick diet on the Isle of May, nor  
447 as far as we are aware, at other colonies in the North Sea (Daan 2015, personal records).

448 Intriguingly the temperature responses of sandeels and clupeids in the North Sea seem  
449 to be the reverse of those in the northeastern Pacific. Thus while in the former warming  
450 conditions have resulted in a shift away from a sandeel dominated system (Heath et al. 2012b),  
451 in the latter the locally prevalent Pacific sandeel species, *A. personatus*, is dominant during  
452 periods of warm ocean conditions but is replaced by alternative forage fish such as clupeids  
453 e.g. the Pacific herring *Clupea pallasii* and/or osmerids especially capelin *Mallotus villosus*  
454 during periods of cooling (Sydeman et al. 2017b). Clearly there is considerable potential for  
455 future research to exploit predator-based sampling from different ocean basins to compare

456 system level responses to global climate change and other anthropogenic pressures (Sydeman  
457 et al. 2017a).

458

#### 459 **Changes in sandeel quality**

460

461 The length and energy density of prey are of key importance for predators when they  
462 are provisioning offspring, particularly in species such as common guillemot that only bring  
463 back one prey item per feeding trip (single prey loaders). Since the relationship between  
464 sandeel length and mass is non-linear the sustained decrease in mean length-at-age of both 0  
465 group and 1+ group sandeels brought in for puffin chicks on the Isle of May indicates a  
466 dramatic deterioration in prey quality over the last 40 yr. Combining annual data for sandeel  
467 length and energy density suggests overall reductions in average energy values of c.70% and  
468 40% for 0 group and 1+ sandeels, respectively between 1973 and 2015. Puffin was the only  
469 species for which sandeel lengths could be measured directly in sufficient numbers for analysis.  
470 However, sandeel lengths estimated from otoliths extracted from shag regurgitates also indicate  
471 a significant decrease in mean length between 1989 and 2014 with the decline more marked in  
472 0 group compared to 1+ group fish (Howells et al. 2017). Isle of May shags typically forage  
473 closer to the shore than puffins (Harris et al. 2102, Bogdanova et al. 2014) suggesting that the  
474 decline in sandeel length has occurred in both inshore and offshore habitats and thus that the  
475 reduction in prey quality will have affected the whole Isle of May seabird community. Further  
476 support for a regional level reduction in sandeel length comes from data from commercial  
477 fishing vessels that also indicate that sandeels in the northwestern North Sea have become  
478 significantly shorter and lighter than those in central and northeastern areas (Rindorf et al.  
479 2016).

480 In this study we did not specifically investigate the mechanisms underlying the decline  
481 in length-at-date of sandeels. However, Frederiksen et al. (2011) previously showed that the  
482 situation was complex with phenological responses predominating in the 1970s to mid-1990s  
483 with sandeel hatch dates becoming later. From the mid -1990s onwards the trend in hatch date  
484 was reversed and instead the decline in length-at-date was driven mainly by lower juvenile  
485 growth rates (Frederiksen et al. 2011).

486

#### 487 **Consequences of dietary changes for community level breeding success**

488

489 Furness & Tasker (2000) quantified the sensitivity of the North Sea seabird community  
490 to reductions in sandeel abundance using an index based on species body size, cost of foraging,  
491 potential foraging range, ability to dive, amount of ‘spare’ time in the daily time budget and  
492 ability to switch diet. Applying these criteria to the Isle of May seabird community ranks the  
493 species in order of increasing sensitivity as shag, guillemot, razorbill, puffin and kittiwake. In  
494 accordance with this, kittiwake the most sensitive species, was the only one to show reduced  
495 breeding success during the period when the sandeel fishery was operating (Daunt et al. 2008,  
496 Frederiksen et al. 2008). However, community level comparisons of breeding success on the  
497 Isle of May revealed synchronised declines from the late 1980s to the late 2000s with the  
498 environmental contribution to overall productivity synchrony driven principally by effects  
499 operating at the chick stage rather than during incubation (Frederiksen et al. 2007, Lahoz-  
500 Montfort et al. 2013). Our analysis demonstrating long-term community level reductions in the  
501 importance of sandeels in chick diet therefore suggests that dietary changes may have played  
502 a role in the decline in productivity. However, interspecific differences in the change in  
503 productivity were also apparent. These suggested that trophic linkages were probably complex

504 and potentially influenced by factors such as interspecific differences in behavioural responses  
505 e.g. time allocation, foraging effort, prey delivery rates and load sizes (Lahoz-Montfort et al.  
506 2013). The community level analyses of productivity have not been updated but breeding  
507 success of all species has generally increased since the mid-2000s (Newell et al. 2017b). The  
508 data on diet composition for the seabird community indicate that these improvements have  
509 occurred despite the continuing decline in both the importance of sandeels, particularly 1+  
510 group, in chick diet and length-at-age of 0 group and 1+ group sandeels used to provision  
511 chicks. Species may be able to compensate for changes in sandeel availability by adjusting  
512 aspects of their provisioning behaviour to a greater or lesser extent. Recent modelling work has  
513 shown that differences in chick provisioning methods and flight costs of guillemots and  
514 razorbills could potentially result in differing responses to changes in sandeel length and  
515 distribution of prey patches (Thaxter et al. 2013). However, taken at face value the dietary data  
516 suggest that the alternative prey (either clupeids in the case of auks and kittiwakes or benthic  
517 species in the case of shags) can currently compensate for decreases in the contribution of  
518 sandeels to chick diet. In accordance with this the dietary quality of the alternative prey are all  
519 broadly comparable in energetic value to sandeels, and indeed are generally energetically  
520 superior to 0 group sandeels (Hislop et al. 1991, Harris et al. 2008; Howells et al. 2017).

521 Changes in length-at-age of sandeels might also be expected to affect breeding success  
522 because of the non-linear relationship between body length and energy value. Guillemot was  
523 the only obligate single prey loader among our study species and thus the one most likely to be  
524 sensitive to changes in energy value of single prey items. In accordance with this, guillemots  
525 showed the most extreme reduction in sandeel in chick diet such that in 12 of the last 13 yr of  
526 the study sandeels made up < 10% of prey biomass. Moreover, the series of years with  
527 exceptionally low guillemot breeding success on the Isle of May (2004–2007; Ashbrook et al.  
528 2010), coincided with the period when sandeel lengths were shortest (Figure 2a) and 2004



529 when energy density was exceptionally low (Figure 2b). Sandeels grow during the seabird  
530 breeding season and hence the long-term decline in length-at-date has meant that, on average,  
531 the date when 0 group (and probably 1+) sandeels reach a given length has become later (Burthe  
532 et al. 2012). Predators such as seabirds could therefore reduce the energetic impacts of this  
533 delay by breeding later so that the period of peak demand (mid-chick-rearing) tracked the  
534 changes in sandeel size. Breeding phenology of all the species in our analysis except shag,  
535 became later between 1983 and 2006 (Burthe et al. 2012). However, these changes were  
536 insufficient to keep pace with the changes in sandeel length and consequently the length (and  
537 energy value) of sandeels during chick rearing showed a net decline over this period (Burthe  
538 et al. 2012). Despite this there was no evidence for an adverse effect on breeding success. Since  
539 the mid-2000s the trend towards later breeding among Isle of May seabirds has ceased (Newell  
540 et al. 2017a) but the decline in sandeel length has continued (Figure 2a). This suggests that the  
541 net decrease in energy value of sandeels during chick rearing will have been exacerbated and  
542 thus it is perhaps surprising that breeding success has generally improved (Newell et al 2017b).  
543 These findings highlight the need to consider energy values of alternative prey and whether  
544 like those of sandeels these have decreased over time due to changes in average length.

545         The aim of the present paper was to use predator-based sampling to elucidate  
546 community level trends in the importance of sandeels in chick diet at a major North Sea colony.  
547 However, as the preceding paragraphs indicate, current evidence for links between breeding  
548 success and chick diet in the Isle of May seabird community is equivocal and productivity has  
549 improved since some of the key analyses were carried out. Updating these analyses and ideally  
550 also considering temporal changes in length and thus energetic quality of the alternative prey  
551 is therefore a research imperative.

552

553

## Conclusions

554

555 Overall, our results add to the growing body of information highlighting the effects of  
556 changing conditions for forage fish stocks on marine predators, particularly seabirds (Cury et  
557 al. 2011, Sydeman et al. 2017a). Such information is vital for ecosystem scale assessments such  
558 as updating food webs linkages, as input data for bioenergetics models and providing advice  
559 on potentially important feeding areas as part of marine spatial planning processes. The species  
560 making up the Isle of May seabird community are typical of many other colonies in the North  
561 Sea (Mitchell et al. 2004). However, generalising from our findings to other colonies needs to  
562 be made with caution as studies of individual species within the region indicate that chick diet  
563 can differ markedly both locally e.g. among kittiwake colonies in the Firth of Forth (Bull et al.  
564 2004) and regionally e.g. among guillemot colonies up the east coast of Britain (Anderson et  
565 al. 2014). Thus while it seems likely that the decline in importance of sandeels in chick diet  
566 will be reflected in other colonies in the North Sea, more community level assessments are  
567 needed to substantiate this and to identify what the alternative prey are.

568 For much of the past 30-40 yr the seabird community on the Isle of May has been  
569 experiencing a deterioration in the quality and quantity of sandeel prey available during the  
570 chick-rearing period. Closure in 2000 of the commercial sandeel fishery off the coast of eastern  
571 Britain adjacent to many seabird colonies, including the Isle of May, resulted in improved  
572 breeding success of kittiwakes, although not the other species (Daunt et al. 2008, Frederiksen  
573 et al. 2008). However, the fishery ban appears not to have reversed the decline in importance  
574 of sandeels in chick diet nor the shift from 1+ group to 0 group. In the case of shags a detailed  
575 analysis demonstrated that the shift from a sandeel dominated diet to a more species diverse  
576 one was associated with rising SST (Howells et al. 2017). Given the climate projections for

577 further rises in SST in the North Sea (IPCC 2014), it seems likely that the diet trajectories for  
578 shags and other seabirds will continue and further diminish the importance of sandeels in chick  
579 diet. Such changes could have consequences for future population and community dynamics  
580 but the magnitude and even the direction of responses are currently difficult to predict and will  
581 depend on the ability of species to exploit alternative prey and the energy value of these prey  
582 compared to sandeels.

583

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593

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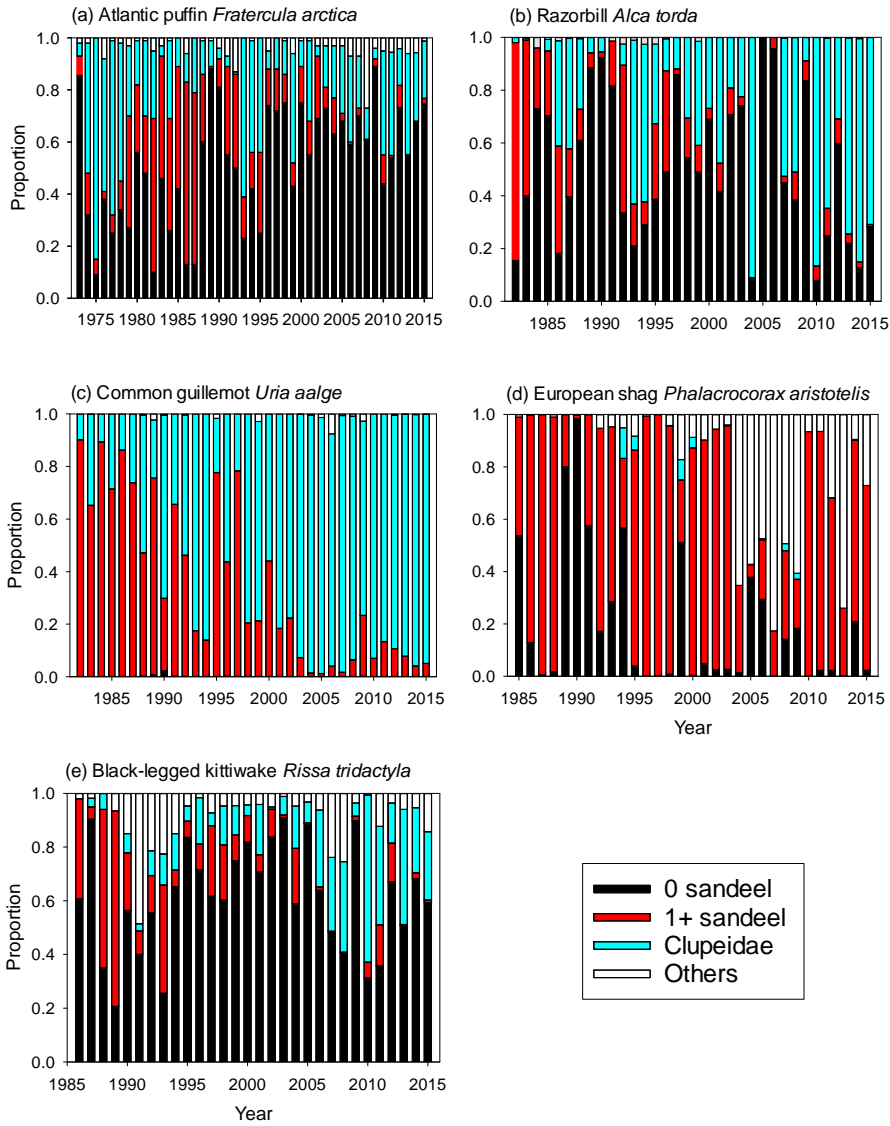
760 Fig. 1. Interannual variation in biomass proportions of 0 group sandeels, 1+ group sandeels,  
761 Clupeidae and other prey in the diet of seabird chicks on the Isle of May. (a) Atlantic puffin  
762 *Fratercula arctica* (1973–2015); (b) razorbill *Alca torda* (1982–2015); (c) common guillemot  
763 *Uria aalge* (1982–2015); (d) European shag *Phalacrocorax aristotelis* (1985–2015); and (e)  
764 black-legged kittiwake *Rissa tridactyla* (1986–2015)

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766

767 Fig. 2. Long-term changes in (a) annual mean length and (b) energy density of 0 group and  
768 1+ group lesser sandeels *Ammodytes marinus* collected from seabirds on the Isle of May  
769 between 1973 and 2015. Lengths of 0 group and 1+ group sandeels are standardized to 1 July  
770 and 1 June, respectively. Samples sizes and SEs are given in the supplementary material

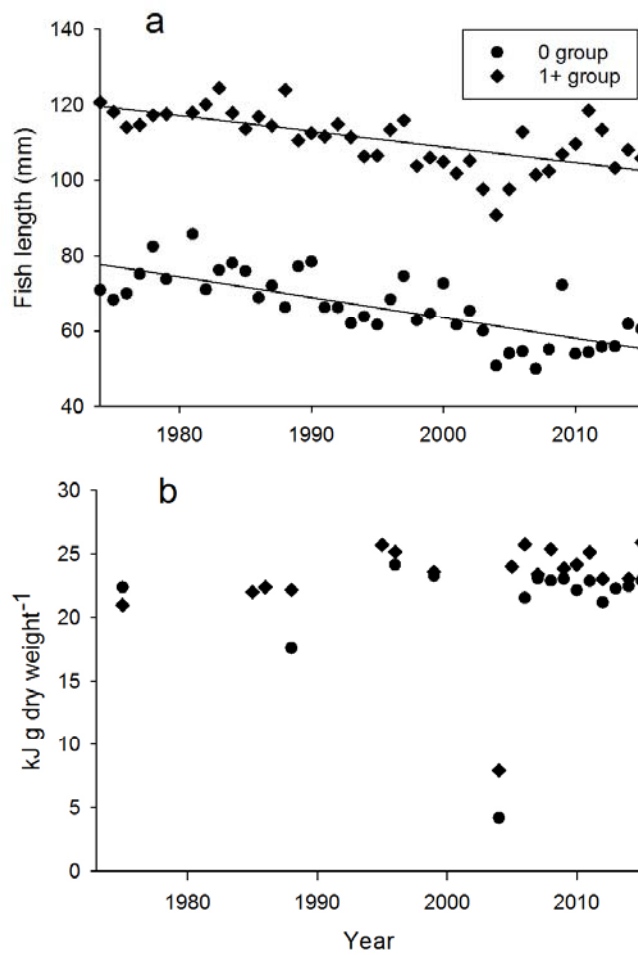
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784 between 1973 and 2015. Lengths of 0 group and 1+ group sandeels are standardized to 1 July  
785 and 1 June, respectively. Samples sizes and SEs are given in the supplementary material.  
786

787 Table 1. Diet samples obtained from seabirds on the Isle of May showing the overall importance of sandeels to the diet of chicks. For Atlantic  
 788 puffin, the frequencies refer to the proportions of all fish (n = 57205) and not samples.

Species	Period	Samples		Frequency in sample			Proportion of biomass		
		No. of samples	Total mass (g)	0 group sandeel	1+ group sandeel	Total sandeel	0 group sandeel	1+ group sandeel	Total sandeel
Atlantic puffin	1973–2015	6489	59329	0.692	0.059	0.823	0.504	0.185	0.690
Razorbill	1982–2015	4854	13849	0.694	0.124	0.825	0.514	0.130	0.644
Common guillemot	1982–2015	33456	228680	0.010	0.386	0.396	0.001	0.330	0.331
European shag	1985–2015	935	35289	0.282	0.759	0.880	0.140	0.698	0.844
Black-legged kittiwake	1986–2015	2020	33805	0.835	0.175	0.904	0.662	0.116	0.778

789



790

791 Table 2 Estimates ( $\pm$  SE) and t- and p-values for effects of year and species on biomass  
792 proportions in the diet of Isle of May seabirds. The intercept corresponds to the value for the  
793 mean study year in black-legged kittiwake when the fishery was not operating. Values are on  
794 the logit scale

795

796 a) Proportion of sandeel

797

798	<b>Parameter</b>	<b>Estimate</b>	<b>SE</b>	<b>t</b>	<b>p</b>
799	Constant	2.026	0.314	6.45	<0.001
800	Year	-0.0945	0.0302	-3.13	0.002
801	Fishery	-0.017	0.208	-0.08	0.934
802	European shag	-0.074	0.423	-0.17	0.862
803	Razorbill	-1.160	0.354	-3.28	0.001
804	Common guillemot	-2.819	0.363	-7.76	<0.001
805	Atlantic puffin	-0.913	0.348	-2.62	0.010
806	Year.European shag	-0.0285	0.0413	-0.69	0.491
807	Year.Razorbill	0.0133	0.0352	0.38	0.707
808	Year.Common guillemot	-0.0482	0.0382	-1.26	0.209
809	Year.Atlantic puffin	0.1121	0.0329	3.41	<0.001

810

811 b) Proportion of 1+ group relative to 0 group

812

813	<b>Parameter</b>	<b>Estimate</b>	<b>SE</b>	<b>t</b>	<b>p</b>
814	Constant	-1.479	0.260	-5.69	<0.001

815	Year	-0.0963	0.0309	-3.12	0.002
816	Fishery	-0.041	0.220	-0.19	0.852
817	European shag	2.533	0.315	8.03	<0.001
818	Razorbill	0.229	0.321	0.71	0.476
819	Common guillemot	6.58	1.04	6.35	<0.001
820	Atlantic puffin	0.099	0.323	0.31	0.759
821	Year.European shag	0.1441	0.0384	3.75	<0.001
822	Year.Razorbill	0.0306	0.0376	0.81	0.418
823	Year.Common guillemot	0.107	0.108	1.00	0.321
824	Year.Atlantic puffin	0.0382	0.0345	1.11	0.270

825

826 c) Proportion of clupeid relation to other non-sandeel prey

827

828	Parameter	Estimate	SE	<i>t</i>	<b>p</b>
829	Constant	0.314	0.225	1.39	0.166
830	Year	0.0681	0.0242	2.81	0.006
831	Fishery	-0.278	0.273	-1.02	0.310
832	European shag	-2.643	0.414	-6.38	<0.001
833	Razorbill	3.041	0.638	4.77	<0.001
834	Common guillemot	4.238	0.817	5.19	<0.001
835	Atlantic Puffin	1.184	0.281	4.21	<0.001
836	Year.European shag	-0.1286	0.0473	-2.72	0.007
837	Year.Razorbill	0.1040	0.0628	1.66	0.100
838	Year.Common guillemot	-0.0729	0.0865	-0.84	0.401
839	Year.Atlantic puffin	-0.0872	0.0290	-3.01	0.00



Supplementary material

Table S1 Details of food samples collected from seabirds on the Isle of May. Dates of first and last food samples are given as Day of the Year (DOY) with Day 1 = 1<sup>st</sup> January

(a) Atlantic puffin *Fratercula arctica*

Year	First date (DOY)	Last date (DOY)	No. of loads	No. of fish	Total mass (g)	Proportion of loads	Proportion of fish		Proportion of biomass		
						with sandeels	0 sandeel	1+ sandeel	0 sandeel	1+ sandeel	Clupeidae
1973	184	200	59	342	564	0.712	0.939	0.009	0.860	0.070	0.050
1974	154	216	101	601	1112	0.782	0.644	0.040	0.320	0.160	0.500
1975	151	198	129	464	1189	0.248	0.170	0.028	0.090	0.060	0.850
1976	155	216	167	694	1185	0.503	0.569	0.009	0.380	0.030	0.510
1977	151	215	119	577	1337	0.529	0.478	0.031	0.250	0.070	0.670
1978	156	207	109	514	1288	0.890	0.498	0.043	0.340	0.110	0.530
1979	175	213	99	445	1463	0.869	0.476	0.191	0.270	0.430	0.270
1980	170	214	56	331	981	0.980	0.647	0.139	0.560	0.260	0.170
1981	155	220	96	457	1152	0.510	0.573	0.083	0.480	0.220	0.290
1982	153	195	90	351	964	0.667	0.311	0.228	0.100	0.590	0.260
1983	153	214	142	619	1549	0.958	0.719	0.134	0.460	0.470	0.040
1984	149	211	214	948	2163	0.724	0.390	0.143	0.260	0.430	0.300
1985	147	213	143	1052	1277	0.951	0.764	0.105	0.420	0.470	0.110

1986	158	196	137	375	792	0.869	0.413	0.229	0.130	0.700	0.110
1987	166	194	137	390	1099	0.664	0.421	0.336	0.130	0.660	0.210
1988	165	186	119	859	1037	0.840	0.825	0.037	0.600	0.260	0.130
1989	165	191	101	630	947	0.990	0.902	0.005	0.880	0.010	0.100
1990	159	188	110	500	776	0.991	0.900	0.028	0.810	0.110	0.040
1991	157	188	130	963	1193	0.985	0.812	0.075	0.550	0.340	0.040
1992	146	197	125	822	1108	0.936	0.729	0.085	0.500	0.360	0.010
1993	160	193	211	1234	1882	0.602	0.590	0.044	0.230	0.160	0.610
1994	170	194	146	1102	1280	0.979	0.686	0.041	0.420	0.140	0.430
1995	169	194	95	577	985	0.737	0.596	0.120	0.250	0.310	0.440
1996	166	198	118	980	1134	0.992	0.869	0.028	0.740	0.140	0.070
1997	154	189	89	732	1056	0.933	0.873	0.034	0.720	0.160	0.120
1998	164	212	333	3112	2664	0.958	0.923	0.025	0.750	0.110	0.130
1999	151	191	212	1960	1759	0.708	0.735	0.016	0.430	0.090	0.420
2000	149	194	230	1984	2479	0.987	0.873	0.041	0.750	0.140	0.100
2001	153	195	219	2288	2193	0.881	0.809	0.035	0.550	0.130	0.310
2002	146	197	189	1805	1506	0.974	0.882	0.057	0.690	0.240	0.040
2003	151	193	223	2516	2034	0.951	0.906	0.024	0.730	0.080	0.160
2004	150	206	271	3843	1736	0.797	0.891	0.033	0.630	0.140	0.200
2005	157	216	226	3040	2004	0.885	0.913	0.006	0.680	0.030	0.260
2006	155	211	172	2289	1529	0.797	0.898	0.001	0.590	0.010	0.330
2007	147	204	132	1881	784	0.917	0.819	0.003	0.700	0.030	0.200
2008	155	217	106	1614	687	0.925	0.606	0.001	0.610	0.000	0.120
2009	145	208	114	1352	1462	0.982	0.907	0.007	0.890	0.030	0.040
2010	144	201	172	1915	1664	0.738	0.661	0.016	0.440	0.110	0.400
2011	143	195	196	2506	1560	0.714	0.690	0.002	0.539	0.010	0.396
2012	145	199	178	2489	1325	0.921	0.895	0.008	0.732	0.086	0.141
2013	168	218	157	2015	1250	0.809	0.755	0.000	0.552	0.000	0.388
2014	149	197	140	1704	1428	0.871	0.808	0.003	0.678	0.002	0.264
2015	155	199	177	2333	1662	0.876	0.870	0.003	0.745	0.023	0.220

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850 (b) Razorbill *Alca torda*

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852

Year	First date (DOY)	Last date (DOY)	No. of loads	No. of fish	Total mass (g)	Proportion of loads with			Proportion of fish		Proportion of biomass		
						0 sandeel	1+ sandeel	Any sandeel	0 sandeel	1+ sandeel	0 sandeel	1+ sandeel	Clupeidae
1982	150	173	42	79	357	0.071	0.881	0.952	0.437	0.543	0.160	0.820	0.020
1983	156	179	124	427	893	0.218	0.742	0.960	0.684	0.276	0.400	0.590	0.008
1984	147	200	62	337	391	0.500	0.371	0.871	0.741	0.109	0.730	0.230	0.000
1985	152	176	107	366	189	0.701	0.262	0.963	0.891	0.087	0.703	0.246	0.043
1986	164	197	49	113	118	0.245	0.592	0.837	0.469	0.292	0.182	0.407	0.398
1987	164	189	46	155	120	0.522	0.283	0.804	0.729	0.097	0.396	0.182	0.418
1988	156	203	143	592	343	0.769	0.154	0.923	0.889	0.047	0.609	0.119	0.268
1989	155	189	68	432	127	0.897	0.074	0.971	0.984	0.012	0.885	0.057	0.058
1990	155	190	65	343	135	0.938	0.031	0.969	0.988	0.006	0.924	0.022	0.055
1991	159	182	45	159	76	0.756	0.200	0.956	0.931	0.057	0.815	0.172	0.000
1992	150	202	92	204	182	0.359	0.500	0.859	0.593	0.343	0.335	0.560	0.081
1993	160	193	38	65	101	0.289	0.211	0.500	0.538	0.169	0.210	0.159	0.621
1994	164	201	51	126	117	0.412	0.098	0.510	0.746	0.056	0.291	0.087	0.596
1995	156	197	33	79	61	0.394	0.364	0.758	0.747	0.152	0.386	0.287	0.302
1996	166	174	48	137	91	0.479	0.438	0.917	0.796	0.175	0.492	0.382	0.121
1997	154	180	188	1155	373	0.910	0.027	0.936	0.984	0.005	0.858	0.023	0.118
1998	165	201	88	321	193	0.625	0.193	0.818	0.888	0.062	0.543	0.151	0.305
1999	160	183	56	184	130	0.571	0.143	0.714	0.864	0.049	0.491	0.100	0.395
2000	156	183	116	505	246	0.793	0.052	0.845	0.950	0.014	0.690	0.041	0.269
2001	154	182	272	906	656	0.559	0.129	0.688	0.853	0.053	0.417	0.106	0.476

2002	155	186	215	1134	364	0.795	0.116	0.912	0.961	0.022	0.708	0.100	0.192
2003	157	196	214	1192	459	0.832	0.037	0.869	0.967	0.009	0.741	0.035	0.224
2004	153	196	249	747	1602	0.281	0.008	0.289	0.482	0.003	0.088	0.002	0.910
2005	165	203	515	2934	1000	0.996	0.004	1.000	0.999	0.001	0.996	0.004	0.000
2006	167	197	703	3780	1339	0.959	0.041	1.000	0.990	0.010	0.958	0.042	0.000
2007	156	185	258	1246	817	0.713	0.031	0.744	0.820	0.011	0.449	0.025	0.524
2008	167	188	160	680	532	0.638	0.156	0.794	0.813	0.057	0.384	0.107	0.508
2009	164	188	139	687	286	0.878	0.079	0.957	0.964	0.022	0.835	0.076	0.088
2010	152	180	148	323	737	0.203	0.122	0.324	0.418	0.087	0.079	0.055	0.865
2011	152	172	46	108	125	0.326	0.196	0.522	0.676	0.083	0.248	0.105	0.645
2012	154	184	165	850	437	0.794	0.115	0.909	0.909	0.033	0.598	0.093	0.309
2013	172	190	109	391	445	0.450	0.101	0.550	0.696	0.028	0.219	0.036	0.742
2014	161	187	62	174	260	0.290	0.032	0.323	0.563	0.023	0.127	0.022	0.845
2015	163	180	138	564	547	0.529	0.065	0.594	0.777	0.032	0.284	0.008	0.708

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855 (c) Common Guillemot *Uria aalge*

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	First date (DOY)	Last date (DOY)	No. of fish	Proportion		Biomass (g)	Proportion of biomass		
				0 sandeel	1+ sandeel		Prop 0	Prop 1+	Clupeidae
1982	150	173	515	0.000	0.915	5270	0.000	0.902	0.098
1983	156	179	1067	0.000	0.753	8876	0.000	0.652	0.347
1984	147	200	708	0.010	0.912	6375	0.001	0.893	0.107
1985	143	198	2111	0.009	0.798	16300	0.001	0.714	0.286
1986	154	204	1066	0.001	0.910	8592	0.000	0.863	0.137
1987	158	206	530	0.000	0.815	5202	0.000	0.739	0.261
1988	151	203	590	0.034	0.537	5480	0.002	0.470	0.524
1989	144	195	818	0.061	0.824	3597	0.008	0.748	0.221
1990	146	190	496	0.173	0.433	2215	0.023	0.276	0.697
1991	142	182	587	0.022	0.733	2658	0.003	0.653	0.344
1992	133	202	637	0.014	0.568	3719	0.001	0.461	0.534
1993	152	190	673	0.000	0.227	4356	0.000	0.175	0.825
1994	158	211	595	0.012	0.171	3218	0.001	0.138	0.861
1995	152	188	478	0.010	0.674	3273	0.001	0.777	0.206
1996	157	197	589	0.019	0.424	3520	0.002	0.436	0.562
1997	149	187	1682	0.004	0.859	10317	0.000	0.784	0.216
1998	154	208	1349	0.007	0.254	6014	0.001	0.204	0.795
1999	152	192	1035	0.011	0.246	5871	0.001	0.211	0.759
2000	151	190	936	0.002	0.581	3898	0.000	0.440	0.560
2001	154	183	1300	0.007	0.300	7709	0.001	0.183	0.815



2002	150	182	1093	0.013	0.379	7049	0.001	0.222	0.776
2003	150	184	1301	0.008	0.165	8453	0.001	0.072	0.925
2004	154	194	1341	0.000	0.016	8449	0.000	0.014	0.982
2005	162	203	2898	0.000	0.041	21129	0.000	0.012	0.975
2006	159	198	1474	0.005	0.147	10682	0.000	0.040	0.884
2007	159	186	745	0.012	0.052	4792	0.001	0.016	0.977
2008	155	199	817	0.000	0.203	9324	0.000	0.064	0.928
2009	153	187	1211	0.016	0.259	7248	0.003	0.230	0.741
2010	142	181	1089	0.000	0.147	8230	0.000	0.070	0.930
2011	145	185	767	0.000	0.196	6574	0.000	0.134	0.865
2012	149	184	771	0.003	0.130	3844	0.000	0.106	0.888
2013	158	188	658	0.002	0.129	5221	0.000	0.078	0.920
2014	153	192	759	0.001	0.050	4334	0.000	0.041	0.957
2015	149	195	770	0.000	0.088	6890	0.000	0.050	0.948

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861 (d) European shag *Phalacrocorax aristotelis*

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	First date (DOY)	Last Date (DOY)	No. of regurgitates	Mass (g)	Frequency in sample			Proportion biomass <sup>1</sup>		
					0 sandeel	1+ sandeel	Any sandeel	0 sandeel	1+ sandeel	Clupeidae
1985	205	228	19	926	0.789	0.632	1.000	0.538	0.453	0.000
1986	194	226	38	1639	0.395	0.921	1.000	0.129	0.868	0.000
1987	149	203	22	1074	0.045	1.000	1.000	0.006	0.994	0.000
1988	167	200	17	686	0.118	1.000	1.000	0.016	0.974	0.000
1989	171	208	30	1027	1.000	0.200	1.000	0.800	0.200	0.000
1990	187	192	20	570	1.000	0.100	1.000	0.985	0.013	0.000
1991	185	199	20	693	0.700	0.550	1.000	0.575	0.425	0.000
1992	173	204	35	1592	0.257	0.857	0.914	0.172	0.776	0.001
1993	132	210	4	202	0.250	0.750	1.000	0.285	0.668	0.000
1994	189	207	23	847	0.696	0.348	0.913	0.566	0.267	0.117
1995	151	191	16	537	0.063	0.813	0.813	0.038	0.826	0.054
1996	169	208	29	1342	0.000	1.000	1.000	0.000	0.993	0.000
1997	128	197	54	1569	0.037	1.000	1.000	0.001	0.999	0.000
1998	133	205	38	1442	0.132	0.974	0.974	0.008	0.948	0.003
1999	189	215	5	166	0.600	0.600	0.800	0.511	0.239	0.077
2000	154	196	37	1647	0.108	0.919	0.919	0.004	0.870	0.040
2001	129	210	68	2524	0.412	0.971	0.985	0.049	0.854	0.000
2002	155	202	48	1430	0.146	1.000	1.000	0.025	0.919	0.001
2003	149	186	38	1591	0.184	0.974	0.974	0.027	0.931	0.003
2004	184	198	9	365	0.222	0.667	0.778	0.014	0.334	0.000

2005	140	216	17	639	0.412	0.118	0.529	0.379	0.046	0.004
2006	135	200	46	1668	0.413	0.391	0.609	0.294	0.228	0.004
2007	163	203	15	750	0.000	0.400	0.400	0.000	0.174	0.000
2008	172	196	35	999	0.371	0.400	0.600	0.142	0.339	0.027
2009	154	182	33	968	0.273	0.242	0.455	0.183	0.188	0.023
2010	127	205	65	2617	0.000	0.923	0.923	0.000	0.935	0.000
2011	136	188	42	1636	0.190	0.976	0.976	0.022	0.914	0.000
2012	148	206	26	1053	0.308	0.731	0.769	0.022	0.659	0.001
2013	181	204	13	423	0.077	0.308	0.308	0.002	0.259	0.000
2014	151	203	21	677	0.381	0.810	0.857	0.209	0.694	0.002
2015	120	191	52	1991	0.173	0.923	0.923	0.023	0.706	0.000

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866 <sup>1</sup>Values differ from Howells et al. (2017; Fig 1a) which presents mean proportion across samples in each year, not proportion after pooling all  
867 the samples for the year which was used here (see Methods).

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870 (e) Black-legged kittiwake *Risaa tridactyla*

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	First date (DOY)	Last date (DOY)	No. of regurgitates	Mass (g)	Proportion with			Proportion of mass		
					0 sandeel	1+ sandeel	Any sandeel	0 sandeel	1+ sandeel	Clupeidae
1986	160	195	35	317	0.829	0.486	0.971	0.606	0.373	0.000
1987	160	187	17	165	0.941	0.059	0.941	0.904	0.046	0.032
1988	178	191	32	354	0.790	0.150	0.940	0.350	0.590	0.060
1989	160	181	25	293	0.600	0.880	1.000	0.207	0.728	0.000
1990	152	207	9	210	0.778	0.222	1.000	0.564	0.214	0.071
1991	170	192	10	91	0.400	0.100	0.500	0.400	0.088	0.026
1992	158	193	26	319	0.615	0.231	0.808	0.555	0.140	0.092
1993	159	188	57	1089	0.404	0.439	0.789	0.256	0.403	0.115
1994	186	202	56	911	0.839	0.054	0.875	0.653	0.062	0.135
1995	171	193	45	731	0.911	0.133	0.956	0.836	0.061	0.057
1996	184	200	43	671	0.907	0.140	0.907	0.714	0.098	0.172
1997	162	197	137	2223	0.810	0.358	0.978	0.617	0.263	0.048
1998	162	195	110	2299	0.782	0.309	0.891	0.602	0.205	0.145
1999	165	195	180	3057	0.867	0.144	0.900	0.749	0.097	0.109
2000	156	208	138	2658	0.935	0.203	1.000	0.818	0.099	0.040
2001	164	219	86	2956	0.826	0.140	0.872	0.707	0.064	0.187
2002	157	199	76	1333	0.895	0.224	0.974	0.837	0.104	0.009
2003	157	216	135	2167	0.978	0.037	0.985	0.909	0.010	0.069
2004	170	209	120	1458	0.892	0.192	0.917	0.589	0.207	0.158
2005	177	213	116	1417	1.000	0.034	1.000	0.886	0.004	0.078

2006	158	211	54	1008	0.815	0.037	0.815	0.638	0.013	0.286
2007	170	205	61	1224	0.672	0.016	0.689	0.485	0.002	0.275
2008	163	198	46	714	0.761	0.022	0.761	0.408	0.001	0.337
2009	167	204	80	1112	0.963	0.038	0.963	0.898	0.017	0.048
2010	152	189	65	1065	0.492	0.200	0.569	0.312	0.059	0.622
2011	145	196	43	924	0.721	0.186	0.860	0.358	0.152	0.367
2012	152	185	59	775	0.915	0.169	0.983	0.671	0.143	0.150
2013	170	203	38	440	0.895	0.053	0.921	0.508	0.003	0.429
2014	172	199	67	848	0.940	0.060	0.940	0.682	0.023	0.242
2015	160	211	61	1038	0.787	0.016	0.787	0.593	0.010	0.254

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877 Table S2 Modelled annual mean lengths, standard errors and sample sizes of 0 group

878 sandeels (standardised to 1 July) and 1+ group sandeels (standardised to 1 June)

879 resulting from fitting linear mixed models using residual maximum likelihood

880 (REML) to fish collected from Atlantic puffins *Fratercula arctica* and common881 guillemots *Uria aalge* on the Isle of May. Year and date (June 1st = 1) were fitted as

882 covariates, and categorical sampling day, categorical year, and date by categorical

883 year as random effects.

	0 group sandeels			1+ sandeel		
	No.	Mean (mm)	SE	No.	Mean (mm)	SE
1973	321	77.92	0.19	3	126.32	0.13
1974	387	71.02	0.10	24	120.68	0.10
1975	79	68.42	0.19	13	118.10	0.11
1976	395	70.12	0.10	6	113.99	0.13
1977	276	75.23	0.11	18	114.73	0.10
1978	256	82.56	0.11	22	117.20	0.10
1979	212	73.89	0.13	85	117.49	0.06
1981	262	85.81	0.12	38	117.86	0.07
1982	109	71.18	0.14	80	120.02	0.07
1983	445	76.35	0.09	83	124.36	0.06
1984	370	78.16	0.11	136	117.82	0.06
1985	804	76.08	0.14	110	113.60	0.07
1986	155	68.95	0.17	86	116.80	0.08
1987	164	72.18	0.19	131	114.39	0.07
1988	709	66.38	0.23	32	123.94	0.09
1989	568	77.30	0.17	3	110.63	0.14
1990	450	78.54	0.20	14	112.46	0.09
1991	782	66.38	0.17	72	111.63	0.07
1992	599	66.37	0.15	70	114.87	0.08
1993	728	62.05	0.19	54	111.43	0.07
1994	756	63.89	0.19	45	106.29	0.07
1995	344	61.63	0.20	69	106.64	0.08
1996	852	68.52	0.17	27	113.38	0.09
1997	639	74.73	0.15	25	115.86	0.09
1998	2871	62.84	0.11	77	103.84	0.06
1999	1441	64.62	0.13	32	106.03	0.08
2000	1732	72.75	0.14	81	104.91	0.07
2001	1852	61.62	0.15	80	101.91	0.09

2002	1592	65.46	0.10	103	105.31	0.09
2003	2280	60.00	0.11	60	97.75	0.08
2004	3425	50.75	0.09	127	90.76	0.07
2005	2777	54.07	0.08	19	97.68	0.10
2006	2055	54.61	0.09	2	112.76	0.13
2007	1541	49.99	0.11	6	101.52	0.12
2008	976	55.14	0.10	1	102.47	0.18
2009	1226	72.35	0.09	10	106.85	0.13
2010	1269	53.97	0.10	27	109.72	0.09
2011	1729	54.35	0.10	5	118.46	0.15
2012	2228	55.81	0.10	19	113.38	0.11
2013	1522	55.90	0.11	0	103.26	0.21
2014	1376	61.85	0.12	4	108.06	0.17
2015	2029	60.54	0.11	8	105.86	0.14

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Table S3 Energy density (kJ g dry weight<sup>-1</sup>) of sandeels dropped by Atlantic puffins *Fratercula arctica* and Common guillemots *Uria aalge* on the Isle of May.

Year	0 group sandeel			1+ group sandeel		
	No.	Mean	SE	No.	Mean	SE
1975	18	22.38	0.20	11	20.96	0.89
1985	0			1	22.00	
1986	0			7	22.36	0.72
1988	1	17.60		9	22.16	0.65
1995	0			1	25.70	
1996	1	24.13		2	25.15	1.19
1999	2	23.27	1.63	1	23.58	
2004	11	4.19	0.17	9	7.91	0.62
2005	0			10	23.99	0.42
2006	50	21.53	0.10	3	25.73	0.46
2007	89	23.07	0.13	4	23.37	0.91
2008	103	22.88	0.08	1	25.36	
2009	115	23.04	0.14	14	23.86	0.49
2010	89	22.13	0.07	23	24.15	0.33
2011	90	22.86	0.12	5	25.11	0.89
2012	117	21.17	0.16	19	23.02	0.37
2013	101	22.27	0.12	0		
2014	115	22.45	0.22	5	23.03	0.75
2015	96	22.90	0.10	8	25.89	0.36

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