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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**

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16   Running head: Decline of sandeels in seabird diet

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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.

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INTRODUCTION

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

In the North Sea, the principal pelagic mid-trophic species is the lesser sandeel *Ammodytes marinus* (hereafter sandeel), a small, lipid-rich, shoaling fish with a complex life cycle after metamorphosis that alternates periods buried in sandy substrates with periods of 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.

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131 **MATERIALS AND METHODS**

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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.

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138 **Diet sampling**

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140 Atlantic puffin

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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 at 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

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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

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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

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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**

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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**

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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^{-1} for fat and 23.7 kJ g^{-1} for protein (Crisp 1971). All energy values

236 were expressed on a dry weight basis.

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238 **Statistical analysis**

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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 (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.

RESULTS

Diet composition

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

Puffin

Except for 1974-78 and 1993, sandeels always made up >50% of the biomass, and only in 1979 and 1982–87 did 1+ group sandeels comprise more of the biomass than 0 group sandeels (Figure 1a, Table S1a). The main alternative prey to sandeels was clupeids (Clupeidae). In 33 of the 42 yr the bulk of these were sprat and only in 1980-1982, 1984 and 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**

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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**

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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.

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310   **Shag**

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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**

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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**

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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).

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350   **Temporal trends in sandeel length**

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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 ± 0.081, F = 30.77,

355    $p < 0.001$; date = 0.245 ± 0.050, F = 24.28, $p < 0.001$; fishery = -0.618 ± 2.336, F = 0.07, p =

356   0.791; REML on 1+ group (mm): year = -0.426 ± 0.137, F = 9.61, p = 0.004; date = 0.449 ±

357   0.064, F = 48.84, $p < 0.001$; fishery = 0.314 ± 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

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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**

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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 ± 0.159, F = 108.94, p < 0.001; year =

367 0.051 ± 0.088, F = 0.34, p = 0.568; fishery = 2.932 ± 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**

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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

20

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

22

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

23

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

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

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

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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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(a) Atlantic puffin *Fratercula arctica*

(b) Razorbill *Alca torda*

(c) Common guillemot *Uria aalge*

(d) European shag *Phalacrocorax aristotelis*

(e) Black-legged kittiwake *Rissa tridactyla*

- 0 sandeel
- 1+ sandeel
- Clupeidae
- Others

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Fig. 1. Interannual variation in biomass proportions of 0 group sandeels, 1+ group sandeels,

Clupeidae and other prey in the diet of seabird chicks on the Isle of May. (a) Atlantic puffin

Fratercula arctica (1973–2015); (b) razorbill *Alca torda* (1982–2015); (c) common guillemot

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778   *Uria aalge* (1982–2015); (d) European shag *Phalacrocorax aristotelis* (1985–2015); and (e)

779   black-legged kittiwake *Rissa tridactyla* (1986–2015)

780

Fig. 2. Long-term changes in (a) annual mean length and (b) energy density of 0 group and
1+ group lesser sandeels *Ammodytes marinus* collected from seabirds on the Isle of May

784 between 1973 and 2015. Lengths of 0 group and 1+ group sandeels are standardized to 1 July

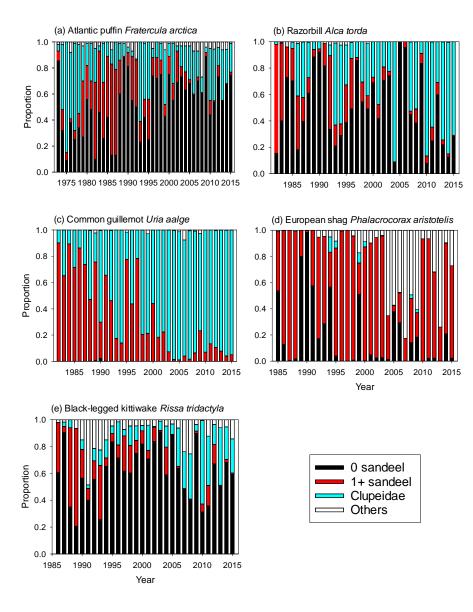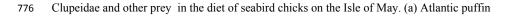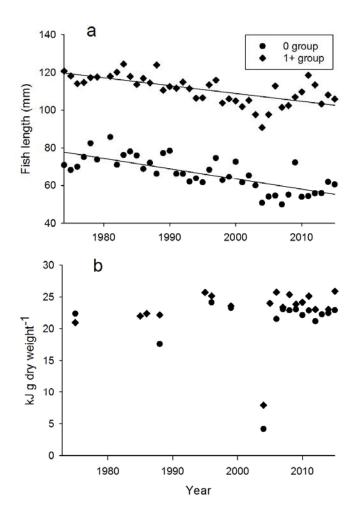785 and 1 June, respectively. Samples sizes and SEs are given in the supplementary material.

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.

		Samples		Frequency in sample			Proportion of biomass		
Species	Period	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

791 Table 2 Estimates (± 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

Parameter	Estimate	SE	*t*	p
Constant	2.026	0.314	6.45	<0.001
Year	-0.0945	0.0302	-3.13	0.002
Fishery	-0.017	0.208	-0.08	0.934
European shag	-0.074	0.423	-0.17	0.862
Razorbill	-1.160	0.354	-3.28	0.001
Common guillemot	-2.819	0.363	-7.76	<0.001
Atlantic puffin	-0.913	0.348	-2.62	0.010
Year.European shag	-0.0285	0.0413	-0.69	0.491
Year.Razorbill	0.0133	0.0352	0.38	0.707
Year.Common guillemot	-0.0482	0.0382	-1.26	0.209
Year.Atlantic puffin	0.1121	0.0329	3.41	<0.001

810

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

812

Parameter	Estimate	SE	*t*	p
Constant	-1.479	0.260	-5.69	<0.001

	Parameter	Estimate	SE	t	p
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

	Parameter	Estimate	SE	t	p
828	**Parameter**	**Estimate**	**SE**	*t*	**p**
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

840

Supplementary material

844 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
845 (DOY) with Day 1 = 1st January

846

(a) Atlantic puffin *Fratercula arctica*

848

Year	First date (DOY)	Last date (DOY)	No. of loads	No. of fish	Total mass (g)	Proportion of loads with sandeels	Proportion of fish		Proportion of biomass		
							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

850   (b) Razorbill *Alca torda*

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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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854

(c) Common Guillemot *Uria aalge*

	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[1]		
					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

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

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 common

881   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^{-1}) of sandeels dropped by Atlantic puffins *Fratercula arctica* and Common guillemots *Uria aalge* on the Isle of May.

| | 0 group sandeel | | | 1+ group sandeel | | |
Year	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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