



UWS Academic Portal

Ragworms and other marine food items in the diet of Herring Gulls *Larus argentatus* breeding on Lady Isle, Firth of Clyde, Scotland

Pennycott, Tom W.; Grant, David; Leopold, Mardik F.; Nager, Ruedi G.

Published in:
Bird Study

DOI:
[10.1080/00063657.2020.1869697](https://doi.org/10.1080/00063657.2020.1869697)

E-pub ahead of print: 12/02/2021

Document Version
Peer reviewed version

[Link to publication on the UWS Academic Portal](#)

Citation for published version (APA):

Pennycott, T. W., Grant, D., Leopold, M. F., & Nager, R. G. (2021). Ragworms and other marine food items in the diet of Herring Gulls *Larus argentatus* breeding on Lady Isle, Firth of Clyde, Scotland. *Bird Study*, 67(3), 402-408. <https://doi.org/10.1080/00063657.2020.1869697>

General rights

Copyright and moral rights for the publications made accessible in the UWS Academic Portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy

If you believe that this document breaches copyright please contact pure@uws.ac.uk providing details, and we will remove access to the work immediately and investigate your claim.

“This is an Accepted Manuscript of an article published by Taylor & Francis Group in Bird Study on 12/02/2021, available online: <http://www.tandfonline.com/10.1080/00063657.2020.1869697>”

1 **Ragworms and other marine food items in the diet of Herring Gulls breeding on Lady**
2 **Isle, Firth of Clyde, Scotland**

3

4 Tom W. Pennycott, Browncarrick Drive, Ayr, KA7 4JA, Scotland.

5 David Grant, University of the West of Scotland, Ayr Campus, Ayr, KA8 0SX, Scotland.

6 Mardik F. Leopold, Wageningen Marine Research, Ankerpark 27, NL-1781 AG Den Helder,
7 The Netherlands.

8 Ruedi G. Nager, Graham Kerr Building, IBAHCM, University of Glasgow, G12 8QQ,
9 Scotland.

10 Email of correspondence author: pennycott740@btinternet.com

11

12

13 *Larus* spp. gulls are opportunistic generalist foragers, at least at the population level (Hunt &
14 Hunt 1973, Götmark 1984) and their diet is highly adaptable so that it can vary in response
15 to variation in food availability (e.g. Stenhouse & Montevecchi 1999, Ronconi *et al.* 2014). A
16 higher proportion of marine resources (marine invertebrates and fish) in their diet can be
17 positively associated with measures of breeding success (Pierotti & Annett 1991, Annett &
18 Pierotti 1999, O'Hanlon *et al.* 2017) and long-term population declines have been associated
19 with dietary shifts away from marine resources (Blight *et al.* 2015, Hobson *et al.* 2015, Foster
20 *et al.* 2017). Thus, knowledge of the marine components of a gull's diet can give insights
21 about changes in the marine foraging environment affecting prey availability and may help to
22 explain changes in the numbers and distribution of gulls.

23 Pennycott *et al.* (2020) found that nearly two-thirds of 314 pellets produced by Herring Gulls
24 *Larus argentatus* breeding on Lady Isle in the Firth of Clyde, southwest Scotland, contained

25 the remains of earthworms; in addition, anthropogenic refuse, cereal and marine items
26 formed at least 25% of the volume of the pellet in 32.2%, 30.6% and 10.2% of pellets,
27 respectively. Given the importance of marine food to the breeding success in this population
28 (O'Hanlon *et al.* 2017), here we describe in greater detail the marine food items in the
29 Herring Gull's diet and record estimates of the numbers, combinations and potential calorific
30 values of prey items present in some pellets.

31 We collected 314 pellets during the incubation period (May) and chick rearing period (June
32 and July, Table 1) in 2018 and 2019. Pellets were collected and analysed as described by
33 Pennycott *et al.* (2020): briefly, pellets were collected from the rocky periphery of Lady Isle,
34 were broken up in water and passed through a sieve, the contents of the sieve examined
35 using a dissecting microscope (magnification 7-45) and the washings through the sieve
36 examined with a binocular microscope (transmitted light, magnification of 100-400). The
37 presence or absence of different categories of marine food items was recorded, and also
38 whether the combined marine items comprised over 25% of the volume of the pellet. The
39 presence of marine prey items in the pellets was compared between years and breeding
40 stages using a GLM with binomial error distribution (R Core Team 2019) and 95%
41 confidence intervals were calculated using the Jeffreys interval (R package binom, Dorai-
42 Raj, 2014).

43 Overall, marine food items were recovered from 24.2% of pellets, although in only 10.2% of
44 pellets did such items make up at least 25% of their volume. In 2018, more pellets from the
45 chick rearing stage contained marine items than pellets from the incubation stage, whereas
46 the reverse was true in 2019 (interaction between breeding stage and year: $\chi^2_1=19.88$,
47 $p<0.001$), reflecting variation in the composition of marine prey items found in different years
48 and breeding stages (Table 1).

49 Twenty-five pellets (8.0% of all pellets examined) contained one or more amber/brown
50 curved serrated pharyngeal jaws of ragworms of the Family Nereidae (Figure 1),

51 approximately 5 mm curved length, 1 mm wide, and with notably square “teeth” typical of the
52 ragworm *Eunereis longissima* (previously referred to as *Nereis longissima*) (Witteveen &
53 Leopold, in prep.). The length of jaw from the base of the first “tooth” to the tip of the jaw (A
54 to B in Figure 1) was 3.1 ± 0.35 mm (mean \pm standard deviation, n=42), indicating an
55 approximate mean ragworm mass of 2.8g (Witteveen & Leopold, in prep.). All pellets
56 containing ragworm jaws were collected during the Herring Gull incubation stage in May, and
57 significantly more pellets contained ragworms in May 2019 than in May 2018 (breeding
58 stage: $\chi^2_1=30.11$, year: $\chi^2_1=14.76$, both $p < 0.001$, Table 1). Fifteen pellets contained up to
59 four ragworm jaws, five pellets contained between five and twenty jaws, a further four had
60 31-50 jaws, and one pellet contained over 50 jaws. Lourenço (2007) noted that estimating
61 ragworm consumption by dividing the number of jaws by two would significantly under-
62 estimate the total consumption of ragworms because not all jaws would survive in pairs. It is
63 likely, therefore, that large numbers of ragworms were taken by some Herring Gulls on Lady
64 Isle, especially in May 2019. Although ragworms usually live in burrows in the sediment, out-
65 with the reach of gulls, during the breeding season they become sexually mature and the
66 males form swarms, often swimming near the surface of the sea where they can be taken by
67 seabirds (Courtens *et al.* 2017). Ragworm spawning is triggered by a rise in sea
68 temperatures after winter and is synchronised to occur when spring tides tend to be
69 especially low at either a full moon or new moon (Bartels-Hardege & Zeeck 1990). Sample
70 collection dates in May in both years were around the time of spring tides, but sea surface
71 temperatures in spring 2018 were lower than in 2019 (<http://climate4you.com/> accessed
72 14/09/2020) which may have caused a later timing of spawning in 2018 and hence a lower
73 availability of ragworms at the time of sampling in May 2018.

74 Ragworms, especially the Harbour or Estuary Ragworm *Hediste diversicolor* (previously
75 referred to as *N. diversicolor*) are an important part of the diet of many wading birds (Goss-
76 Custard *et al.* 1977, Le V. Dit Durrell & Kelly 1990, De Vlas *et al.* 1996, Dierschke *et al.*
77 1999, Scheiffarth 2001, Lourenço 2007, Duijns *et al.* 2013), and ragworms have also been

78 recorded in the diet of other groups of coastal and marine birds such as Great Cormorant
79 *Phalacrocorax carbo* and European Shag *P. aristotelis* (Barrett *et al.* 1990, Leopold & van
80 Damme 2003), Shelduck *Tadorna tadorna* (Buxton & Young 1981), Northern Fulmar
81 *Fulmarus glacialis* (Camphuysen & van Franeker 1997) and Atlantic Puffin (Harris *et al.*
82 2015). However, although recorded as prey items of gulls and terns in the North Sea off The
83 Netherlands, Germany and Belgium (Spaans 1971, Kubetzki & Garthe 2003, Markones *et al.*
84 2009, Camphuysen 2013, Courtens *et al.* 2017), the Tagus Estuary in Portugal (Moreira
85 1995), North America (Ambrose 1986) and Japan (Iwamatsu *et al.* 2007), published records
86 of the consumption of ragworms by gulls in the British Isles appear to be limited. Most relate
87 to Black-headed Gulls *Chroicocephalus ridibundus* foraging on *H. diversicolor* (Vernon 1972,
88 Mudge & Ferns 1982, Curtis & Thompson 1985), although Harris (1965) mentioned *H.*
89 *diversicolor* and *N. pelagica* as prey items of Herring Gulls in Wales but did not give further
90 details. Thus, the frequent detection of *E. longissima* in Herring Gull pellets in our study is
91 the first such report from the British Isles and adds to our understanding of the diet of
92 Herring Gulls. Jaws of this species of ragworm have been recovered in large numbers from
93 the faeces of breeding Sandwich Terns *Thalasseus sandvicensis* from five colonies in
94 Belgium and The Netherlands, mostly in May (Courtens *et al.* 2017), and from pellets from a
95 mixed gull colony in The Netherlands (Camphuysen 2013); in the latter study, jaws of *E.*
96 *longissima* were found in 22% of pellets from Lesser Black-backed Gulls in the pre-hatching
97 phase and 8% of Lesser Black-backed Gull pellets in the post-hatching phase, but in under
98 1% of pellets from Herring Gulls. It is unclear whether the detection of *E. longissima* in
99 pellets from Herring Gulls on Lady Isle represents a change in foraging behaviour in gulls at
100 this location, perhaps in response to a reduction in other marine food resources, or whether
101 earlier studies in the British Isles did not detect or report *E. longissima* jaws in gull pellets or
102 faeces because the timing of sample collection missed the short period of ragworm
103 spawning.

105 Thirty pellets (9.6%) contained the remains of Langoustines *Nephrops norvegicus*, including
106 fragments of carapace, legs, chelae (claws), rostra, eyes and antennae. Based on their
107 appearance, Langoustine claws could be identified as being from the upper or lower
108 crushing or cutting claw, enabling an estimation to be made of the minimum number of
109 Langoustines contributing to the pellet. Most pellets contained only one or two Langoustines,
110 but two pellets contained claws from a minimum of four and five Langoustines, respectively,
111 and a combination of Langoustines and fish was detected in seven pellets. The mean length
112 of 17 upper claws recovered from pellets was 17.9 ± 2.35 mm (mean \pm standard deviation):
113 although this may have slightly underestimated claw size if they were worn down in the
114 upper digestive tract, this was smaller than the mean of 19.1 ± 3.01 mm for 100 upper claws
115 from discarded whole undersized Langoustines ($t_{115}=6.87$, $p<0.001$). The mean size of claws
116 from pellets was also smaller than a mean of 23.2 mm for 100 upper claws from the
117 cephalothorax of discarded “tailed” Langoustines and a mean of 27.0 ± 4.47 mm for 20 upper
118 claws from Langoustines marketed as whole medium-sized Langoustines ($t_{35}=12.16$,
119 $p<0.0001$) (T. Pennycott, reference collection), suggesting that the gulls most likely fed on
120 small undersized whole Langoustines discarded by the local fishery. Significantly more
121 pellets contained Langoustines in the chick-rearing phase than the incubation phase, but the
122 presence of Langoustines did not differ between the two years (breeding stage: $\chi^2_{1}=10.98$,
123 $p<0.001$; year: $\chi^2_{1}=0.58$, $p=0.446$; Table 1). The differences between the two phases may
124 reflect seasonal variation in the landing of Langoustines at the nearby port of Troon
125 (approximately 6 km from Lady Isle): 200 and 276 tonnes were landed in April/May 2018 and
126 April/May 2019 (incubation phase), respectively, rising to 432 tonnes in June/July 2018 and
127 375 tonnes in June/July 2019 (chick-rearing phase) (data provided by Marine Scotland
128 Compliance, Edinburgh).

129

130 Fish fragments such as vertebrae, ribs, fin rays, bones of the head (dentaries, pre-maxillae,
131 pre-opercula), earstones (otoliths) and pharyngeal teeth were found in 28 pellets (8.9% of all

132 examined pellets) and the presence of fish in pellets varied between year and breeding
133 stage (year-by-breeding stage interaction: $\chi^2_1=7.21$, $p=0.007$; Table 1). Fish was most
134 frequently present in pellets from the 2019 incubation period but, although less than in 2019,
135 fish was more frequent during chick rearing than incubation in 2018. Where possible, the fish
136 were further identified using descriptions and images provided by Camphuysen &
137 Henderson (2017). The remains of multiple fish, sometimes of different species, were
138 confirmed in eight individual pellets and may have been present in other pellets with fish
139 remains not identified to the Family level. Otoliths from at least two gadoid fish (codfishes of
140 the Family Gadidae) were identified in four pellets, and one pellet contained evidence of at
141 least one Common Dragonet *Callionymus lyra*, four wrasse (Family Labridae, most likely
142 Goldsinny *Ctenolabrus rupestris*) and three gadoids of two different species. Another two
143 pellets each contained the remains of at least two gadoids and one wrasse, and otoliths from
144 at least seven gadoids, most likely Poor Cod *Trisopterus minutus*, were recovered from an
145 eighth pellet along with the pharyngeal teeth of a wrasse. These are all demersal species
146 and although they have previously been identified in pellets from Herring Gulls breeding in
147 the Firth of Clyde (Nogales *et al.* 1995, O'Hanlon *et al.* 2017), our study has highlighted that
148 a single pellet can contain the remains of multiple fish, sometimes of different species or
149 concurrently with Langoustines. Based on measurements of otoliths, pharyngeal teeth and
150 head bones, and compared with reference collections and with figures provided by
151 Camphuysen & Henderson (2017), the Poor Cod were approximately 10 cm long, smaller
152 gadoids were under 10 cm, Goldsinny and Common Dragonet approximately 12 cm, and
153 larger gadoids (mostly Haddock *Melanogrammus aeglefinus*) approximately 17 cm,
154 suggesting that the fish remains found in gull pellets were acquired as discards from the
155 Troon trawler and creel fishery targeting Langoustines, European Lobsters *Homarus*
156 *gammarus* and Edible (Brown) Crabs *Cancer pagurus*.

157

158 Whole or parts of crab legs, claws or fragments of exoskeleton were recovered from 11
159 pellets (3.5% of all examined pellets). Five contained the remains of Green Shore Crabs
160 *Carcinus maenus*, fragments of Velvet Swimming Crab *Necora puber* were found in one
161 pellet, and in five pellets the species of crab could not be identified. Most pellets appeared to
162 contain fragments from only one crab but one pellet contained claws from at least five Green
163 Shore Crabs. Green Shore Crabs have frequently been found in pellets from Herring Gulls
164 and Lesser Black-backed Gulls in the British Isles and elsewhere (Harris 1965, Spaans
165 1971, Sibly & McCleery 1983, Kubetzki & Garthe 2003, Coulson & Coulson 2008,
166 Camphuysen 2013), acquired by foraging in the intertidal zone (Kubetzki & Garthe 2003).
167 Portions of Velvet Swimming Crab have been recorded much less frequently in gull pellets
168 from the British Isles, although they were included (as *Portunus puber*) by Harris (1965) in
169 the comprehensive list of items consumed by Herring Gulls in Wales, and were found in five
170 out of 43 pellets produced by Lesser or Great Black-backed Gulls on Lady Isle in 2018 (T.
171 Pennycott, unpublished data).

172

173 The energetic demands of an adult Herring Gull weighing 1 kg are estimated to be 980
174 kJ/day during the incubation phase, rising to 1220 kJ/day during brooding and 1430 kJ/day
175 at the crèche stage (https://ruthedunn.shinyapps.io/seabird_fmr_calculator/ , accessed
176 14/11/20). Converting the estimated fish lengths into fish mass (Silva *et al.* 2013) and with a
177 theoretical calorific value of 3.5 – 5.0 kJ/g (Camphuysen 2013), each Poor Cod might
178 contribute 35 – 50 kJ, each Common Dragonet 50 – 70 kJ, each Goldsinny 100 – 145 kJ,
179 and each Haddock 160 – 230 kJ. Although the calorific content of some individual fish may
180 be low, their contribution to the daily energy requirements of the gulls is likely to be
181 significant if, as found in the pellet analysis, multiple fish are consumed. The mean mass of
182 Langoustine consumed by the gulls was estimated by weighing whole discarded
183 Langoustines with claws slightly larger than those found in gull pellets, giving a mean of
184 7.6 ± 2.76 g (mean \pm standard deviation, n=50). Based on a theoretical calorific value for

185 whole Langoustines of 3.7 kJ/g wet weight (Björnsson & Alvaro 2004), the total calorific
186 value of each consumed Langoustine was only approximately 28 kJ. In addition,
187 Langoustines contain a large amount of poorly digestible chitin in their exoskeleton, reducing
188 their nutritional value. Björnsson & Alvaro (2004) found that the growth rate of Atlantic Cod
189 *Gadus morhua* experimentally fed Langoustines was under half of those fed Capelin
190 *Mallotus villosus*, partly due to the lower percentage of fat and higher levels of ash and chitin
191 in Langoustines, and also because it was more difficult for the Cod to pack their stomachs
192 with Langoustines compared with Capelin because of the tough exoskeleton and
193 appendages of the Langoustines: the same may also be true for Herring Gulls consuming
194 Langoustines. Shore crabs have a fairly low individual calorific value (<3.5 kJ/g,
195 Camphuysen 2013) and the size of crab consumed by the gulls is unknown but likely to be
196 small based on the size of claws recovered from the pellets. Individual ragworms have a low
197 calorific value (<3 kJ/g wet weight, Camphuysen 2013), indicating an energy content of only
198 approximately 8 kJ per ragworm based on an estimated mean mass of 2.8g, suggesting that
199 their contribution to the total calorific intake of the gulls was low unless consumed in large
200 numbers.

201 O'Hanlon *et al.* (2017) cite a number of papers in which seabirds switched to a more
202 nutritious diet when rearing chicks, typically providing more marine items to increase the fat
203 and protein content. However, seasonal changes in availability of different food items will
204 also influence prey selection. Thus, for Herring Gulls breeding on Lady Isle, factors such as
205 rainfall can affect access to earthworms on the mainland (Pennycott *et al.* 2020), rising sea
206 temperatures in the spring combined with a new or full moon will influence whether gulls can
207 readily obtain ragworms, and seasonal changes in the activities of the local fishing fleet
208 could affect the quantity of fish and Langoustine discards available to foraging gulls.

209 Comparisons with earlier studies on the diets of Herring Gulls in this part of the Firth of Clyde
210 are difficult due to the different methodologies used. In our study on Lady Isle, marine items
211 constituted at least 25% of the bulk of the pellet in 10.2% of pellets, similar to the findings of

212 O'Hanlon *et al.* (2017, Figure 3) who detected marine items in approximately 10% of gull
213 pellets from Lady Isle in the 2014 breeding season, but less than the figure of approximately
214 25% of pellets from the island of Pladda, 27 km in a westerly direction from Lady Isle
215 (O'Hanlon *et al.* 2017, Figure 3). When considered as presence/absence of marine items,
216 our study detected marine food items in 24.2% of pellets examined from the 2018 and 2019
217 breeding seasons on Lady Isle, compared with Nogales *et al.* (1995) who found marine food
218 items, mostly fish, in 32.8% of pellets from adult Herring Gulls during the 1991 breeding
219 season on Ailsa Craig (39 km to the southwest of Lady Isle). The ratio of fish to Langoustine
220 remains also differed: in 1991 on Ailsa Craig, fish remains were found approximately six
221 times more frequently than Langoustine remains, whereas in our study in 2018 and 2019 fish
222 and Langoustines were equally represented. This most likely reflected the change in the
223 nature of commercial fishing in the Firth of Clyde during the 1990s when vessels converted
224 from demersal fishing to targeting Langoustines, to the extent that by 2005 most of the
225 demersal fish catch was bycatch from the Langoustine fishery (Hunter *et al.* 2015). As a
226 result, discards of larger numbers of undersized demersal fish and highly nutritious offal
227 (liver and intestines) from gutted demersal fish would be replaced by smaller numbers of
228 undersized demersal fish and larger numbers of Langoustines, reducing the nutritional
229 quality available to the gulls.

230 It is clear from this and other studies that the presence of marine food items and their
231 composition can vary substantially for different dates and sites of sampling, suggesting that
232 breeding Herring Gulls respond to variations in food availability. Therefore, a large number of
233 samples collected over multiple dates, examined using appropriate methodology, will be
234 required before a truly representative assessment of the diet of a Herring Gull population can
235 be made.

236

237 **Acknowledgements**

238 We are grateful to SAC Consulting Veterinary Services for access to the Olympus binocular
239 microscope, and to Klaudyna Maniszewska, Rachel Scott, James Scarlett and Roselle Smith
240 for collection of some of the pellets.

241

242

243 **References**

244

245 **Ambrose, W.G.Jr.** 1986. Estimate of removal rate of *Nereis virens* (Polychaeta: Nereidae)
246 from an intertidal mudflat by gulls (*Larus* spp.). *Mar. Biol.* **90**: 243-247.

247

248 **Annett, C.A. & Pierotti, R.** 1999. Long-term reproductive output in western gulls:
249 consequences of alternate tactics in diet choice. *Ecology* **80**: 288–297.

250

251 **Barrett, R.T., Røv, N., Loen, J., & Montevecchi, W.A.** 1990. Diets of shags *Phalacrocorax*
252 *aristotelis* and Cormorants *P. carbo* in Norway and possible implications for gadoid stock
253 recruitment. *Mar. Ecol. Prog. Ser.* **66**: 205–218.

254

255 **Bartels-Hardege, H.D. & Zeeck, E.** 1990. Reproductive behaviour of *Nereis diversicolor*
256 (Annelida : Polychaeta). *Mar.Biol.* **106**: 409-412.

257

258 **Björnsson, B. & Alvaro, M.A.D.** 2004. Quality of *Nephrops* as food for Atlantic Cod (*Gadus*
259 *morhua*) with possible implications for fisheries management. *ICES J. Mar. Sci.* **61**:983-991.

260

261 **Blight, L.K., Hobson, K.A., Kyser, T.K. & Arcese, P.** 2015. Changing gull diet in a
262 changing world: a 150-year stable isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) record from feathers collected in the
263 Pacific Northwest of North America. *Global Change Biol.* **21**: 1497–1507.

264

265 **Buxton, N.E. & Young, C.M.** 1981. The food of the Shelduck in north-east Scotland. *Bird*
266 *Study* **28**: 41-48

267

268 **Camphuysen, C.J.** 2013. A historical ecology of two closely related gull species (Laridae):
269 multiple adaptations to a man-made environment. PhD thesis. University of Groningen,
270 Groningen.

271

272 **Camphuysen, C.J. & van Franeker, J.A.** 1997. Notes on the diet of northern fulmars
273 *Fulmarus glacialis* from Bjørnøya (Bear Island). *Sula* **11**:1-10.

274

275 **Camphuysen, C.J. & Henderson, P.A.** 2017. North Sea fish and their remains. Royal
276 Netherlands Institute for Sea Research & Pisces Conservation Ltd. ISBN-13 978-1-904690-
277 65-8.

278

279 **Coulson, J.C. & Coulson, B.A.** 2008. Lesser black-backed gulls *Larus fuscus* nesting in an
280 inland urban colony: the importance of earthworms (Lumbricidae) in their diet. *Bird Study* **55**:
281 297-303.

282

283 **Courtens, W., Verstraete, H., Vanermen, N., Van de walle, M. & Stienen, E.W.M.** 2017.
284 Faecal samples reveal the diet of breeding adult Sandwich terns *Thalasseus sandvicensis* in
285 Belgium and the southern part of the Netherlands. *J. Sea Res.* **127**: 182–193.

286

287 **Curtis, D.J. & Thompson, B.A.** 1985. Spacing and foraging behaviour of Black-headed
288 Gulls *Larus ridibundus* in an estuary. *Ornis Scand.* **16**: 245-252.

289

290 **De Vlas, S.J., Bunscoeke, E.J., Ens, B.J. & Hulscher, J.B.** 1996. Tidal changes in the
291 choice of *Nereis diversicolor* or *Macoma balthica* as main prey species in the diet of the
292 Oystercatcher *Haematopus ostralegus*. *Ardea* **84**: 105-116.

293

294 **Dierschke, V., Kube, J., Probst, S. & Brenning, U.** 1999. Feeding ecology of dunlins
295 *Calidris alpina* staging in the southern Baltic Sea. I. Habitat use and food selection. *J. Sea*
296 *Res.* **42**: 49-64.

297

298 **Dorai-Raj, S.** 2014. binom: Binomial Confidence Intervals For Several Parameterizations. R
299 package version 1.1-1. <https://CRAN.R-project.org/package=binom>

300

301 **Duijns, S., Hidayati, N.A. & Piersma, T.** 2013. Bar-tailed godwits *Limosa lapponica* eat
302 polychaete worms wherever they winter in Europe. *Bird Study* **60**: 509-517.

303

304 **Foster, S., Swann, R.L. & Furness, R.W.** 2017. Can changes in fishery landings explain
305 long-term population trends in gulls? *Bird Study* **64**: 90–97.

306

307 **Goss-Custard, J.D., Jones, R.E. & Newbery, P.E.** 1977. The ecology of the Wash. I.
308 Distribution and diet of wading birds (Charadrii). *J. App. Ecol.* **14**: 681-700.

309

310 **Götmark, F.** 1984. Food and foraging in five European *Larus* gulls in the breeding season: a
311 comparative review. *Ornis Fenn.* **61**: 9–18.

312

313 **Grant, D., Robertson, D., Nager, R. & McCracken, D.** 2013. The status of breeding gulls
314 on Lady Isle, Ayrshire. 2012. *Scott. Birds* **33**: 298-307.

315

316 **Harris, M.P.** 1965. Food of some gulls. *Ibis* **107**: 43-52.

317

318 **Harris, M.P., Leopold, M.F., Jensen, J.-K., Meesters, E.H. & Wanless, S.** 2015. The
319 winter diet of the Atlantic Puffin *Fratercula arctica* around the Faroe Islands. *Ibis* **157**: 468-
320 479.

321

322 **Hobson, K.A., Blight, L.K. & Arcese, P.** 2015. Human-induced long-term shifts in gull diet
323 from marine to terrestrial sources in North America's coastal Pacific: more evidence from
324 more isotopes ($\delta^2\text{H}$, $\delta^{34}\text{S}$). *Environmental & Science Technology* **49**: 10834–10840.

325

326 **Hunt, G.L. Jr, & Hunt, M.** 1973. Habitat partitioning by foraging gulls in Maine and
327 Northwestern Europe. *Auk* **90**: 827–839.

328

329 **Hunter, A., Speirs, D.C. & Heath, M.R.** 2015. Fishery-induced changes to age and length
330 dependent maturation schedules of three demersal fish species in the Firth of Clyde. *Fish.*
331 *Res.* **170**: 14-23

332

333 **Iwamatsu, S., Suzuki, A. & Sato, M.** 2007. Nereidid polychaetes as the major diet of
334 migrating shorebirds on the estuarine tidal flats at Fujimae-Higata in Japan. *Zoological*
335 *Science* **24**: 676-685.

336

337 **Kubetzki, U. & Garthe, S.** 2003. Distribution, diet and habitat selection by four sympatrically
338 breeding gull species in the south-eastern North Sea. *Mar. Biol.* **143**: 199-207.

339

340 **Leopold, M.F. & van Damme, C.J.G.** 2003. Great Cormorants *Phalacrocorax carbo* and
341 polychaetes: can worms sometimes be a major prey of a piscivorous seabird? *Marine*
342 *Ornithology* **31**: 83-87.

343

344 **Le V. Dit Durrell, S.E.A. & Kelly, C.P.** 1990. Diets of Dunlin *Calidris alpina* and Grey Plover
345 *Pluvialis squatarola* on The Wash as determined by dropping analysis. *Bird Study* **37**: 44-47.

346

347 **Lourenço, P.M.** 2007. Analysing faecal samples of Ragworm predators: not just a matter of
348 counting mandibles. *Ardea* **95**: 151-155.

349

350 **Markones N., Guse, N., Hüppop, O., & Garthe, S.** 2009. Unchanging diet in a stable
351 colony: contemporary and past diet composition of black-legged kittiwakes *Rissa tridactyla* at
352 Helgoland, south-eastern North Sea. *Helgol. Mar. Res.* **63**: 199–206.

353

354 **Moreira, F.** 1995. Diet of Black-headed Gulls *Larus ridibundus* on emerged intertidal areas
355 in the Tagus Estuary (Portugal): predation or grazing? *J. Avian Biol.* **26**: 277-282

356

357 **Mudge, G. P. & Ferns, P.N.** 1982. The feeding ecology of five species of gulls (Aves: Larini)
358 in the inner Bristol Channel. *J. Zool.* **197**: 455-461.
359

360 **Nogales, M., Zonfrillo, B. & Monaghan, P.** 1995. Diets of adult and chick Herring Gulls
361 *Larus argentatus argenteus* on Ailsa Craig, south-west Scotland. *Seabird* **17**: 56-63.
362

363 **O’Hanlon, N.J., McGill, R.A.R. & Nager, R.G.** 2017. Increased use of intertidal resources
364 benefits breeding success in a generalist gull species. *Mar. Ecol. Prog. Ser.* **574**: 193-210.
365

366 **Pennycott, T. W., Grant, D. & Nager, R.W.** 2020. Earthworms in the diet of Herring Gulls
367 *Larus argentatus* breeding on an off-shore island. *Bird Study* **67**: 131-134.
368

369 **Pierotti, R. & Annett, C.A.** 1991. Diet choice in the herring gull: constraints imposed by
370 reproductive and ecological factors. *Ecology* **72**: 319–328.
371

372 **R Core Team** (2019). R: A language and environment for statistical computing. R
373 Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
374

375 **Ronconi, R.A., Steenweg, R.J., Taylor, P.D. & Mallory, M.L.** 2014. Gull diets reveal
376 dietary partitioning, influences of isotopic signatures on body condition, and ecosystem
377 changes at a remote colony. *Mar. Ecol. Prog. Ser.* **514**: 247–261.
378

379 **Scheiffarth, G.** 2001. The diet of Bar-tailed Godwits *Limosa lapponica* in the Wadden Sea:
380 combining visual observations and faeces analyses. *Ardea* **89**: 481-494.

381

382 **Sibly, R.M. & McCleery, R.H.** 1983. The distribution between feeding sites of Herring Gulls
383 breeding at Walney Island, UK. *J. Anim. Ecol.* **52**: 51-68.

384

385 **Silva, J.F., Ellis, J.R. & Ayers, R.A.** 2013. Length-weight relationships of marine fish
386 collected from around the British Isles. *Sci. Ser. Tech. Rep., CEFAS Lowestoft.* **150**: 109pp.

387

388 **Spaans, A.L.** 1971. On the feeding ecology of the Herring Gull *Larus argentatus* Pont. in the
389 northern part of The Netherlands. *Ardea* **55**: 73-188.

390

391 **Stenhouse, I.J., & Montevecchi, W.A.** 1999. Indirect effects of the availability of capelin
392 and fishery discards: gull predation on breeding storm- petrels. *Mar. Ecol. Prog. Ser.* **184**:
393 303–307.

394

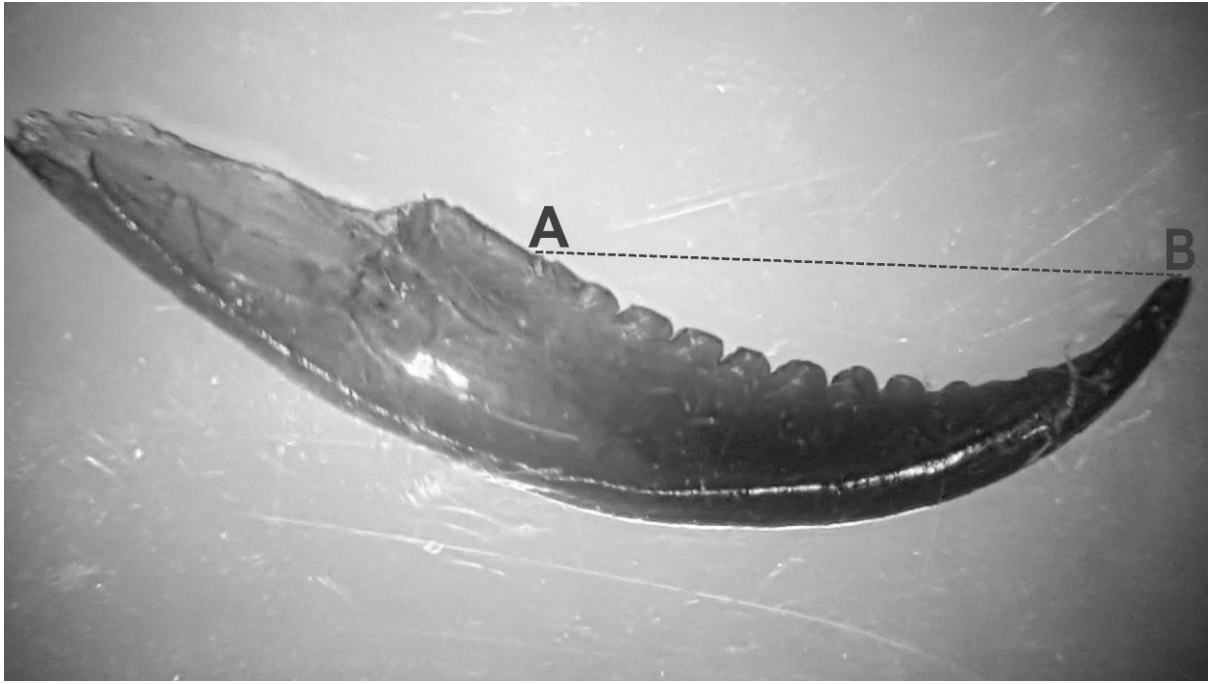
395 **Vernon, J.D.R.** 1972. Feeding habitats and food of the Black-headed and Common Gulls.
396 Part 2 – Food. *Bird Study* **19**: 173-186

397

398 **Witteveen, L. & Leopold, M.F.** Handbook of North Sea Polychaete Jaw Identification and
399 Biomass Estimation for Diet Studies. *Wageningen Marine Research Report* (in prep.), The
400 Netherlands.

401

402



403

404 Figure 1.