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11 **Changing Numbers of Three Gull Species in the British Isles**

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24 **Abstract.**—Between-population variation of changes in numbers can provide insights
25 into factors influencing variation in demography and how population size or density is
26 regulated. Here, we describe spatio-temporal patterns of population change of Herring Gull
27 (*Larus argentatus*), Lesser Black-backed Gull (*L. fuscus*) and Great Black-backed Gull (*L.*
28 *marinus*) in the British Isles from national censuses and survey data. The aim of this study
29 was to test for density-dependence and spatial variation in population trends as two possible,
30 but not mutually exclusive, explanations of population changes with important implications
31 for the understanding of these changes. Between 1969 and 2013 the three species showed
32 different population trends with Herring Gulls showing a strong decline, Great Black-backed
33 Gulls a less pronounced decline and Lesser Black-backed Gulls an increase until 2000 but
34 then a decline since. Population changes also varied between different regions of the British
35 Isles, with the Atlantic coast showing declines and the North Sea coast increases in all three
36 species. Population changes were density-dependent in the Herring Gull, and Lesser Black-
37 backed Gulls showed faster population increases at lower Herring Gull densities. Contrasting
38 numbers of gulls nest in coastal habitats or on roofs (mainly in urban habitats). Herring Gulls
39 seem to seek refuge in urban environments, whereas Lesser Black-backed Gulls expand their
40 range into the urban environment. The large declines in hitherto abundant species create a
41 dilemma for conservation bodies in prioritizing conservation policies. The spatial variation in
42 population changes and the differences between species suggest that there is no single cause
43 for the observed changes, thus requiring region-specific conservation management strategies.

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47 **Key words.**—density-dependence, Great Black-backed Gull, Herring Gull, *Larus*
48 *argentatus*, *Larus fuscus*, *Larus marinus*, Lesser Black-backed Gull, population trends,
49 productivity, roof-nesting.

50

51 **Running Head:** TRENDS IN LARGE BRITISH GULLS

52 Most species show between-population variation in demography, but case studies
53 covering a substantial part of a species' range are rare (but see Dhondt 2001). Exploration of
54 spatial variation in demography over a large range may provide insights into factors
55 influencing variation in demography and how population size or density is regulated because
56 throughout a larger range the populations are likely to be exposed to a larger range of
57 environmental conditions increasing the power of the study (Bairlein 2003). Here, we want to
58 explore the spatial variation in population trends of the three large gull species, Herring Gull
59 (*Larus argentatus*), Lesser Black-backed Gull (*L. fuscus*) and Great Black-backed Gull (*L.*
60 *marinus*) breeding in the British Isles, northeastern Atlantic.

61 The British Isles host more seabirds than comparable areas at similar latitudes in
62 continental Europe because they are surrounded by highly productive seas. Some of the
63 seabird species have shown large fluctuations in numbers over the last century. Because of
64 their colonial nesting behavior, which allows collection of large numbers of birds and eggs,
65 seabirds were particularly vulnerable to human exploitation that peaked in the 19th century
66 in the British Isles (Newton 2013). After protective legislation was put in place to curb
67 human exploitation, and an upsurge in food supplies mainly resulting from human fishing
68 activities, many seabird populations increased again and spread in the latter half of the 20th
69 century (Cramp *et al.* 1974; Lloyd *et al.* 1991; Mitchell *et al.* 2004). Three of the seabirds
70 that showed such large fluctuations were the large *Larus* species: Great Black-backed Gull,
71 Herring Gull, and Lesser Black-backed Gull. The British Isles host a significant proportion of
72 their biogeographic population (from 16% in *L. marinus* to 63% for *L. fuscus*; Mitchell *et al.*
73 2004). Insofar as we know, the three large *Larus* species were not uncommon in the British
74 Isles during the 19th century, with their main distribution being to the north of Scotland and
75 on the western seaboard of Scotland, Wales and Ireland (Holloway 1996). During most of
76 the 20th century, following the implementation of protective legislation in the early 1900s,

77 their populations expanded and colonized new areas and/or reoccupied areas from which they
78 had been driven by persecution (Cramp *et al.* 1974). For example, the Herring Gull is
79 considered to have increased annually by ~13% from the 1930s to the 1970s (Chabrzyk and
80 Coulson 1976). Reasons for this increase are thought to be increased protection and increased
81 food availability, mainly from human sources, refuse and fisheries discards (Furness and
82 Monaghan 1997; but see Coulson this volume). Most recently, however, worrying declines
83 for all three species were recorded (Eaton *et al.* 2013).

84 The population dynamics of marine top predators, like the *Larus* species, may reflect
85 environmentally induced changes in resource availability (Davoren and Montevecchi 2003),
86 or they may be self-regulated through local prey depletion (Birt *et al.* 1987). Changes in a top
87 predator's environment may cascade through bottom-up control (i.e., from prey to predator).
88 If spatio-temporal variation in resource availability is mainly determined by environmental
89 effects, colonies exploiting the same local resources would be expected to show similar
90 population trends and, therefore, geographic clusters would show similar dynamics (regional
91 variation hypothesis). On the other hand, demographic parameters of top predators may be
92 negatively correlated with their density, possibly through local prey depletion or reduced
93 resource availability through interference (Furness and Birkhead 1984; Lewis *et al.* 2001;
94 Ainley *et al.* 2003), so that there is a top-down control (i.e., from predator to prey). These two
95 mechanisms have profoundly different implications for population control, and determining
96 which of these mechanisms is most important is critical for our understanding of the
97 population dynamics of *Larus* species (Montevecchi 1993).

98 The aim of this study was to test for spatial variation and density-dependence in
99 population change in the three large *Larus* species in the British Isles between 1969 and 2013
100 to gain insights into two possible, but not mutually exclusive explanations for the observed
101 population changes. By including different species that differ in their general ecology (only

102 the Lesser Black-backed Gull is migratory; all three species differ in their use of food
103 supplies (Furness *et al.* 1992; Noordhuis and Spaans 1992; Kim and Monaghan 2006)),
104 variation in population changes among species and among regions may point toward potential
105 causes of changes in population abundance in the British Isles.

106

107

METHODS

108 We used two sources of data to evaluate the changes in abundance of the large gulls in
109 Great Britain, Isle of Man, Channel Islands and Ireland, hereafter referred to as the British
110 Isles. First, comprehensive counts of seabirds nesting in the British Isles were carried out in
111 1969-1970 (Operation Seafarer; Cramp *et al.* 1974), in 1985-1988 (Seabird Colony Register;
112 Lloyd *et al.* 1991) and 1998-2002 (Seabird 2000; Mitchell *et al.* 2004). And secondly, we
113 used more recent surveys from the Seabird Monitoring Programme (SMP; Joint Nature
114 Conservation Committee 2014a) that give an index to estimate the trends in gull populations
115 since Seabird 2000.

116 Operation Seafarer, Seabird Colony Register and Seabird 2000 all followed the same
117 essential methodologies to quantify numbers of coastal nesting gulls. Essentially, the entire
118 coastline within 5 km of the high-water line (on Orkney, Shetland and Western Isles all
119 colonies were considered coastal even if more than 5 km from the coastline) where there
120 were previous reports on seabird presence were surveyed and all apparently occupied nests
121 (AON, well-constructed nest either containing eggs or young or capable of holding eggs, a
122 well-constructed nest attended by an adult, or an adult apparently incubating) were counted
123 during the daytime in the peak incubation period when most gulls were expected to be on
124 eggs (Mitchell *et al.* 2004). Coastlines in remote and sparsely populated areas (e.g., north and
125 northwest Scotland, western and southern Ireland) were incompletely surveyed in Operation
126 Seafarer and Seabird Colony Register; therefore, total abundance might have been slightly

127 underestimated in the 1970s and 1980s. Seabird 2000 ensured that the coverage of those
128 regions was much improved and where some gaps remained, notably western and southern
129 Ireland, only few gulls had been previously recorded from that area (Hannon *et al.* 1997).
130 Therefore, abundances of coastal breeding large gulls are comparable across 1969-2002.
131 Seabird 2000 also covered roof-nesting gulls (colonies on man-made structures, mostly roofs)
132 and gulls nesting at inland sites. Additional specialist national surveys of roof-nesting gulls
133 were also carried out in 1974-1976 (Monaghan and Coulson 1977) and in 1994-1995 (Raven
134 and Coulson 1997) allowing us to separate population changes between different breeding
135 habitats (coastal nesting vs. roof-nesting pairs). AON counts were provided per
136 administrative areas which correspond to the English and Welsh counties, Scottish and
137 Northern Ireland districts and Irish vice-counties.

138 To look at changes in population abundance of gulls since Seabird 2000, we included
139 information of the SMP surveys. Started in 1986, SMP monitors an extensive sample of
140 colonies each year, supplemented with more intensive monitoring of demographic parameters
141 at key colonies. It covers 26 seabird species that regularly breed in the British Isles. For gulls,
142 annual count data from an extensive sample of gull colonies are compiled and values for
143 missing years (where these existed) were estimated using an ‘imputation’ method (Thomas
144 1993). The estimates of population abundance from the SMP is an index expressed as a
145 percentage of the first year in the time series (1986) that was set as 100%. Note that SMP
146 data only cover the U.K., whereas Operation Seafarer, Seabird Colony Register and Seabird
147 2000 cover the British Isles. However, by the mid-1980s the numbers of gulls breeding in the
148 Republic of Ireland were so small (typically < 10% of the count of the whole of the British
149 Isles) that the differences between U.K. and British Isles numbers were negligible. Based on
150 the absolute number of gulls in Seabird Colony Register (1985-1988), when the SMP
151 population index was set at 100%, and the SMP population index for 2000, we can calculate

152 the number of gulls estimated by the SMP survey and compare this to the more exhaustive
 153 total count by Seabird 2000 to assess how representative is the SMP population index. We
 154 then used the SMP population index for 2013 (Joint Nature Conservation Committee 2014a)
 155 to estimate the total number of gulls in 2013 and investigate population trends in the three
 156 larger gulls since 2002. The SMP also records data on productivity and we extracted annual
 157 productivity rates for Herring, Lesser Black-back and Great Black-backed gulls in order to
 158 test for temporal changes in productivity between 1986 and 2012 (the period for which data
 159 are available).

160 Within the database, seabird population estimates can be determined over two scales;
 161 the individual colony and the administration area, with the exception of the administration
 162 areas around Glasgow where population estimates were combined and categorized as the
 163 Clyde. Changes in abundance are expressed in two ways. To compare changes between
 164 intervals of different duration we calculated percentage change per annum (% pa) as
 165 $\sqrt[t]{N(t)/N(0)}$ where $N(0)$ is the initial count and $N(t)$ is the count t years later. Secondly, we
 166 calculated population growth rate (GR) from the late 1960s to 2000 using the following
 167 formula based on Guillaumet *et al.* (2014):

$$168 \quad \text{GR} = (N_{t+1} - N_t) / \text{Maximum} [N_{t+1}, N_t]$$

169 where N_{t+1} and N_t are two counts and $\text{Maximum} [N_{t+1}, N_t]$ is either the earlier or later count,
 170 whichever was the higher value. GR were calculated per administrative area instead of
 171 individual colony to buffer against short-distance movements between neighboring colonies.
 172 The equation based on Guillaumet *et al.* (2014) was used instead of the more conventional
 173 calculation for population growth as it deals better with administrative areas with gull
 174 populations (e.g., Lancashire, West Sussex, Hampshire, Suffolk, East Sussex, Dorset) newly
 175 established during the study period, whilst still providing a good estimate of the population
 176 change (Guillaumet *et al.* 2014). Our estimate of GR is monotonically related to the

177 conventional measure of population growth (N_{t+1}/N_t) with Spearman correlation coefficient r_s
178 = 1.0 in all three species. GR thus provides provides an adequate alternative to describing
179 population trends where new populations are established during the study period but as it
180 requires both N_t and N_{t+1} , it does not provide a tool for predicting future abundance
181 (Guillaumet *et al.* 2014).

182 We then clustered administrative areas into distinct biogeographic zones, each having
183 a specific oceanography (primarily temperature, depth and current) that supports
184 characteristic biological communities (Dinter 2001). Coastal waters around the British Isles
185 are included in two regions of the northeastern Atlantic by the OSPAR Commission (2014):
186 Greater North Sea east of 5° W and Celtic Sea west of 5° W. For U.K. waters only, the Joint
187 Nature Conservation Committee identified Regional Seas Regions (RSR; Joint Nature
188 Conservation Committee 2014b) on a finer scale based on the same biogeographic principles
189 as the OSPAR Commission regions. For the purpose of our analyses, we used the following
190 RSRs (maintain the same numbers as Joint Nature Conservation Committee 2014b; Fig. 2): 1.
191 *Northern North Sea* between Duncansby Head and Flamborough; 2. *Southern North Sea*
192 between Flamborough and Dover Straits; 3. *Eastern English Channel* between Dover Straits
193 and the line between Weymouth to Cherbourg; 4. *Western English Channel & Celtic Sea*
194 west of the line between Weymouth to Cherbourg and bounded in the northeast by the Celtic
195 Sea front; 6. *Irish Sea* bounded in the south by the Celtic Sea front and in the north by the
196 line from the Mull of Kintyre to Fair Head; 7. *Minches & West Scotland* bounded in the south
197 by the line from the Mull of Kintyre to Fair Head and in the north by the line from the Butt of
198 Lewis to Cape Wrath; and 8. *Scottish Continental Shelf* north of the line from the Butt of
199 Lewis to Cape Wrath and west of Duncansby Head. The Joint Nature Conservation
200 Committee's RSRs do not include waters of the Republic of Ireland, and although the
201 *Western English Channel & Celtic Sea* appears to extend around Ireland, initial analyses

202 showed that some trends in Irish gull colonies differed from those in the rest of the *Western*
203 *English Channel & Celtic Sea* (analyses not shown). We therefore included Irish vice-
204 counties not bordering the Celtic Sea (north-west of Cork) in a separate RSR (referred as 4a),
205 and vice-counties bordering the Celtic Sea were included in RSR 4. Because for each RSR
206 we had multiple measures of GR (one for each administrative area) we could calculate a
207 mean GR and 95% confidence interval of the mean per RSR. If the 95% confidence interval
208 does not overlap with 0 than we can say that the population in that RSR increased (positive
209 GR) or declined (negative GR). For population trend between 2000 and 2013 based on the
210 SMP Index we have only one value at the start and end for that period and we cannot judge
211 whether observed changes in numbers are statistically significant or not.

212 To test for spatial variation in population trends, we compared GRs between RSRs
213 using ANOVAs with administrative area GRs as response variable and RSR as a fixed factor,
214 carried out separately for each of the three species. For the effects of density on GRs, we
215 analyzed the data separately for the periods of Operation Seafarer to Seabird Colony Register
216 and Seabird Colony Register to Seabird 2000, and related GRs to the absolute abundance at
217 the beginning of each interval (Operation Seafarer and Seabird Colony Register,
218 respectively). To account for regional variation in both population size and GR, we analyzed
219 for the effect of population size on GR using a general linear model with RSR as a fixed
220 effect. To investigate the relationship between numbers of pairs in different breeding habitats
221 we analyzed a relationship between number of roof-nesting pairs in Seabird 2000 against
222 change in number of coastal-nesting pairs between 1969 and 2002 across all species using a
223 general linear model including species as a factor. This analysis only included Herring and
224 Lesser Black-backed gulls as insufficient numbers for the Great Black-backed Gull were
225 available. Because changes in annual productivity can cause changes in population size we
226 explored temporal changes in annual productivity rates of each species using correlations. All

227 statistical analyses were carried out using SPSS (IBM Corp. 2013). A significance level of P
228 = 0.05 was used, and results are presented as means \pm 95% confidence intervals of means.

229

230

RESULTS

231 There have been changes in numbers of breeding pairs of Herring, Great Black-
232 backed and Lesser Black-backed Gulls in the British Isles between 1969 and 2002, but
233 they differ between the three species (Fig. 1). Operation Seafarer (1969-1970) recorded
234 343,600 AON of coastal nesting Herring Gulls (Cramp *et al.* 1974). By the mid-1980s, the
235 number of coastal-nesting Herring Gulls declined to nearly half that number (177,000 AON;
236 Lloyd *et al.* 1991; 1.1% decline per annum) and by Seabird 2000, it decreased further to
237 147,100 AON; Mitchell *et al.* 2004; 1.4% decline per annum). Overall the Herring Gull
238 population of the British Isles showed a negative average GR of -0.27 with a 95% confidence
239 interval (-0.43 to -0.11, $n = 72$ administrative areas) that did not overlap with 0. Coastal-
240 nesting Great Black-backed Gulls were less numerous than Herring Gulls and showed a less
241 pronounced decline in numbers: Operation Seafarer = 22,200 AON (Cramp *et al.* 1974);
242 Seabird Colony Register = 20,900 AON (Lloyd *et al.* 1991; 0.4% decline per annum); and
243 Seabird 2000 = 19,700 AON (Mitchell *et al.* 2004; 0.5% decline per annum since Seabird
244 Colony Register). The average GR of Great Black-backed gulls was 0.055 with a 95%
245 confidence interval (-0.12 to 0.23, $n = 58$ administrative areas) which overlapped with 0.
246 Coastal-nesting Lesser Black-backed Gulls showed an increase in numbers by 29% (1.5% per
247 annum) from Operation Seafarer (50,000 AON; Cramp *et al.* 1974) to Seabird Colony
248 Register (64,400 AON; Lloyd *et al.* 1991) and by 42% (2.7% per annum) from Seabird
249 Colony Register to Seabird 2000 (91,300 AON; Mitchell *et al.* 2004). The average GR of
250 coastal-nesting Lesser Black-backed Gulls of the British Isles was 0.37 with a 95%
251 confidence interval (0.21 to 0.53, $n = 64$ administrative areas) that did not overlap with 0.

252 Between Operation Seafarer and Seabird 2000, the GR of Herring Gulls differed
253 between RSRs (ANOVA: $F_{7,63} = 2.78$, $P = 0.014$; Table 1; Fig. 2a). Numbers of coastal-
254 nesting Herring Gulls decreased in the northern and western parts of the British Isles but did
255 not show clear trends elsewhere (Table 1; Fig. 2a). Coastal-nesting Great Black-backed
256 Gulls showed population increases in the Northern North Sea and the Eastern English
257 Channel, but no clear trends elsewhere with the differences in GR between RSRs marginally
258 significant (ANOVA: $F_{6,47} = 2.28$, $P = 0.050$; Table 1; Fig. 2c). Although the GR of coastal-
259 nesting Lesser Black-backed Gulls did not differ significantly between RSRs (ANOVA: $F_{7,56}$
260 $= 1.96$, $P = 0.076$), Lesser Black-backed Gull numbers increased in RSRs in the southern part
261 of the British Isles, but declined Minches and West Scotland and no clear trends in the other
262 regional seas (Table 1; Fig 2b).

263 We found density-dependent GR for coastal-nesting Herring Gulls during both
264 sampling intervals (Operation Seafarer to Seabird Colony Registry and Seabird Colony
265 Registry to Seabird 2000) with administrative areas that held the largest numbers of Herring
266 Gulls showed the greatest per capita declines in local abundance (Table 2). There was no
267 evidence of negative correlations between GR and population abundance in the other two
268 species (Table 2). We also found weak evidence for an interaction between Lesser Black-
269 backed and Herring gulls; local Lesser Black-backed Gull populations increased the least in
270 administrative areas with the highest numbers of Herring Gulls in the period between Seabird
271 Colony Registry and Seabird 2000, but all other species interactions were not significant
272 (Table 2).

273 Data on roof-nesting gulls suggested few birds were nesting on man-made structures
274 in the 1970s (Fig. 1). In the 1980s and 1990s, the number of roof-nesting gulls increased
275 dramatically in Herring and Lesser Black-backed gulls (Fig. 1). The relationship between
276 number of roof-nesting pairs in Seabird 2000 and changes in numbers of coastal-nesting pairs

277 per RSR differed significantly between Herring and Lesser Black-backed gulls (interaction
278 species by absolute change in coastal-breeding numbers: GLM: $F_{1,14} = 10.43$, $P = 0.006$; Fig.
279 3). In Herring Gulls, RSR that lost the largest number in coastal-nesting pairs were also the
280 areas with the largest number of roof-nesting gulls in Seabird 2000 (correlation: $r = -0.75$, $n =$
281 8 RSR, $P = 0.019$). In contrast, for the Lesser Black-backed Gull the RSRs with the largest
282 increases in coastal-nesting pairs also held the highest numbers of roof-nesting pairs in 2000
283 ($r = 0.82$, $n = 8$, $P = 0.007$). However, the number of roof-nesting pairs in Herring and Lesser
284 Black-backed gulls are smaller than the changes in population abundance in the coastal areas
285 (Fig. 3).

286 To assess the trends in gull numbers since 2000, we used the SMP index . Because the
287 SMP covers only a sample of colonies, we first compared the projections of the SMP index
288 from 1986-2000 with the more extensive data from Seabird 2000. The agreement between the
289 trend in gull numbers between the estimate from the SMP index and Seabird 2000 was very
290 good for all three species (Fig. 1). Between 2000 and 2013, the numbers of Herring Gulls
291 further declined (30% decline between 2000 and 2013 or 3.0% per annum) as did the
292 numbers of Great Black-backed Gulls (24% decline between 2000 and 2013 or 3.0% per
293 annum). Since 2000, the number of Lesser Black-backed Gulls also started to decline (48%
294 decline between 2000 and 2013 or 5.0% per annum).

295 Annual productivity rates declined between 1986 and 2012 for Herring Gulls
296 (correlation: $r = -0.44$, $n = 23$ years, $P = 0.036$) and Great Black-backed Gulls ($r = -0.66$, $n =$
297 22 years, $P < 0.001$) but did not change over time in Lesser Black-backed Gulls ($r = 0.18$, n
298 $= 23$ years, $P = 0.411$).

299

300

DISCUSSION

301 We found considerable variation in changes in population trends between species, and
302 within species variation between regions and habitats in the three *Larus* species Herring,
303 Lesser Black-backed, and Great Black-backed gulls in the British Isles. The variation in GR
304 between species and regions suggests that there is no one overall cause of the changes in
305 abundance in Herring, Lesser Black-backed, and Great Black-backed gulls for the whole of
306 the British Isles.

307 The changes in numbers of coastal-nesting pairs of Herring, Great Black-backed and
308 Lesser Black-backed gulls between 1969 and 2013 differed between the three species.
309 Herring Gulls exhibited a steep and significantly negative growth rate (GR), Great Black-
310 backed Gulls showed a small and non-significant change whereas over that same period the
311 population of the Lesser Black-backed Gull significantly increased. The numbers of Herring
312 and Great Black-backed gulls possibly peaked in the 1960s and 1970s following a period of
313 increased protection and food availability, while the Lesser Black-backed Gull continued is
314 spread throughout the 20th century in the British Isles, as elsewhere in its range, possibly
315 benefiting from reduced exploitation and increased protection and in the British Isles may
316 have peaked in 2000 (JNCC 2014a).. Based on the SMP index, the current projections for the
317 period 2000-2013 suggest that between 2000 and 2013 all three species declined, but since
318 there is only one estimate for the whole of the UK we cannot calculate a confidence interval
319 for those changes. The most recent estimates (2013) of number of coastal-breeding birds are
320 lower than they were in 1969-1970 in all three species. The SMP index mostly contains
321 coastal colonies (Eaton *et al.* 2013) and may not be fully representative of the overall
322 populations that also breed on roofs in built-up areas and in inland colonies (i.e., colonies
323 more than 5 km from the high water line). This might be particularly true for Herring and
324 Lesser Black-backed gulls that breed in large numbers on roofs and inland (Mitchell *et al.*
325 2004) and might explain why their projected absolute numbers by the SMP index for 2000

326 appeared slightly lower than the Seabird 2000 census. Most importantly, however, the SMP
327 index accurately reflected the population trends between the Seabird Colony Register and
328 Seabird 2000, therefore their projections of the current population trends are likely true. For
329 all three species the British Isles represent a significant proportion of the world population of
330 these species and thus hosts internationally important numbers (Mitchell *et al.* 2004). Yet, the
331 Herring Gull has recently been added to the U.K.'s Red List (Eaton *et al.* 2009). The Lesser
332 Black-backed and Great Black-backed gulls are on the Amber List. Other North Atlantic
333 population of large gulls showed similar temporal changes in abundance (Bond *et al.* this
334 volume; Mittelhauser *et al.* this volume; Regular *et al.* this volume; Wilhelm *et al.* this
335 volume).

336 In addition to differences between species, we also found regional differences in GR
337 for at least the Herring Gull and the Great Black-backed gulls. Between 1969 and 2002
338 Herring Gulls declined in the west and the north with the possible exception of the Irish sea
339 where the population decline was not significant, and no significant changes in the east and
340 the south. Although the regional differences in GR of Great Black-backed Gulls was
341 marginally significant, it is clear that populations along the British North Sea increased
342 whereas the numbers tended to decrease, although not statistically significant, along the
343 Atlantic coast. In contrast most regions exhibited significantly increasing numbers of Lesser
344 Black-backed Gulls between 1969-2002, but there was also a significant decline in the
345 Minches and Western Scotland (see also Thom 1986). Regional variation in population
346 changes in Herring and Great Black-backed gulls is further supported by recent avian atlas
347 work that also showed that their distribution within Britain has changed (Balmer *et al.* 2013).
348 Herring and Great Black-backed gulls used to be concentrated along the western seaboard
349 and along the northern coast of the British Isles where the largest declines occurred. Both
350 species used to be much rarer on the eastern seaboard along the North Sea coast and the

351 southern coast of England where some colonies are now expanding and new colonies are
352 forming in previously unoccupied areas. Thus some areas which were previously by a low
353 proportion of the British population may now contain significant numbers of the British
354 population (e.g., Grant *et al.* 2013).

355 Furthermore there were also distinct shifts in the habitat occupied by Herring and
356 Lesser Black-backed gulls (Mitchell *et al.* 2004, Balmer *et al.* 2013). Both Herring and
357 Lesser Black-backed gulls now nest in larger numbers on artificial structures (Mitchell *et al.*
358 2004; Rock 2005). Lesser Black-backed Gulls can also nest inland in substantial numbers
359 (22% of the total population in Seabird 2000) whereas less than 2% of Herring and Great
360 Black-backed gulls breed inland (Mitchell *et al.* 2004). However, inland colonies have only
361 been systematically surveyed for the Seabird 2000. Inland colonies of Lesser Black-backed
362 Gulls may have been under-represented in Operation Seafarer and Seabird Colony Register
363 and if so, those counts are possibly too low, and the estimated population increase of Lesser
364 Black-backed Gulls between 1969 and 2002 has possibly been over-estimated. Interestingly,
365 we found relationships between changes in numbers of coastal- and roof-nesting numbers of
366 Herring and Lesser Black-backed gulls when considering RSRs. The more coastal-nesting
367 Herring Gulls lost in a RSR between 1970 and 2000, the larger the number of roof-nesting
368 Herring Gulls in that same RSR in 2000. This could mean that artificial structures now act as
369 refuges, with urban sites possibly offering more food and safer nesting sites from predators
370 (Monaghan and Coulson 1977; Raven and Coulson 1997). However, the increases in roof-
371 nesting Herring Gulls are by far not sufficient to make up for losses in coastal-nesting
372 Herring Gulls. Counting gulls in urban areas is tricky, and it has been suggested that the
373 available estimates seriously underestimate the true number of urban nesting gulls (Rock
374 2005; Calladine *et al.* 2006). In contrast, over the same period coastal-nesting Lesser Black-
375 backed Gulls expanded and they have expanded their populations into both coastal- and roof-

376 nesting sites as shown by the positive relationship between changes in coastal- and roof-
377 nesting pairs in that species, maybe for the same reasons that Herring Gulls take refuge
378 nesting on roofs in built-up areas.

379 What are the possible causes for the changes in population size in Herring, Great
380 Black-backed and Lesser Black-backed gulls? Populations maybe constraint by
381 environmental conditions that affect the birds directly or indirectly through bottom-up control
382 the availability of their resources (i.e., from prey to predator), or populations may be self-
383 regulated through local prey depletion (density-dependence) . We found little evidence for
384 density dependence, and only for the Herring Gull. For Herring Gulls, RSR with the highest
385 abundance showed the strongest declines, and this was still true when statistically accounting
386 for spatial variation in abundance (i.e., the decline was not only strong in its former
387 strongholds). Density-dependence in GR has also been shown in British colonies of Black-
388 legged Kittiwakes (*Rissa tridactyla*) (Coulson 1983, but see Frederiksen *et al.* 2005 for more
389 recent analyses)and Northern Gannets (*Morus bassanus*) (Moss *et al.* 2002). The density-
390 dependence was reflected in increased foraging ranges around larger Northern Gannets
391 colonies (Lewis *et al.* 2001) and more depleted fish shoals around larger Black-legged
392 Kittiwake colonies (Ainley *et al.* 2003). The reason why Herring Gulls showed negative
393 density-dependence, but not Lesser Black-backed and Great Black-backed gulls, is unclear,
394 but this could point to differences in spatial variation in resource utilization between the three
395 species or differences in behavioral processes responding to conspecifics (Frederiksen *et al.*
396 2005). Negative density-dependence, however, could also be due to larger groups being more
397 susceptible to other factors, for example being more vulnerable to conspecific nest predation
398 or more likely to contract a parasite or disease.

399 Competition between gull species has been hypothesized to have led to the decline of
400 Herring Gulls. The analyses of local GR and absolute counts at the local scale of

401 administrative areas did not support this hypothesis. Interestingly, between the Seabird
402 Colony Register and Seabird 2000, increases in Lesser Black-backed Gulls were slowed
403 down by high Herring Gull numbers. The effect of high Herring Gull density on reducing
404 Lesser Black-backed Gull population growth could be due to exacerbated competition for
405 resources within and between species.

406 The results also partly support the spatial variation hypothesis that population trends
407 may be related to environmental factors that vary across the British Isles. The differences
408 between species and RSR in GR suggest that there is unlikely one cause of the declines in the
409 large gulls. There may be a whole range of possible factors related to population trends of
410 these gulls. Food supply is one of the most important factors determining changes in all
411 animal populations (Sinclair and Krebs 2002). There might be regional variation in changes
412 of food resources. Fisheries discards and landfill sites that possibly fuelled the population
413 increase up to the 1970s have declined (Furness and Monaghan 1987; Oro *et al.* 2004; Votier
414 *et al.* 2004). This may have been made up for, at least locally, by an alternative food resource,
415 namely swimming crabs of the subfamily Polybiinae (Luczak *et al.* 2012) and changes in
416 agricultural operations (Coulson and Coulson 2008). Differences in foraging ecology
417 between Herring, Lesser Black-backed and Great Black-backed gulls may also explain
418 differences in population trends, if different components of the marine ecosystem were
419 differentially affected by environmental change. Moreover, the three species also depend on
420 different non-breeding areas with the Lesser Black-backed Gulls migrate south while Herring
421 and Great Black-backed gulls depend on British waters in the winter. The more recent
422 decline in the Lesser Black-backed Gull may coincide with them becoming less migratory
423 (Banks *et al.* 2009) or due to environmental changes on their wintering grounds. However,
424 this does not explain the difference in the rate of decline between Herring and Great Black-
425 backed gulls.

426 There are several factors that can directly affect vital rates (survival and productivity)
427 which may vary spatially and between species, therefore potentially explaining differential
428 population trends. We showed that across the U.K. productivity of Herring and Great Black-
429 backed gulls declined through the 1990s and 2000s, whereas during the same period
430 productivity of the Lesser Black-backed Gull did not change. Temporal trends in adult
431 survival are only available for one site, the large population breeding on Skomer, in
432 southwestern Wales where between 1994 and 2003 survival rates of Herring and Lesser
433 Black-backed gulls declined and coincided with a rapid decline in their numbers breeding at
434 that site (Joint Nature Conservation Committee 2014c). We know very little about spatial
435 variation in survival and productivity of larger gulls. Vital rates can be affected by culling,
436 disease and predation. In the 1970s and 1980s, gulls were culled for conservation and public
437 health reasons that could have contributed to population declines (Mitchell *et al.* 2004), and
438 some culling is still ongoing but at a reduced rate. Some diseases have been proposed to be
439 important factors in local population declines like avian botulism possibly being the main
440 cause for the large losses of Herring Gulls at some of the Irish colonies (Mitchell *et al.* 2004)
441 and thiamine deficiency syndrome, proposed being responsible for the declines of Herring
442 Gulls in the Baltic Sea (Balk *et al.* 2009). Predation, particularly by non-native predators,
443 may also have contributed to population declines. For example American mink (*Mustela*
444 *vison*) may have been responsible for widespread breeding failures and colony abandonment
445 in gulls in West Scotland, and removal of American mink has positively affected breeding
446 productivity and colony size in Herring Gulls (Craik 1998). How factors that affect fecundity
447 and survival of gulls interact in driving their population dynamics are poorly understood
448 (Camphuysen and Gronert 2012), and future work needs to focus on these factors for a better
449 understanding of the drivers of populations of large gulls in the British Isles. These potential
450 large declines in a hitherto abundant species have taken many people by surprise and now

451 clearly mark this species as one of high conservation concern, while it was formerly treated
452 as a pest species. This creates a dilemma for conservation bodies used to assigning gulls a
453 low priority in comparison to other species with which they interact. Differential changes in
454 population abundance between species RSR and nesting habitat point to changes in the gulls'
455 traditional habitats, but the exact drivers of these changes are far from clear. To better
456 understand these changes, we will need good information on what ecological factors affect
457 fecundity and survival in gulls, which are currently poorly explored, and future research
458 needs to pay particular attention to these topics. We urgently need to better understand why
459 the observed population changes have occurred and what this tells us about changes in coastal
460 ecosystems in which the gulls live. The regional variation in population dynamics observed
461 here will necessitate area-specific management strategies rather than one national
462 conservation strategy. We also need to revise existing conservation policies to ensure that the
463 right balance is struck between conservation of the large gulls and management of the
464 environmental problems with which they can be associated.

465

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473

474

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621 southeastern Canada. *Waterbirds* (Special Publication 1).

622 **Table 1.: Population growth rate (GR) for Herring, Lesser Black-backed and Great**
 623 **Black-backed Gulls separately for each Regional Seas Regions (RSR, 1: Northern North**
 624 **Sea, 2: Southern North Sea, 3: Eastern English Channel, 4: Western English Channel &**
 625 **Celtic Sea, 4a: westcoast of Republic of Ireland, 6: Irish Sea, 7: Minches & West**
 626 **Scotland, 8: Scottish Continental Shelf). For each RSR, average GR (lower and upper**
 627 **95% confidence interval) was calculated over all the administrative units contained in**
 628 **that RSR; where the 95% confidence interval did not overlap with 0 are shown in bold**
 629 **and represent RSR where abundance increased or decreased.. RSR 2 only had one**
 630 **administrative unit with active Great Black-backed Gull colonies and was therefore**
 631 **excluded from analysis.**

RSR	GR		
	Herring Gull	Lesser Black-backed Gull	Great Black-backed Gull
1	-0.32 (-0.59; -0.05)	0.27 (-0.14; 0.68)	0.42 (0.03; 0.81)
2	0.60 (-0.11; 1.31)	0.99 (0.98; 1.00)	
3	0.16 (-0.47; 0.79)	0.77 (0.39; 1.15)	0.73 (0.39; 1.07)
4	-0.33 (-0.72; 0.06)	0.47 (0.05; 0.89)	-0.19 (-0.73; 0.36)
4a	-0.89 (-0.94; -0.84)	0.42 (0.10; 0.74)	-0.31 (-0.67; 0.05)
6	-0.21 (-0.69; 0.27)	0.40 (-0.06; 0.86)	-0.02 (-0.57; 0.53)
7	-0.52 (-0.98; -0.06)	-0.47 (-0.76; -0.18)	-0.22 (-0.67; 0.23)
8	-0.58 (-0.78; -0.38)	-0.15 (-0.40; 0.10)	-0.29 (-0.68; 0.10)

633 **Table 2. Association between population growth rate (GR) and the total number of**
 634 **apparently occupied nests (AON) at the first census for each of two periods (1970-1985**
 635 **is from Operation Seafarer to Seabird Colony Registry, and 1985-2000 is from Seabird**
 636 **Colony Registry to Seabird 2000) accounting for Regional Seas Regions (RSR) (General**
 637 **Linear Model with RSR as fixed effect). Shown are the estimates of change in GR per**
 638 **10,000 AONs ± SE. Significant associations are in bold. Patterns were similar across all**
 639 **RSRs (all interactions between RSR and abundance were non-significant).**
 640

Total Numbers of AON at Start of Interval			
	Herring Gull	Lesser Black-backed Gull	Great Black-backed Gull
GR			
Herring Gull			
1970-1985	-0.303 ± 0.104	-0.146 ± 0.292	-0.382 ± 0.75
	$F_{1,60} = 8.57, P = 0.005$	$F_{1,56} = 0.25, P = 0.620$	$F_{1,46} = 0.12, P = 0.734$
1985-2000	-0.599 ± 0.232	-0.082 ± 0.294	-0.690 ± 0.75
	$F_{1,63} = 6.65, P = 0.012$	$F_{1,58} = 0.08, P = 0.782$	$F_{1,46} = 0.23, P = 0.587$
Lesser Black-backed Gull			
1970-1985	-0.071 ± 0.128	-0.319 ± 0.340	-0.577 ± 0.75
	$F_{1,53} = 0.30, P = 0.584$	$F_{1,53} = 0.88, P = 0.353$	$F_{1,43} = 0.17, P = 0.686$
1985-2000	-0.458 ± 0.223	-0.365 ± 0.272	-0.343 ± 0.75
	$F_{1,55} = 4.23, P = 0.044$	$F_{1,55} = 1.81, P = 0.184$	$F_{1,43} = 0.09, P = 0.772$
Great Black-backed Gull			
1970-1985	-0.029 ± 0.120	0.077 ± 0.303	-0.64 ± 0.75
	$F_{1,43} = 0.06, P = 0.812$	$F_{1,43} = 0.07, P = 0.800$	$F_{1,43} = 0.09, P = 0.772$
1985-2000	-0.193 ± 0.266	0.227 ± 0.314	0.318 ± 0.75
	$F_{1,46} = 0.53, P = 0.471$	$F_{1,46} = 0.52, P = 0.473$	$F_{1,46} = 0.05, P = 0.819$

641

642 FIGURE CAPTIONS

643

644 **Figure 1. Changes in coastal-nesting populations of (A) Herring Gull, (B) Lesser Black-**
645 **backed Gull and (C) Great Black-backed Gull between 1970 and 2013. The solid line**
646 **and closed symbols give the observed number of apparently occupied nests (AON) for**
647 **coastal colonies from Operation Seafarer, Seabird Colony Register and Seabird 2000.**
648 **The open symbols and dashed line show the changes in roof-nesting gulls (data from**
649 **Monaghan and Coulson (1977) for 1976, Raven and Coulson (1997) for 1993-1995 and**
650 **Mitchell *et al.* (2004) for 1998-2002). The stars and dotted line give the predicted**
651 **changes in number based on the Seabird Monitoring Programme (SMP) index relative**
652 **to the Seabird Colony Register Count. Note that SMP data only cover the U.K., whereas**
653 **the absolute counts cover the British Isles. However, by the mid-1980s the numbers of**
654 **gulls breeding in the Republic of Ireland were so small (typically < 10%) that the**
655 **differences between U.K. and British Isles numbers were negligible.**

656

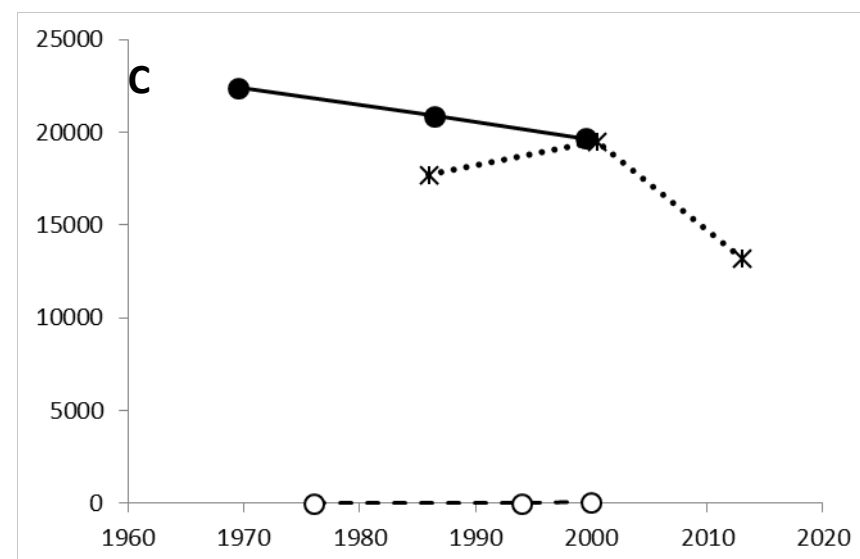
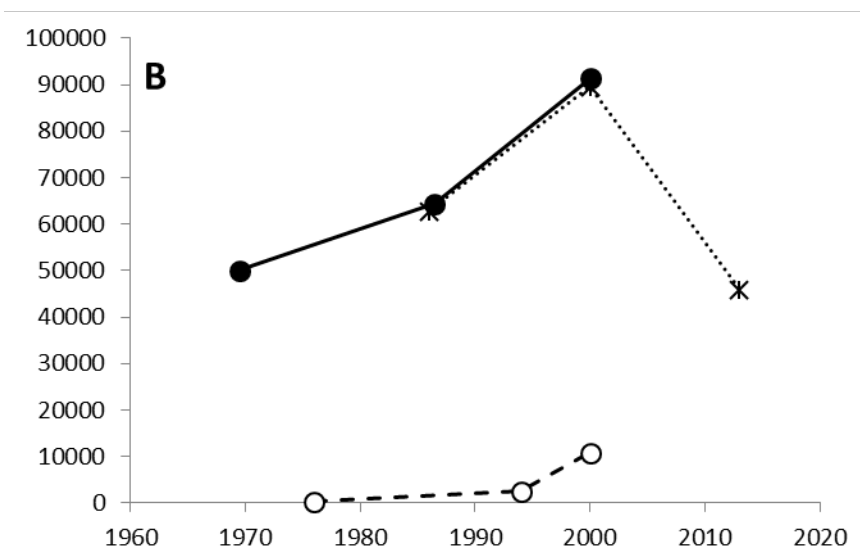
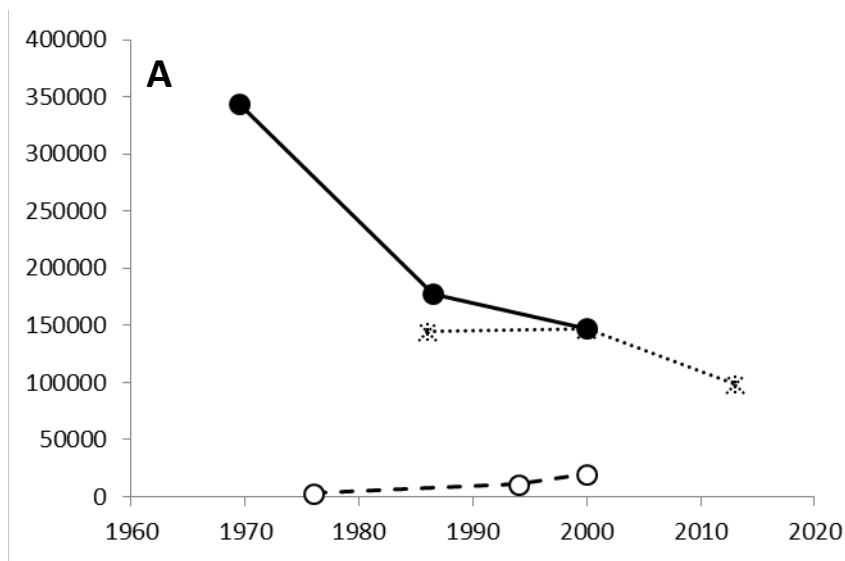
657 **Figure 2. Spatial variation in population growth rate (GR) by administrative unit for**
658 **(A) Herring Gull, (B) Lesser Black-backed Gull and (C) Great Black-backed Gull. The**
659 **darker the color of the administrative unit on the map, the greater the population**
660 **decrease, with the lightest colors representing population declines and the darkest**
661 **colors population increases. Administrative units are grouped into Regional Seas**
662 **Regions (RSR), which are indicated by the different numbers and lines around the**
663 **coast. Significant differences in GRs between RSRs are shown in Table 1.**

664

665 **Figure 3. Relationship between number of roof-nesting gulls in Seabird 2000 and the**
666 **absolute number of apparently occupied nests (AON) of coastal nesting gulls that were**

667 **lost (left part of the horizontal axis) or gained (right part of the horizontal axis) between**
668 **Operation Seafarer and Seabird 2000 for each of the Regional Seas Regions for Herring**
669 **Gulls (gray symbols) and Lesser Black-backed Gulls (black symbols); insufficient**
670 **numbers of Great Black-backed Gulls nest on roofs for this analysis.**
671

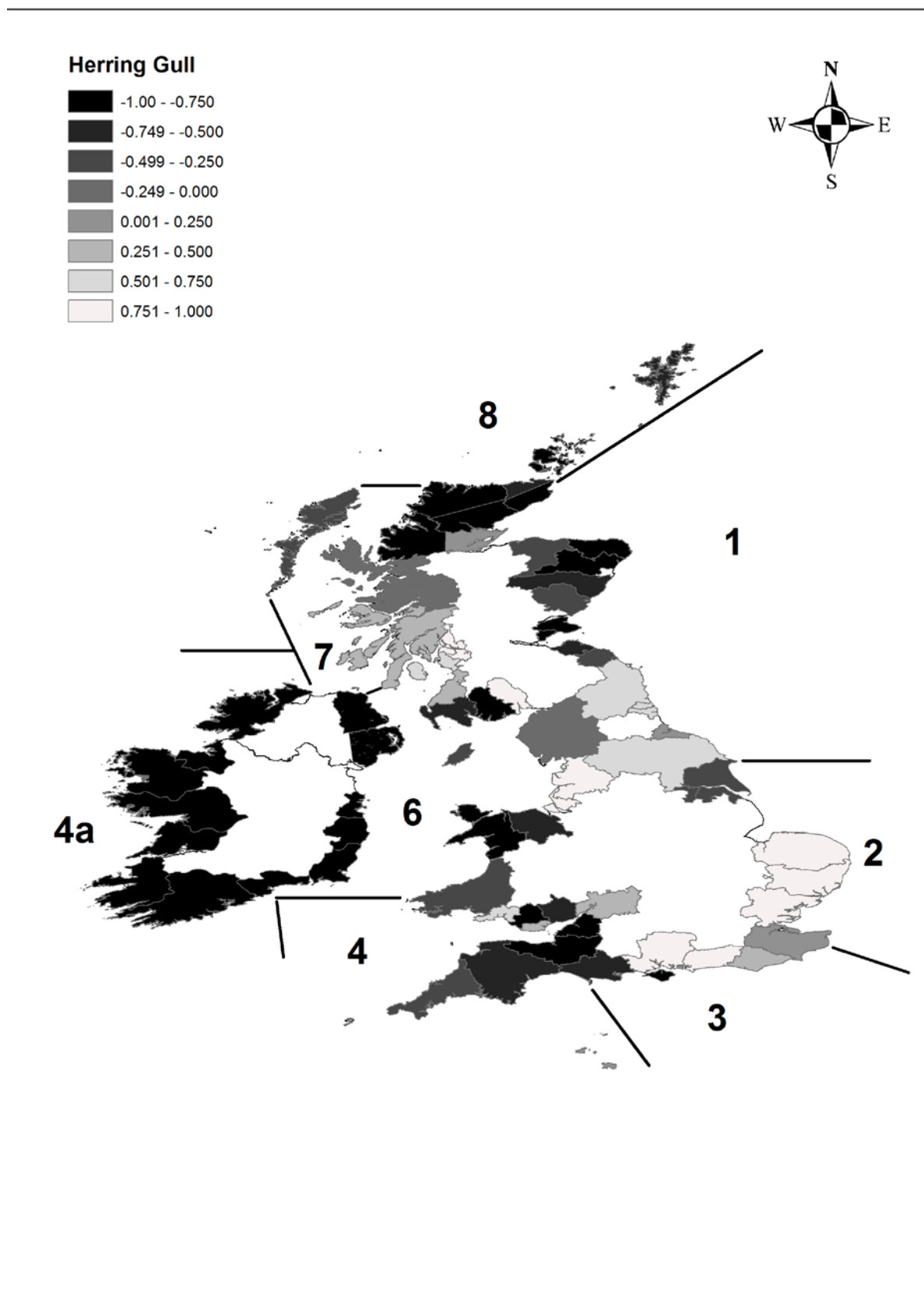
672 Figure 1.



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675 Figure 2a.

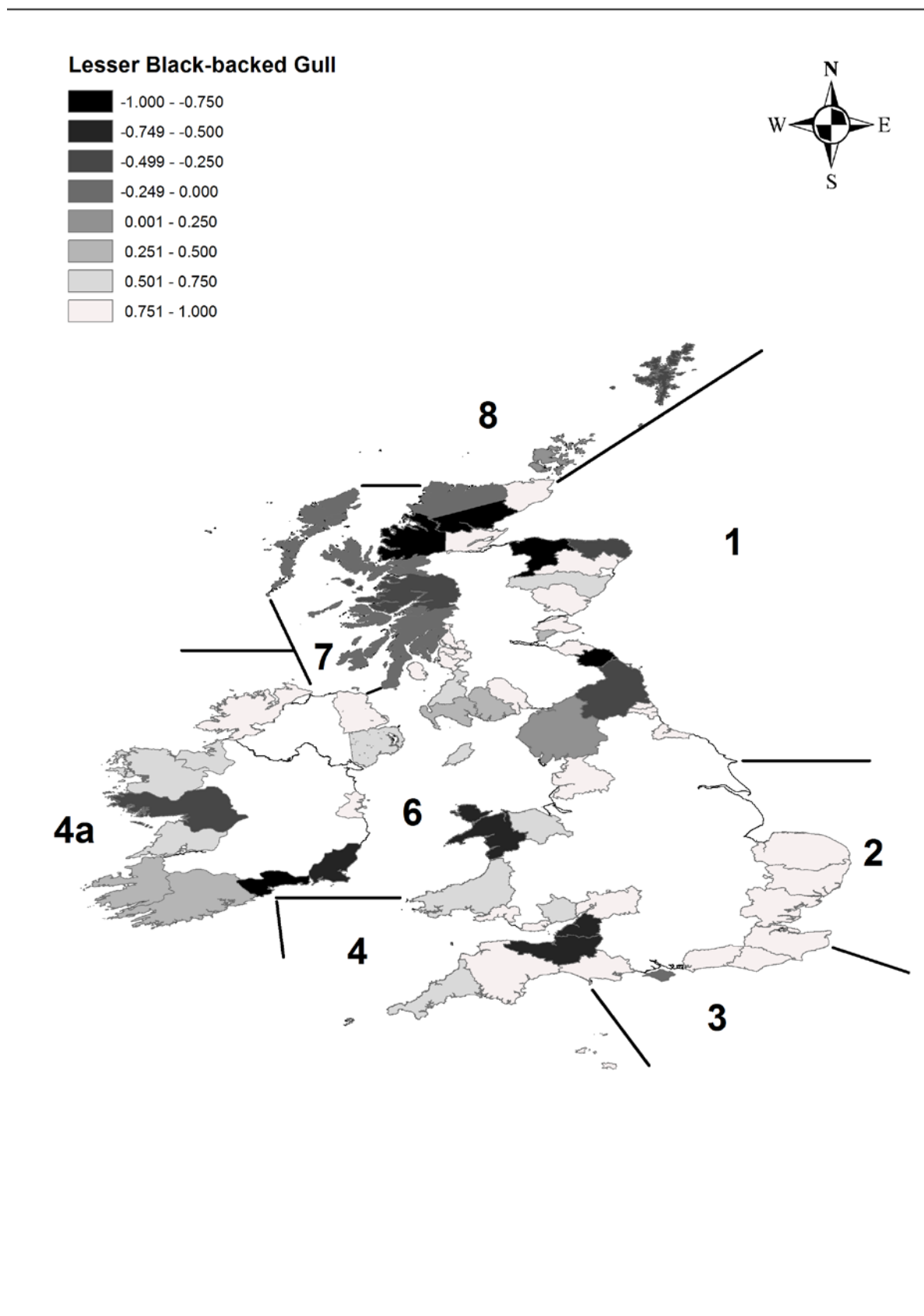


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679 Figure 2b.

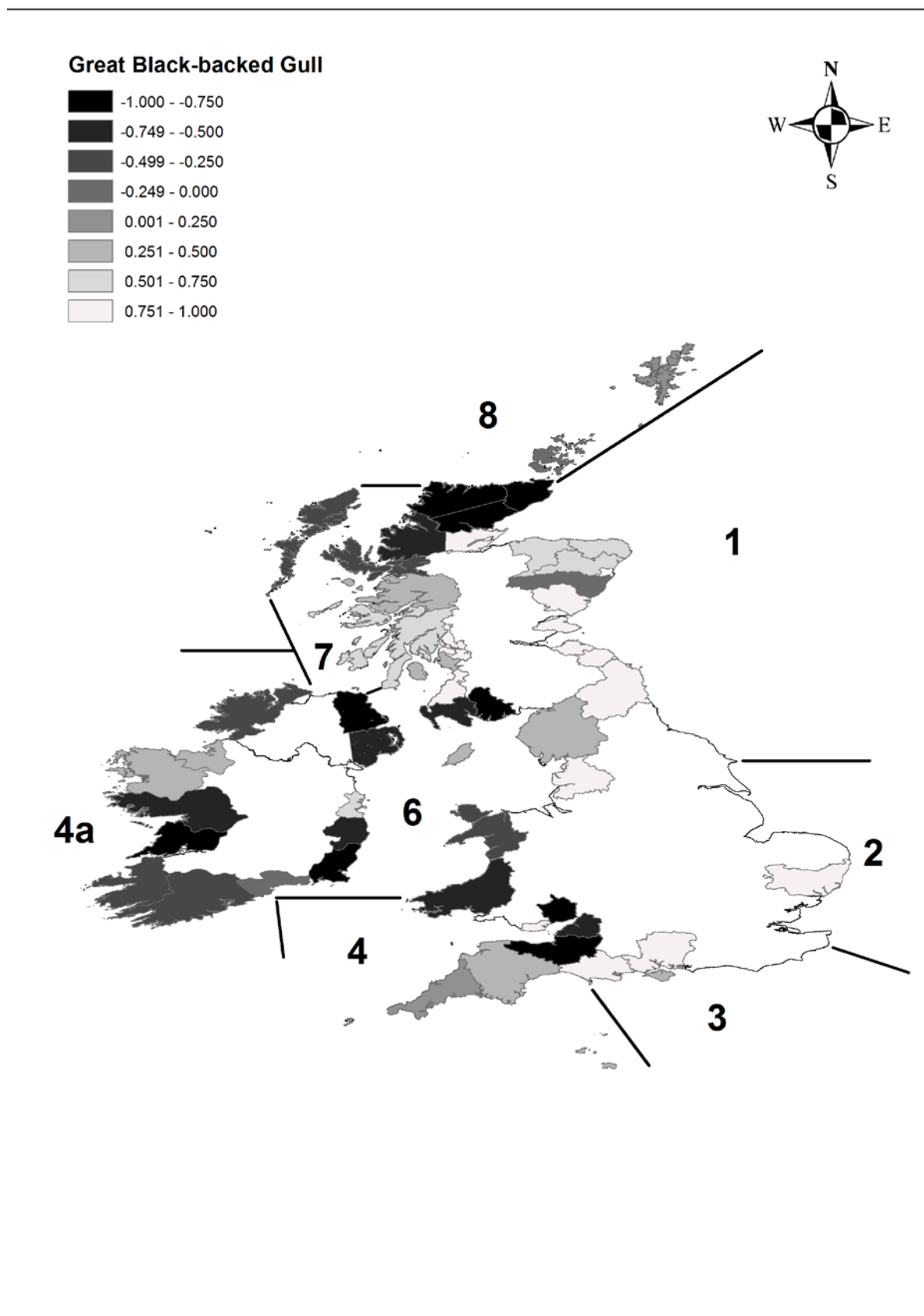


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683 Figure 2c.

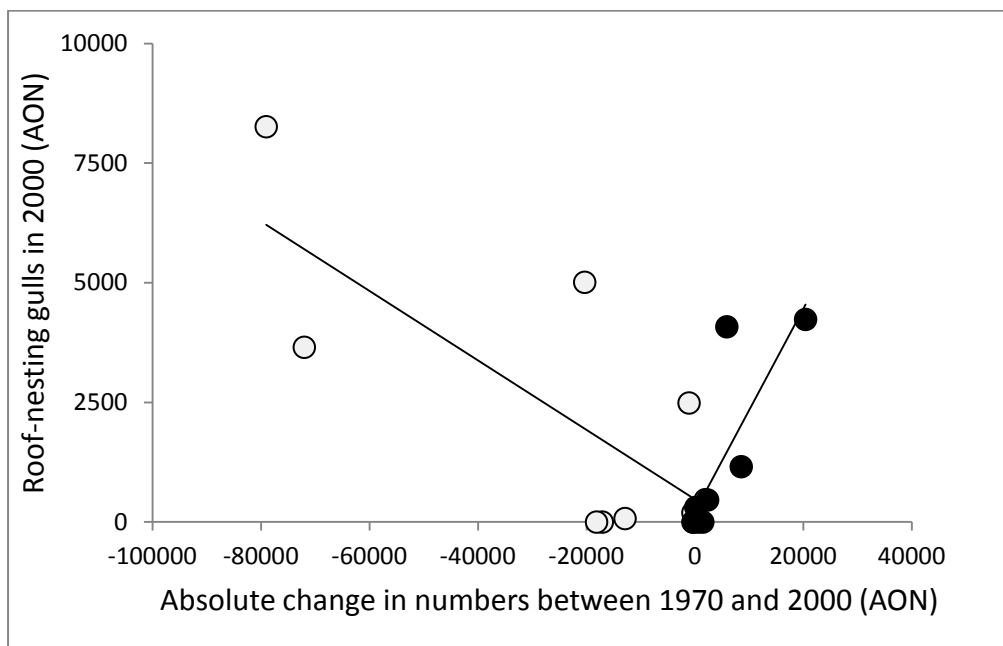


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687 Figure 3.



688