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Identifying environmentally-driven spatial clustering in population trends of large gulls in south-west Scotland and Northern Ireland

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Running head: Spatial clustering in gull trends

17   **Capsule** Spatial clustering was observed in colony growth rates of three large UK gull

18   species with proxies of local marine and intertidal resources explaining part of this variation

19   in two species.

20   **Aims** To investigate spatial clustering in colony growth rates of three gull species and

21   determine which environmental variables may explain any spatial clustering observed.

22   **Methods** Colony growth rates were calculated for Herring Gull *Larus argentatus*, Lesser

23   Black-backed Gull *L. fuscus* and Great Black-backed Gull *L. marinus* to identify spatial

24   synchrony and to relate to proxies of local foraging conditions in coastal habitats.

25   **Results** Spatial clustering in growth rates was found in the gull species. Herring Gull

26   colonies located in areas with greater availability of intertidal prey and fishery activity had

27   higher growth rates. Lesser Black-backed Gull colonies in areas of higher chlorophyll a

28   concentrations experienced more negative growth rates suggesting a negative effect in areas

29   of potential local runoff from agriculture and built-up areas.

30   **Conclusion** Spatial clustering in the gulls' colony growth rates indicated that local colonies

31   did experience similar environmental conditions; helping identify variables influencing

32   coastal populations of two gull species, highlighting the importance of marine habitats. These

33   results highlight the need for species and area-specific management for these species of

34   conservation concern.

35

Introduction

Animal population changes vary over time and space, with patterns often differing over different temporal and spatial scales (McArdle *et al.* 1990, Sutherland & Baillie 1992, Brown *et al.* 1995). Variation in population trends can be driven by differences in environmental variables as well as by density-dependent processes, such as competition and predation (Furness & Birkhead 1984, Brown *et al.* 1995, Sibly & Hone 2002, Crespin *et al.* 2006). Often drivers of population changes are identified using long-term data sets from single populations which can compromise the generality of the findings. Alternatively, spatial clustering in population trends between different populations of the same species, or co-occurring populations of different species can provide a 'pseudo-experimental' approach that treats spatial contrasts in population trajectories as 'treatments' (Baum & Worm 2009). This spatial approach can identify factors that correlate with between-population differences (Frederiksen *et al.* 2005, Robinson *et al.* 2013) and help in understanding larger-scale changes in a species' abundance (Liebhold *et al.* 2004).

Differences in environmental variables, particularly climatic conditions and food availability, can drive variation in population trends (Newton, 1998). In recent decades, many ecosystems are also being impacted upon by anthropogenic influences; affecting population sizes through over-exploitation of resources, introduction of invasive species and habitat destruction/modification (Butchart *et al*. 2010). Different environmental variables are likely to impact populations over different spatial scales, from predation and disturbance acting at a local level to severe or unusual weather events which can act over small and larger spatial scales. When spatially distinct populations fluctuate synchronously this may indicate that populations are connected by dispersal or that similar environmental conditions are occurring over the scale being measured (Moran effect), affecting those multiple populations similarly (Harald *et al.* 2002, Liebhold *et al.* 2004). Contrasting abundance trajectories between spatially distinct populations may, conversely, indicate the local environmental conditions that may drive this variation differ between the distinct populations (Ens *et al*. 2009) or that some populations are able to buffer themselves more effectively against adverse conditions (Burger & Piatt 1990). For instance, generalists, which typically consume the most abundant food, may switch to an alternative resource. Spatial clustering in population trends may be more likely in species which are affected by drivers acting over smaller spatial scales and in species which show higher site fidelity (Erwin *et al.* 1981, Parsons *et al.* 2008).

69

70   The extent of spatial clustering has important implications for the understanding of

71   changes in abundance across the distribution of a species and their population management.

72   For species that shows spatial clustering in population trends, if this is due to variation in

73   environmental conditions, then there might be multiple drivers of population changes

74   depending on the local environment. Population management strategies, if required, will

75   therefore depend on local environmental conditions. Populations of apex predators, such as

76   seabirds, often depend on conditions at lower trophic levels (Boyd *et al*. 2006, Fossi *et al*.

77   2012) and if the local environment varies between geographically distinct populations,

78   findings from one population may not necessarily apply to others. Spatial variation in

79   demographic traits have been found to exist in seabird populations across different scales

80   with inter-population differences found in adult survival, productivity and population growth

81   rate (Frederiksen *et al.* 2005, Harris *et al.* 2005, Bertram *et al.* 2015, Cordes *et al.* 2015,

82   Nager & O'Hanlon in press).   However, spatial variation in population trends is generally

83   still poorly understood with the extent to which it occurs in populations likely to depend on

84   the species and habitats of interest.

85

86   Within the foraging environments used by seabirds coastal habitats are particularly

87   affected by anthropogenic and natural pressures due to their accessibility and location at a

88   boundary between marine and terrestrial ecosystems, resulting in being impacted from both

89   environments (Thompson *et al*. 2002, Lopez y Royo *et al*. 2009). Species utilising this

90   coastal habitat have experienced declines in recent decades (Lotze *et al.* 2006, van Roomen *et*

91   *al.* 2012). Among seabirds that particularly rely on coastal habitats for foraging, and have

92   experienced recent declines, are the large gulls: Great Black-backed Gull *Larus marinus*,

93   Lesser Black-backed Gull *L. fuscus* and Herring Gull *L. argentatus* (Eaton *et al*. 2015). As

94   gulls are generalist and opportunistic foragers, exploiting both marine and terrestrial

95   resources (Götmark 1984, Pearson 1968), their populations may be affected by the

96   environment at both sides of the boundary between land and sea. However, the three large

97   gull species differ in their traditional foraging habits. Herring Gulls mostly rely on intertidal

98   foraging habitats whereas Lesser and especially Great Black-backed Gulls scavenge on

99   fishery discards to a greater extent than Herring Gulls; whilst Lesser Black-backed Gulls also

100   forage more frequently inland on farmland, built-up areas and landfill sites (Hunt 1972,

101   Kubetzki & Garthe 2003, McLellan & Shutler 2009). If food resources from their traditional

102   marine intertidal and offshore habitats provide higher quality resources than terrestrial-

4

103   anthropogenic habitats (Pierotti & Annett 1991, Annett & Pierotti 1999) then we expect a

104   predominant influence of these habitats on population changes. Alternatively, if terrestrial

105   anthropogenic habitats provide more predictable and abundant food (Burger & Gochfeld

106   1983, Horton *et al*. 1983), even if of potentially lower quality, these alternative foraging

107   habitats may buffer populations against poor availability of their traditional marine food

108   resources.

109

110   This study focuses on the coastal habitats of a region in north-west Europe which has

111   experienced particularly high levels of anthropogenic pressure (Halpern *et al*. 2008). Here we

112   aim to determine whether spatial clustering occurs in the population trends of the three large

113   gull species within a region that shows variation in the coastal habitat that the gulls depend on

114   for breeding and foraging. Where spatial clustering occurs we will explore whether local

115   environmental variables reflecting terrestrial anthropogenic (area of farmland and built-up

116   land, number of landfill sites) and traditional marine food resources (quality of intertidal

117   habitat, fish abundance, marine productivity) might explain between-colony differences in

118   population trends; and whether terrestrial anthropogenic resources, where present, can buffer

119   for poor availability of traditional marine food resources. As the three study species differ in

120   their foraging ecologies we expect each species to be affected by different environmental

121   variables. We will also explore whether colony trends are affected by intra-specific

122   competition for limited resources. This study can provide insights into potential drivers of

123   population trends in the larger gulls that can inform management decision for these species of

124   current conservation concern.

125

Materials and methods

Study region and study species

128   The study region incorporates an area of south-west Scotland and Northern Ireland covering

129   two biogeographically distinct regional seas (the north Irish Sea and the south Minches and

130   West Scotland Sea; JNCC 2014), within an area of approximately 200 by 250 km (Fig. 1),

131   providing variation in environmental conditions within a relatively small geographic area. At

132   this regional scale it is known that the three large gull species have experienced contrasting

133   population changes, both between and within species (Mitchell *et al*. 2004, Nager &

134   O'Hanlon in press); therefore providing a suitable region to investigate spatial clustering in

135   gull population abundance at the colony level.

136

137   It is uncommon to have simultaneous colony counts from multiple colonies over a

138   larger geographical area. No regular counts exist for the gull colonies in the study region,

139   therefore the seabird censuses of the UK and Ireland (Mitchell *et al*. 2004) provides a rare

140   opportunity to investigate multiple colonies within a larger area. Breeding Herring, Lesser

141   Black-backed and Great Black-backed Gulls within this region were counted as part of three

142   national censuses across the UK and Ireland between 1969 and 2002: Operation Seafarer in

143   1969 (Cramp *et al*. 1974), Seabird Colony Register in 1985-1989 (Lloyd *et al*. 1991), and

144   Seabird 2000 in 1998-2002 (Mitchell *et al*. 2004). All three censuses had complete coverage

145   of the region and for each of the selected species used the same survey methodologies

146   (Mitchell *et al*. 2004). We used the adjusted counts of Apparently Occupied Nests (AON) per

147   colony from the Seabird Monitoring Programme (Walsh *et al*. 1995, JNCC 2012) and

148   additional data for Operation Seafarer from JNCC (Roddy Mavor, pers. comm.). Only

149   coastal colonies within 5 km of the coast were included as we were interested in the interface

150   between marine and terrestrial coastal habitats. Although the temporal resolution with three

151   censuses over three decades is relatively low, changes in colony size were consistent between

152   the censuses for two of the three gull species (see results).

153

154   **Spatial variation in colony growth rates**

155   To estimate long-term population trends for each of the three gull species we extracted

156   species-specific counts of individual breeding colonies from the three national seabird

157   censuses. During the seabird censuses grid references of all counted colonies were recorded.

158   We matched counts from the same colony in different censuses by importing the grid

159   references into ArcGIS (ArcMap ver.10. ESRI, USA) and extracted the location of all counts.

160   Only where locations between censuses matched, by name or grid reference within 500m, we

161   assumed successive counts for the same colony. For small islands and sea-lochs (less than 5

162   km^2 in area), where the level of sub-sites counted was different between censuses, we totalled

163   all counts within such sites into one value so that total counts were comparable between

164   censuses.

165

166   Over the three census periods some colonies were newly established whilst others

167   went extinct, which could be identified if their absence (a count of zero) was recorded.

6

168 However, where no record of a zero count was made we could not be certain that the colony

169 had been monitored within that census, therefore these colonies were not included in the

170 analysis. The number of colonies with no information was largest in the Seabird Colony

171 Registry and therefore, in the analysis we only included colonies that reported a count,

172 including a zero count, in Operation Seafarer (1969-1970) and in Seabird 2000 (1998-2002).

173 This ensured that colony growth was estimated for all colonies over the same period of time,

174 and therefore were comparable, and maximised our sample sizes. The total number of

175 individual colonies for each species within the study region, for which data was available in

176 the first and last census, are displayed in Table 1.

177

178 The conventional calculation of growth rate lambda, (N_{t+1}/N_t), is not defined for

179 newly established colonies. We therefore calculated colony growth rates (GR) for individual

180 colonies using a formula based on Guillaumet *et al*. (2013):

181 $$GR = (N_t - N_{t-1})/\text{Maximum } [N_t, N_{t-1}]$$

182 where N_t is the count in Seabird 2000, N_{t-1} the count in Operation Seafarer, and Maximum

183 [N_t, N_{t-1}] is the highest count from either Operation Seafarer or Seabird 2000. This

184 calculation of GR avoids the issue of undefined growth rate for newly established colonies

185 and GR = 0 for extinct colonies (Guillaumet *et al*. 2013), both of which occurred at the

186 colony level. GR values were monotonically related to the calculated lambda with $r_s = 1.0$ in

187 all species.

188

189 **Environmental correlates of colony growth rates**

190 Where spatial synchrony in population changes occurred, we also wanted to identify any

191 environmental factors, reflecting availability of resources used by gulls, that might explain

192 inter-colony variation. As all three large gull species are generalist foragers (Pearson 1968;

193 Götmark 1984, Camphuysen 1995), we selected environmental factors that covered the range

194 of known resource use of the gulls: marine invertebrates in intertidal habitats; fish in offshore

195 marine habitats and farmland and anthropogenic food sources in the terrestrial habitats.

196

197 An important foraging habitat for large gulls, and in particular for Herring Gulls, is

198 the intertidal zone where they forage on a large diversity of invertebrate prey (Götmark

199 1984). We extracted information both on the area of intertidal habitat and the average wave

200 fetch as a proxy for food availability in the intertidal zone. The area of intertidal habitat was

201 obtained from Landcover 2000, which uses computer classification of satellite images to

202 quantify different land uses in the UK (Fuller et al. 2002). Wave fetch, a measure of the
203 exposure of the coastline that depends on topography, was included as a proxy for potential
204 intertidal foraging habitat quality. For rocky shoreline, which is the predominant coastal
205 habitat in the study region, low wave fetch supports a greater abundance and diversity of
206 potential intertidal prey species (Burrows *et al*. 2012). Wave fetch was available for quadrats
207 of 200m^2 along the coastline by Burrows (2009).

208

209 All three species also forage out at sea, with Lesser and Great Black-backed Gulls to a
210 greater extent than Herring Gulls, where they can feed on small pelagic fish but mainly
211 scavenge on fishing discards (Spaans 1971, Camphuysen 1995, Tasker *et al.* 2000, Kubetzki
212 & Garthe 2003, Tyson *et al.* 2015). To characterise local marine foraging habitats we
213 included sea surface temperature (SST), chlorophyll a concentration and fishery data. SST
214 (11µ night-time) and chlorophyll a concentration (mg/m^3) were included as proxies for
215 primary productivity in the marine environment. SST influences marine processes associated
216 with thermoclines and upwelling which will affect the distribution and abundance of potential
217 prey species, whilst chlorophyll a concentration acts as a proxy for primary productivity at
218 the base of marine food webs (Huot *et al*. 2007). We extracted summer seasonal composites
219 of SST and chlorophyll a concentration for 2002, to relate to marine productivity during the
220 breeding season, from Aqua MODIS at 4 km resolution
221 (http://oceancolor.gsfc.nasa.gov/cgi/l3). For the UK there are no publically available data on
222 discard tonnages (Gibson *et al*. 2015) and landing data are only available on a coarser spatial
223 level than we use here. Instead we assumed that fishery activity is greater where fish are more
224 abundant and therefore extracted demersal fish abundance from the International Bottom
225 Trawl Survey (IBTS) data at the ICES (International Council for the Exploration of the Sea)
226 sea area level (Fig. 1; data obtained from https://datras.ices.dk/Home/Descriptions.aspx).
227 Our study region encompassed four of these sea areas and for each we averaged the total
228 catch per unit effort (CPUE) of all fish age classes trawled during the spring survey (Quarter
229 1) for 1998-2002.

230

231 Gulls also exploit resources from terrestrial habitats by foraging on fields, where they
232 take earthworms and grain, and by scavenging on landfill sites and other built-up areas such
233 as in coastal towns (Pons 1992, Belant *et al*. 1993, Coulson & Coulson 2008). We therefore
234 extracted farmland and built-up areas from Landcover 2000 (Fuller *et al*. 2002). Built-up area
235 is defined as the area covered by buildings and gardens in suburban/rural developed areas and

236   continuous urban areas. Farmland was categorised as the area covered by agriculture and

237   improved grassland.   The number of landfill sites for Scotland was obtained from the

238   Scottish Environment Protection Agency (SEPA, 2015) and for Northern Ireland from the

239   Northern Ireland Environment Agency (NIEA, Eugene Kelly, pers. comm.).

240

241   Each environmental variable was extracted from within the gulls' potential foraging

242   range around each of the colonies. The average maximum foraging distance from the colony

243   for breeding Herring Gulls is estimated at 50 km (Pearson 1968, Götmark 1984, Camphuysen

244   1995, Thaxter *et al.* 2012). We also observed foraging trips of up to 40 km from the colony

245   for a small subsample of Herring Gulls in our study region. As all three species can access

246   resources as far as 50 km considering smaller foraging ranges would therefore likely ignore

247   resources potentially available to the birds. Lesser and Great Black-backed Gulls can have

248   larger average maximum foraging ranges, especially foraging further offshore than Herring

249   Gulls (Camphuysen 1995, Thaxter *et al.* 2012). Therefore, for colonies that were less than

250   50 km from the boundary between two ICES sea areas we selected the higher CPUE value of

251   the two ICES sea areas within their foraging range. Spatially-explicit environmental data for

252   the whole study region are difficult to obtain, and are generally only available for the more

253   recent years. We could only extract static environmental data for the end of the census period

254   rather than extracting information on the change in these variables over time, therefore we

255   investigated potential drivers of the spatial variation in colony GR at the end of the census

256   period.

257

258   Data on proxies for the gulls' resource availability may have changed over the seabird

259   census period; however spatially-explicit data was only available at the end of this period.

260   We cannot therefore determine directly what the drivers of spatial clustering in colony GR

261   within the region were. However, they can still be informative when investigating spatial

262   clustering in colony trends at the end of the census period. The amount of farmland and

263   built-up area and number of landfill sites, as a proxy for terrestrial anthropogenic food

264   availability are based on information from 2000, at the end of the period of interest.

265   Although the absolute values of these variables have likely changed over time levels relative

266   to each other are thought to have remained largely the same, with areas with the greatest

267   human impact in the late 1960s also being the areas with the greatest human impact in 2000.

268   Although Landcover data was available for 1990 (Fuller *et al*. 1994) it could not be included

269   in the analysis as it did not cover Northern Ireland. However, for Scotland, there was a

270   significant positive correlation between the amount of built-up area around the gull colonies

271   during 1990 to that in 2000 ($r_{149} = 0.87$, $P < 0.001$). Data for SST and chlorophyll a

272   concentration was also only available for the end of the census period, extracted for 2002 as

273   this was the earliest data was available for at the required resolution. The values of these two

274   variables will also vary annually, however we are more interested in the relative spatial

275   variation in marine productivity rather than absolute values; with relative values for SST and

276   chlorophyll a concentration in the following ten years similar across the region.

277

278   **Statistical analysis**

279   All statistical analyses were performed in R, Version 3.1.1 (R Development Core Team

280   2015).   To investigate spatial clustering in colony GR on an objective basis we used spatial

281   autocorrelation analyses. For each species we calculated a Moran's *I* Index using the *lctools*

282   package in R (Paradis *et al*. 2004).   Moran's *I* Index is a measure of spatial autocorrelation,

283   based on each species' colony GR and the colony's latitude and longitude. Moran's *I* Index

284   ranges from -1 (spatially dispersed, where neighbouring colonies have different values of

285   GR) to +1 (spatially clustered, where neighbouring colonies have similar values of GR)

286   (Moran 1950, 1953, Legendre & Fortin 1989). A *I* value of zero indicates a random spatial

287   pattern of GR. To statistically test whether Moran's *I* Index differs from 0 it can be

288   transformed to Z-scores with values greater than 1.96 indicating *I* is significantly greater than

289   0 (spatially clustered) or smaller than −1.96 then indicating *I* is significantly less than 0

290   (spatially dispersed), indicating significant spatial autocorrelations at $P < 0.05$. To visualise

291   the spatial clustering of the three gull species we carried out K-means clustering (MacQueen

292   1967) using the kmeans function from the *stats* package in R. To identify the most

293   appropriate number of clusters, k, the elbow criterion was used which considers the amount

294   of variance explained by different number of clusters based on a plot of the within group

295   sums of squares. To visualise the spatial variation in colony GR across the study region for

296   each species the locations of colonies were plotted in ArcMap 10.1 and shaded based on the

297   GR clusters.

298

299   To test which characteristics of the coastal environment were related to within-species

300   variation in colony GR we used general linear models with colony GR as the response

301   variable and environmental variables (SST, chlorophyll a, CPUE, wave fetch, built-up area,

302   farmland and number of landfill sites) as explanatory variables.   As the effect of environment

303 conditions on colony GR may depend on the number of individuals competing for that

304 resource, we also included colony size and its interaction with the environmental variables in

305 the model. We used colony size from Seabird 2000 to match the time frame environmental

306 information was available, as we were investigating the structure at the end of the census

307 period for when spatially-explicit environmental information available. We tested for

308 multicollinerity between explanatory variable in the *car* package (Fox & Weisberg 2011)

309 removing variables with a Variance Inflation Factor (VIF) greater than three (Zuur *et al*.

310 2010). This resulted in the number of landfill sites being removed from all statistical models;

311 chlorophyll a concentration being removed from the Herring Gull and Great Black-backed

312 Gull models; and built-up area being removed from the Lesser Black-backed Gull model.

313

314   Starting with the most complex model, including biologically relevant second-order

315 interactions, backwards stepwise model selection, to establish the minimal adequate model,

316 was carried out using Likelihood Ratio tests to determine whether the exclusion of a term

317 resulted in a significantly poorer fit of the model (Crawley, 2007). Significance thresholds

318 were set at $P < 0.05$, and only significant interaction terms are shown. Residual plots were

319 inspected to ensure no deviations from homoscedasticity or normality occurred, and if

320 necessary data were transformed (colony size was natural logarithm transformed).

321

322 **RESULTS**

323 **Population growth rates**

324 Between the first and last national seabird census the abundance of all three large gull species

325 declined (Table 1); although this was only significant for the Herring Gull ($t_{67} = 2.53$, $P =$

326 0.014). For the analysis we assumed that colony GR across the census period was monotonic

327 (annual counts for the included colonies were not available over this period); the most recent

328 population change (GR between 1985-2000 available for a subset of colonies) was correlated

329 with the change over the whole census period (1970-2000) for Herring Gulls ($r_{49} = 0.62$, $P <$

330 0.001) and Great Black-backed Gulls ($r_{31} = 0.79$, $P < 0.001$), but not for Lesser Black-backed

331 Gulls ($r_{20} = 0.33$, $P = 0.126$). Therefore, when investigating which environmental variables

332 could explain spatial variation in the colony GR of Lesser Black-backed Gulls across the

333 region colony GR from the reduced sample of 21 colonies between the second (1985-1989)

334 and last (1998-2002) censuses were instead included as the response variable.

335

336   In all three species we found a statistically significant spatial clustering of colony GR

337   over the entire census period across the study region (Table 1). Colonies of all species

338   generally increased around the Firth of Clyde with declines around the northern Solway Firth.

339   Both Herring and Great Black-backed Gulls declined across Northern Ireland to a greater

340   extent than the Lesser Black-backed Gull, whereas the trends for colonies in the Southern

341   Hebrides were more variable between the species (Figure 2). Herring and Great Black-

342   backed Gull, but not Lesser Black-backed Gull, colonies mainly declined in their former

343   strongholds; we found negative effects of colony size in 1969-1971 on the colony GR

344   between 1969-1971 and 1998-2002 from linear regressions: Herring Gull: $F_{1,66} = 16.85$, $P <$

345   0.001; Great Black-backed Gull: $F_{1,46} = 10.34$, $P = 0.002$; Lesser Black-backed Gull: $F_{1,31} =$

346   2.73, $P = 0.109$.

347

348   **Environmental correlates of population growth rates**

349   Different proxies of local food availability within the colony's foraging range were found to

350   explain part of the spatial variation in colony GR for the three gull species. In Herring Gulls

351   (Table 2b) there was a significant, negative relationship of colony GR with average local

352   wave fetch (Fig. 3a); and significant positive relationships with CPUE (Fig. 3b) and SST

353   (Fig. 3c). Herring Gull colonies with increasing GR were recorded in more sheltered

354   locations with lower wave fetch and in areas where the CPUE of benthic fish were higher.

355   In addition, colony declines were greater at locations with lower mean SST within the

356   foraging range of the colony. In Lesser Black-backed Gulls colony GR was negatively

357   correlated with chlorophyll a concentration (Table 2c); with colonies declining to a greater

358   extent in areas of higher mean chlorophyll a concentration within the colony's foraging range

359   (Fig. 4). In Herring and Great Black-backed Gull, but not in Lesser Black-backed Gulls,

360   colonies which experienced the highest GR also had the largest colony counts in Seabird

361   2000. However, colony size did not interact with any of the environmental variables

362   suggesting no evidence for limited resources in any of the species (Table 2).

363

364   **DISCUSSION**

365   We found evidence for spatial clustering of colonies of two of the three gull species with

366   respect to colony GR across south-west Scotland and Northern Ireland; for Great Black-

367   backed and Herring Gulls, however the pattern was not statistically significant for Lesser

368   Black-backed Gulls. This spatial clustering suggests that over the census period gull colonies

369   in close proximity were likely to experience similar environmental conditions which

370   influenced their colony GR. We also identified environmental variables that were related to

371   the spatial clustering for Herring Gulls: colonies had higher growth rates when located in

372   areas with more sheltered coasts; near areas where there was potentially a greater abundance

373   of demersal fish and in areas where average local SST was higher. For the Lesser Black-

374   backed Gulls, colonies had higher growth rates in areas of lower chlorophyll a concentrations

375   in the marine environment. None of the environmental variables we included were associated

376   with variation in Great black-Backed Gull colony GR. These results suggest that relatively

377   small scale variation in environmental conditions can affect changes in population abundance

378   in gulls and that the different species are affected by different drivers.

379

380   We found spatial variation in colony growth for all three gull species on a relatively

381   small spatial scale, with clustering based on the direction and extent of individual colony GR,

382   and this pattern was statistically significant in the Herring and Great Black-backed Gull.

383   There were both similarities and differences between the spatial clustering of the Great

384   Black-backed, Herring and Lesser Black-backed Gulls. Spatial synchrony in population

385   trends has been observed in other seabird species, and over larger spatial scales (Frederiksen

386   *et al.* 2005, Cook & Robinson 2010, Bertram *et al.* 2015); and in the large gull species on the

387   scale of the British Isles (Nager & O'Hanlon in press) indicating that nearby seabird colonies

388   may frequently be influenced similarly by what is occuring in the local environment. This

389   has implactions for conservation stratergies for these speices of conservation concern as one

390   common stratergy across a large geographic scale is unlikely to be effective for all

391   populations.

392

393   Geographic variation in colony growth, as found in the three gull species, could be

394   due to spatial variation in deterministic processes, such as strength of density dependence,

395   and/or due to spatial variation in environmental conditions (Moran effect) (Brown *et al.* 1995,

396   Williams *et al.* 2003, Liebhold *et al.* 2004). We found a significant negative relationship

397   between colony growth and the size of the colony at the start of the census period for the

398   Herring and Great Black-backed Gulls indicating that the colonies which declined the most

399   over the census period were those that were the largest during the first census. Evidence for

400   density-dependent population changes have also been found at the national level in the

401   Herring Gull and the Lesser Black-backed Gull (Nager & O'Hanlon in press). Larger

402   colonies may deplete local food sources more strongly and experience higher levels of

403 competition resulting in reduced colony growth (e.g. Furness & Birkhead 1984, Birt *et al.*
404 1987, Lewis *et al.* 2001).   It would be expected that such processes would be indicated by
405 interactive effects of colony size and environmental conditions on colony growth, however
406 we did not find evidence in support of this. Deterministic processes are therefore unlikely to
407 explain the observed spatial clustering in colony trends of the large gull species. Instead,
408 spatially variable environmental conditions may be responsible for the geographic differences
409 in colony trends of the gulls.
410
411   Environmental variables acting as proxies of resource availability associated with
412 marine, intertidal and terrestrial habitats, explained part of the variation in colony GR of
413 Herring and Lesser Black-backed Gulls. In Herring Gulls, colonies that were associated with
414 lower average wave fetch in their foraging range had higher colony GR. Wave fetch predicts
415 the composition of rocky shore communities due to the influence of wave exposure on these
416 communities (Burrows *et al.* 2008). Low wave fetch reflects a more sheltered intertidal
417 habitat that generally supports a greater abundance and diversity of intertidal prey species on
418 which the gulls forage (Burrows *et al.* 2008, Burrows 2012). Herring Gulls forage more
419 extensively within intertidal habitats than the other two gull species (Hunt & Hunt 1973,
420 Kubetzki & Garthe 2003) and therefore colonies close to sheltered intertidal habitats may
421 experience higher potential local food availability which results in higher colony GR. In
422 addition, Herring Gulls on more sheltered shorelines may breed more successfully possibly
423 due to these colonies being more sheltered from adverse weather events which could impact
424 upon egg and chick survival or affect the gulls foraging ability (Schreiber 2001). In Herring
425 Gulls increasing colonies were also located within sea areas of higher demersal fish
426 abundance. Higher abundance of demersal fish may mean higher fishery activity and
427 therefore more opportunities to scavenge on discards; a higher quality resource than what the
428 gulls are likely to consume in terrestrial habitats (Hüppop & Wurm 2000, Oro *et al*. 1996).
429 This was with the exception of ICES area 47 where the CPUE was relatively high but the
430 colonies located within this area had experienced large declines. One potential explanation is
431 that this ICES sea area covers a larger area, incorporating areas for away from those occupied
432 by Herring gulls and therefore may not be representative of the potential food availability
433 accessible to them. Both Great and Lesser Black-backed Gulls scavenge more intensively on
434 discards than Herring Gulls (McLellan & Shutler 2009, Ramírez *et al*. 2015, Tyson *et al*.
435 2015, Washburn *et al*. 2013) and therefore we expected that the colony GR of these species
436 would also relate to CPUE. However, this was not found to be the case potentially due to the

437   coarse resolution of CPUE we included. In addition, within the study region greater numbers

438   of Herring Gulls were found associated with fishing boats, potentially due to the higher

439   numbers of this species in the regions (Furness *et al.* 1988).

440

441   In Herring and Lesser Black-backed Gulls, colony GR were associated with measure

442   of marine productivity, however in both cases the relationships were opposite to what we

443   would expect. Typically, higher chlorophyll a concentrations and lower SST reflect high

444   marine productivity; with higher chlorophyll a concentration relates to more productive

445   marine waters (Huot *et al.* 2007), resulting in potentially higher availability of marine prey

446   (Bustamante *et al.* 1995). Whilst, lower SST is typically related to higher marine

447   productivity associated with the timing of thermal stratification and spring blooms

448   (Townsend *et al.* 1994). In Lesser Black-backed Gull colonies one possible explanation for

449   the opposite pattern observed could be attributed to nutrient runoff into coastal waters and

450   sea-lochs masking actual chlorophyll a concentration, as the satellite data cannot distinguish

451   between chlorophyll from phytoplankton and nutrient runoff (Smith *et al.* 1998, Nielsen *et al.*

452   2002). If this high chlorophyll a concentration does reflect high runoff from local agriculture

453   as well as domestic and industrial waste (Grantham & Tett 1993) this may lead to a decline in

454   benthic marine prey (Hiscock *et al.* 2004, Burrows *et al.* 2008). The model did not include

455   any terrestrial anthropogenic habitats therefore the effect of chlorophyll a concentration on

456   colony GR could also possibly reflect proximity to built-up areas. The observed pattern in

457   the Herring Gull is more difficult to explain. If higher SST in certain locations are attributed

458   to runoff, rather than reflecting natural marine productivity, then, unlike the Lesser Black-

459   backed Gulls, Herring Gulls may benefit from runoff entering coastal waters. As higher

460   nutrient levels can potentially benefit the abundance of some marine invertebrate species,

461   such as starfish (Brodie *et al.* 2005, Chiu *et al.* 2008), which Herring Gulls forage on.

462

463   Therefore, for the Herring Gull increasing colonies were located in areas with access

464   to marine resources in terms of potential discards and intertidal prey; and declined in areas

465   where the availability of these resources were lower. This may suggest that Herring Gulls do

466   benefit from having high quality marine resources within the vicinity of the breeding colony

467   (Annett & Pierotti 1999, Blight *et al.* 2015) potentially buffering them from other impacts in

468   the local environment. This may also be the case for the Lesser Black-backed Gull, with

469   areas away from potential high runoff, having between foraging conditions.

470

471   In colonies in close proximity to built-up areas it may also have been expected that

472   the presence of potential terrestrial anthropogenic food sources such as landfill sites may

473   benefit the gulls resulting in more favourable colony growth rates. Anthropogenic resources,

474   especially in relation to the vicinity of landfill sites are known to benefit opportunist gulls

475   species in terms of colony size, breeding traits and body conditions (Pons 1992, Duhem *et al.*

476   2008, Weiser & Powell 2010, Steigerwald *et al.* 2015). Despite these resources generally

477   being thought of as lower quality to the gulls than marine resources (Pierotti & Annett 1991,

478   Annett & Pierotti 1999), they can potentially provide a predictable and abundant food source

479   (Burger & Gochfeld 1983, Horton *et al.* 1983). However, we found no relationship between

480   colony GR and potential terrestrial resources within the vicinity of the colonies o Herring and

481   Great Black-backed Gulls. The negative relationship between the Lesser Black-backed Gull

482   colony GR and chlorophyll a concentration may however potentially indicate that colonies

483   with a high amount of built-up area within the colony range may negatively impact upon this

484   species through runoffs entering the local marine environment; although potentially not for

485   the Herring Gull. This suggests that the two gull species may respond differently to local

486   marine conditions at least in terms of runoff into coastal habitats.

487

488   Not all monitored colonies within the study region were included in the analysis due

489   to incomplete records of colony counts; which could be due to the colony not being counted

490   or not being in existence at the time. However, it is thought that the selected colonies do

491   reflect the regional population trends (unpubl. data). For this analysis we selected the

492   average maximum foraging range taken from values in the literature, as well as unpublished

493   tracking data of Herring Gulls from the study region. This means that the average maximum

494   of foraging range of 50km results in the foraging ranges of neighbouring colonies to overlap.

495   However, studies on other seabird species have found that neighbouring colonies do not

496   overlap in their forging areas (Wanless & Harris 1993, Wakefield *et al.* 2013 but see Ainley

497   *et al.* 2004, Evans *et al.* 2015). In addition, foraging ranges are likely to vary with colony

498   size (Jovani *et al.* 2015); with individuals from larger colonies potentially travelling further

499   due to competition and local food depletion in the vicinity of the colony (Furness & Birkhead

500   1984). It is therefore difficult to accurately estimate the foraging range for every colony

501   however, selecting the maximum foraging distance of breeding gulls will account for all

502   resources that are potentially accessible around the colony.

503

504   In opportunistic and generalist species, such as the gulls, the resources most widely

505   available within the foraging range of the colony will likely be the most consumed

506   (Osterblom et al., 2008, White, 2008). The results from this study suggests that when the

507   resources in the vicinity of Herring Gull and Lesser Black Back Gull colonies are from

508   marine and intertidal habitats their GR is more favourable than those which have more

509   terrestrial resources available. This highlights the importance of an intact marine coastal

510   environment to these two species; and especially for the Herring Gull the importance of the

511   intertidal habitat.

512

513   We found spatial clustering in at least two of the three large gull species within a

514   relatively small region of 200 by 200km.   The results suggest that colony growth rates of

515   Herring and Lesser Black-backed Gulls are sensitive to spatially variable environmental

516   conditions at the interface of marine and terrestrial ecosystems. Identifying the

517   environmental drivers of population changes is challenging and the spatial clustering

518   indicates that these drivers may vary even on a small spatial scale. This study demonstrates

519   that investigating spatial variation in colony growth is a promising approach and highlights

520   the potential of monitoring multiple colonies and identifying spatial variation in population

521   trajectories to help investigate relevant environmental variables that might explain spatial

522   differences in population changes. It also warns that common conservation management

523   might not be equally effective at all sites and highlights the need for area-specific

524   conservation measures.

525

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Table 1. Moran's *I* Index (measure of spatial autocorrelation) to determine the extent of spatial variation in colony population growth rates (GR ± standard error SE) for seven coastal seabird species. Moran's *I* index values range from +1 (clustered) to -1 (dispersed) with values close to 0 indicating a random pattern.

Species	GR ± SE	N[a]	Moran's *I*	*Z* value	*P* value
Great Black-backed Gull	-0.098±0.09	48	0.458	2.618	**0.009**
Herring Gull	-0.228±0.09	68	0.410	2.740	**0.007**
Lesser Black-backed Gull	-0.032±0.14	33	0.370	1.830	**0.067**

[a]N relates to number of individual colonies included within the analysis with population counts, including counts of zero, in Operation Seafarer (1969-1970) and Seabird 2000 (1998-2002).

Table 2. Final models from general linear regression models relating colony GR to environmental variables and colony size (log transformed) in Seabird 2000 for (a) Great Black-backed Gull (n = 48), (b) Herring Gull (n = 68) and (c) Lesser Black-backed Gull (n=21).

Species	Coefficients	Estimate	Std. Error	t	P	R^2
(a) Great Black-backed Gull	Intercept	-0.3639	0.0847	-4.298	**<0.001**	
	Colony Size	0.2098	0.0355	5.908	**<0.001**	0.42
(b) Herring Gull	Intercept	-7.9414	2.9615	-2.682	**0.009**	
	Wave fetch[a] (km)	-0.0008	0.0002	-3.837	**<0.001**	
	SST[b] (°C)	0.5759	0.2256	2.553	**0.013**	
	CPUE[c]	0.0003	0.0001	2.200	**0.032**	
	Colony Size	0.1291	0.0244	5.296	**<0.001**	0.50
(c) Lesser Black-backed Gull	Intercept	0.2744	0.1939	1.415	0.173	
	Chl. A (mg/m^3)[d]	-0.0533	0.0234	-2.280	**0.034**	0.17

Models started with all variables including interactions between each environmental variable and colony size. [a]Mean wave fetch within 50km of the colony. [b]Mean sea surface temperature (SST) within 50km of the colony. [c]Catch per unit effort (CPUE) during the spring (quarter 1) from International Bottom Trawl Surveys per ICES sea area. [d]Mean chlorophyll a concentration (mg/m^3) within 50km of the colony. The following environmental variables were removed from model (a) Wave fetch P = 0.96, CPUE P = 0.61, Chlorophyll a P = 0.44, Farmland P = 0.23, Built-up area P = 0.12; model (b) Farmland P = 0.86, Chlorophyll a P = 0.71, Built-up area P = 0.11 and model (c) SST P = 0.92, Wave fetch P = 0.91, Built-up P = 0.84, CPUE P = 0.66. Colony GR was calculated for the period between 1969-1970 and 1998-2002 except for the Lesser Black-backed Gull where we took GR between 1985-1989 and 1998-2002 (see text).

Figure 1. Study region (in grey) where spatial clustering in population trends were assessed for the three large gull species between 1969 and 2002. The study region spanned two Regional Seas: Minches and West Scotland (including ICES sea areas 45, 46 and 47) in the North and Irish Sea (ICES sea area 50) in the South.

Figure 2. Locations of colonies with sufficient count information (see text) included in the spatial autocorrelation analysis across the study region for (a) Great Black-backed Gull, (b) Herring Gull and (c) Lesser Black-backed Gull. The shade of the circle depicts the extent of colony growth rate between 1969-1970 and 1998-2002; along a gradient of white (strongest increase) to black (strongest decline); categories based on a kmeans cluster analysis (see text). The size of the circle reflects the size of the colony during the first Seabird census, 1969-1970 (separate scales for each species).

Figure 3. Relationship between Herring Gull colony growth rate, between 1969-1970 and 1998-2002, and (a) average wave fetch (km) within the foraging range of the colony, (b) bottom trawler survey CPUE (catch per unit effort) per ICES sea area and (c) mean sea surface temperature (SST °C) within 50km of the colony (km^2). Data are binned for categories of 200 km wave fetch and per ICES area for CPUE for illustration only. Solid line indicates the trend line with 95% confidence intervals (dashed lines) predicted from a Linear Model.

Figure 4. Relationship between Lesser Black-backed Gull colony growth rate, between 1985-1989 and 1998-2002, and mean chlorophyll a concentration (mg/m^3) within 50km of the colony (km^2). Data are binned for categories of 2.5 mg/m^3 chlorophyll a concentration for illustration only. Solid line indicates the trend line with 95% confidence intervals (dashed lines) predicted from a Linear Model.

Southern Hebrides

45 South Minch

47 Northern Ireland

46 Cyde

Solway Firth

50 Irish Sea

N

0   75   150   300 Kilometers

(a)

(b)