



Title	What can cetacean stranding records tell us? A study of UK and Irish cetacean diversity over the past 100 years
Authors	Coombs, Ellen J; Deauville, R; Sabin, RC; Allan, Louise; O'Connell, M; Berrow, S; Smith, B; Brownlow, A; Ten Doeschate, M; Penrose, R; Williams, R; Perkins, MW; Jepson, PD; Cooper, N
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1 **What can cetacean stranding records tell us? A study of UK and Irish cetacean**
2 **diversity over the past 100 years**

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4 Ellen J. Coombs^{1,2*}, Rob Deaville³, Richard C. Sabin², Louise Allan², Mick O'Connell⁴, Simon
5 Berrow^{4,5}, Brian Smith², Andrew Brownlow⁶, Mariel Ten Doeschate⁶, Rod Penrose⁷, Ruth
6 Williams⁸, Matthew W. Perkins³, Paul D. Jepson³ and Natalie Cooper²

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9 1 University College London, Genetics, Evolution and Environment Department, Gower Street, WC1E 6BT, UK

10 2 Department of Life Sciences, Natural History Museum, London, Cromwell Road, London, SW7 5BD. UK.

11 3 UK Cetacean Strandings Investigation Programme, The Wellcome Building, Institute of Zoology, Zoological
12 Society of London, Regent's Park, London NW1 4RY. UK.

13 4 Irish Whale and Dolphin Group, Merchants Quay, Kilrush V15 E762, County Clare, Ireland

14 5 Marine and Freshwater Research Centre, Galway-Mayo Institute of Technology, Dublin Road, Galway H91
15 T8NW, Ireland.

16 6 Scottish Marine Mammal Stranding Scheme, SRUC Wildlife Unit, Drummondhill, Inverness, IV2 4JZ

17 7 Marine Environmental Monitoring, Penwalk, Llechryd, Cardigan, West Wales SA43 2PS

18 8 Cornwall Wildlife Trust, Five Acres, Allet, Truro, TR4 9DJI, UK

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21 *Corresponding author

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39 **Abstract**

40 There are many factors that may explain why cetaceans (whales, dolphins, and porpoises)
41 strand. Around the UK and Ireland, over 20,000 stranding records have been collected since
42 1913, resulting in one of the longest, continuous, systematic stranding data sets in the world.
43 We use this dataset to investigate temporal and spatial trends in cetacean strandings and
44 use generalized additive models (GAMs) to investigate correlates of strandings. We find a
45 dramatic increase in strandings since the 1980s, most likely due to increases in recording
46 effort, and the formation of formal strandings networks. We found no correlation between the
47 numbers of cetaceans stranding each year and several potential environmental and
48 anthropogenic predictors: storms, geomagnetic activity, North Atlantic Oscillations, sea-
49 surface temperature, and fishing catch. We suggest that this is because the scale of change
50 in the variables is too coarse to detect any potential correlations. It may also highlight the
51 idiosyncratic nature of species' responses to external pressures, and further the need to
52 investigate other potential correlates of strandings, such as bycatch and military sonar.
53 Long-term cetacean stranding data provide vital information on past and present diversity for
54 common, rare, and inconspicuous species. This study underlines the importance of
55 continued support for stranding networks.

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57 Keywords: cetaceans, strandings, diversity, generalized additive models, macroecology

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64 Introduction

65 Cetaceans (whales, dolphins, and porpoises) are major components of oceanic ecosystems
66 (Roman *et al.* 2014). They are top predators and their distributions can provide an indication
67 of prey abundance and wider ocean health (Friedlaender *et al.* 2006, Burek *et al.* 2008,
68 Roman *et al.* 2014). Unfortunately, many cetacean species are threatened (Reeves *et al.*
69 2003, IUCN SSC, 2018) and are vulnerable to anthropogenic impacts, such as incidental
70 entanglement in fishing gear (bycatch), ship strikes, hunting, chemical or noise pollution and
71 environmental changes across their ranges (Parsons *et al.* 2010, Ramp *et al.* 2015). It is
72 therefore important to monitor cetaceans to determine the impacts of these pressures on
73 their abundance and behavior (Bejder *et al.* 2006). As with other marine species, cetaceans
74 can prove difficult to study as they are often wide-ranging and spend most of their lives
75 submerged under water (Evans and Hammond, 2004). Frequently employed monitoring
76 techniques, such as surveying from boats, are not only expensive and time consuming, but
77 are often biased towards conspicuous species or those that respond positively to boat
78 presence, such as bottlenose dolphins (*Tursiops truncatus*) and short-beaked common
79 dolphins (*Delphinus delphis*; Evans and Hammond, 2004). One approach to these
80 constraints is to use strandings data, *i.e.*, records of cetaceans that have washed ashore.
81
82 Stranding records are the primary source of information for many elusive species, such as
83 beaked whales (Ziphiidae; Morin *et al.* 2017) and can provide an indication of relative
84 abundance and richness in extant cetacean communities (Evans and Hammond, 2004,
85 Maldini *et al.* 2005, Pyenson, 2011). Globally, there are several long-term, regional stranding
86 datasets: the northwest Pacific USA, *e.g.*, Norman *et al.* (2004) who reported 904 records,
87 concluding that most reports are made in summer time when sampling effort is higher;
88 Hawaii, *e.g.*, Maldini *et al.* (2005); who documented 202 odontocete strandings; the
89 Netherlands, *e.g.*, Murphy *et al.* (2006) who have ~10,000 strandings records to date, the
90 majority of which are harbor porpoises; and Australia, *e.g.*, Evans *et al.* (2005), who
91 analyzed 639 stranding events comprising 39 taxonomic groups. The Australian dataset only

92 has 21 records gathered prior to 1960 (Lloyd and Ross, 2015), while the Hawaiian and North
93 American datasets have limited accuracy prior to the 1960s and 70s when systematic
94 recording of strandings became more standardized (Pyenson, 2010). The Dutch dataset has
95 systematic records dating back to at least the 1920s (Murphy *et al.* 2006), with some records
96 dating back hundreds of years. Similarly, the Irish Whale and Dolphin Group (IWDG)
97 stranding records date back to the 18th Century. Although globally there are several long-
98 term stranding datasets the majority of them are not systematic, nor as long-term as the one
99 we present here. The Natural History Museum, London (NHM) has maintained a database of
100 UK strandings since 1913, making it one of the longest, continuous, systematic cetacean
101 stranding datasets in the world (NHM, 2018). The program became part of the Cetacean
102 Strandings Investigation Programme (CSIP) in 1990, which continues to record cetacean
103 strandings in the UK to the present day and investigates the causes of strandings through
104 systematic postmortem examinations, under contract to the UK government (CSIP, 2019).
105 The IWDG has been systematically recording strandings since 1990 (IWDG, 2019).
106 Despite records being available up to 2015, no comprehensive studies of temporal changes
107 in cetacean strandings exist for this full time period, *i.e.*, from 1913-2015. The unique
108 characteristics of this data set are ideal for investigating trends and inter-annual variability in
109 cetaceans strandings alongside anthropogenic and/or environmental changes.

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120 **Potential correlates of strandings**

121 Many studies have investigated possible causes of cetacean strandings. Strandings may be
122 triggered by geomagnetic storms affecting the orientation of cetaceans that navigate by
123 these means (Vanselow *et al.* 2017). Other (*i.e.*, meteorological) storms may exhaust,
124 displace, or physically injure cetaceans, increasing the risk of disorientation and stranding
125 (Mignucci-Giannoni *et al.* 2000, Bogomolni *et al.* 2010, Schumann *et al.* 2013). Fluctuations
126 in the North Atlantic Oscillation (NAO) can lead to storms and wind and sea surface
127 temperature (SST) changes, that may in turn influence prey abundance and distributions
128 (Hurrell, 1995, Pierce *et al.* 2007) that can alter cetacean distributions and lead to strandings
129 (Simmonds and Elliott, 2009, Schumann *et al.* 2013). Anthropogenic impacts such as military
130 sonar can cause cetaceans to surface quickly resulting in fatal decompression sickness
131 (Jepson *et al.* 2003). Further, direct physical contact with ships (*i.e.*, ship strike) (Laist *et al.*
132 2001) has also been attributed to deaths in a number of stranding records. Starvation is a
133 known cause of death recorded in stranding necropsies (Leeney *et al.* 2008, Deaville *et al.*
134 2015), which may be linked to overfishing. Other effects of human fishing efforts *e.g.*,
135 bycatch, are well documented (Read *et al.* 2017). Entanglement in fisheries nets, and other
136 commercial debris (Leeney *et al.* 2008, Deaville *et al.* 2015) causes either immediate
137 asphyxiation (often the case in smaller cetaceans) or exaggerated energy expenditure from
138 the drag of nets, often leading to emaciation and asphyxiation (Moore and van Der Hoop,
139 2012). Pollution and plastic contamination have also been attributed to cetacean death and
140 subsequent stranding (Simmonds, 2012).

141
142 Our overall objective is to explore broad-scale patterns and correlates of cetacean
143 strandings through time. Combining all three datasets for the first time, we present over 100
144 years of data, and show spatio-temporal patterns in the number of individuals stranding in
145 the UK and Ireland. We also used Generalized Additive Models (GAMs) to explore
146 correlates of strandings.

147

148 **Methods**

149 **Study area**

150 All stranding records were recorded from UK and Irish coastlines between 49°N and 61°N,
151 and 11°W and 3°E. The predominant ocean current in this region is the North Atlantic drift,
152 which travels eastwards with prevailing winds towards the western UK and Ireland. Further,
153 there are powerful currents associated with submarine canyons to the extreme southwest of
154 the UK, near the edge of the continental shelf. Bed stress (disturbance to the sea floor by
155 tidal currents) is lowest in the more sheltered, shallower waters of the Irish sea, English
156 Channel, and the southern North Sea, near East Anglia (Connor *et al.* 2006). The UK
157 continental shelf includes parts of the North Sea, Irish Sea, English Channel, and North
158 Atlantic, and is under 200 m deep around most of the UK. This continental shelf slopes down
159 into a deep-sea zone off the west coast of Ireland (Connor *et al.* 2006).

160

161 **Strandings datasets**

162 During the early 20th century most UK stranding reports were sent to the NHM by HM
163 Coastguard. Information was collected *via* standardized forms that showed the basic data
164 requirements. Members of the public also submitted reports *via* the coastguard. As
165 photography became more widely used, more reports to the NHM were supported by
166 images. With the development of Wildlife Trusts around the UK, wardens, officers, and
167 rangers became key reporters of strandings. When CSIP and the IWGD were set up in
168 1990, wider publicity was given to the work on strandings, raising public awareness and
169 understanding. Reporting strandings *via* online forms, telephone, and social media became
170 common practice and is still used today. Many reported strandings are attended by the CSIP
171 and IWDG teams.

172

173 We used stranding data from the NHM, CSIP and IWDG to investigate temporal and spatial
174 patterns of cetacean strandings around the UK and Ireland. In the present study, a stranding

175 is defined as any individual found beached or washed up onto land (beaches, mudflats,
176 sandbanks *etc.*) either alive or dead, and also includes a small number of records where the
177 individual was re-floated. All three datasets contain information on the stranded species, the
178 date it was discovered, the latitude and longitude of the stranding location, and whether the
179 animal was alive or dead on discovery. For some specimens, the NHM and CSIP datasets
180 also have information on whether the individual stranded alone or with others of the same
181 species (a mass stranding, *i.e.*, more than one individual, excluding mother-calf pairs), the
182 decomposition condition of the carcass, sex, and body length. The NHM dataset contains
183 4,311 UK and Irish stranding records from 1913-1989 (NHM, 2018). The CSIP dataset
184 contains 13,084 UK, and seven Irish stranding records from 1990-2015 (CSIP, 2018), and
185 the IWDG dataset contains 2,973 Irish cetacean records for the period 1913-2015 (IWDG,
186 2018). We combined the datasets and removed 220 duplicate records found in both the
187 NHM and IWDG datasets.

188

189 Before analyses, we cleaned the data by removing any records where species were listed as
190 'unknown', 'unknown cetacean', or similar. Then we removed any species that are rarely
191 seen in UK waters, defined using Reid *et al.* (2003) and OBIS-SEAMAP (Halpin *et al.* 2009);
192 Supplemental information: Table S1, S2). These are likely to represent one-off events that
193 will not contribute to general patterns, or may be misidentifications, especially in the
194 historical data. These species were: narwhal (*Monodon monoceros*), beluga (*Delphinapterus*
195 *leucas*), dwarf sperm whale (*Kogia sima*), Blainville's beaked whale (*Mesoplodon*
196 *densirostris*), Gervais' beaked whale (*Mesoplodon europaeus*), Fraser's dolphin
197 (*Lagenodelphis hosei*), and melon-headed whale (*Peponocephala electra*). Where possible,
198 we converted grid references and detailed location descriptions into latitudes and longitudes
199 for records that did not have this information. We sense-checked all anomalous strandings,
200 such as those with localities far inland, and removed any that were not near a viable water
201 source. Lastly, we standardized the date formats and scientific names across the combined

202 dataset, using YYYY-MM-DD for dates and the taxonomy of Reid *et al.* (2003) for scientific
203 names.

204

205 **Correlates of strandings through time**

206 We plotted changes in the total number of stranded individuals through time for all species
207 combined, for each species separately, and for mysticetes (baleen whales) and odontocetes
208 (toothed whales). Next, we explored the spatio-temporal patterns in strandings for all
209 species combined, and for mysticetes and odontocetes separately, across the UK and
210 Ireland at 25-year intervals and decadal intervals (Fig. S3).

211

212 We considered drivers of changes in strandings through time. We fitted models of numbers
213 of individuals stranded against various predictor variables thought to correlate with cetacean
214 strandings (Table 1, Fig.1). We included the following predictors because they have been
215 reported to potentially influence strandings, and because we could collate data for them on a
216 yearly basis for the UK and Ireland for the full-time span of our dataset (1913-2015)
217 (Supplemental information: Data Collection). **(1) Geomagnetic activity.** Some cetaceans,
218 such as sperm whales (*Physeter macrocephalus*) may use Earth's geomagnetic fields for
219 navigation (Kirschvink *et al.* 1986, Kremers *et al.* 2014, Vanselow *et al.* 2017), thus changes
220 in geomagnetic activity, e.g., solar storms, may affect their navigation and increase the
221 likelihood of strandings (Vanselow *et al.* 2017). **(2) Sea surface temperature (SST).**
222 Changes in SST (°C) can affect prey abundance, resulting in net movements of cetaceans
223 as they follow their prey (Pierce *et al.* 2007, Simmonds and Elliott, 2009), which could result
224 in changes in cetacean distribution and therefore the spatial distribution of strandings. **(3)**
225 **Storm events.** Storm conditions, hurricane events and associated oceanographic
226 disturbances may increase strandings (Mignucci-Giannoni *et al.* 2000, MacLeod *et al.* 2004,
227 Bogomolni *et al.* 2010) as individuals suffer from exhaustion, disorientation, or direct
228 physical injury. Further, these impacts can also affect food sources (Lawler *et al.* 2007,
229 Evans *et al.* 2005), which may alter cetacean distributions and therefore the likelihood of

230 strandings. **(4) North Atlantic Oscillations (NAO)**. Fluctuations in the NAO can affect prey
231 distribution and abundance via associated wind and temperature changes (Hurrell, 1995,
232 Pierce *et al.* 2007). Low NAO indexes have been associated with physiological stress in
233 North Atlantic right whales (*Eubalaena glacialis*). Note that although NAO and storms, and
234 NAO and SST are related, they are not strongly correlated ($r^2 < 0.16$ and $r^2 < 0.001$
235 respectively; Supplemental information; Environmental variables). Therefore, we included all
236 three variables. **(5) Fishing catch**. Over-fishing can have a direct impact on cetaceans due
237 to a reduction of their prey (Evans, 1990, Weir *et al.* 2007), causing starvation, or a shift in
238 cetacean distribution as they search for prey elsewhere. Further, discarded or fixed fishing
239 nets and creel lines are partly responsible for cetacean mortality as bycatch (Leeney *et al.*
240 2008). Note that ideally, we would have included sonar use, bycatch, and chemical
241 pollution, but none of these variables were available for every year in our dataset (*i.e.*, 1913
242 - 2015), particularly for the historical data. We ran a model that included a proxy for shipping
243 traffic, but these data were only available for 1950-2015 (Supplemental Information;
244 Shipping model). Sources and units of the main model dataset are in Table 1.

245

246 <Table 1>

247 <Figure 1>

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254 **Generalized additive models (GAMs)**

255 We modelled the effects of our predictors on the number of individuals stranded using
256 GAMs. GAMs allow for smooth relationships between multiple explanatory variables and the
257 response variable (Wood, 2017). Like generalized linear models (GLMs), GAMs use a link
258 function. GAMs use this link function to establish a relationship between a 'smoothed'
259 function of the predictor variable(s) and the mean of the response variable (Guisan *et al.*
260 2002). A GAM is substantially more flexible because the relationships between independent
261 and dependent variables are not assumed to be linear (Wood, 2017). Our initial data
262 exploration found that relationships between the individual predictors and the number of
263 individuals stranded were nonlinear.

264 We modelled the total number of stranded individuals as a sum of smooth functions of
265 covariates in a GAM framework (1). In an attempt to account for changes in the potential for
266 detection of stranded cetaceans through time we included yearly UK population size based
267 on the assumption that as population size increases, or activity in an area increases, it is
268 more likely that strandings will be observed and reported (Norman *et al.* 2004, Maldini *et al.*
269 2005, Pyenson, 2011, McGovern *et al.* 2016). Stranding studies highlight the importance of
270 considering population growth as a proxy for observer effort (Maldini *et al.* 2005, Pyenson,
271 2011). However, it is often difficult to obtain accurate population estimates over the time
272 frame of these stranding databases or in regions where populations have varied
273 considerably (*e.g.*, the Hawaiian Islands, Maldini *et al.* 2005)., we used yearly UK human
274 population size (Table 1) as an offset in the model. To further investigate the impacts of
275 sampling effort, we ran two case study models that look at differences in population between
276 the populated southern UK, and the less populated northern UK (Supplemental information;
277 Regional study 1 & 2). Smooths were modelled using a thin plate spline basis with shrinkage
278 (Marra and Wood, 2011), which allowed terms to be removed from the model (*i.e.*, their
279 effect size shrunk to zero) during fitting, thus terms were selected during model fitting. As we
280 wanted to model species-specific effects, we included a factor-smooth interaction between

281 year of stranding and species; this term fitted a smooth of time for each species but allowed
 282 common smooths to be fitted for the other covariates. An advantage of this approach is that
 283 the per-species smooths are estimated as deviations from a base-level smooth, so some
 284 information is shared between species. We fitted models with the following candidate
 285 response count distributions: Poisson, quasi-Poisson, negative binomial, and Tweedie. We
 286 used standard residual checks for GAMs (Q-Q plot, histogram of residuals, residuals vs.
 287 linear predictors, response vs. fitted values) to decide between response distributions and
 288 assess model fit. We report the results using the negative binomial distribution as this was
 289 the best fit for the data (Supplemental information: GAM candidate response distributions)
 290 with each of the different response distributions (Supplemental information: Fig. S7:S10).
 291 The total number of stranded individuals was modelled as a sum of smooth functions of the
 292 k explanatory variables z_{tk} using a GAM with the general formulation:

293 (1)

$$294 \quad s_{t, \text{ species}} = \exp \left[\log(p_t) + \beta_0 + \sum_{k=1}^K f_k(z_{tk}) + f_{t, \text{ species}}(t, \text{ species}) \right]$$

295

296 Where $s \sim$ negative binomial (θ), s is the number of stranded individuals, t is year, species is
 297 the cetacean species in the stranding dataset, p is an offset of human population size, β_0 is
 298 the intercept and f_k are smooths of the K explanatory variables. The explanatory variables
 299 for inclusion in the models were smooth functions of year, with the additional species smooth
 300 as mentioned and shown in (1), and storm events, geomagnetic activity, sea surface
 301 temperature, North Atlantic oscillation, and fishing catch.

302

303 We fitted models using Restricted Maximum Likelihood (REML) in the R `mgcv` package
 304 version 1.8.17 (Wood, 2011). REML was preferable because when models contain highly
 305 correlated covariates, REML finds an optimal degree of smoothing (Reiss and Ogden 2009).
 306 In a GAM, k is the maximum complexity of the basis used to represent the smooth term. If
 307 the k value is high enough, we can be sure that there is enough flexibility in the model. We

308 can find out if k is high enough by increasing the k value and refitting the original model
309 (Supplemental information: Setting the k parameter). After refitting the model and analyzing
310 the GAM output, we set the k parameter for storm events and geomagnetic activity to k = 7
311 and k = 4, respectively. The k parameter did not need to be set for NAO, SST, or fishing
312 catch because these terms had more unique covariate combinations than the specified
313 maximum degrees of freedom. To avoid fitting overly complex models, the maximum basis
314 size for the smooth terms were limited to these values. Finally, we plotted the residuals by
315 covariate (Supplemental information; GAM model checking) to confirm the goodness of our
316 model fit. These plots showed low variation in the covariate residuals suggesting that the
317 model is a good fit (Fig. S11).

318 We removed 'rare' and 'unknown' records from the final model to account for possible
319 misidentifications in the stranding record. These records were also removed because of the
320 effect one or two records could have on skewing the species smooth. We also ran a GAM
321 with all 'rare' and 'unknown' records included (2,664 records) to investigate the effect of
322 these additional strandings.

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331 **Sensitivity analyses**

332 There are many different ways to subdivide the dataset, and many possible sources of error.
333 Therefore, we ran a series of additional analyses on subsets of the data, or different
334 arrangements of the data, to identify any obvious issues. These are described briefly below;
335 for more details see the supplementary information.

336

337 *Species identification models*

338 We ran the model with all stranding records at genus-level to account for possible
339 misidentification at the species-level, particularly in the historical data. Because species
340 identifications by dedicated strandings networks are likely to be more reliable than those in
341 the historic data, we also ran a model using CSIP and IWDG stranding records only (1990 –
342 2015).

343

344 *Species specific models*

345 47% of the dataset were harbor porpoise (*Phocoena phocoena*) records, as these small
346 cetaceans are widespread and abundant in UK and Irish waters (Fig. S4). To ensure that our
347 results were not merely reflecting a signal in the harbor porpoise data we repeated our
348 analyses after removing this species from the dataset, and then for the harbor porpoise data
349 separately. For completeness we also fitted models for all other species with over 100
350 stranding records in the dataset (we excluded five species with fewer than 100 strandings
351 records; sei whale (*Balaenoptera borealis*), blue whale (*Balaenoptera musculus*), pygmy
352 sperm whale (*Kogia breviceps*), humpback whale (*Megaptera novaeangliae*), and True's
353 beaked whale (*Mesoplodon mirus*), because they had insufficient data to fit the models.

354

355 *Ship strike models*

356 To investigate ship strike effects on strandings we ran a model that included a proxy for
357 shipping traffic around the UK. These data were only available from 1950-2015; therefore,

358 the other predictors and the response were constrained accordingly, and shipping was not
359 included in the full model. Note that we use shipping traffic as a proxy for ship strikes
360 because direct ship strike data was not available historically, and even those data available
361 mainly focus on mysticetes or are geographically restricted.

362

363 *Stranding events models*

364 In the main model the response is all individual stranding records, with each and every
365 cetacean in a mass stranding recorded by species, location, and date. Cetaceans that mass
366 strand are generally pelagic odontocetes (Jepson *et al.* 2013), and we felt it was important to
367 assess the effects of correlates on these mass strandings. We therefore also fitted a model
368 with the number of stranding events as the response (with a single mass stranding event
369 recorded as a '1' for all individuals of the same species at that location and date) to
370 investigate whether the correlates had a different effect on single and mass strandings, and
371 to see whether our results were reflecting a signal of multiple mass strandings of pelagic
372 odontocetes.

373

374 *Suborder models*

375 The cetaceans were split by suborder (*i.e.*, Mysticeti or Odontoceti) to investigate whether
376 the predictors affected the numbers of strandings differently in each suborder. The two
377 suborders are generally different ecologically (*e.g.*, diet specialization and larger body size in
378 the mysticetes), and it has been suggested that only some genera (*e.g.*, *Delphinus*,
379 *Grampus*, and *Ziphius*; Kirschvink *et al.* 1986), of which all are odontocetes, use
380 geomagnetic features to navigate, with *Balaenoptera* (a mysticete), to a lesser extent
381 (Kirschvink *et al.* 1986). We therefore investigate the differences in this and the other
382 correlates of strandings for the two suborders.

383

384

385

386 *Habitat models*

387 We ran a model with a smooth of habitat (*i.e.*, oceanic, coastal, or both) (Table S2) rather
388 than a species smooth because some of the predictors *e.g.*, storms, may have had more of
389 an effect on species in certain habitats. For example, shallow water species, such as
390 porpoises, may be more likely to strand due to severe weather as they are less able to
391 escape from storm impacts (Lawler *et al.* 2007, Schumann *et al.* 2013). Species habitat data
392 were from Reid *et al.* (2003).

393

394 *Regional models*

395 Finally, we ran two regional models for strandings from; 1) the south west coast of the UK
396 where cetacean stranding records and human population have increased, and 2) the north
397 west coast of the UK where cetacean stranding records have increased, but human
398 population has decreased. These models were run to assess the possible effects that using
399 one standard UK human population size may have had in the original model and to see if
400 correlates of strandings were different in different regions of the UK and Ireland. The same
401 predictors were used in these models but were constrained to 1991-2015 as county-level
402 human population data are only available for this time period.

403 All data required to reproduce our analyses are available from the NHM Data Portal
404 (data.nhm.ac.uk, Coombs *et al.* 2018). We performed all data cleaning, data exploration,
405 plotting and analyses in R version 3.4.0 (R Core Team, 2017). A fully reproducible workflow
406 is available on GitHub (<https://github.com/EllenJCoombs/cetacean-strandings-project>) and
407 Coombs *et al.* (2019).

408

409

410

411 Results

412 Data exploration

413 Temporal and spatial patterns in the strandings data

414 A total of 17,491 strandings comprising 21 species were recorded. The dataset contains 786
415 mysticete records from five species, and 16,705 odontocete records from 16 species.

416 Temporal and spatial patterns in strandings varied across and within species (Fig. 2, 3).

417

418 <Figure 2>

419 <Figure 3>

420

421 Some species e.g., blue whales and false killer whales (*Pseudorca crassidens*), stranded in
422 the earlier parts of the time series but then disappear from the strandings record (Fig. 3).

423 Conversely, some species appear for the first time in the latter half of the century. For
424 example, the first humpback whale stranding record was in 1982 and the first pygmy sperm
425 whale stranding was recorded in 1966 (Fig. 2, 3). Species such as northern bottlenose
426 whales (*Hyperoodon ampullatus*) and Cuvier's beaked whales (*Ziphius cavirostris*) have
427 stranded consistently throughout the century, with an increase in records towards the
428 present day.

429 Overall, cetacean strandings records have increased over the past century, with a rapid rise
430 from the late 1980s to the present (Fig. 4). There were several prominent spikes in stranding
431 numbers before the 1990s (Fig. 4) caused by mass strandings. In 1927, there was a mass
432 stranding of 150 false killer whales, with further mass strandings of this species in 1934 and
433 1935, the largest being 41 individuals. In 1950 there were two long-finned pilot whale

434 (*Globicephala melas*) mass strandings (totaling 245 individuals; Fig. 2, 4), with further mass
435 strandings of this species in 1983. All of these mass strandings occurred in Scotland, which
436 accounts for the high numbers in that region from 1926-1950 (Fig. 5).

437 The most frequently stranded species were harbor porpoise (*Phocoena phocoena*; $n =$
438 8,265; 47% of all stranding records), short-beaked common dolphin (*Delphinus delphis*; $n =$
439 3,110; 18% of all stranding records) and long-finned pilot whale (*Globicephala melas*; $n =$
440 1,606; 9% of all stranding records) (Fig. 2, 3). Mysticete strandings were much less frequent
441 (Fig. 4) and accounted for around 4% of total strandings records. Mysticete strandings
442 showed an overall decline throughout the century until the 1980s. Generally stranding
443 records of all odontocetes increased throughout the 1990s to the present. The exceptions
444 were false killer whale, as previously mentioned, and killer whale (*Orcinus orca*) that
445 stranded intermittently in low numbers, with one mass stranding event ($n = 11$) in 1994 in
446 Scotland. 1990 was the first year that mysticete stranding records reached double figures.
447 There was an increase in mysticete strandings after 1987 and throughout the 1990s to the
448 present. Minke whales (*Balaenoptera acutorostrata*) accounted for 79% of all mysticete
449 strandings and also accounted for the majority of the post-1990 rise in mysticete strandings.
450 Mysticete records remained low throughout the 1950s and 60s (Fig. 4). There was a slight
451 decline in the number of odontocete stranding records during the early period of WWII, but
452 there are other years throughout the time period that reported lower numbers of odontocete
453 strandings. The CSIP and IWDG programs began in 1990, after which there was an
454 increase in stranding records for both mysticetes and odontocetes (Fig. 3, 4).

455 <Figure 4>

456 <Figure 5>

457

458 Most strandings were of odontocetes, therefore the plot for odontocetes and all species
459 combined show a similar pattern (Fig. 4). Most strandings occurred around the south coast
460 of England and the west coasts of Ireland and Scotland (Fig. 5, S6). This pattern was
461 particularly evident in common dolphin and harbor porpoise strandings (Fig. S4, S5).
462 Stranding hotspots in southern and southwest England were first documented from 1926-
463 1950 (Fig. 5). Over the next 25 yr (1951-1975) there was an increase in stranding records
464 around northern England. Over the next few decades (1976-2000) stranding density
465 increased along the northeast and north of Scotland (Fig. 5). From the 1990s, stranding
466 records can be observed around most of the coastline concomitant with the advent of the
467 modern stranding programs. Mysticete strandings increased around southwest England,
468 southwest and western Ireland and western Scotland in the last few decades (2001-2015;
469 Fig. 5). East Anglia, Wales and eastern Ireland have fewer records for mysticete strandings
470 compared to other parts of the UK and Ireland (Fig. 5).

471

472 **Correlates of strandings through time**

473 We found significant effects for NAO, SST, and fish catch ($P < 0.05$, $P < 0.001$, $P = 0.02$,
474 respectively) suggesting the smooth of these variables were significantly different from “no
475 effect” (Table 2). However, the estimated degrees of freedom (EDF) were very low (*i.e.*, less
476 than, or not much greater than 1) indicating that the number of individuals that strand was
477 not strongly influenced by any of our predictor variables apart from year of stranding (Table
478 2, Fig. 6). The factor smooth term $s(\text{Year}, \text{Species})$ has an estimated degrees of freedom
479 (EDF) of 103 (Table 2; deviance explained = 84.5%, $n = 2,163$). The results of the GAMs
480 were qualitatively similar when we included all ‘rare’ and ‘unknown’ records, except fishing
481 catch had an EDF a little higher than 1 (Table S4, S15, Fig. S15).

482

483

484 <Table 2>

485 <Figure 6>

486

487 **Sensitivity analyses**

488 We found significant P -values for some variables in our sensitivity analyses (see below for
489 details) suggesting the smooth of these variables were significantly different from “no effect”.

490 However, the EDFs for all variables (with a few exceptions; see below) were low, indicating that
491 across all sensitivity analyses the number of individuals that strand was not strongly

492 influenced by any of our predictor variables, except year of stranding, *i.e.*, our results

493 were qualitatively identical to those for the full model described above. This was true

494 across all sensitivity analyses (Tables S4, S5, S7-S12, S15 and Fig. S15, S16, S18-

495 S23); therefore, we only report the differences below. All results are compiled in Table

496 S15.

497

498 *Species identification models*

499 In the genus-level models we found significant effects for SST, NAO index, and fishing catch

500 ($P < 0.001$, $P = 0.01$, $P = 0.01$, respectively) (Table S5, Fig. S16). For the CSIP and IWDG

501 (1990 – 2015) data we found significant P -values for storms, NAO, fishing catch, and shipping

502 traffic (Table 3, Fig. S17).

503

504 *Species specific models*

505 When we removed harbor porpoises from the dataset we found significant effects for SST,

506 NAO, and fishing catch ($P < 0.001$, $P = 0.001$, $P = 0.07$, respectively) (Table S7, Fig. S18) and

507 showed that the original model was not merely reflecting a signal in the harbor porpoise data. When

508 we modelled harbor porpoise only, we found a significant P -value for SST ($P < 0.01$) but no

509 influence of any of the other predictor variables. When modelling each species

510 separately, we found no influence of any of the predictor variables (Table 4).

511

512 *Ship strike models*

513 We found significant P -values for all of the variables; storms ($P < 0.005$), geomagnetic k-index ($P <$
514 0.01), SST ($P < 0.01$), NAO ($P < 0.01$), fishing catch ($P < 0.001$), and shipping traffic ($P < 0.001$)
515 (Table S9, Fig. S20), however, all variables (except fishing catch) had low EDFs (Table S9). The
516 EDF for fishing catch was 5.57, but the relationship was not particularly “wiggly” meaning we can
517 also interpret this as having little effect on the number of stranded individuals (Wood, 2017).

518

519 *Stranding events models*

520 Our model with the number of stranding events as the response (with a single mass
521 stranding event recorded as a ‘1’) had a significant P -value for maximum SST, NAO and fishing
522 catch ($P = 0.005$, $P < 0.001$, $P = 0.04$, respectively) (Table S10, Fig. S21) but EDFs were low.
523 The correlates did not have a different effect on single and mass strandings. Further, our
524 results were not merely reflecting a signal of multiple mass strandings of pelagic
525 odontocetes.

526

527 *Suborder models*

528 We found a significant effect for maximum SST, and fishing catch ($P < 0.005$, $P < 0.001$,
529 respectively) (Table S11, Fig. S22) but otherwise the models for odontocetes and mysticetes
530 were qualitatively similar to those for the full dataset.

531

532 *Habitat models*

533 We found significant effects for maximum SST, and fishing catch ($P = 0.001$, $P < 0.001$,
534 respectively) but overall the results were the same as in the models without a habitat smooth
535 (Table S12, Fig. S23).

536

537 *Regional models*

538 The two regional models had different EDFs, with higher EDFs found in the southwest (region 1)
539 model (Table 3). We found significant P -values for all of the variables except for maximum k-index

540 and maximum SST in both models (Table S13, S14). The region 1 model had an EDF of 6.62 for
541 NAO but the relationship was not particularly “wiggly”. We therefore interpret this as having little effect
542 on the number of stranded individuals (Wood, 2017). The EDFs for the other variables were still too
543 low to be fully conclusive (Table 3, Fig. S24, S25).

544

545 <Table 3>

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547 <Table 4>

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567 **Discussion**

568 We looked at 17,491 UK and Irish cetacean stranding records from 1913-2015 from the
569 Natural History Museum (NHM), the Cetacean Stranding Investigation Programme (CSIP),
570 and the Irish Whale and Dolphin Group (IWDG). We found that stranding numbers
571 increased throughout the century, with hotspots along the southern and western coast of the
572 UK and Ireland. We investigated several potential environmental and anthropogenic
573 predictors: storms, geomagnetic activity, North Atlantic Oscillations, sea-surface
574 temperature, and fishing catch. Except for year of stranding, we found no significant
575 correlation between the numbers of cetaceans stranding each year and these potential
576 predictors.

577

578 **Temporal and spatial patterns in the strandings data**

579 We found that temporal and spatial variation in cetacean strandings has occurred over the
580 last 100 yr (from 1913-2015) on the shores of the UK and Ireland. Generally, cetacean
581 strandings have increased throughout the century.

582 A reduction in mysticete strandings in the 1950s is likely to be related to a substantial
583 increase in post-WWII commercial whaling that affected North Atlantic stocks (Braham,
584 1984, Amundsen *et al.* 1995), reducing the number of individuals available to strand.
585 Mysticete stranding numbers increase after 1987, the year after the International Whaling
586 Commission moratorium on whaling came into effect.

587 Stranding events along the north and west coasts of Britain, south and west coasts of
588 Ireland (McGovern *et al.* 2016), and around the English Channel, Irish Sea, and Sea of the
589 Hebrides may in part be due to the passive transport of carcasses by the North Atlantic drift
590 (MacLeod *et al.* 2004). Further, these areas support a higher abundance and diversity of
591 cetaceans, particularly the deep, prey rich waters off the west coasts and continental shelf

592 (Evans, 1980, Wall *et al.* 2009, Hammond *et al.* 2013). Many cetaceans including fin and
593 sperm whales migrate along the west coasts of Ireland and Scotland (Evans, 1980) and are
594 therefore more likely to strand in these regions.

595

596 Studies have highlighted the impacts of bycatch and entanglement as a cause of strandings
597 (Leeney *et al.* 2008, Parsons *et al.* 2010, Deaville and Jepson 2011, Prado *et al.* 2016).

598 Strandings of harbor porpoise and common dolphin were particularly frequent around
599 Cornwall and the southwest coast of England (Leeney *et al.* 2008, Deaville *et al.* 2015) and
600 the Isles of Scilly (Sabin *et al.* 2005). This spatial pattern has been attributed to
601 entanglement in bycatch and intense fishing pressures off the southwest coast, one of the
602 most heavily fished regions of the UK (Leeney *et al.* 2008, Deaville *et al.* 2015). Incidences
603 of bycatch and entanglement in fishing gear for smaller cetacean species are generally
604 higher in these regions (Leeney *et al.* 2008, Deaville and Jepson, 2011, Deaville *et al.* 2015).
605 Despite an increase in bycatch monitoring and recording effort through initiatives such as the
606 Agreement on the Conservation of Small Cetaceans of the Baltic, North East Atlantic, Irish,
607 and North Seas (ASCOBANS), monitoring of cetacean bycatch in the majority of fisheries
608 and areas is still insufficient (Read *et al.* 2017). Entanglement in fishing gear also affects
609 larger species and there has been a documented rise in the number of humpback whales
610 caught in static creel lines in Scottish waters (Ryan *et al.* 2016). Entanglement was the
611 cause of fatality in half of all baleen whales examined at necropsy in Scotland (Northridge *et al.*
612 *et al.* 2010), which may help explain high mysticete stranding rates in this region or reflect
613 higher densities of these species in this region. It is also important to note that the proximity
614 of the Atlantic shelf-edge to the Scottish islands, coupled with the influence of the Gulf
615 Stream, make this a particularly rich area for migrating and feeding mysticetes (Evans, 1980,
616 Pollock *et al.* 2000).

617

618 **Correlates of strandings through time**

619 To further investigate spatial and temporal variation, we examined several possible
620 correlates of strandings: storm events, geomagnetic fluctuations, North Atlantic Oscillation
621 (NAO), maximum sea surface temperature (SST), and fishing catch data. However, none of
622 these potential predictors explained the variation in cetacean strandings once we accounted
623 for time. We suggest that this is because the scale of change in the variables is too coarse
624 to detect any potential correlations. Due to the availability of human population data (used as
625 a proxy of sampling effort in our models) we were constrained to examining correlates at
626 yearly intervals. Similar results and criticisms arose from the CSIP and IWDG (1990-2015)
627 data only model, despite this model suffering less from the biases inherent in historical data.
628 Further, the genus-level model and the model with 'rare' and 'unknown' records showed
629 qualitatively similar results most likely due to the coarse, yearly constraints of the models.
630 Below we discuss each correlate in turn.

631

632 **Storms**

633 We found no significant indication of storms as a correlate for strandings records. Storm
634 events have been reported to have a greater effect on smaller, shallow water species
635 (Lawler *et al.* 2007, Schumann *et al.* 2013). However, we found no such effect in any of our
636 16 species-specific models, including our harbor porpoise only model, nor in our suborder
637 model despite odontocetes generally having a smaller body size. Further, we found no effect
638 of storms on strandings in our habitat model, despite storms potentially affecting shallow,
639 coastal water species to a greater extent (Lawler *et al.* 2007). We suggest that these effects
640 may be population, location, or season-specific. Further, carcasses of offshore species may
641 be blown onshore during storm events making species-specific impacts harder to identify;
642 consistent data on carcass condition would be required to analyze this. Stormy weather can
643 increase the chances of mass stranding events in some species, sometimes with multiple

644 species stranding together (Bogomolni *et al.* 2010, Schumann *et al.* 2013), however, we
645 found no effect of storms when we included mass strandings as multiple events (*i.e.*, each
646 species in that location, on that date is a single record). Again, it is likely that the scale of
647 change in our variables is too coarse to model these effects.

648

649 ***Geomagnetic fluctuations***

650 We found no significant indication of geomagnetic fluctuations as a correlate for strandings.
651 Geomagnetic fluctuations may increase the likelihood of stranding in some species, *e.g.*,
652 sperm whales (Smeenk, 1997, Pierce *et al.* 2007, Vanselow *et al.* 2017). Only some genera
653 (*e.g.*, *Delphinus*, *Grampus*, and *Ziphius*; Kirschvink *et al.* 1986) likely use geomagnetic
654 features to navigate, with others to a lesser extent (*e.g.*, *Balaenoptera*; Kirschvink *et al.*
655 1986), however, this was not detected in our species-specific models, nor in our suborder
656 model. It should be noted that many of these studies focus on one species in one ocean
657 basin *e.g.*, the effect of geomagnetic activity on sperm whales stranding in the North Sea
658 (Vanselow *et al.* 2017) and that these regional and species-specific definitions were not
659 investigated in our macroecological study. We did not find a correlation between
660 geomagnetic fluctuations and strandings in our regional models, perhaps because these
661 effects are population, or season-specific.

662

663 ***North Atlantic Oscillation (NAO)***

664 In contrast to other studies (Pierce *et al.* 2007, Truchon *et al.* 2013), we found only a slight
665 effect of NAO on the number of stranding events in our main model. However, this was so
666 small that it was inconclusive. Previously, positive NAO indices have been positively
667 correlated with high stranding frequencies for seasonal migratory cetaceans (such as minke
668 whales) in the Atlantic (Truchon *et al.* 2013). Further, incidences of sperm whale strandings

669 in the North Sea are higher during warm periods (associated with the NAO and higher SST),
670 a likely reflection on changes in distribution of their prey (Robinson *et al.* 2005, Pierce *et al.*
671 2007). Again, this may be because many of these previous studies focus on one species, in
672 a specific geographical region (*e.g.*, the North Sea only (Smeenk, 1997, Pierce *et al.* 2007,
673 Vanselow *et al.* 2017), and show regional, and seasonal definitions that are not detected in
674 our wider macroecological study.

675

676 ***Sea surface temperature (SST)***

677 We found only a slight correlation between SST and stranding records in our main model.
678 The EDF was so low, that this is not a conclusive correlate of strandings. Studies that have
679 investigated SST and cetacean strandings are species, and region specific. For example, in
680 western Scotland, the relative frequency of strandings of white-beaked dolphins, a colder
681 water species, have declined whilst strandings of common dolphins, a warmer water
682 species, have increased (MacLeod *et al.* 2005). We found no such species-specific effects.
683 We also found no effects of SST on strandings in our regional models (southwest UK and
684 northwest UK). The effects of an increase in SST may be particularly profound in species
685 that are constrained to shelf-waters and are unable to retreat to deeper, oceanic waters
686 (MacLeod *et al.* 2009). However, we saw no such effect of SST in our habitat model. Again,
687 it is likely that the scale of change in our variables is too coarse to model these effects, and
688 further, that seasonal definitions are not investigated in our model.

689

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691

692

693 ***Fishing catch***

694 We found only a small correlation between stranding events and fishing catch. It is well
695 known that over-fishing can directly impact cetaceans by reducing their prey (Evans, 1990,
696 Weir *et al.* 2007), which can lead to starvation, or a shift in cetacean distribution as they
697 search for prey elsewhere. Starvation is a common cause of death recorded in stranding
698 reports (Kirkwood *et al.* 1997, Deaville and Jepson, 2011, Deaville *et al.* 2015), with many
699 cases ascertaining that no other significant disease processes could explain the animal's
700 poor nutritional status (Jepson, 2005, Deaville and Jepson, 2011). We found a correlation
701 between fishing catch and strandings in the southwest regional model, the habitat model,
702 and the model with all 'rare' and unknown records included, although these correlations are
703 too small to be conclusive. Future studies should investigate the effects of fishing catch at a
704 finer seasonal, and regional scale, and importantly, in conjunction with bycatch data.

705

706 ***Model criticisms***

707 Our models may have failed to fully explain the variation in cetacean strandings because we
708 did not include other possible predictors such as reported bycatch numbers, or sonar use.
709 Other causes of death, and of strandings include infections from bacteria and other
710 pathogens, impacts of legacy chemical contaminants, particularly in top predators such as
711 killer whales and false killer whales which have seen a decline in stranding records, physical
712 trauma from boat strikes, in addition to interspecific aggression, and starvation (Sabin *et al.*
713 2005, Deaville and Jepson, 2011, Jepson *et al.* 2016, Law *et al.* 2012). Other studies have
714 shown that beaked whales and pilot whales are particularly sensitive to sound pollution from
715 ship sonar and military exercises, causing fatal gas bubble lesions from rapid ascents
716 (Jepson *et al.* 2003, McGeady *et al.* 2016, Harris *et al.* 2017). However, responses varied
717 between, and within, individuals and populations (Harris *et al.* 2017). We were unable to
718 include these variables because data were not available for the full time period of our

719 stranding dataset at a yearly resolution. In addition, they have been addressed elsewhere
720 through the work of the current UK strandings program (e.g., Deaville and Jepson, 2011,
721 Jepson *et al.* 2016).

722 Our results may be confounded by the way we performed our analyses. First, we were
723 unable to account, in a satisfactory way, for sampling effort, instead using yearly UK
724 population size as a proxy. This is problematic as it cannot take into account social and
725 attitudinal changes over the 103-year period that are likely to have had a significant impact
726 on reporting effort. In addition, we used a population measure for the whole UK, which
727 shows that apart from the years 1916-1918 (*i.e.*, WWI), the human population rose every
728 year (Supplemental information: Human population data). A total UK population count
729 misrepresents some rural counties that have seen population fluctuations (for example
730 Anglesey, Wales) or declines (for example Argyll and Inverclyde, Scotland; and Donegal,
731 Ireland). Our two regional models, one for the southwest UK where human population has
732 increased over the century, and one for the northwest of Scotland where human population
733 has decreased over the century, were designed to account for this, but we did not find much
734 variation in our results. A better model would incorporate monthly human population data for
735 each county with a coastline, for the period 1913-2015, and therefore represent changing
736 sampling effort in that region over the century. This would also allow us to model the other
737 variables at monthly intervals. We could not incorporate these data because county-level
738 population data dating back to 1913 is only available decadal in UK and Irish Census data,
739 and county (and country) boundaries have changed in this time. Further, fluctuations in
740 stranding records may be attributable to uneven observer effort caused by specific events,
741 for example reduced effort during and after both world wars (Klinowska 1985).

742 We also highlight that the spatio-temporal difference between the death of the animal and its
743 discovery may affect stranding records, but that this is too variable to model. This includes
744 factors such as initial location of the animal at the time of death, buoyancy of the

745 carcass/species, and proximity of the carcass to strong currents, all of which determine
746 where and if the animal washes up.

747

748 ***Sampling effort***

749 It is most likely that the increase in stranding records throughout the 1980s to the present
750 was due to an increase in observer effort (Leeney *et al.* 2008, Deaville and Jepson, 2011,
751 Pyenson, 2011) and dedicated recording effort from the CSIP and the IWDG from 1990
752 onwards. It may also be the result of an increase in interest and reporting (O'Connell and
753 Berrow, 2007), and knowledge of the public (Norman *et al.* 2004, Leeney *et al.* 2008). An
754 increase in stranding records from the late 1980s onwards was also reported from southeast
755 Australia (Evans *et al.* 2005), the northwest Pacific in the USA (Norman *et al.* 2004), and
756 from the Hawaiian Islands (Maldini *et al.* 2005). These increases are also associated with an
757 increase in observer effort, and the formation of formal strandings networks. We see this
758 pattern in the UK and Irish stranding data.

759 Overall, we found numerous potential drivers of cetacean stranding events, but that the
760 causes of strandings often remain undetermined (Dolman *et al.* 2010). Cetaceans in UK
761 and Irish waters are facing numerous challenges such as reductions in prey stocks,
762 increases in chemical and noise pollution, and bycatch/entanglement (Parsons *et al.* 2010,
763 Deaville and Jepson, 2011). It is likely that the number of stranded cetaceans will continue to
764 rise as reporting effort and public interest in cetaceans continue to increase, and further, as
765 environmental and anthropogenic pressures on cetaceans persist. We suggest that future
766 studies continue to consider these anthropogenic threats that are likely to affect the numbers
767 of cetaceans that strand.

768 Long-term strandings data provides vital information on past and present cetacean diversity
769 and distribution for common, rare, and inconspicuous species, highlighting the importance of

770 stranding programs. Such data on cetaceans can provide an indication of wider ecosystem
771 health (Friedlaender *et al.* 2006, Roman *et al.* 2014) making these an important data source
772 to consider when informing conservation decisions.

773

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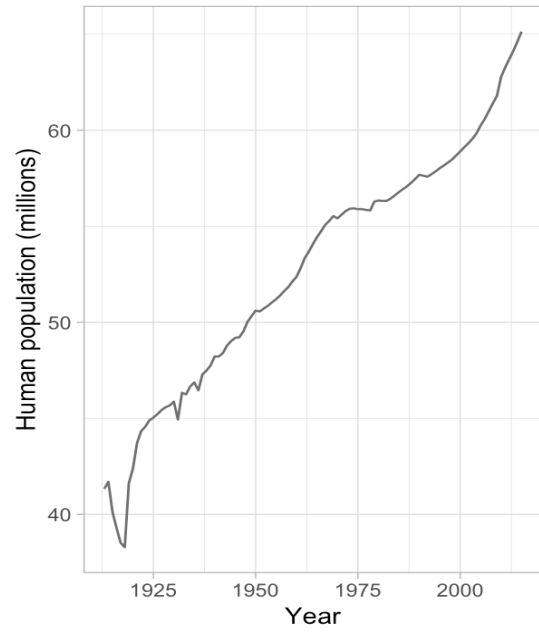
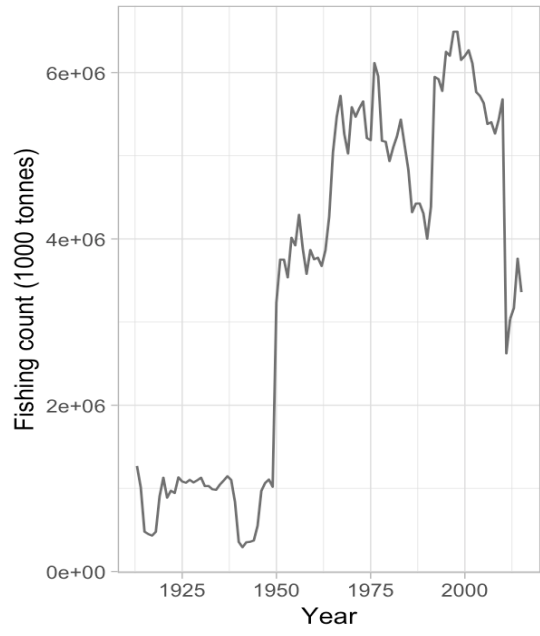
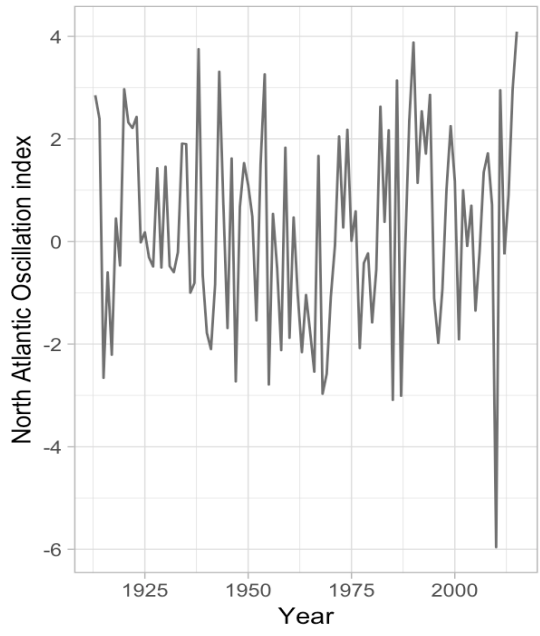
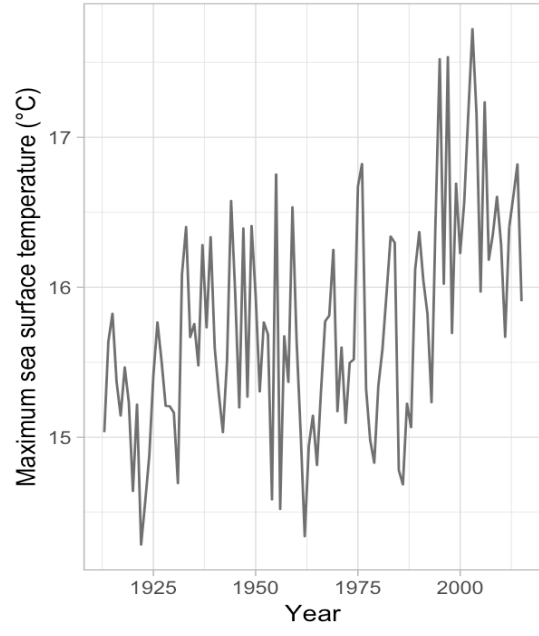
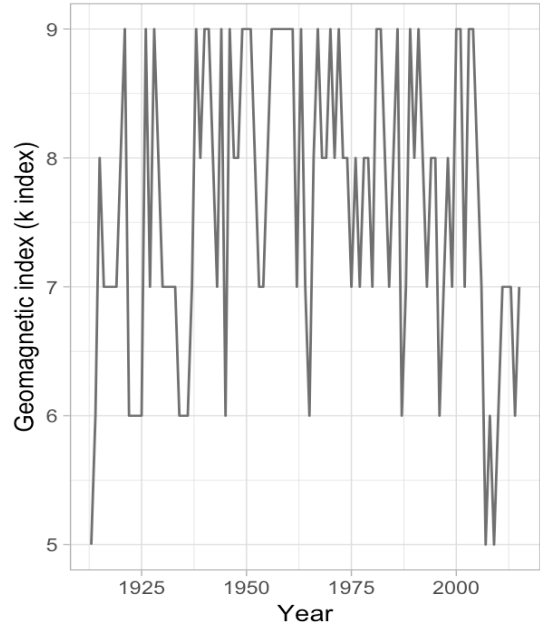
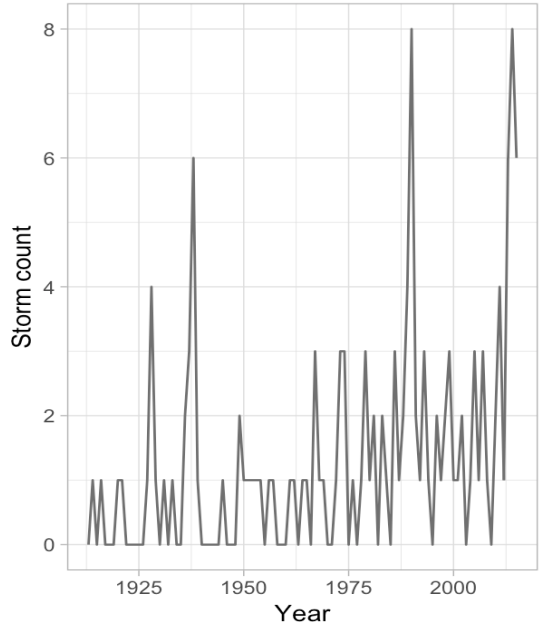
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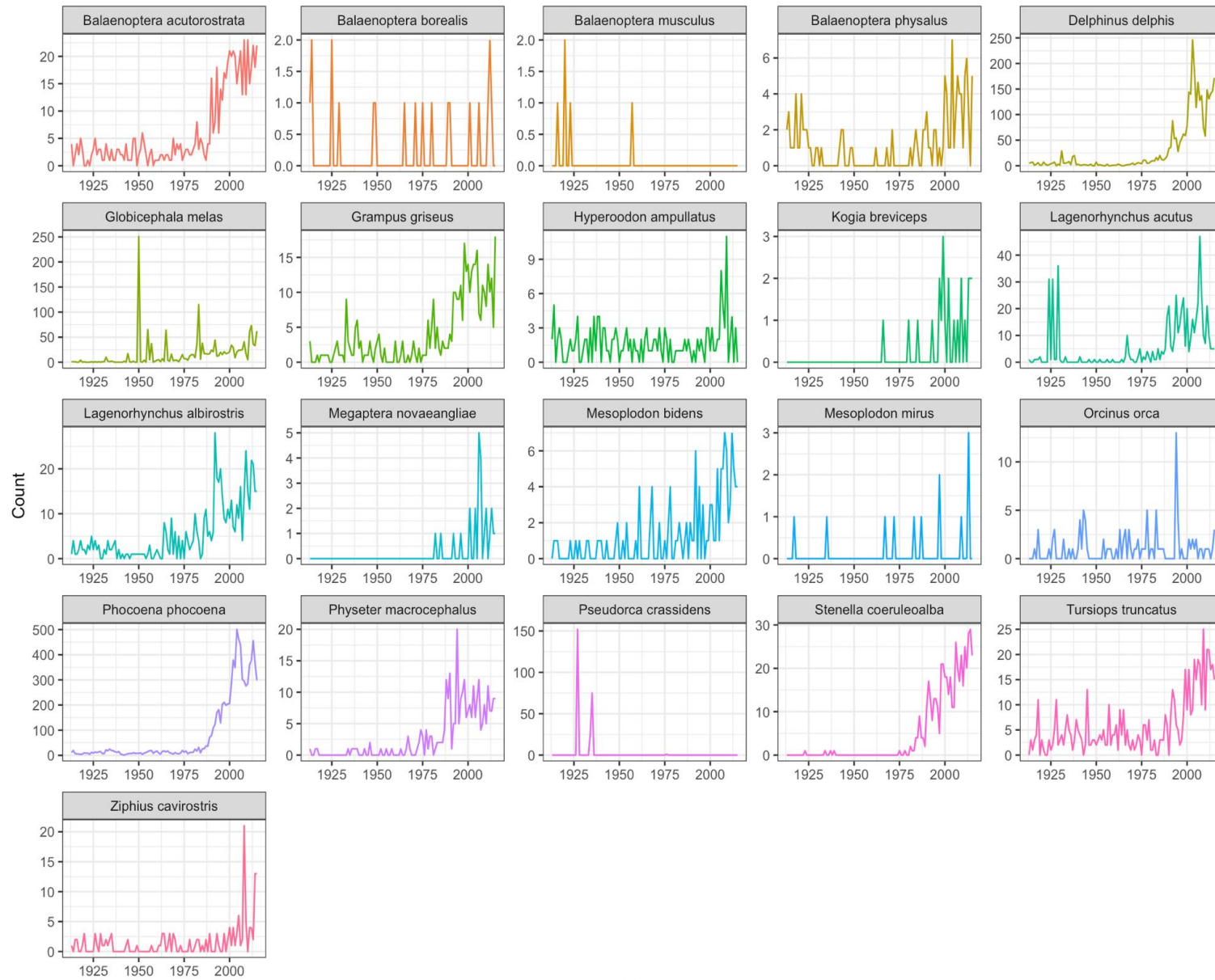
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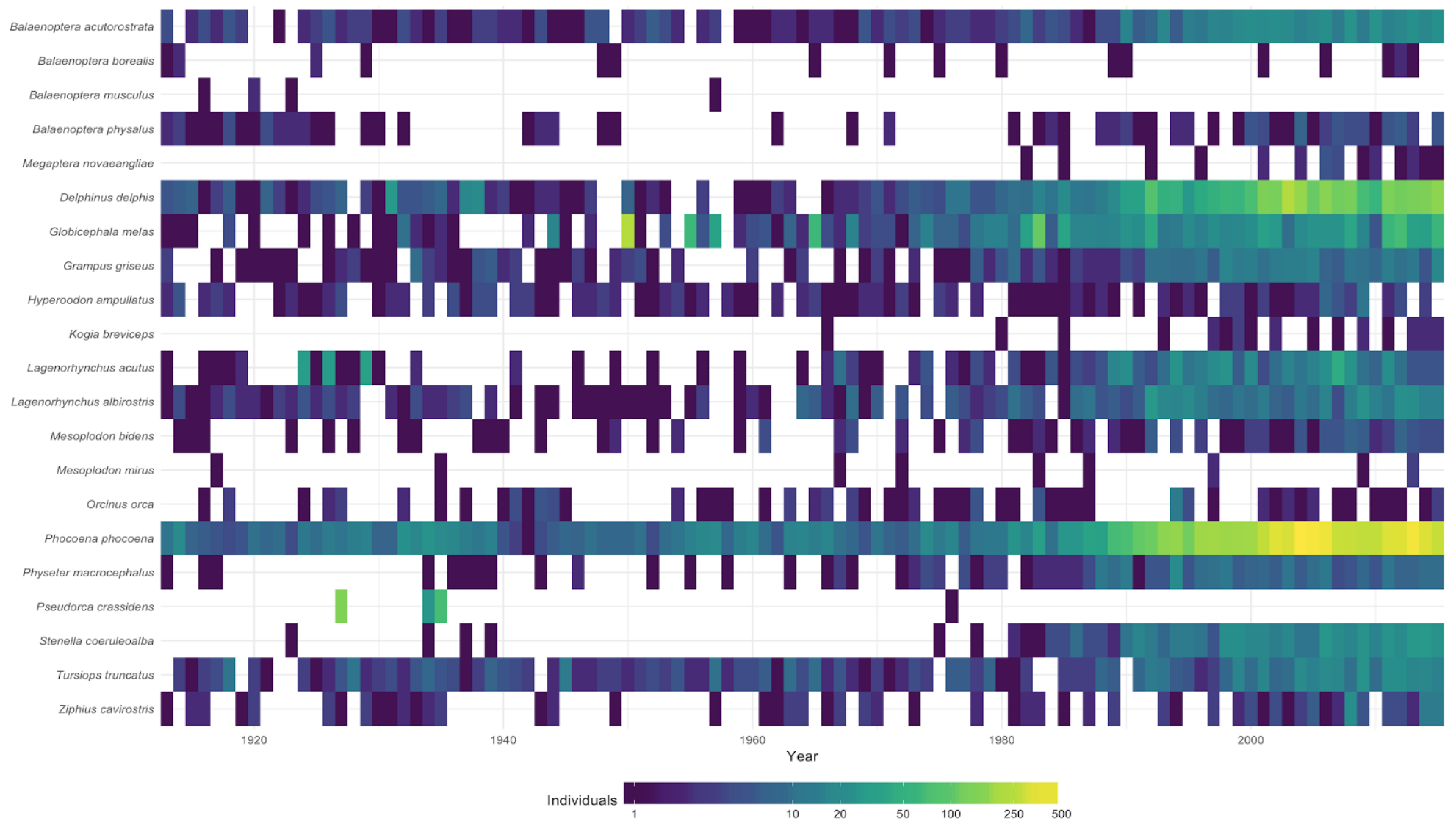
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1009 **Figure 1.** Predictor variables thought to correlate with cetacean strandings. From top left to
1010 bottom right: Storm count, Geomagnetic index (k-index), maximum sea surface temperature
1011 (° C), North Atlantic Oscillation index, Fishing count (1,000 tons), and human population
1012 (millions). All variables show data for the UK and Ireland, apart from Geomagnetic index and
1013 human population which show data for the UK only. All data are shown from 1913 – 2015.
1014 Details on how the data were obtained is in Table 1 and the Supplemental Information; Data
1015 collection. Extra details on each of the variables are in the Supplemental information; Data
1016 collection.



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1019 **Figure 2.** Temporal stranding patterns of each cetacean species stranding in the UK and
1020 Ireland from 1913-2015. The y-axis shows total stranding count per year, the x-axis shows
1021 the year. Note that y-axis scales are different for different species.

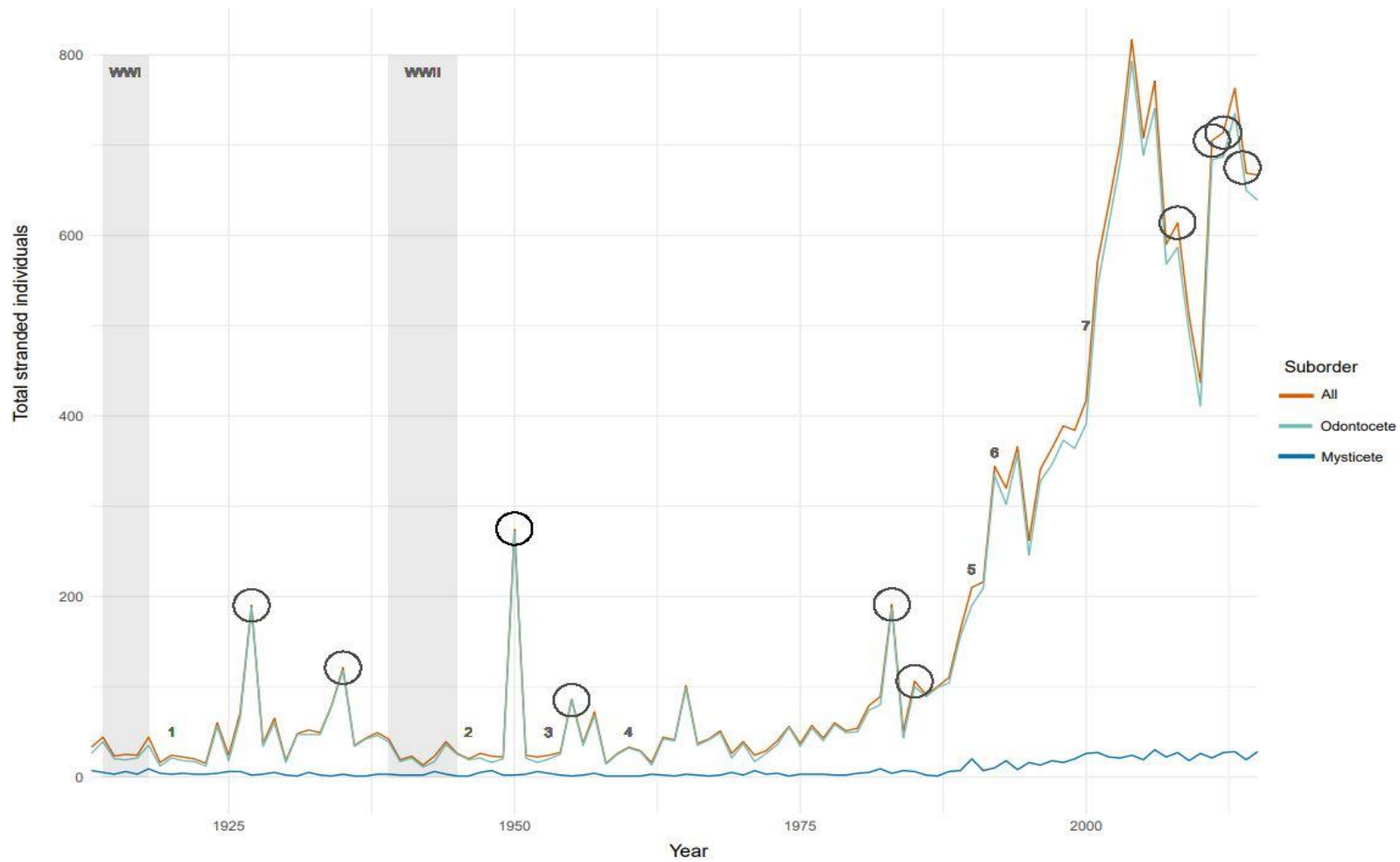


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1025 **Figure 3.** Stranding events of cetacean species in UK and Irish waters from 1913-2015. The
1026 x axis shows the years 1913-2015 with individual tiles representing one year. The y axis
1027 shows the species found in the UK and Irish stranding records. The first five species are
1028 mysticetes (baleen whales), and the rest of the species are odontocetes (toothed whales).
1029 The colored boxes show the number of individuals that stranded each year. Dark blue shows
1030 one to a few individuals, yellow shows more than 200 individuals.

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1. 1920s: Sonar use in French and UK waters
2. 1946: NATO military testing in European waters: submarine, sonar, & torpedo testing increase
3. 1950s: Increase in post-war fishing & whaling effort
4. 1960s: Increase in use of polychlorinated biphenyls (PCBs) and other chemical pollutants
5. 1985/86 season: Moratorium on whaling comes into effect
6. 1990: The CSIP and IWDG programmes start
7. 2000s: Increase in pile-driving for offshore wind turbines

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1037 **Figure 4.** Temporal variation in cetacean strandings records for all species, odontocetes

1038 (toothed whales), and mysticetes (baleen whales) in the waters around the UK and Ireland

1039 from 1913-2015. 1913 is when the NHM started to record cetacean strandings. The plot

1040 shows strandings through time for all species (orange), odontocetes (blue), and mysticetes

1041 (green). The y axis shows total number of individuals that stranded each year. Key

1042 anthropogenic events are labelled with numbers, with the corresponding key below the plot.

1043 Key periods are shaded in light grey. WWI is World War I, WWII is World War II, CSIP is the

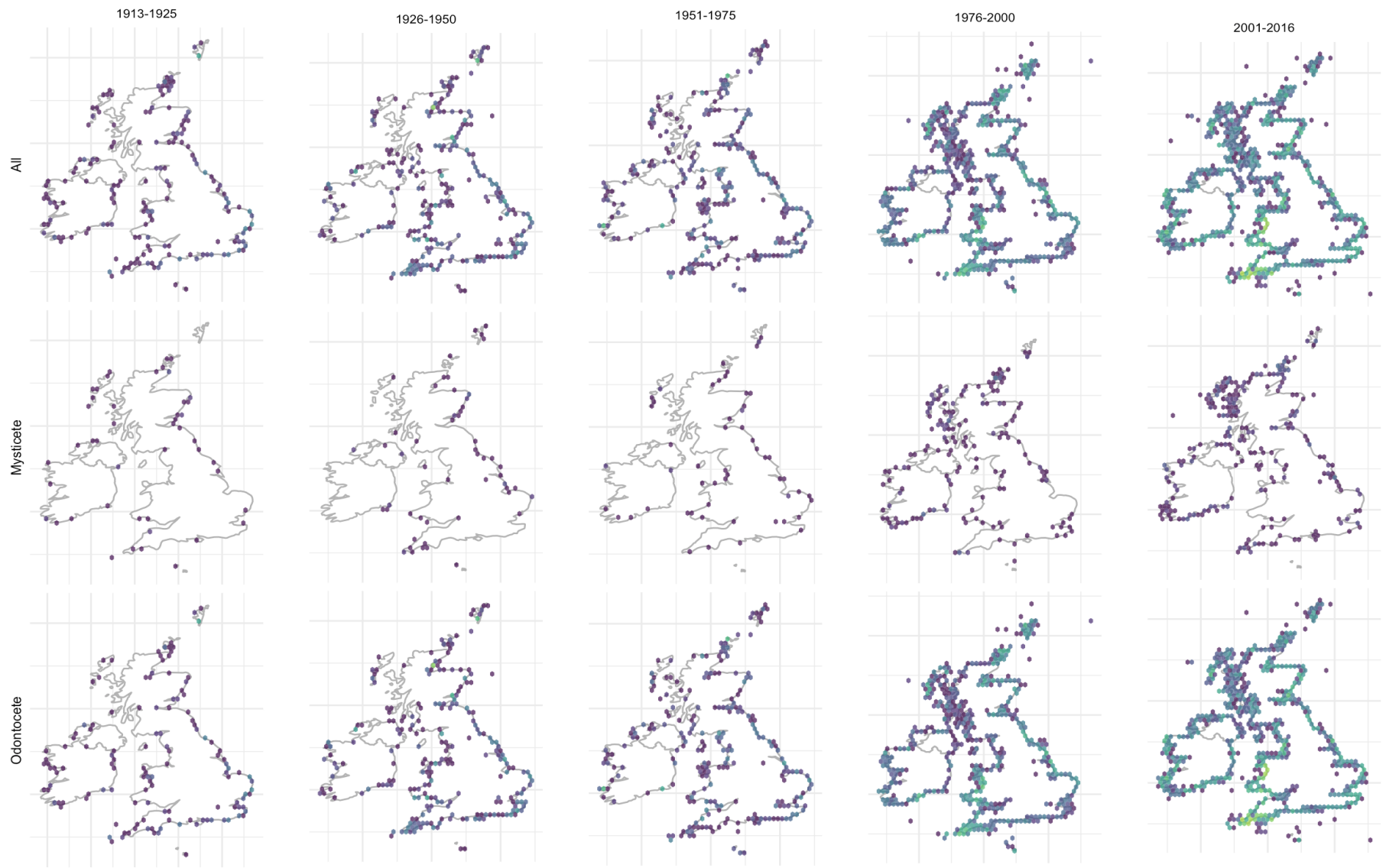
1044 Cetacean Stranding Investigation Programme, IWDG is the Irish Whale and Dolphin Group

1045 Cetacean Stranding Scheme. The circles highlight years with mass strandings of > 20

1046 individuals.

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1051 **Figure 5.** Temporal and spatial variation in cetacean stranding records for all species,
1052 odontocetes (toothed whales), and mysticetes (baleen whales) in the waters around the UK
1053 and Ireland from 1913-2015 at 25-year intervals. Low numbers of strandings are shown as
1054 dark blue, higher numbers of strandings shown in light green, the highest numbers of
1055 strandings are shown in yellow.

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1059 **Table 1.** Predictor variables thought to correlate with cetacean strandings. Units, data type,
1060 and source of raw data are shown. SST is sea surface temperature, NAO is North Atlantic
1061 Oscillation. Human population data are used as an offset in our models. Details on how each
1062 of these variables were sourced and calculated can be found in the Supplemental
1063 information: Data analysis.

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1065 <Table on next page>

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Variable	Data	Sources
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(units)		
Storm events (count/year)	Storm events over 47 knots	Lamb and Frydendahl (1991) Met Office, UK Multiple sources: https://github.com/EllenJCoombs/strandings-project
Geomagnetic activity (K - index)	The K-index is used to characterize the magnitude of geomagnetic storms. The range is 0–9, with 1 being calm and 5 or more indicating a geomagnetic storm Three-hourly readings obtained from: 1913 - 1925: Greenwich 1926 - 1939: Abinger 1940 - 1956: Abinger, Eskdalemuir and Lerwick 1957 - 2015: Hartland, Eskdalemuir and Lerwick A mean maximum yearly K-index reading was used in the model	British Geological Survey
Sea surface temperature (°C)	Maximum yearly SST from 14 UK and Irish locations (Supplemental information; Fig. S1). A mean maximum yearly reading was used in the model (Supplemental information; Fig. S2).	Met Office: HadISST
North Atlantic Oscillation (mb)	Yearly readings The NAO is based on the difference of	University Corporation for Atmospheric Research

	normalized sea level pressure (SLP) between Stykkisholmur/Reykjavik, Iceland, and Lisbon, Portugal.	
Yearly fishing catch (1000 tonnes)	Total yearly catch (1000 tonnes) data of ~ 58 species in UK and Ireland. Combined datasets for England and Wales, Scotland, Northern Ireland, and Ireland to get a yearly total.	International Council for the Exploration of the Sea (ICES)
UK and Ireland yearly human population	1913-1922 are figures for England, Wales and Scotland; from 1922, onwards Northern Ireland is included	Office of National statistics (ONS)

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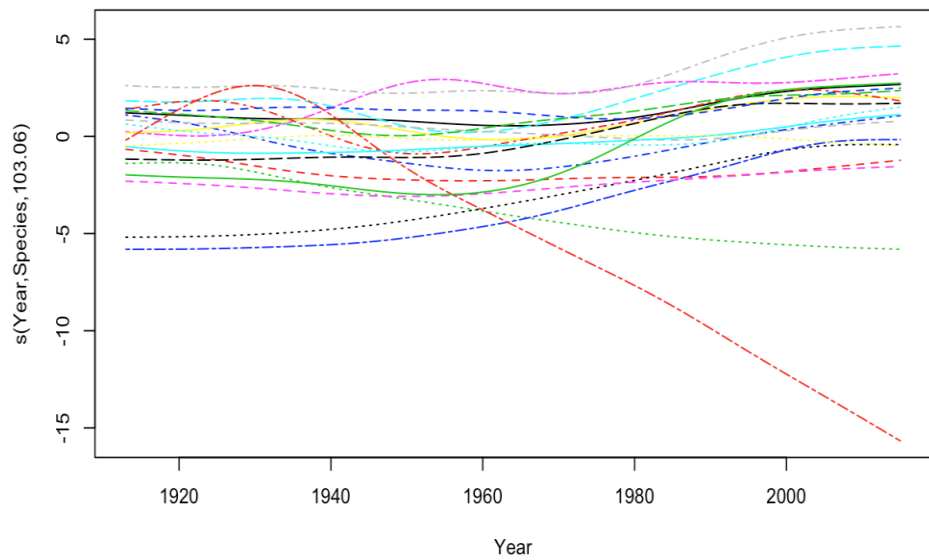
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s(Storms)	< 0.001	0.94	6.0
s(Max_K_index)	< 0.001	0.79	4.0
s(Max_SST)	2.40	< 0.001	9.0
s(NAO_index)	0.92	< 0.05	9.0
s(Fish_catch)	0.79	0.02	9.0
s(Year, Species)	103	< 0.001	210

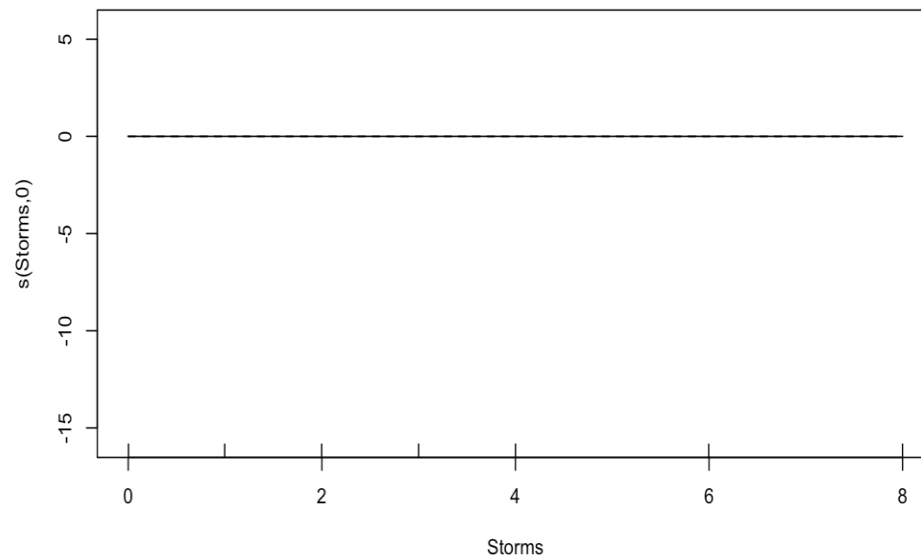
1082 **Table 2** Generalized additive model (GAM) outputs from a model of correlates of strandings
1083 for the UK and Ireland, from 1913-2015. s() are smooths of the explanatory variables.
1084 'Storms' refer to the storm count for each year, 'Max_K_Index' is the geomagnetic reading
1085 (where the K-index is used to characterize the magnitude of geomagnetic storms),
1086 'Max_SST' is the yearly maximum sea surface temperature (°C), 'NAO_index' is the North
1087 Atlantic Oscillation which is the difference of normalized sea level pressure (SLP) between
1088 Stykkisholmur/Reykjavik, Iceland, and Lisbon, Portugal, 'Fish_catch' is annual fish catch
1089 (1,000 tons) for the UK and Ireland, 'Year' is the years 1913-2015, 'Species' are the 21
1090 cetacean species that make up the data set. This table shows the estimated degrees of
1091 freedom (EDF) for each of the different predictor variables. The *P*-values show whether the
1092 smooth of that variable is significantly different from "no effect", *i.e.*, if we estimated the
1093 smooth as a flat line at zero. k shows the maximum basis complexity.

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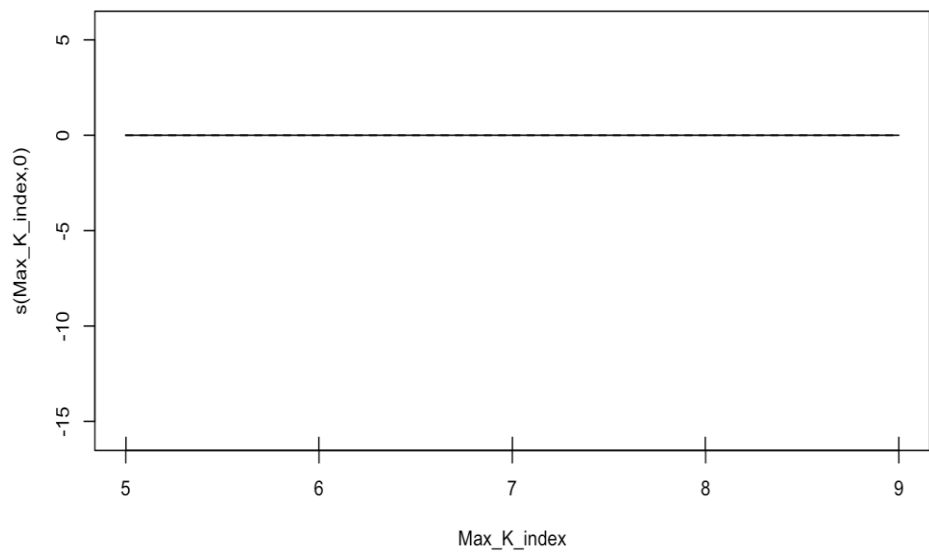


b)

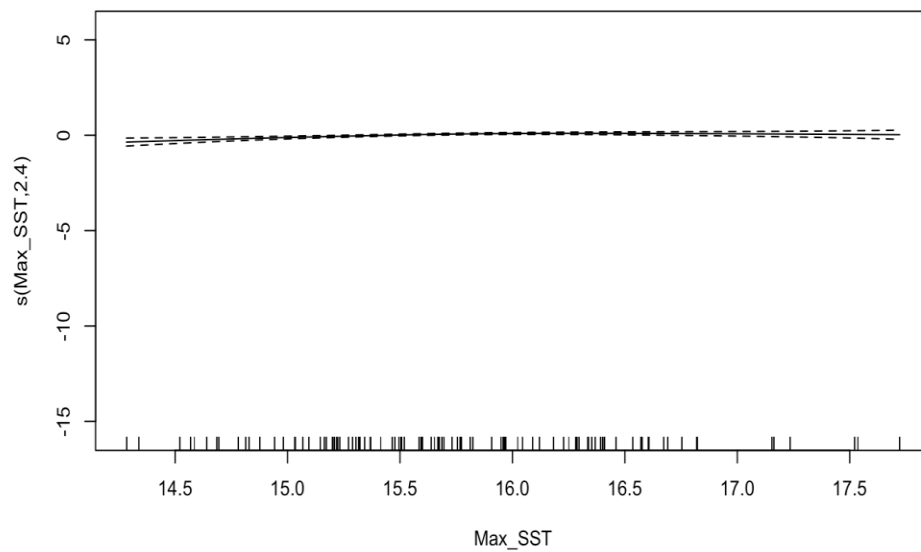


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c)

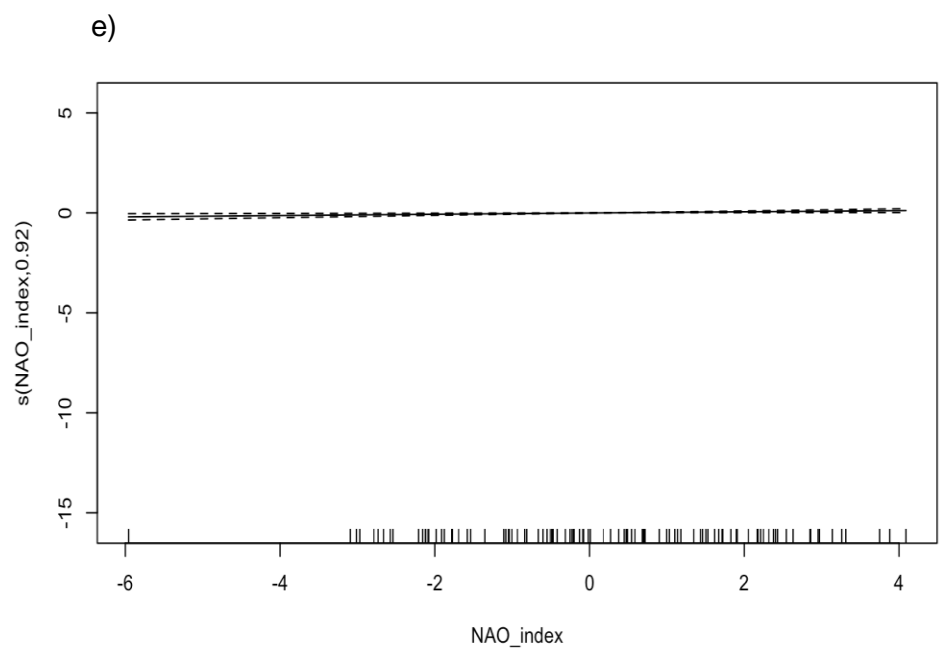


d)

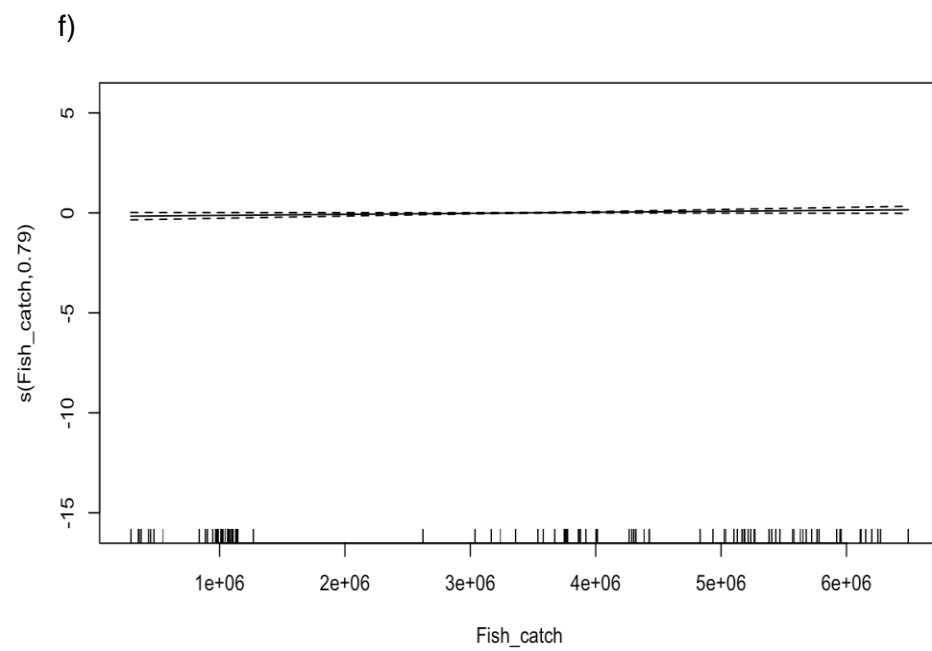


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1101 **Figure 6.** Generalized Additive Model (GAM) summary plots for variables included in the
1102 final model of correlates of cetacean strandings; a) Year, Species smooth, b) Storm events
1103 s(Storms), c) Geomagnetic index, s(Max_K_index), d) Maximum sea surface temperatures,
1104 s(Max_SST), e) North Atlantic Oscillation index, s(NAO_index), f) Annual fishing catch,
1105 s(Fish_catch). X-axis shows the values for that variable (*i.e.*, the year 1913-2015 (a), storm
1106 counts (b), maximum k-index value (c), Maximum sea surface temperature (°C) (d), NAO
1107 index value (e), and fishing catch (1,000 tons) (f). The y-axis shows the smooth and the
1108 estimated degrees of freedom (EDF) (*e.g.*, s(Max_SST, 2.4). These EDF values are also
1109 reported in Table 2. Modelled using the negative binomial response count distribution. The
1110 model has a deviance explained of 84.5%, $n = 2163$.

1111 **Table 3.** Generalized additive model (GAM) outputs from additional models. ‘1990s model’ is
 1112 correlates of stranding GAM using only CSIP and IWDG stranding data (1990 – 2015).
 1113 ‘Regional model 1’ is correlates of stranding GAM using data from the south west of the UK.
 1114 ‘Regional model 2’ is correlates of stranding GAM using data from the north west of the UK.
 1115 s() are smooths of the explanatory variables. ‘Storms’ refer to the storm count for each year,
 1116 ‘Max_K_Index’ is the geomagnetic reading (where the K-index is used to characterize the
 1117 magnitude of geomagnetic storms), ‘Max_SST’ is the yearly maximum sea surface
 1118 temperature (°C), ‘NAO_index’ is the North Atlantic Oscillation which is the difference of
 1119 normalized sea level pressure (SLP) between Stykkisholmur/Reykjavik, Iceland, and Lisbon,
 1120 Portugal, ‘Fish_catch’ is annual fish catch (1,000 tons) for the UK and Ireland, ‘Year’ is the
 1121 years 1990-2015 in the 1990s model, and 1991-2015 in the Regional models. ‘Ships_tons’ is
 1122 the combined yearly weight of ships over 500 tons in the UK, as a proxy for ship strike.
 1123 ‘Species’ are the cetacean species that make up the strandings dataset. This table shows
 1124 the estimated degrees of freedom (EDF) for each of the different variables. The *P*-values
 1125 show whether the smooth of that variable is significantly different from “no effect”, *i.e.*, if we
 1126 estimated the smooth as a flat line at zero.

Correlates as modelled	1990s model	Regional model 1	Regional model 2
s(Storms)	0.79*	0.93*	0.81*
s(Max_K_index)	0.38	< 0.001	0.12
s(Max_SST)	< 0.001	< 0.001	< 0.001
s(NAO_index)	1.36**	6.62**	1.11**
s(Fish_catch)	0.79*	3.95**	2.38**
S(Ships_tons)	1.13**	4.40**	1.07**
s(Year, Species)	43.0**	40.1**	25.5**

1127 **P* < 0.05; ***P* < 0.01

Species	Year			Storms			Geomagnetic k-index			Maximum SST (°C)			NAO index			Fishing catch		
	EDF	P-value	k	EDF	P-value	k	EDF	P-value	k	EDF	P-value	k	EDF	P-value	k	EDF	P-value	k
<i>Balaenoptera acutorostrata</i>	4.98	< 0.001	9	0.51	0.14	4	0.23	0.25	3	0.71	0.06	9	< 0.001	0.96	9	0.79	0.02	9
<i>Balaenoptera physalus</i>	3.57	< 0.001	9	0.94	< 0.005	4	0.58	0.13	3	< 0.001	0.58	9	0.93	< 0.005	9	0.79	0.02	9
<i>Delphinus delphis</i>	7.03	< 0.001	9	0.58	0.11	4	0.87	0.02	3	< 0.005	0.48	9	0.13	0.30	9	0.84	0.01	9
<i>Globicephala melas</i>	< 0.001	0.93	9	< 0.001	0.86	4	< 0.001	1.00	3	1.02	< 0.001	9	< 0.001	0.76	9	0.67	< 0.001	9
<i>Grampus griseus</i>	56.3	< 0.001	9	< 0.001	0.53	4	0.84	0.02	3	< 0.001	0.56	9	< 0.001	0.18	9	0.66	0.05	9
<i>Hyperoodon ampullatus</i>	< 0.001	0.95	9	0.36	0.22	4	1.03	< 0.001	3	< 0.001	0.33	9	< 0.001	0.43	9	< 0.001	0.59	9
<i>Lagenorhynchus acutus</i>	7.21	< 0.001	9	0.50	0.16	4	< 0.001	0.21	3	< 0.001	0.91	9	< 0.001	0.60	9	< 0.001	0.59	9
<i>Lagenorhynchus albirostris</i>	3.70	< 0.001	9	< 0.001	0.57	4	0.14	0.28	3	< 0.001	0.77	9	< 0.001	0.82	9	0.61	0.08	9
<i>Mesoplodon bidens</i>	1.20	< 0.001	9	< 0.001	0.46	4	< 0.001	0.66	3	< 0.001	0.54	9	< 0.001	0.09	9	< 0.001	0.40	9
<i>Orcinus orca</i>	0.64	0.10	9	0.75	0.05	4	< 0.001	0.47	3	< 0.001	0.38	9	< 0.001	0.80	9	< 0.001	0.76	9
<i>Phocoena phocoena</i>	8.27	< 0.001	9	0.74	0.05	4	< 0.005	0.67	3	0.89	0.01	9	0.04	0.32	9	0.39	0.19	9
<i>Physeter macrocephalus</i>	4.19	< 0.001	9	0.71	0.05	4	< 0.001	0.80	3	< 0.001	0.44	9	< 0.005	0.31	9	< 0.001	0.75	9
<i>Pseudorca crassidens</i>	1.04	0.05	9	< 0.001	0.88	4	< 0.001	0.46	3	0.99	0.07	9	< 0.001	0.76	9	< 0.001	0.93	9
<i>Stenella coeruleoalba</i>	5.45	< 0.001	9	< 0.001	0.89	4	< 0.001	0.83	3	< 0.001	0.75	9	0.76	0.05	9	0.18	0.24	9
<i>Tursiops truncatus</i>	3.54	0.001	9	< 0.001	0.92	4	< 0.001	0.90	3	< 0.001	0.77	9	< 0.001	0.79	9	< 0.001	0.79	9
<i>Ziphius cavirostris</i>	2.70	0.001	9	< 0.001	0.95	4	< 0.001	1.00	3	< 0.001	1.00	9	< 0.001	0.45	9	< 0.001	0.76	9

1128 **Table 4.** Generalized additive model (GAM) outputs from a model of correlates of strandings for the UK and Ireland, from 1913-2015 for each
1129 individual species. ‘Storms’ refer to the storm count for each year, ‘Geomagnetic k-index’ is the geomagnetic reading (where the K-index is
1130 used to characterize the magnitude of geomagnetic storms), ‘Maximum SST’ is the yearly mean maximum sea surface temperature (°C), ‘NAO
1131 index’ is the North Atlantic Oscillation which is the difference of normalized sea level pressure (SLP) between Stykkisholmur/Reykjavik, Iceland,
1132 and Lisbon, Portugal, ‘Fishing catch’ is annual fish catch from the UK and Ireland (1,000 tons), ‘Year’ is the years 1913-2015, ‘Species’ are the
1133 16 cetacean species which had 100 or more strandings in the dataset. Rarer species were removed because they had insufficient data to fit the
1134 models. This table shows the estimated degrees of freedom (EDF) for each of the different predictor variables. The P-values show whether the
1135 smooth of that variable is significantly different from “no effect”, *i.e.*, if we estimated the smooth as a flat line at zero. k shows the maximum
1136 basis complexity.
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