What can cetacean stranding records tell us? A study of UK and Irish cetacean diversity over the past 100 years

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Abstract

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

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

Introduction

Cetaceans (whales, dolphins, and porpoises) are major components of oceanic ecosystems (Roman *et al.* 2014). They are top predators and their distributions can provide an indication of prey abundance and wider ocean health (Friedlaender *et al.* 2006, Burek *et al.* 2008, Roman *et al.* 2014). Unfortunately, many cetacean species are threatened (Reeves *et al.* 2003, IUCN SSC, 2018) and are vulnerable to anthropogenic impacts, such as incidental entanglement in fishing gear (bycatch), ship strikes, hunting, chemical or noise pollution and environmental changes across their ranges (Parsons *et al.* 2010, Ramp *et al.* 2015). It is therefore important to monitor cetaceans to determine the impacts of these pressures on their abundance and behavior (Bejder *et al.* 2006). As with other marine species, cetaceans can prove difficult to study as they are often wide-ranging and spend most of their lives submerged under water (Evans and Hammond, 2004). Frequently employed monitoring techniques, such as surveying from boats, are not only expensive and time consuming, but are often biased towards conspicuous species or those that respond positively to boat presence, such as bottlenose dolphins (*Tursiops truncatus*) and short-beaked common dolphins (*Delphinus delphis*; Evans and Hammond, 2004). One approach to these constraints is to use strandings data, *i.e.*, records of cetaceans that have washed ashore.

Stranding records are the primary source of information for many elusive species, such as beaked whales (Ziphiidae; Morin *et al.* 2017) and can provide an indication of relative abundance and richness in extant cetacean communities (Evans and Hammond, 2004, Maldini *et al.* 2005, Pyenson, 2011). Globally, there are several long-term, regional stranding datasets: the northwest Pacific USA, *e.g.*, Norman *et al.* (2004) who reported 904 records, concluding that most reports are made in summer time when sampling effort is higher; Hawaii, *e.g.*, Maldini *et al.* (2005); who documented 202 odontocete strandings; the Netherlands, *e.g.*, Murphy *et al.* (2006) who have ~10,000 strandings records to date, the majority of which are harbor porpoises; and Australia, *e.g.*, Evans *et al.* (2005), who analyzed 639 stranding events comprising 39 taxonomic groups. The Australian dataset only has 21 records gathered prior to 1960 (Lloyd and Ross, 2015), while the Hawaiian and North American datasets have limited accuracy prior to the 1960s and 70s when systematic recording of strandings became more standardized (Pyenson, 2010). The Dutch dataset has systematic records dating back to at least the 1920s (Murphy *et al.* 2006), with some records dating back hundreds of years. Similarly, the Irish Whale and Dolphin Group (IWDG) stranding records date back to the 18th Century. Although globally there are several long-term stranding datasets the majority of them are not systematic, nor as long-term as the one we present here. The Natural History Museum, London (NHM) has maintained a database of UK strandings since 1913, making it one of the longest, continuous, systematic cetacean stranding datasets in the world (NHM, 2018). The program became part of the Cetacean Strandings Investigation Programme (CSIP) in 1990, which continues to record cetacean strandings in the UK to the present day and investigates the causes of strandings through systematic postmortem examinations, under contract to the UK government (CSIP, 2019). The IWDG has been systematically recording strandings since 1990 (IWDG, 2019). Despite records being available up to 2015, no comprehensive studies of temporal changes in cetacean strandings exist for this full time period, *i.e*., from 1913-2015. The unique characteristics of this data set are ideal for investigating trends and inter-annual variability in cetaceans strandings alongside anthropogenic and/or environmental changes.

Potential correlates of strandings

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

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

Methods

Study area

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

Strandings datasets

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

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

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

Correlates of strandings through time

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

We considered drivers of changes in strandings through time. We fitted models of numbers of individuals stranded against various predictor variables thought to correlate with cetacean strandings (Table 1, Fig.1). We included the following predictors because they have been reported to potentially influence strandings, and because we could collate data for them on a yearly basis for the UK and Ireland for the full-time span of our dataset (1913-2015) (Supplemental information: Data Collection). **(1) Geomagnetic activity.** Some cetaceans, such as sperm whales (*Physeter macrocephalus*) may use Earth's geomagnetic fields for navigation (Kirschvink *et al.* 1986, Kremers *et al.* 2014, Vanselow *et al.* 2017), thus changes in geomagnetic activity, *e.g.,* solar storms, may affect their navigation and increase the likelihood of strandings (Vanselow *et al.* 2017). **(2) Sea surface temperature (SST)**. Changes in SST (°C) can affect prey abundance, resulting in net movements of cetaceans as they follow their prey (Pierce *et al.* 2007, Simmonds and Eliott, 2009), which could result in changes in cetacean distribution and therefore the spatial distribution of strandings. **(3) Storm events.** Storm conditions, hurricane events and associated oceanographic disturbances may increase strandings (Mignucci-Giannoni *et al.* 2000, MacLeod *et al.* 2004, Bogomolni *et al.* 2010) as individuals suffer from exhaustion, disorientation, or direct physical injury. Further, these impacts can also affect food sources (Lawler *et al.* 2007, Evans *et al.* 2005), which may alter cetacean distributions and therefore the likelihood of strandings. **(4) North Atlantic Oscillations (NAO).** Fluctuations in the NAO can affect prey distribution and abundance via associated wind and temperature changes (Hurrell, 1995, Pierce *et al.* 2007). Low NAO indexes have been associated with physiological stress in North Atlantic right whales (*Eubalaena glacialis*). Note that although NAO and storms, and NAO and SST are related, they are not strongly correlated ($r^2 < 0.16$ and $r^2 < 0.001$ respectively; Supplemental information; Environmental variables). Therefore, we included all three variables. **(5) Fishing catch.** Over-fishing can have a direct impact on cetaceans due to a reduction of their prey (Evans, 1990, Weir *et al.* 2007), causing starvation, or a shift in cetacean distribution as they search for prey elsewhere. Further, discarded or fixed fishing nets and creel lines are partly responsible for cetacean mortality as bycatch (Leeney *et al.* 2008). Note that ideally, we would have included sonar use, bycatch, and chemical pollution, but none of these variables were available for every year in our dataset (*i.e.,* 1913 - 2015), particularly for the historical data. We ran a model that included a proxy for shipping traffic, but these data were only available for 1950-2015 (Supplemental Information; Shipping model). Sources and units of the main model dataset are in Table 1.

<Table 1>

<Figure 1>

Generalized additive models (GAMs)

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

We modelled the total number of stranded individuals as a sum of smooth functions of covariates in a GAM framework (1). In an attempt to account for changes in the potential for detection of stranded cetaceans through time we included yearly UK population size based on the assumption that as population size increases, or activity in an area increases, it is more likely that strandings will be observed and reported (Norman *et al.* 2004, Maldini *et al.* 2005, Pyenson, 2011, McGovern *et al.* 2016). Stranding studies highlight the importance of considering population growth as a proxy for observer effort (Maldini *et al.* 2005, Pyenson, 2011). However, it is often difficult to obtain accurate population estimates over the time frame of these stranding databases or in regions where populations have varied considerably (*e.g.,* the Hawaiian Islands, Maldini *et al.* 2005)., we used yearly UK human population size (Table 1) as an offset in the model. To further investigate the impacts of sampling effort, we ran two case study models that look at differences in population between the populated southern UK, and the less populated northern UK (Supplemental information; Regional study 1 & 2). Smooths were modelled using a thin plate spline basis with shrinkage (Marra and Wood, 2011), which allowed terms to be removed from the model (*i.e.,* their effect size shrunk to zero) during fitting, thus terms were selected during model fitting. As we wanted to model species-specific effects, we included a factor-smooth interaction between year of stranding and species; this term fitted a smooth of time for each species but allowed common smooths to be fitted for the other covariates. An advantage of this approach is that the per-species smooths are estimated as deviations from a base-level smooth, so some information is shared between species. We fitted models with the following candidate response count distributions: Poisson, quasi-Poisson, negative binomial, and Tweedie. We used standard residual checks for GAMs (Q-Q plot, histogram of residuals, residuals *vs.* linear predictors, response *vs.* fitted values) to decide between response distributions and assess model fit. We report the results using the negative binomial distribution as this was the best fit for the data (Supplemental information: GAM candidate response distributions) with each of the different response distributions (Supplemental information: Fig. S7:S10).

The total number of stranded individuals was modelled as a sum of smooth functions of the k explanatory variables z_{tk} using a GAM with the general formulation:

(1)

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

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

We fitted models using Restricted Maximum Likelihood (REML) in the R mgcv package version 1.8.17 (Wood, 2011). REML was preferable because when models contain highly correlated covariates, REML finds an optimal degree of smoothing (Reiss and Ogden 2009). In a GAM, k is the maximum complexity of the basis used to represent the smooth term. If the k value is high enough, we can be sure that there is enough flexibility in the model. We can find out if k is high enough by increasing the k value and refitting the original model (Supplemental information: Setting the k parameter). After refitting the model and analyzing the GAM output, we set the k parameter for storm events and geomagnetic activity to k = 7 and k = 4, respectively. The k parameter did not need to be set for NAO, SST, or fishing catch because these terms had more unique covariate combinations than the specified maximum degrees of freedom. To avoid fitting overly complex models, the maximum basis size for the smooth terms were limited to these values. Finally, we plotted the residuals by covariate (Supplemental information; GAM model checking) to confirm the goodness of our model fit. These plots showed low variation in the covariate residuals suggesting that the model is a good fit (Fig. S11).

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

Sensitivity analyses

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

Species identification models

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

Species specific models

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

Ship strike models

To investigate ship strike effects on strandings we ran a model that included a proxy for shipping traffic around the UK. These data were only available from 1950-2015; therefore, the other predictors and the response were constrained accordingly, and shipping was not included in the full model. Note that we use shipping traffic as a proxy for ship strikes because direct ship strike data was not available historically, and even those data available mainly focus on mysticetes or are geographically restricted.

Stranding events models

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

Suborder models

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

Habitat models

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

Regional models

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

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

Results

Data exploration

Temporal and spatial patterns in the strandings data

A total of 17,491 strandings comprising 21 species were recorded. The dataset contains 786 mysticete records from five species, and 16,705 odontocete records from 16 species. Temporal and spatial patterns in strandings varied across and within species (Fig. 2, 3).

<Figure 2>

<Figure 3>

Some species *e.g.,* blue whales and false killer whales (*Pseudorca crassidens*), stranded in the earlier parts of the time series but then disappear from the strandings record (Fig. 3). Conversely, some species appear for the first time in the latter half of the century. For example, the first humpback whale stranding record was in 1982 and the first pygmy sperm whale stranding was recorded in 1966 (Fig. 2, 3). Species such as northern bottlenose whales (*Hyperoodon ampullatus*) and Cuvier's beaked whales (*Ziphius cavirostris*) have stranded consistently throughout the century, with an increase in records towards the present day.

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

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

The most frequently stranded species were harbor porpoise (*Phocoena phocoena*; *n* = 8,265; 47% of all stranding records), short-beaked common dolphin (*Delphinus delphis*; *n* = 3,110; 18% of all stranding records) and long-finned pilot whale (*Globicephala melas*; *n* = 1,606; 9% of all stranding records) (Fig. 2, 3). Mysticete strandings were much less frequent (Fig. 4) and accounted for around 4% of total strandings records. Mysticete strandings showed an overall decline throughout the century until the 1980s. Generally stranding records of all odontocetes increased throughout the 1990s to the present. The exceptions were false killer whale, as previously mentioned, and killer whale (*Orcinus orca*) that stranded intermittently in low numbers, with one mass stranding event (*n* = 11) in 1994 in Scotland. 1990 was the first year that mysticete stranding records reached double figures. There was an increase in mysticete strandings after 1987 and throughout the 1990s to the present. Minke whales *(Balaenoptera acutorostrata*) accounted for 79% of all mysticete strandings and also accounted for the majority of the post-1990 rise in mysticete strandings.

Mysticete records remained low throughout the 1950s and 60s (Fig. 4). There was a slight decline in the number of odontocete stranding records during the early period of WWII, but there are other years throughout the time period that reported lower numbers of odontocete strandings. The CSIP and IWDG programs began in 1990, after which there was an increase in stranding records for both mysticetes and odontocetes (Fig. 3, 4).

<Figure 4>

<Figure 5>

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

Correlates of strandings through time

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

<Table 2>

<Figure 6>

Sensitivity analyses

We found significant *P*-values for some variables in our sensitivity analyses (see below for details) suggesting the smooth of these variables were significantly different from “no effect". However, the EDFs for all variables (with a few exceptions; see below) were low, indicating that across all sensitivity analyses the number of individuals that strand was not strongly influenced by any of our predictor variables, except year of stranding, *i.e.,* our results were qualitatively identical to those for the full model described above. This was true across all sensitivity analyses (Tables S4, S5, S7-S12, S15 and Fig. S15, S16, S18-S23); therefore, we only report the differences below. All results are compiled in Table S15.

Species identification models

In the genus-level models we found significant effects for SST, NAO index, and fishing catch ($P < 0.001$, $P = 0.01$, $P = 0.01$, respectively) (Table S5, Fig. S16). For the CSIP and IWDG (1990 – 2015) data we found significant *P*-values for storms, NAO, fishing catch, and shipping traffic (Table 3, Fig. S17).

Species specific models

When we removed harbor porpoises from the dataset we found significant effects for SST, NAO, and fishing catch ($P < 0.001$, $P = 0.001$, $P = 0.07$, respectively) (Table S7, Fig. S18) and showed that the original model was not merely reflecting a signal in the harbor porpoise data. When we modelled harbor porpoise only, we found a significant *P*-value for SST ($P < 0.01$) but no influence of any of the other predictor variables. When modelling each species separately, we found no influence of any of the predictor variables (Table 4).

Ship strike models

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

Stranding events models

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

Suborder models

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

Habitat models

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

Regional models

The two regional models had different EDFs, with higher EDFs found in the southwest (region 1) model (Table 3). We found significant *P*-values for all of the variables except for maximum k-index and maximum SST in both models (Table S13, S14). The region 1 model had an EDF of 6.62 for NAO but the relationship was not particularly "wiggly". We therefore interpret this as having little effect on the number of stranded individuals (Wood, 2017). The EDFs for the other variables were still too low to be fully conclusive (Table 3, Fig. S24, S25).

<Table 3>

<Table 4>

Discussion

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

Temporal and spatial patterns in the strandings data

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

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

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

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

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

Correlates of strandings through time

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

Storms

We found no significant indication of storms as a correlate for strandings records. Storm events have been reported to have a greater effect on smaller, shallow water species (Lawler *et al.* 2007, Schumann *et al.* 2013). However, we found no such effect in any of our 16 species-specific models, including our harbor porpoise only model, nor in our suborder model despite odontocetes generally having a smaller body size. Further, we found no effect of storms on strandings in our habitat model, despite storms potentially affecting shallow, coastal water species to a greater extent (Lawler *et al.* 2007). We suggest that these effects may be population, location, or season-specific. Further, carcasses of offshore species may be blown onshore during storm events making species-specific impacts harder to identify; consistent data on carcass condition would be required to analyze this. Stormy weather can increase the chances of mass stranding events in some species, sometimes with multiple species stranding together (Bogomolni *et al.* 2010, Schumann *et al.* 2013), however, we found no effect of storms when we included mass strandings as multiple events (*i.e.,* each species in that location, on that date is a single record). Again, it is likely that the scale of change in our variables is too coarse to model these effects.

Geomagnetic fluctuations

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

North Atlantic Oscillation (NAO)

In contrast to other studies (Pierce *et al.* 2007, Truchon *et al.* 2013), we found only a slight effect of NAO on the number of stranding events in our main model. However, this was so small that it was inconclusive. Previously, positive NAO indices have been positively correlated with high stranding frequencies for seasonal migratory cetaceans (such as minke whales) in the Atlantic (Truchon *et al.* 2013). Further, incidences of sperm whale strandings in the North Sea are higher during warm periods (associated with the NAO and higher SST), a likely reflection on changes in distribution of their prey (Robinson *et al.* 2005, Pierce *et al.* 2007). Again, this may be because many of these previous studies focus on one species, in a specific geographical region (*e.g.,* the North Sea only (Smeenk, 1997, Pierce *et al.* 2007, Vanselow *et al.* 2017), and show regional, and seasonal definitions that are not detected in our wider macroecological study.

Sea surface temperature (SST)

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

Fishing catch

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

Model criticisms

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

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

We also highlight that the spatio-temporal difference between the death of the animal and its discovery may affect stranding records, but that this is too variable to model. This includes factors such as initial location of the animal at the time of death, buoyancy of the carcass/species, and proximity of the carcass to strong currents, all of which determine where and if the animal washes up.

Sampling effort

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

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

Long-term strandings data provides vital information on past and present cetacean diversity and distribution for common, rare, and inconspicuous species, highlighting the importance of stranding programs. Such data on cetaceans can provide an indication of wider ecosystem health (Friedlaender *et al.* 2006, Roman *et al.* 2014) making these an important data source to consider when informing conservation decisions.

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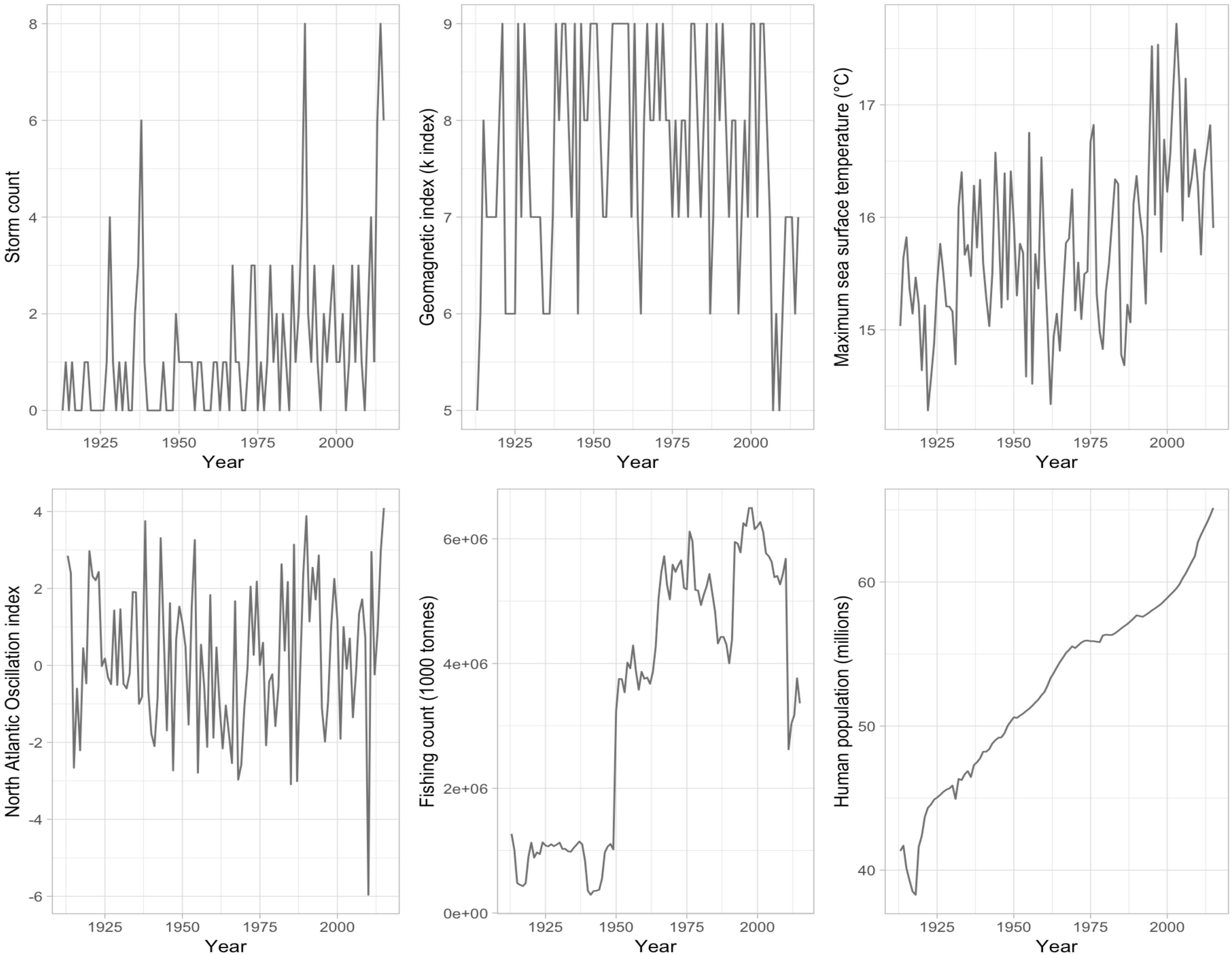

Storm count
Year
Geomagnetic index (k index)
Year
Maximum sea surface temperature (°C)
Year
North Atlantic Oscillation index
Year
Fishing count (1000 tonnes)
Year
Human population (millions)
Year

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

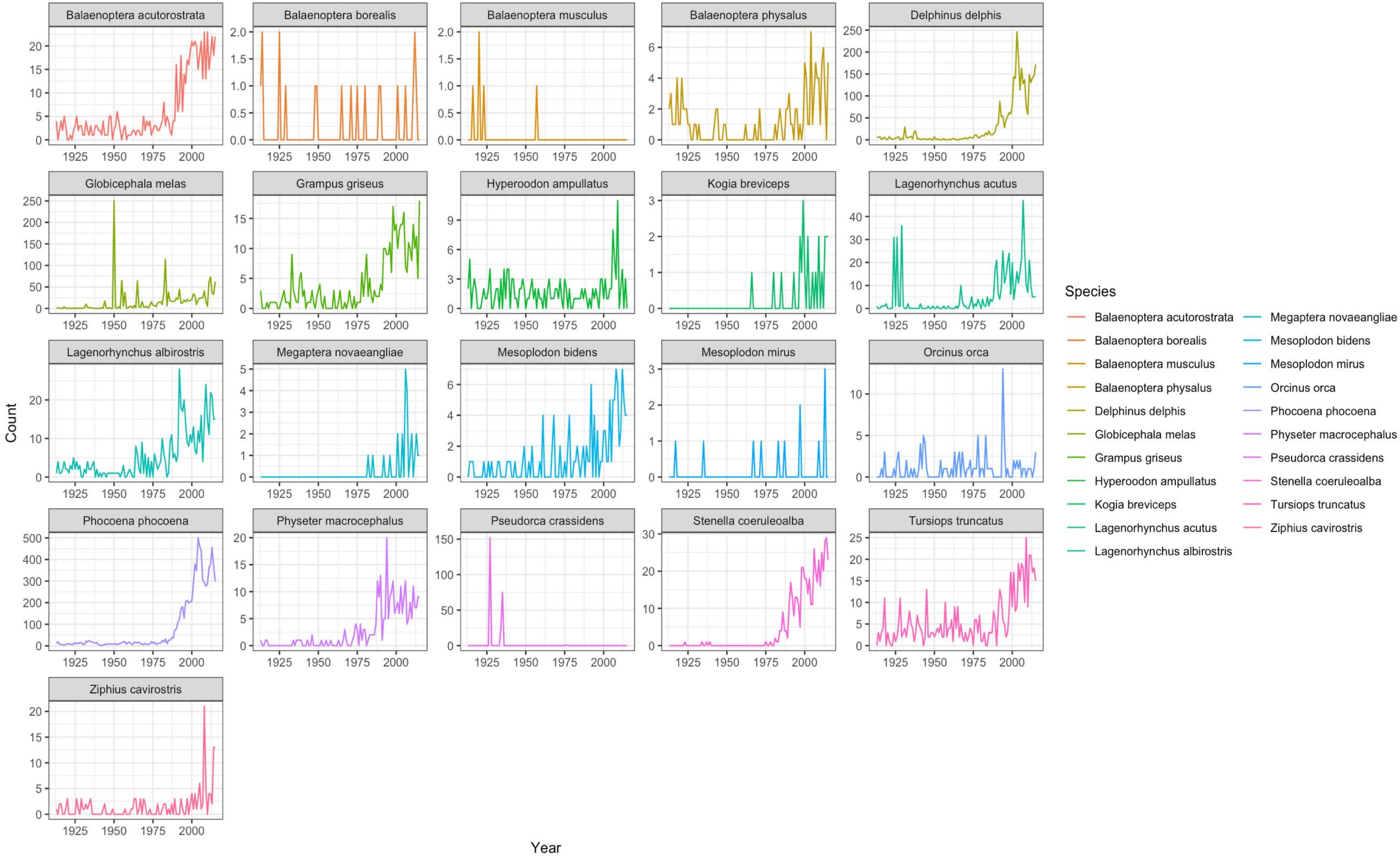
Balaenoptera acutorostrata
Balaenoptera borealis
Balaenoptera musculus
Balaenoptera physalus
Delphinus delphis
Globicephala melas
Grampus griseus
Hyperoodon ampullatus
Kogia breviceps
Lagenorhynchus acutus
Lagenorhynchus albirostris
Megaptera novaeangliae
Mesoplodon bidens
Mesoplodon mirus
Orcinus orca
Phocoena phocoena
Physeter macrocephalus
Pseudorca crassidens
Stenella coeruleoalba
Tursiops truncatus
Ziphius cavirostris
Count
Year
Species
Balaenoptera acutorostrata
Balaenoptera borealis
Balaenoptera musculus
Balaenoptera physalus
Delphinus delphis
Globicephala melas
Grampus griseus
Hyperoodon ampullatus
Kogia breviceps
Lagenorhynchus acutus
Lagenorhynchus albirostris
Megaptera novaeangliae
Mesoplodon bidens
Mesoplodon mirus
Orcinus orca
Phocoena phocoena
Physeter macrocephalus
Pseudorca crassidens
Stenella coeruleoalba
Tursiops truncatus
Ziphius cavirostris

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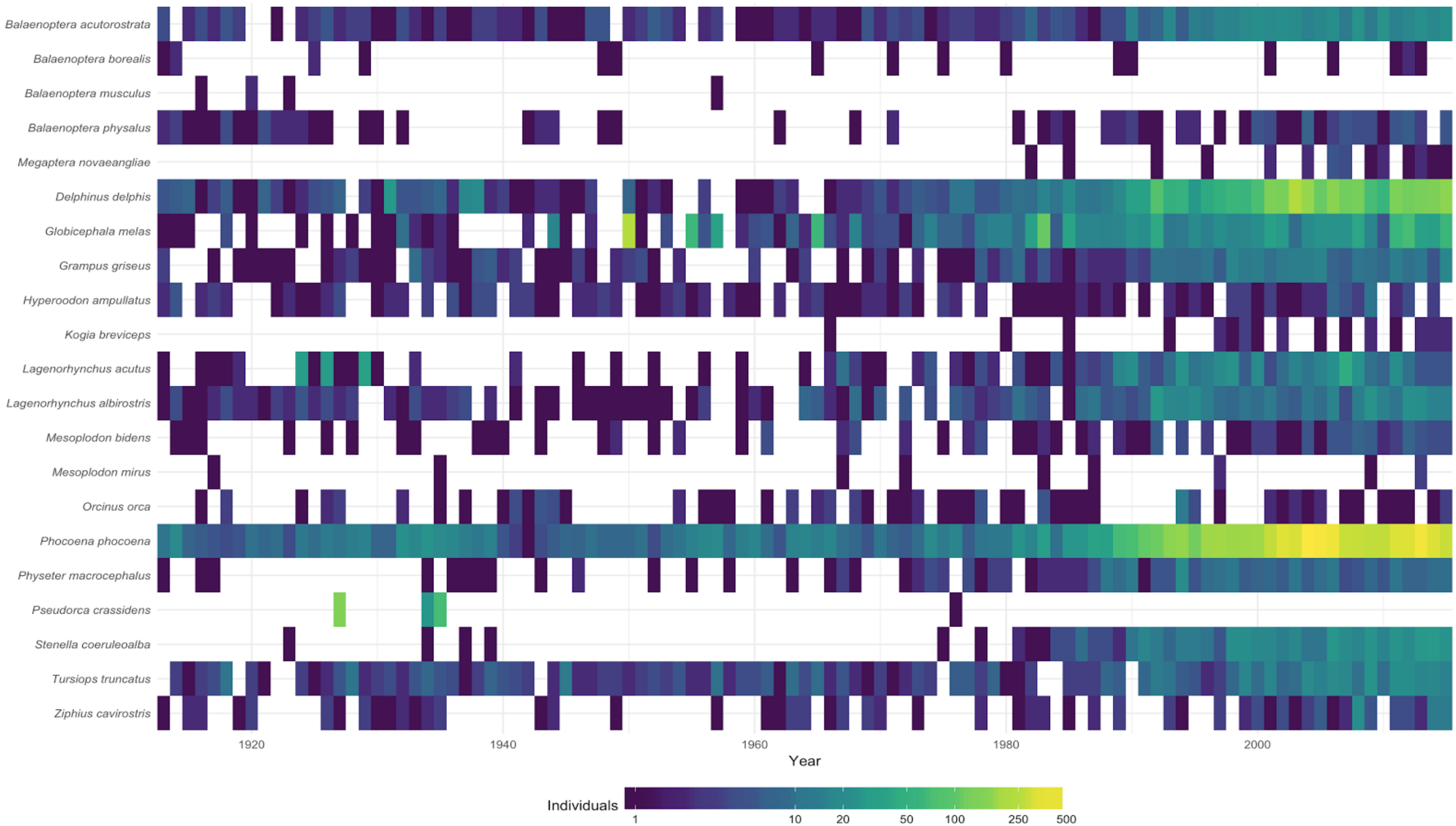
Figure 2. Temporal stranding patterns of each cetacean species stranding in the UK and Ireland from 1913-2015. The y-axis shows total stranding count per year, the x-axis shows the year. Note that y-axis scales are different for different species.



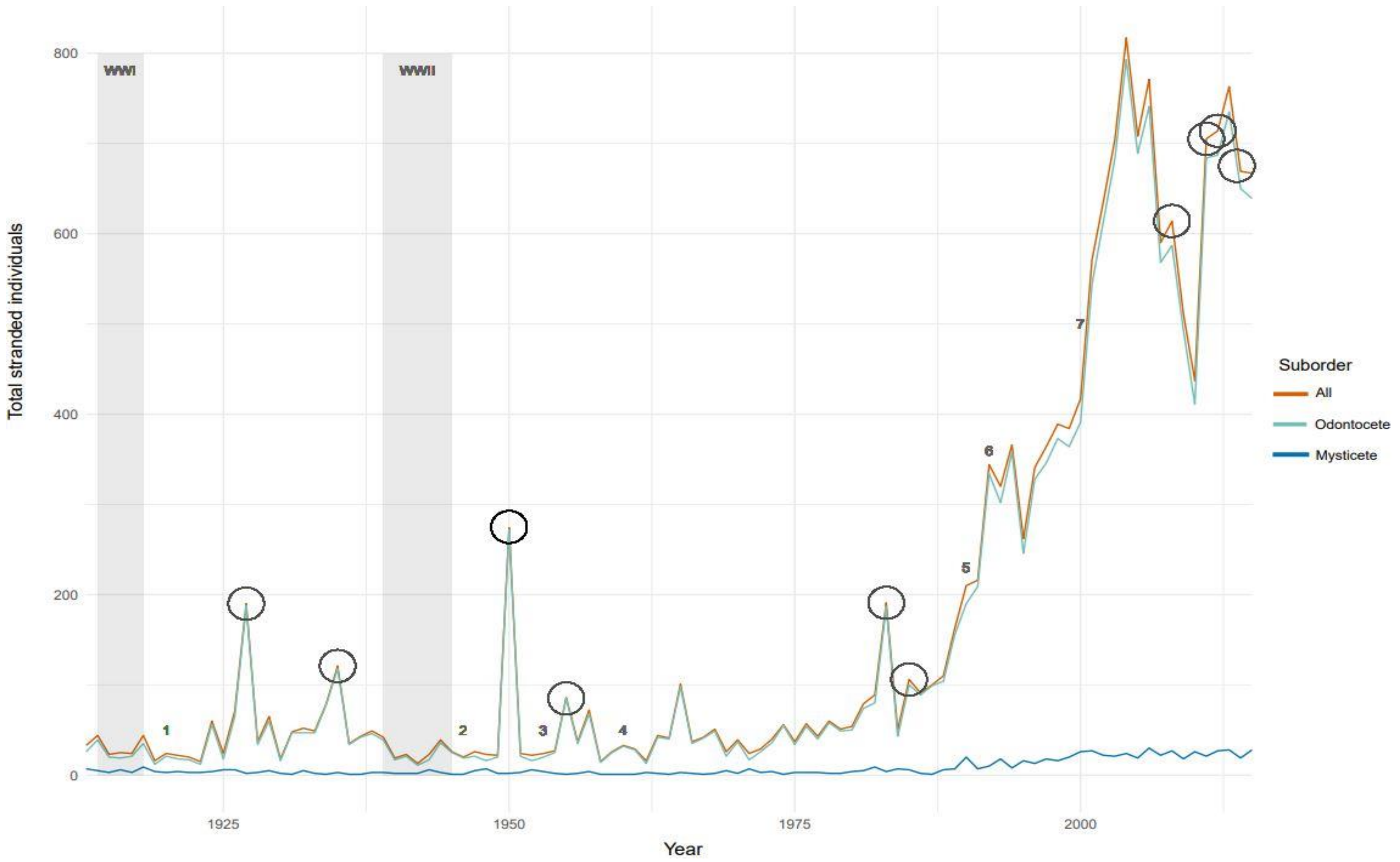
Balaenoptera acutorostrata
Balaenoptera borealis
Balaenoptera musculus
Balaenoptera physalus
Megaptera novaeangliae
Delphinus delphis
Globicephala melas
Grampus griseus
Hyperoodon ampullatus
Kogia breviceps
Lagenorhynchus acutus
Lagenorhynchus albirostris
Mesoplodon bidens
Mesoplodon mirus
Orcinus orca
Phocoena phocoena
Physeter macrocephalus
Pseudorca crassidens
Stenella coeruleoalba
Tursiops truncatus
Ziphius cavirostris
1920
1940
1960
1980
2000
Year
Individuals
1
10
20
50
100
250
500

1022

1023

<Plot on previous page>

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



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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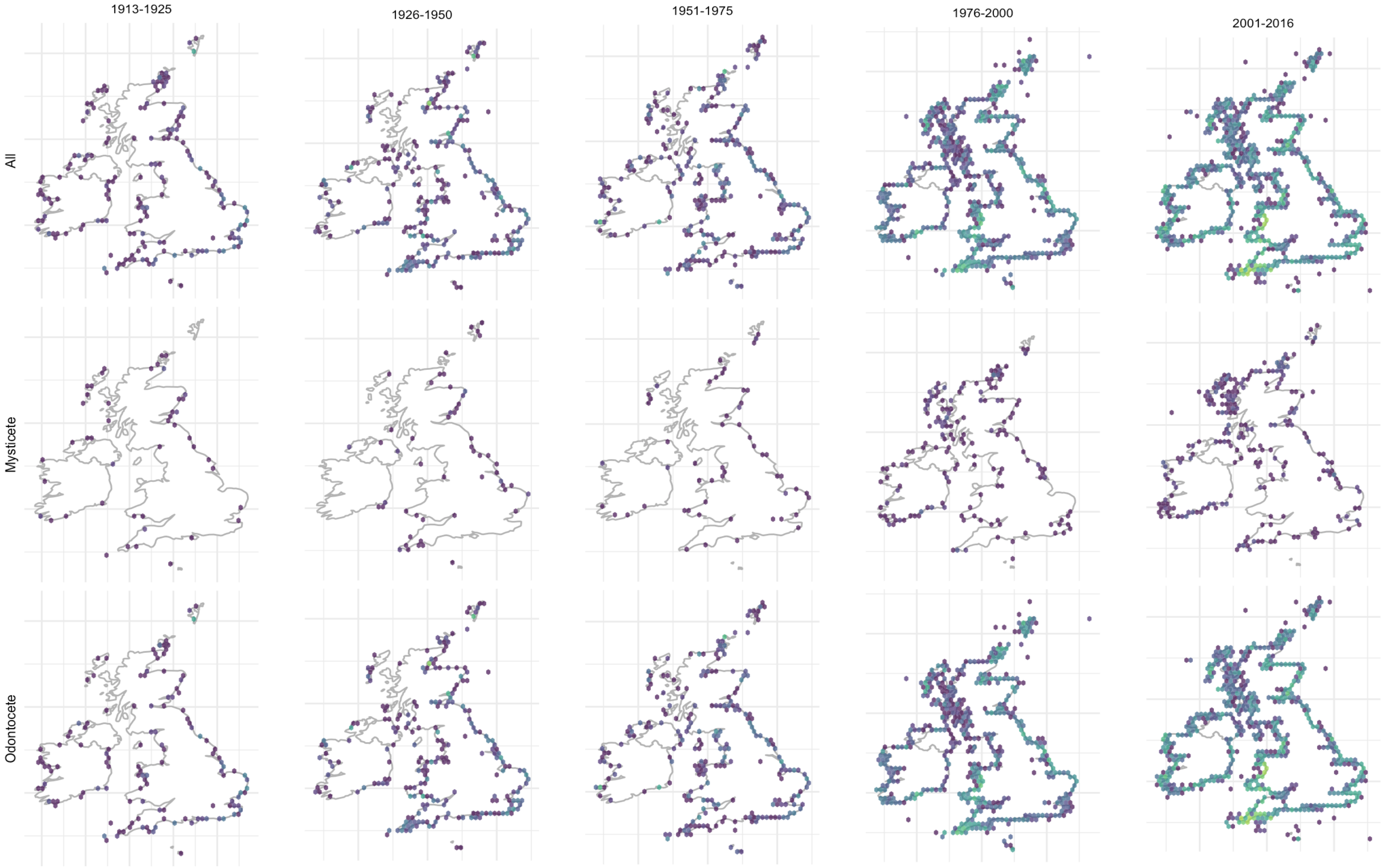
Figure 4. Temporal variation in cetacean strandings records for all species, odontocetes (toothed whales), and mysticetes (baleen whales) in the waters around the UK and Ireland from 1913-2015. 1913 is when the NHM started to record cetacean strandings. The plot shows strandings through time for all species (orange), odontocetes (blue), and mysticetes (green). The y axis shows total number of individuals that stranded each year. Key anthropogenic events are labelled with numbers, with the corresponding key below the plot. Key periods are shaded in light grey. WWI is World War I, WWII is World War II, CSIP is the Cetacean Stranding Investigation Programme, IWDG is the Irish Whale and Dolphin Group Cetacean Stranding Scheme. The circles highlight years with mass strandings of > 20 individuals.


1913-1925
1926-1950
1951-1975
1976-2000
2001-2016
All
Mysticete
Odontocete

<Plot on previous page>

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

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

<Table on next page>

Variable	**Data**	**Sources**

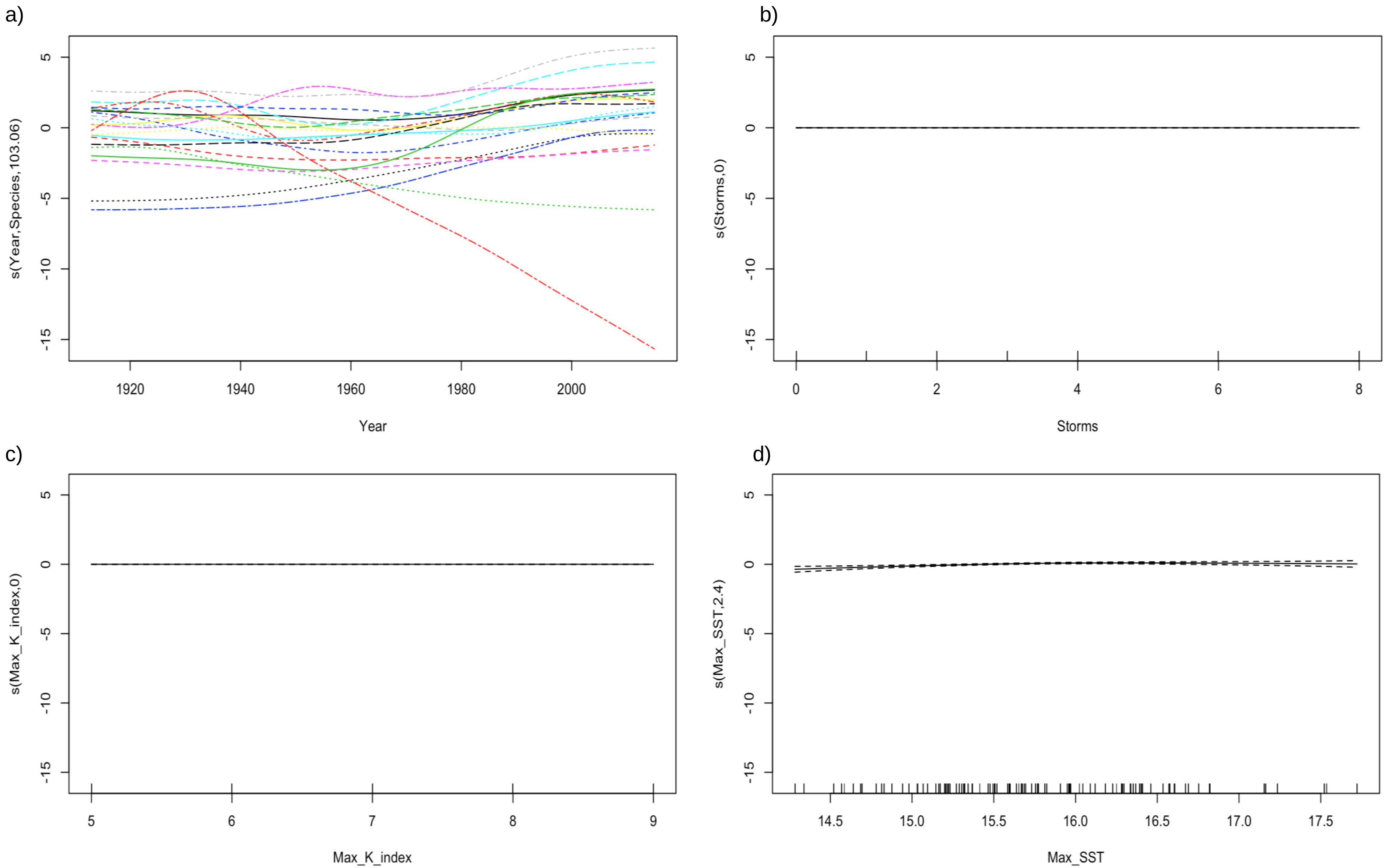
(units)		
Storm events (count/year)	Storm events over 47 knots	Lamb and Frydendahl (1991) Met Office, UK Multiple sources: https://github.com/EllenJCoombs/strandings-project
Geomagnetic activity (K - index)	The K-index is used to characterize the magnitude of geomagnetic storms. The range is 0–9, with 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)

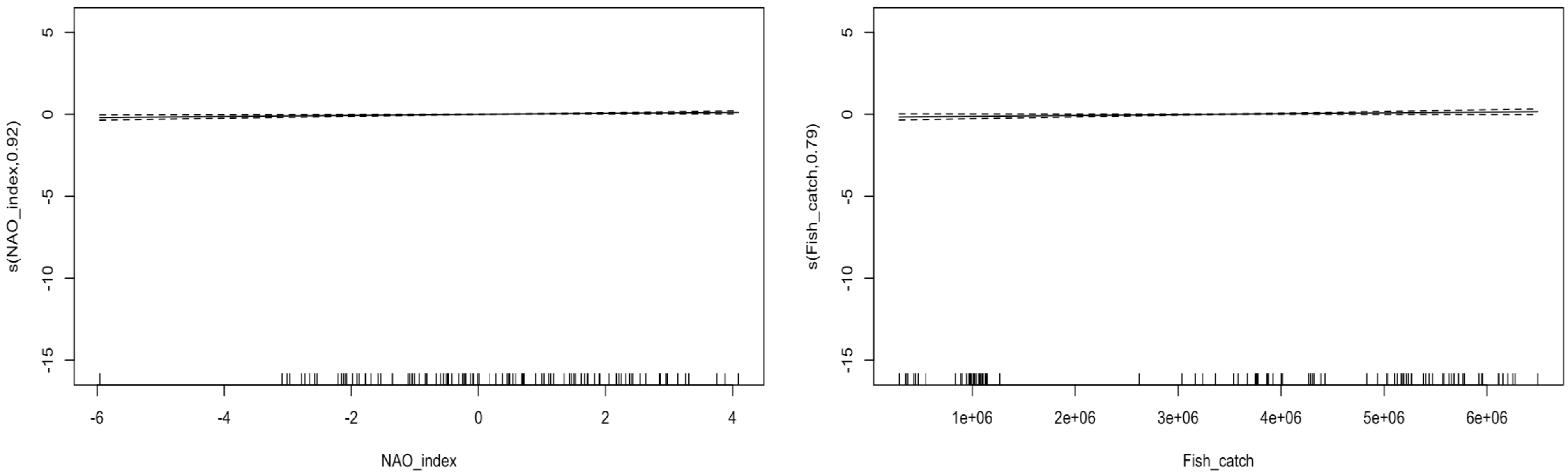
Correlates as modelled	**EDF**	***P*-value**	**k value**

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

Table 2 Generalized additive model (GAM) outputs from a model of correlates of strandings for the UK and Ireland, from 1913-2015. s() are smooths of the explanatory variables. 'Storms' refer to the storm count for each year, 'Max_K_Index' is the geomagnetic reading (where the K-index is used to characterize the magnitude of geomagnetic storms), 'Max_SST' is the yearly maximum sea surface temperature (°C), 'NAO_index' is the North Atlantic Oscillation which is the difference of normalized sea level pressure (SLP) between Stykkisholmur/Reykjavik, Iceland, and Lisbon, Portugal, 'Fish_catch' is annual fish catch (1,000 tons) for the UK and Ireland, 'Year' is the years 1913-2015, 'Species' are the 21 cetacean species that make up the data set. This table shows the estimated degrees of freedom (EDF) for each of the different predictor variables. The *P*-values show whether the 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 basis complexity.


a)
b)
c)
d)
s(Year,Species,103.06)
Year
1920
1940
1960
1980
2000
s(Storms,0)
Storms
0
2
4
6
8
s(Max_K_index,0)
Max_K_index
5
6
7
8
9
s(Max_SST,2.4)
Max_SST
14.5
15.0
15.5
16.0
16.5
17.0
17.5
5
0
-5
-10
-15

e) f)



5
0
-5
-10
-15
s(NAO_index,0.92)
-6
-4
-2
0
2
4
NAO_index
5
0
-5
-10
-15
s(Fish_catch,0.79)
1e+06
2e+06
3e+06
4e+06
5e+06
6e+06
Fish_catch

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

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

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

	Year			Storms			Geomagnetic k-index			Maximum SST (°C)			NAO index			Fishing catch		
Species	EDF	*P*-value	k	EDF	*P*-value	k	EDF	*P*-value	k	EDF	*P*-value	k	EDF	*P*-value	k	EDF	*P*-value	k
Balaenoptera acutorostrata	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
Balaenoptera physalus	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
Delphinus delphis	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
Globicephala melas	< 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
Grampus griseus	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
Hyperoodon ampullatus	< 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
Lagenorhynchus acutus	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
Lagenorhynchus albirostris	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
Mesoplodon bidens	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
Orcinus orca	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
Phocoena phocoena	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
Physeter macrocephalus	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
Pseudorca crassidens	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
Stenella coeruleoalba	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
Tursiops truncatus	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
Ziphius cavirostris	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

Table 4. Generalized additive model (GAM) outputs from a model of correlates of strandings for the UK and Ireland, from 1913-2015 for each individual species. ‘Storms’ refer to the storm count for each year, ‘Geomagnetic k-index’ is the geomagnetic reading (where the K-index is used to characterize the magnitude of geomagnetic storms), ‘Maximum SST’ is the yearly mean maximum sea surface temperature (°C), ‘NAO index’ is the North Atlantic Oscillation which is the difference of normalized sea level pressure (SLP) between Stykkisholmur/Reykjavik, Iceland, 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 16 cetacean species which had 100 or more strandings in the dataset. Rarer species were removed because they had insufficient data to fit the models. This table shows the estimated degrees of freedom (EDF) for each of the different predictor variables. The *P*-values show whether the 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 basis complexity.