Analysis of stranding data of harbour porpoises along the North Sea for a better understanding of the population structure

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In collaboration with:

Summary

Harbour porpoises (*Phocoena phocoena*) are the most abundant species of cetacean in the North Sea and protected under several international conventions. Expansion of anthropogenic activities in their habitat, including pile driving for offshore development, have raised concerns among conservationists and policy makers aiming at conserving the species. Monitoring of harbour porpoise demographics is focussed on topics as suggested under the Agreement on the Conservation of Small Cetaceans of the Baltic, North East Atlantic, Irish and North Seas (ASCOBANS), and includes research into seasonal movements, habitat preference, and pressures and threats to the population. Analysis of stranding frequencies provides an opportunity to assess smaller-scale spatiotemporal patterns. Therefore, we analysed available stranding data of the countries bordering the North Sea aiming to gain a better insight in the population structure and baseline mortality numbers of porpoises in the North Sea.

Stranding records from the Netherlands, United Kingdom, Belgium, Germany and Denmark were collected which included data on strandings date and location as a minimum, with additional data on sex and age class (based on total length) when available. This is the first time that data from the individual stranding schemes are combined to allow an ecosystem wide assessment. The North Sea coastline was divided into six regions (A-F) similar to those assigned during large-scale decadal population abundance surveys (SCANS). Spatiotemporal variation in stranding frequencies was examined from 1990 to 2017, also in terms of biological parameters.

A total number of 16247 harbour porpoises strandings were recorded. Stranding numbers increased annually in all regions, with a sharp increase in especially the southern region since 2004. Generalized Additive Mixed modelling revealed a seasonal pattern which was region specific throughout the study period. In addition we conclude that the majority of neonate strandings occurred in two regions (those including the Danish, German and Dutch Wadden and mainland coastlines); suggestive of areas of importance for calving. The General Linear modelling revealed an additional heterogeneity in age-specific sex ratio across the study area, with high male juvenile mortality in mainly the most southern regions. This could indicate that these areas are a less optimal habitat for harbour porpoises, reflecting a potential population sink. We conclude that the rise in stranding numbers cannot be explained solely by a shift in distribution of or increase in abundance of harbour porpoises and therefore seem to reflect an increase in mortality.

We can only speculate about underlying causes of the observed heterogeneity in the composition of the stranded population and without data on environmental and physical variables as well as health parameters, our findings need to be interpreted with caution. We have shown that it was possible to detect seasonality and elevations in stranding rates. This is a first step in revealing trends in harbour porpoise population structure and habitat use. Following this process there is a unique opportunity to assess changes in mortality, including those of anthropogenic origin that could eventually be used as a reference framework for future monitoring. Other metrics to assess population health status include data on nutritional condition, parasitism, and disease, would allow profiling the health status of individuals and spatiotemporal variation in this. Besides, to be able to effectively address population demographics, parameters like life history and prey preference and abundance will contribute to our understanding of habitat use and optimal areas. Only the knowledge of when, where and to what extent threats and pressure occur will allow assessment of future population impacts, especially taken into account the predicted increase in offshore wind industries and other anthropogenic activities at sea; this seems a vital step in effectively monitoring and protecting of the species.

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1   Introduction

Marine ecosystems are globally affected by a range of anthropogenic pressures including shipping, fisheries, oil and gas exploitation, chemical and noise pollution, and more indirectly by effects of a rise in water temperature as a result of global warming (Aguirre & Tabor 2004; Moore 2008; Wassmann et al. 2011). More recently, a requirement for alternative energy resources has resulted in a rising wind energy sector, with increasing interest in the development of especially offshore wind farms (Snyder & Kaiser 2009). While expansion of offshore renewable energy devices is required in order to meet the 2015 Paris Agreement of the United Nations Framework Convention on Climate Change (UNFCCC 2015), particularly the construction phase of such developments likely has negative impacts on the marine environment and its populations (Gill 2005; Snyder & Kaiser 2009).

Human activities can affect the ecosystem by direct and indirect means, through direct lethal impacts of marine life as well as long term loss of ecosystem viability (Halpern et al. 2008). Monitoring of ecosystems is complex, and often done through surveillance of indicator species. Marine mammals are useful ocean sentinels as they are mobile, relatively long-lived, and feed at- or near the top of the food chain (Aguirre & Tabor 2004; Moore 2008; Bossart 2011). In the North Sea, harbour porpoises (*Phocoena phocoena*) are the most abundant species of cetaceans. Through large-scale decadal population surveys, the North Sea population of harbour porpoises is estimated at around 350.000 individuals without obvious declines or increases in the past three decades (Hammond et al. 2002; 2013; 2017). Despite these apparent stable population numbers, harbour porpoises are protected and included under several international, European and national conventions, especially given their frequent exposure to offshore human activities (Reijnders et al. 2009; Green et al. 2012; IAMMWG et al. 2015; IJsseldijk et al. 2018a).

In the North Sea, monitoring of harbour porpoise demographics is focussed on topics as suggested under the Agreement on the Conservation of Small Cetaceans of the Baltic, North East Atlantic, Irish and North Seas (ASCOBANS), and includes research into seasonal movements, habitat preference, and pressures and threats to the population. Population demographics are independent of national borders or administrative management units, therefore population monitoring and management should be conducted on a spatial scale that makes ecological sense in order to be effective (IJsseldijk et al. 2018a). The large-scale SCANS abundance estimates are a key example of that (Hammond et al. 2002; 2013; 2017), however, assessment of smaller-scale spatiotemporal changes, both in terms of abundance and distribution, can only be achieved when conducted on a higher spatial and temporal resolution. Analysis of stranding frequencies provides an opportunity to assess smaller-scale spatiotemporal patterns, as demonstrated previously in ten Doeschate et al. (2017); IJsseldijk et al. (2018b) and Warlick et al. (2018).

Efficient systems for the reporting and retrieving of bycaught and stranded specimens are established on a national basis throughout the ASCOBANS agreement area (ASCOBANS 1992). Profiling these strandings data can reveal vital clues about the possible processes underlying the demographics of the harbour porpoise population in the North Sea, and assessing spatiotemporal stranding frequencies and the biological characteristics of stranded specimens therefore has the potential to inform about the structure and distribution of the population from an ecosystem perspective. This information is essential to be able to understand baseline variation in population demographics and allows detection of unusual mortality, and changes in parameters of interest.

1.1 Research aims and questions

In this research call, an analysis of the available stranding data of the countries bordering the North Sea will be conducted aiming to gain a better insight in the population structure and baseline mortality of the harbour porpoises in the North Sea. The analysis will be carried out with stranding data from the independent stranding networks of the Netherlands, United Kingdom, Belgium, Germany and Denmark. This includes information on stranding date, location, and, when available, biological metrics such as sex and size of the stranded animals, in order to answer the following research questions:

1. What is the spatiotemporal variation in stranding frequencies of harbour porpoises in the different countries along the North Sea in terms of biological parameters?
2. Can these biological parameters be used to infer whether or not there are sub-populations or how harbour porpoises are distributed across the different parts of the North Sea?
3. Is it possible to develop a model that is able to detect changes in mortality at a relevant spatial and/or ecological level, and have such changes (increases of decreases) in mortality frequency been present in the past decade?
4. Based on these results, which information or research focus is recommended, e.g. on other factors i.e. physical and sociological factors (e.g. chance of detection), in order to improve our understanding of the underlying causes of the observed changes in stranding rates? Is this data available for the baseline period?
5. What would the cause of death results add to the model? In which way could cause of death information be used to derive information about anthropogenic influences on the population?
6. What additional information is needed to improve our understanding of biological parameters and mortality in porpoises in relation to anthropogenic factors, and what data is available in the different countries (e.g. through tissue-banking or other projects) and under what conditions could this be made available for a follow-up from this study?

2 Methods

2.1 Data collection

2.1.1 National stranding schemes

Stranding records are collected and maintained at a national level by stranding networks. For this study, the stranding databases of Belgium, Denmark, Schleswig-Holstein (Germany), the Netherlands and the United Kingdom (UK) were combined. Data held by the following institutes were collated: Royal Belgian Institute of Natural Sciences (Belgium); the Fisheries and Maritime Museum of Esbjerg (Denmark); the Institute for Terrestrial and Aquatic Wildlife Research, University of Hannover Foundation (Location Büsum, Schleswig-Holstein, Germany); Naturalis Biodiversity Centre Leiden and Faculty of Veterinary Medicine, Utrecht University (the Netherlands) and Cetacean Strandings Investigation Programme (CSIP, UK). For the UK, only cases with a stranding location along the east coast (North Sea coastline) were included, starting at Romney Marsh (Kent) in the south of England, to Skerray (Sutherland) on the north coast of Scotland, and including the Orkney islands. Shetland was not included. For Denmark, strandings along the east coast, including those along the Baltic Sea, were not included.

2.1.2 Data preparation

To ensure equal temporal coverage across all areas, stranding records were selected from the first full year of the most recently initiated stranding network, until the last full year of data collection. This resulted in data on stranding frequencies from the last 28 years (period of 01-01-1990 to 31-12-2017). Data submitted by each stranding scheme included as a minimum stranding date (day, month, year) and location, and, if available, also data on sex, length (in cm), and/or age class. Animals that were reported as floating or bycaught at sea were excluded. The combined data from all stranding schemes were checked for missing values and outliers. Where outliers were detected the scheme the data point derived from was consulted to check whether these were due to incorrect data entry, and outliers were corrected where possible. If the source of the outlier could not be traced the value was treated as "unknown".

While standardised protocols for strandings data collection are in place across Europe, data derived from the stranding schemes can be expected to show some variation in surveillance methods with individual countries facing different (logistical) challenges. In order to treat the data as comparable, some assumptions therefore had to be adopted. Strandings are recorded opportunistically, and reporting effort has likely improved over time with increasing public awareness, technological developments which facilitate submission of stranding reports, and interest in marine animal conservation. This is unquantified for all schemes, yet there is no indication that this expected increase in reporting effort has been significantly different between the individual countries, and it was therefore assumed that variation in effort was homogenous across areas hence the data comparable.

Data on total length was inconsistently recorded for all stranding schemes. It was measured for some cases, estimated for others, and of unknown accuracy for the majority of the individuals included in the analysis. It was therefore assumed that absolute length was not the most reliable parameter of age and the attributed age class was used instead. Animals that did have a length recorded but for which an age class was not determined by the stranding schemes themselves were assigned to a class, based on the total length estimate with animals <91 cm being neonates, 91 to 130 cm considered juvenile, and >130 cm classed as adults.

Harbour porpoise demographics are driven by ecological and environmental processes which are independent of the national borders. Yet, strandings data is collected in national databases. Therefore, for this analysis six regions (A-F, Fig. 1) of roughly equal coastal length were established. These regions were assigned following regions as described by Hammond et al. (2017) to allow comparison with estimates of decadal large scale population abundance surveys (SCANS), and based on homogenous habitat (mainly focussed on water depth). It was assumed that while movement between regions is plausible, animals stranded within a particular region have died within that region.
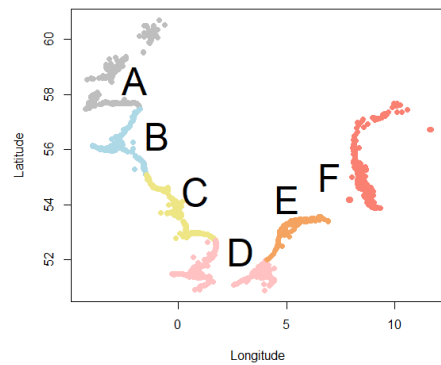

Figure 1: Assigned regions in the study area

2.2 Data analyses

Data exploration was applied following Zuur et al. (2010) prior to analysis. Data exploration and analyses were performed using R version 3.4.4 (R Core Team 2017).

2.2.1   Data exploration

Maps of the study area were created using the ggplot2 (Wickham 2009) and ggmap (Kahle & Wickham 2013) libraries available in R. To better visualise point density, kernel density estimation was performed using the stat_density_2d function integrated within ggmap. This method estimates the underlying probability density function of a stranding at a particular location and visualises potential shifts in distribution over the study period. To facilitate data interpretation, the study period was divided in three periods firstly (1990-1999; 2000-2009; 2010-2017); then six periods (1990-1995; 1996-2000; 2001-2005; 2006-2010; 2011-2015; 2016-2017); a two monthly interval (Jan-Feb, Mar-Apr, May-Jun, Jul-Aug, Sept-Oct, Nov-Dec) as well as all of above's time periods per sex (male, female) and per age class (neonate, juvenile, adult). This allowed an extensive investigation of spatial temporal coverage of the stranding frequency and underlying population demographics of these. For this report a selection of the most informative maps are presented in the main body of text. Other maps can be found as part of the Supplementary material.

To investigate whether any potential areas of importance for calving could be assigned within the study area, a literature search was conducted to set the timeframe and neonatal size scale. According to Lockyer (2003), porpoises are born at a length of 65-75 cm. Reported parturition in different areas of the North Sea ranged from May to August (Sørensen & Kinze 1994; Addink et al. 1995; Lockyer 2003). We therefore selected all porpoises within the database with a length between 60-80 cm, that stranded in the months May-August, for analysis of potential high density areas of neonate strandings. Spatial visualisation was done using methodology similar to the maps described above.

2.2.2   Data analyses

Spatiotemporal variation in stranding frequencies of harbour porpoises along the North Sea coastline was examined from 1990 to 2017. A Generalised Additive Mixed Model (GAMM) was applied to the stranding data using the nlme (Pinheiro et al. 2018) and mgcv (Wood et al. 2016) packages available in R. GAMMs allow the modelling of non-linear relationships and nested data structures while being able to account for temporal auto-correlation commonly associated with time series data (Wood 2006; Zuur et al. 2007), and is therefore a suitable method of modelling seasonal and long term temporal trends in stranding frequencies. A count of number of strandings was modelled as a function of month to capture a potential seasonal effect, year to examine long term trends, and regions as described above. The model was fitted using a Poisson error distribution with a log-link function, and the appropriate level of smoothness was found by utilising the integrated smoothness estimation and cross validation function available within the mgcv library. Autocorrelation can be expected in time series data, and this was assessed following each model fit and appropriate correlation structures were added if required. Model selection was carried out by comparing different forms of inclusion of the

variables month, year, and region applied through a backwards model selection process. Data exploration indicated that there is a potential seasonality in all regions, but these patterns were not identical and interactions between the three variables were therefore considered in the model selection. The most appropriate model structure best describing the data was identified through examination of scaled residuals, parameter estimates, and evaluation of the Akaike Information Criterion (AIC, Akaike 1974). GAMM procedures generate no overall goodness of fit measure and r2 values are also approximations. Model validation was therefore carried out mainly by evaluating diagnostic plots and residual variance using normalised pearson residuals to verify underlying model assumptions and evaluate model fit. The residual scaled deviance to the residual degrees of freedom-ratio was calculated to examine possible over- or under dispersion.

The composition of the stranded population in terms of biological parameters was examined to explore whether these could provide insight into the population structure of harbour porpoises in the North Sea. To assess the sex ratio of porpoise strandings in the different regions and differences in strandings of different age classes (neonate, juvenile, adult) per region, yearly proportions were calculated, corrected for the number of available cases for which this information was available per region per year. As mentioned before, harbour porpoises were subdivided into age classes based on their total length. Cases with an unknown length and/or age class were not included in this analysis. These data were further analysed using generalised linear models (GLM) fitted with a binomial error distribution and logit link. Sex (recorded as 1 for males and 0 for females) was modelled as a function of body length as a proxy for age, month to examine seasonal differences, year to assess potential long term changes over time, and region to evaluate potential heterogeneity between regions. Neonates (length <91cm) were excluded from this analysis. Model selection was carried out by comparing different forms of inclusion of these variables including interaction terms, by means of a backward stepwise selection using the AIC to select the optimal model. Model validation was applied to verify the underlying model assumptions by evaluation of calculated dispersion parameters and diagnostic plots using Pearson residuals.

3   Results

3.1 Spatiotemporal analysis

Between 1990 and 2017, a total of 16247 harbour porpoise strandings were recorded comprising 1362 animals from Belgium, 1317 from Denmark, 2500 from Schleswig-Holstein (Germany), 8375 from the Netherlands and 2693 from the United Kingdom (with 1456 from England and 1237 from Scotland). Annual stranding frequencies varied greatly over the study period. Annual totals slowly increased from around 150 in 1990 to almost 500 in 2004, after which a steeper increase in numbers was observed. Peak stranding years were 2011 and 2013, with a total of 1317 and 1374 stranded harbour porpoises respectively (Figure 2,Figure 3). The monthly distribution of all stranding records also varies, indicating seasonality in the number of strandings along the North sea coastline (Figure 4).

When we map the stranding records over six timeframes it becomes clear that over time, a change in stranding frequencies throughout the study area occurred, especially after the period of 2001-2005 (Figure 5). From 1990-1995, numbers were generally low but particularly in the most southern region (region D; southeast England, Belgium and southwest Netherlands), and the highest density was observed around Schleswig-Holstein, Germany, and Denmark (region F), with relatively higher numbers also in northeast Scotland (region A) compared to other regions. Density distribution changed spatially from 1996-2005, when stranding numbers started to concentrate more towards the southern areas. Absolute stranding numbers along the Scottish, Danish and German coastlines at that time period remained at a similar level. From 2005 however, an overall increase in harbour porpoise strandings is observed throughout the study area, yet with particularly higher numbers recorded in region D and E, resulting in the highest density of strandings occurring in this region. From this time onwards, the largest proportion of the total annual strandings is consistently observed in regions D and E.
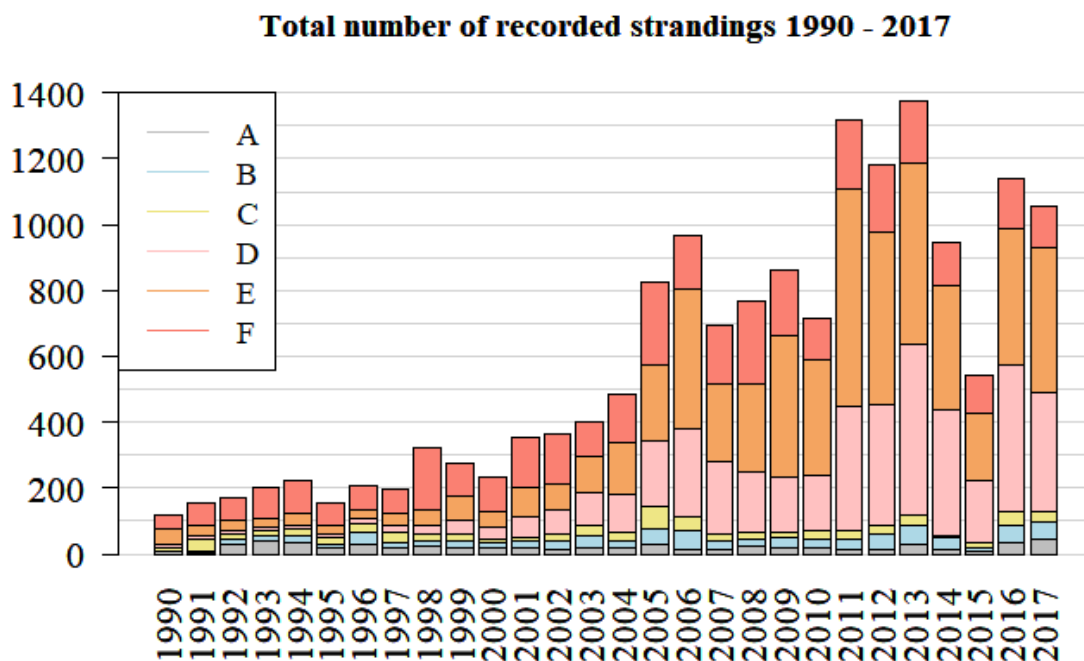

Figure 2: Barchart with total number of stranded harbour porpoises in the entire study area per year, stacked per region.

Cumulative number of Strandings per WoZEP Region

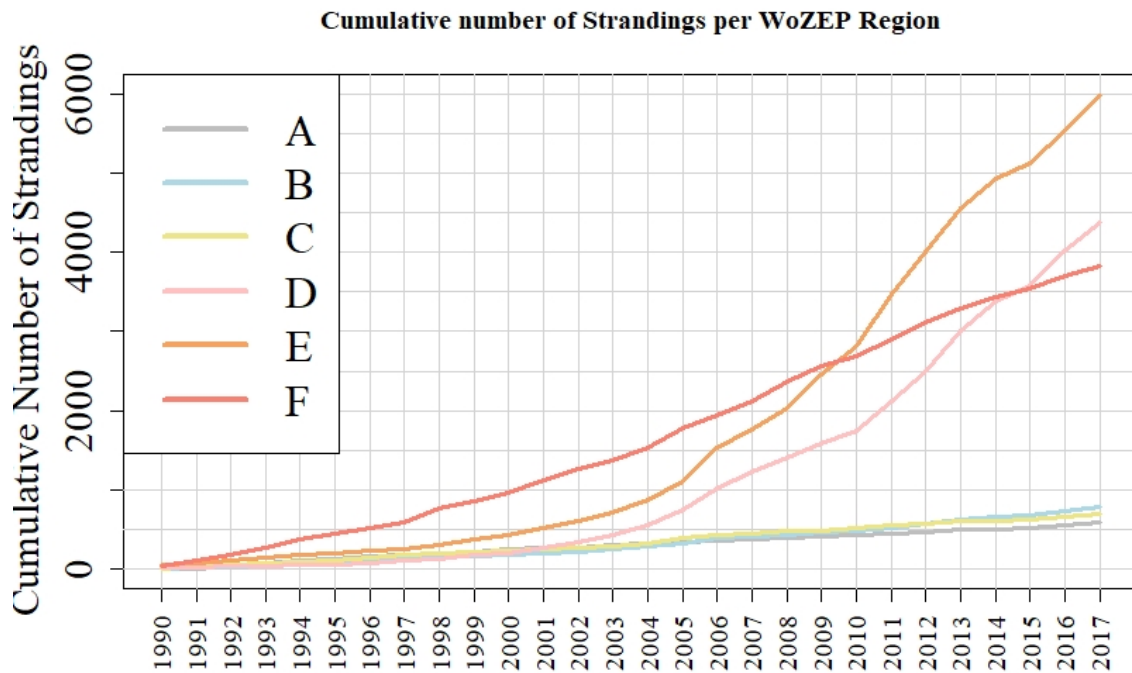*Figure 3: Cumulative number of stranded harbour porpoises per region over the study period*

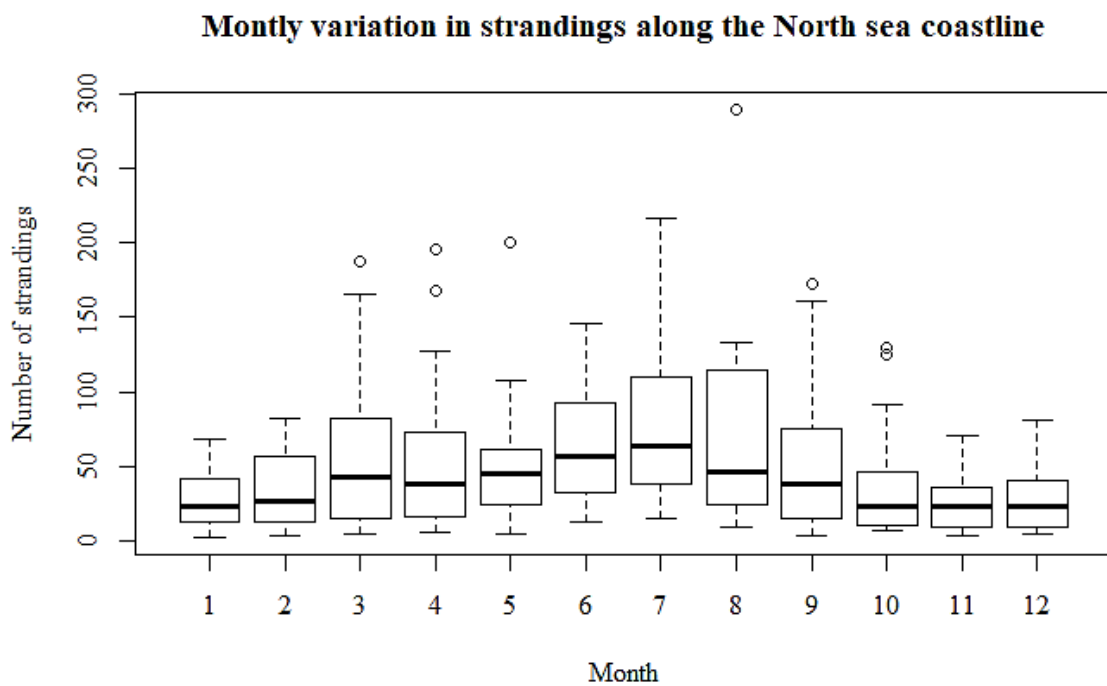**Montly variation in strandings along the North sea coastline**

Figure 4: Boxplot showing monthly variation in stranding numbers in the entire study area and period (1990-2017).
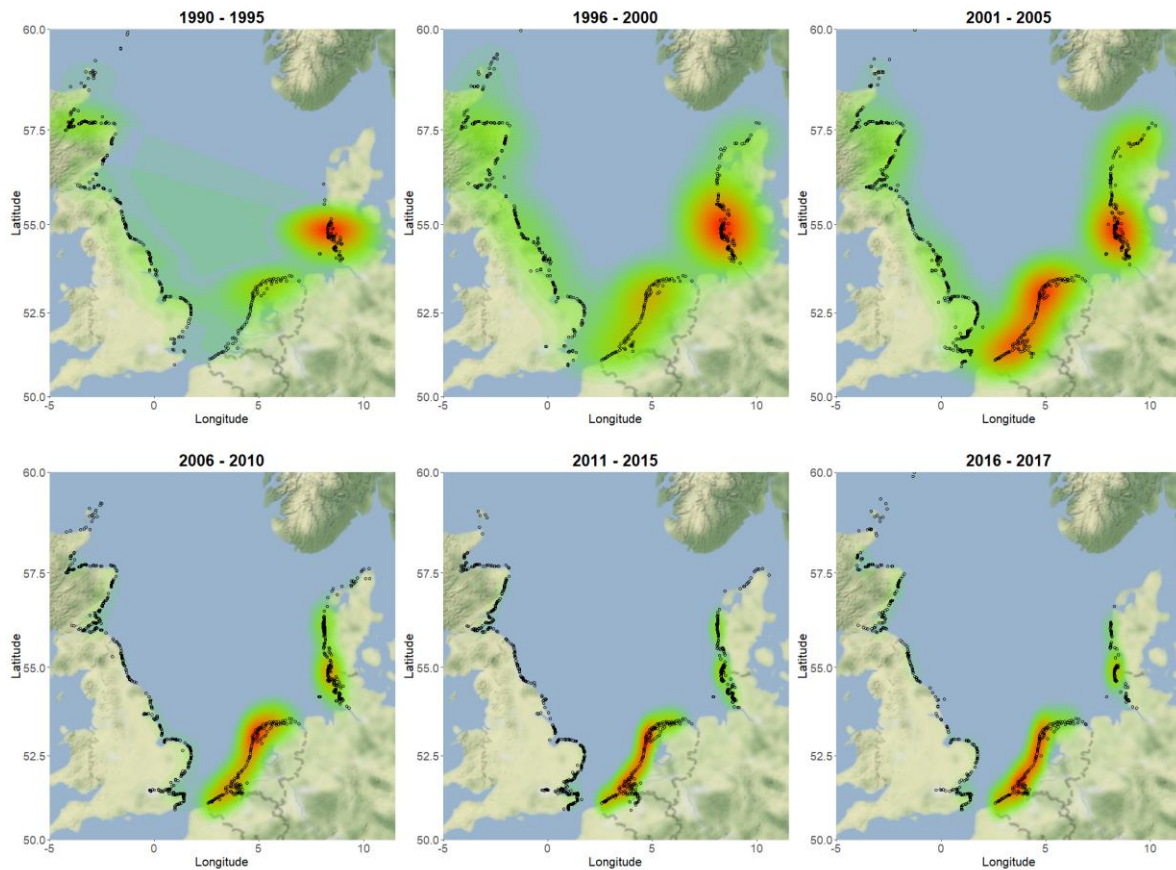
Figure 5: Study area showing the distribution density of harbour porpoise strandings over six time periods (1990-1995; 1996-2000; 2001-2005; 2006-2010; 2011-2015; 2016-2017). Red represent the highest density areas per time frame. High densities are present throughout the study area until 2006, after which stranding frequencies seem to centre mainly around the south-eastern area (region D).

Seasonality over the study period and throughout the North sea shows high densities in the southern North sea (region D and E) in most months compared to the other regions, most likely as a result of the highest annual number of strandings being recorded in these areas. Apparent changes are noted in the months May to August in region F, when stranding densities increase there. Along the UK coastline (regions A, B and C), densities are particular low from July to December (Figure 6).
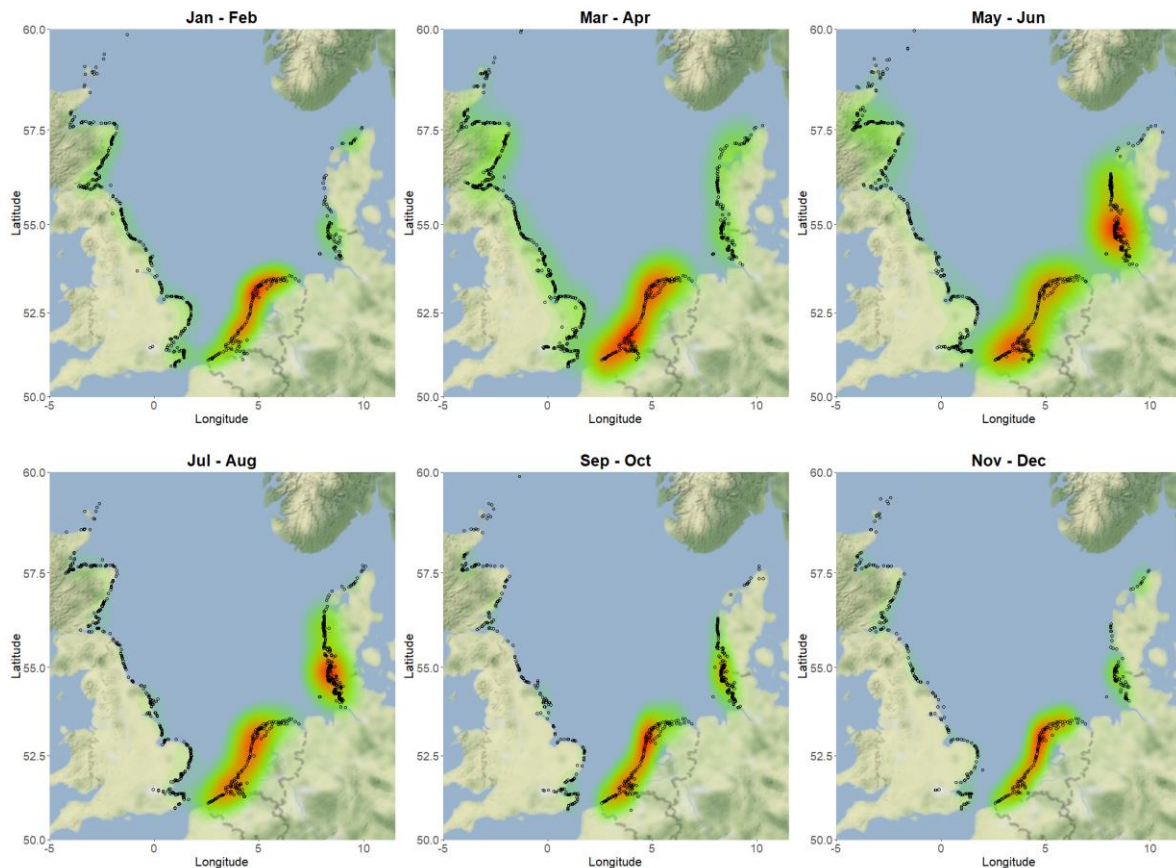
Figure 6: Study area showing the distribution of harbour porpoise strandings per two month interval, with high densities throughout all months in region D but apparent increases in region F in the months May-July.

The spatiotemporal model best describing the data incorporated a smooth seasonal effect per region, and a long term trend for each region individually. All smoothers were significant at the $p<0.001$ level (Table 1). This provides evidence that there is seasonality in stranding frequencies and that this variation significantly differs between regions (Figure 7), and additionally confirms that the long term trend in annual stranding frequencies has not been homogenous across regions. This model was preferred over a model incorporating an interaction between month and year, suggesting the observed seasonality within each region has been relatively consistent throughout the study period. The final model was fitted with an AR1 correlation structure, describing the correlation between residuals separated by one month, and normalised residuals were further assessed for serial correlation through partial autocorrelation plots. Results indicated there was no evidence of autocorrelation left in the residuals and this was the appropriate structure for these data. Plotting model residuals versus fitted values showed patterns indicative of heterogeneity of variance in one of the explanatory variables. Assessment of model residuals versus the variables included in the model indicated this was most likely driven by heterogeneity between regions, where the spread in residual variation was much larger for regions D, E, and F than for regions A, B, and C. Adding a variance structure to a GAMM is computationally highly intensive (Zuur et al. 2007), and there were convergence issue with a model allowing a different variance per each individual region. Due to their similarity it was decided to group region A with region B and C, and region D with region E and F, and incorporate a variance structure allowing for heterogeneity between these two areas instead. This variance structure removed the majority of the heterogeneity in the residuals and was accepted as the final model. The residual scaled deviance to the residual degrees of freedom-ratio was calculated at 0.99 meaning the model was not under- or over-dispersed.

Seasonality in regions A, B and C showed to be similar with a peak in March and April following which numbers slowly decrease towards constant low numbers throughout the winter months (Figure 7). Regions D and E are characterised by a double peak in stranding numbers, with high numbers being recorded in March and April after which numbers decrease, and increase again around August. The spring peak appears absent from region F, which shows a clear peak in the summer months with

numbers increasing from May to August following which numbers decrease and are relatively low throughout the rest of the year.
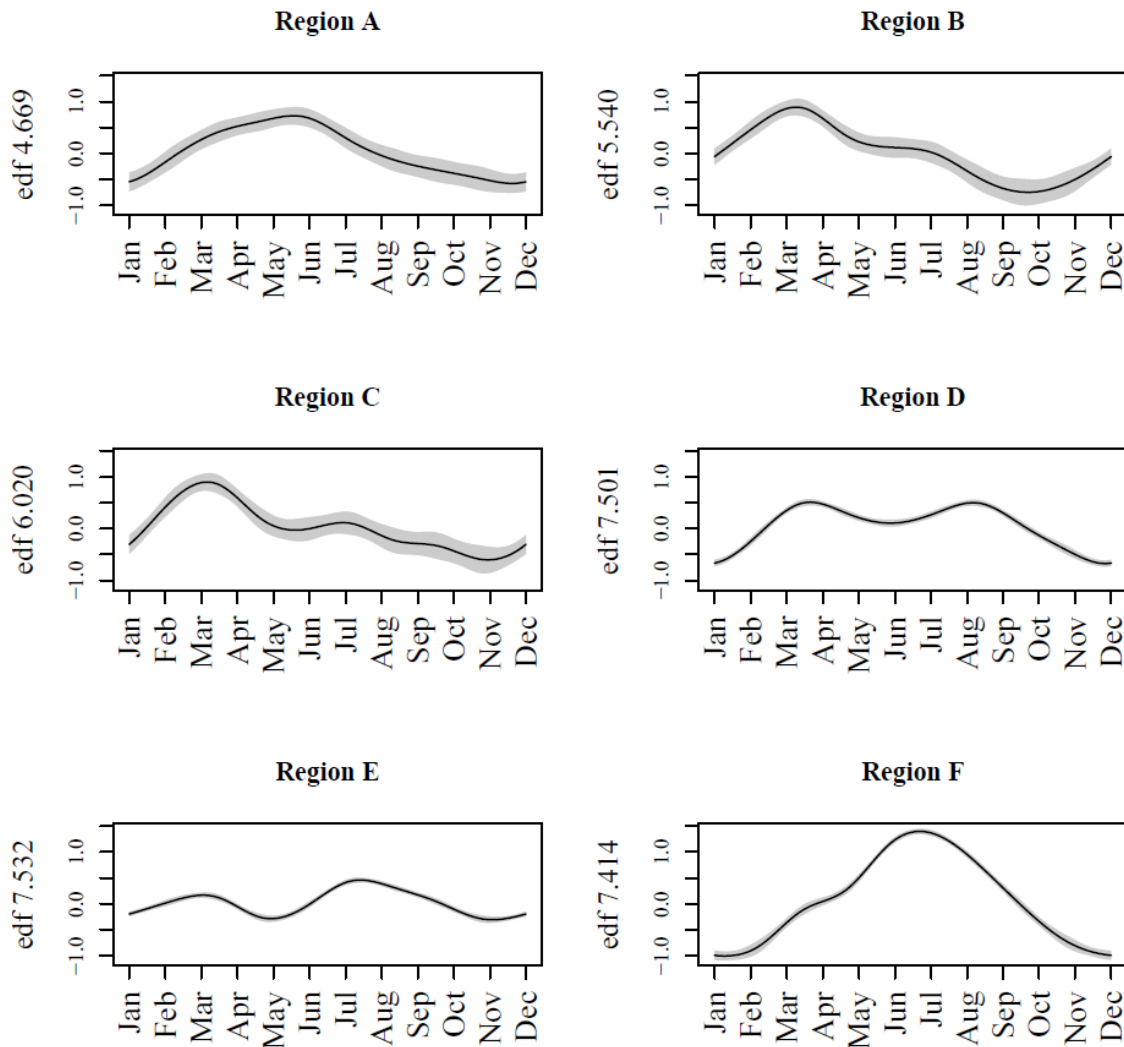

Figure 7: Estimated smoothing curves for the final model which incorporated a smoother for month for each region individually, showing seasonal patterns in number of strandings per region. The shaded area represents 95% confidence bands.

Table 1: Smooth term results of the final model which incorporated a smoother for month for each region individually (circular cubic spline).

	Edf	F	p
s (Region A)	4.669	15.26	<0.001
s (Region B)	5.540	22.96	<0.001
s (Region C)	6.020	19.50	<0.001
s (Region D)	7.501	137.4	<0.001
s (Region E)	7.532	87.72	<0.001
s (Region F)	7.414	529.16	<0.001

The model residuals are representative of variation in stranding numbers not explained by the variables included in the model and interactions between these. Extracting the normalised residuals from this final model thereby allows assessment of unusual variation within the time series. This does not only allow the identification of periods of high or low mortality out width normal variation, but additionally facilitates evaluation of the order of magnitude of an event compared to other years. **Error! Reference source not found.** shows this for region D, where points outside the dotted confidence bands can be considered unusual variation. There are a number of months in particular years where numbers where somewhat higher or lower than expected by the model, and the highly unusual months and years can clearly be identified. In region D, this included August 2011, May 2013, and March in 2014 and 2016). These graphs are available for the remaining regions in Supplementary material.
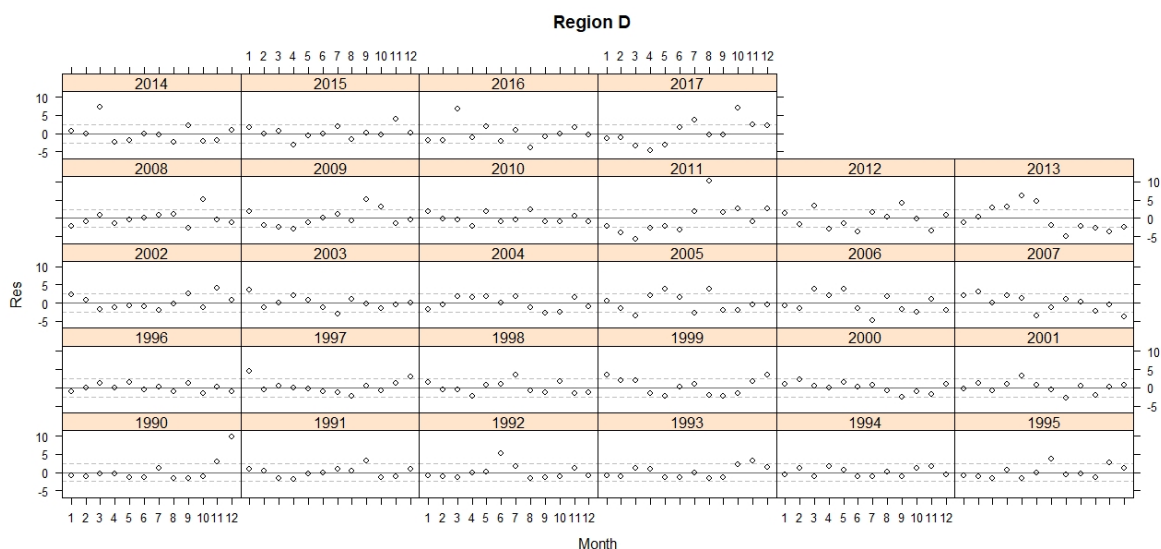

Figure 8: Pearson residuals from the spatiotemporal GAMM for region D per month for each year.

3.2 Biological parameters

Sex ratio and length distribution

Sex was recorded for 9546/16247 individuals (58.8%), comprising of n=5325 males and n=4222 females in the entire dataset. Length was measured or estimated for 10915/16247 (67.2%). The distribution of lengths varies per region (Figure 9). In most regions but especially in region D and E, the majority of the stranded population comprises juvenile individuals with a length of around 100 – 120 cm. Region A, B and C show a relatively equal distribution of lengths between 90 – 160 cm, yet with a slightly higher proportion of juvenile animals between 100 – 120 cm particularly for region B. Proportionally very few individuals <90cm were found in these regions. Region D and E are dominated by juvenile animals between 100 – 120 cm with only few adult individuals of around 150cm and even less animals with a length <90cm. In contrast, region F is characterized by a high number of porpoises with a length of 60-80cm corresponding to the length of neonates at the time of birth (Lockyer 2003), particularly compared to the other regions, and an equal amount of adults and juvenile individuals. Sex ratio appears to be relatively equal, though more males are found with a length of around 100-120 cm in region D and especially E, and hardly any adult males are present in these two regions. Looking at figure 8, sex ratio does not appear to differ among age categories for the other regions. Females tend to grow larger than males in general in harbour porpoises (Lockyer 2003), and the largest individuals tend to be female across all regions in this dataset as well.

Age class was known or identified for 11220 individuals comprising n=1444 neonates, n=6630 juveniles and n=3146, leaving n=5327 cases with unknown age class. Annual proportions were calculated to assess the sex ratio of strandings per region. Annual proportions were also calculated for the age classes (neonate, juvenile, adult) per region, corrected for the number of available cases,

which varied across regions (Table 2). Stacked bar charts per region were composed for both sex ratio and age groups to visualise the spread of proportions (supplementary files).
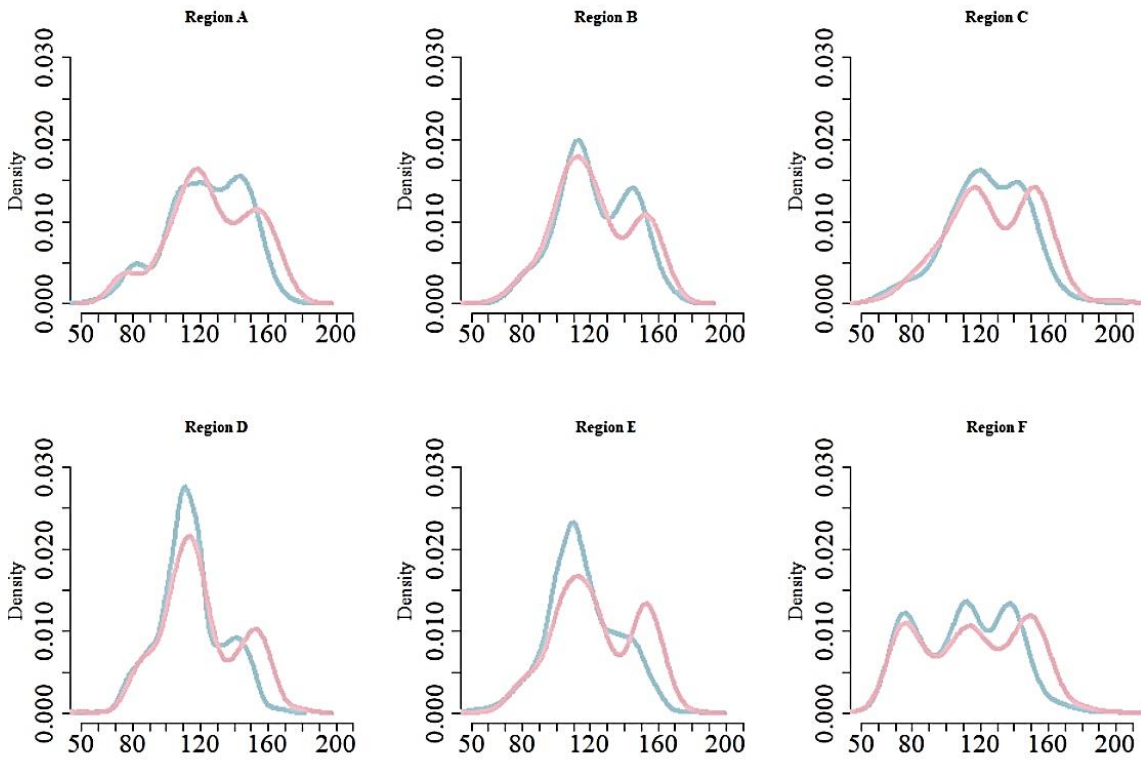

Figure 9: Density graph of total length of stranded population per region. Pink line represents the females and the blue line represents the males.

Table 2: Sex and age class per region. Number of cases available for assessment of sex (females, males, unknown sex) and for the different age classes (adult, juvenile, neonate, unknown) per region.

Region	Sex			Age class				Total
	Female	*Male*	*Unknown*	*Adult*	*Juvenile*	*Neonate*	*Unknown*	
A	183	214	197	196	269	46	83	594
B	172	221	387	199	366	45	170	780
C	156	201	337	206	306	42	140	694
D	1188	1645	1550	620	1831	252	1680	4383
E	1251	1552	3176	1034	2437	375	2133	5979
F	1271	1492	1054	891	1121	684	1121	3817
Total	4221	5325	6700	3146	6630	1444	5327	16247

Neonates

To further assess specific areas of importance for neonatal porpoises, we selected all cases with a length of >59 and <81cm, which resulted in a sample size of n=966. Porpoises with a size of <81cm were found in all regions, however, in small numbers in regions A, B and C, moderate numbers in region D and highest numbers in regions E and F (Figure 10,Figure 11). From the neonates of which sex is known (n=684), the proportion of males and females is given in Table 3.
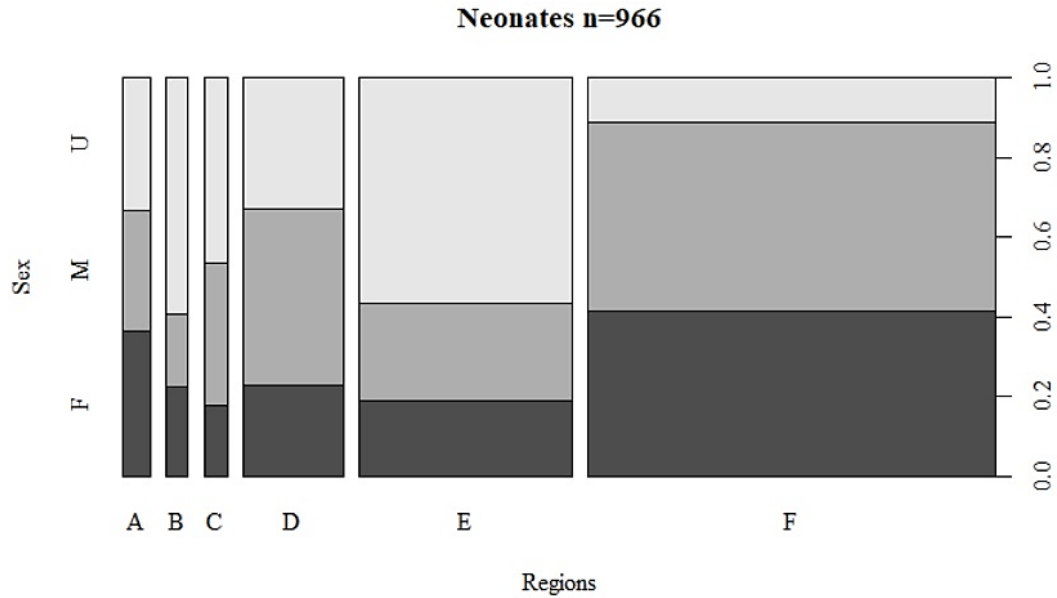

Figure 10: Stacked barchart of stranded porpoises (60 – 80 cm) per region (x-axis). The width reflects the total number of porpoises in the individual areas proportional to the North Sea total.
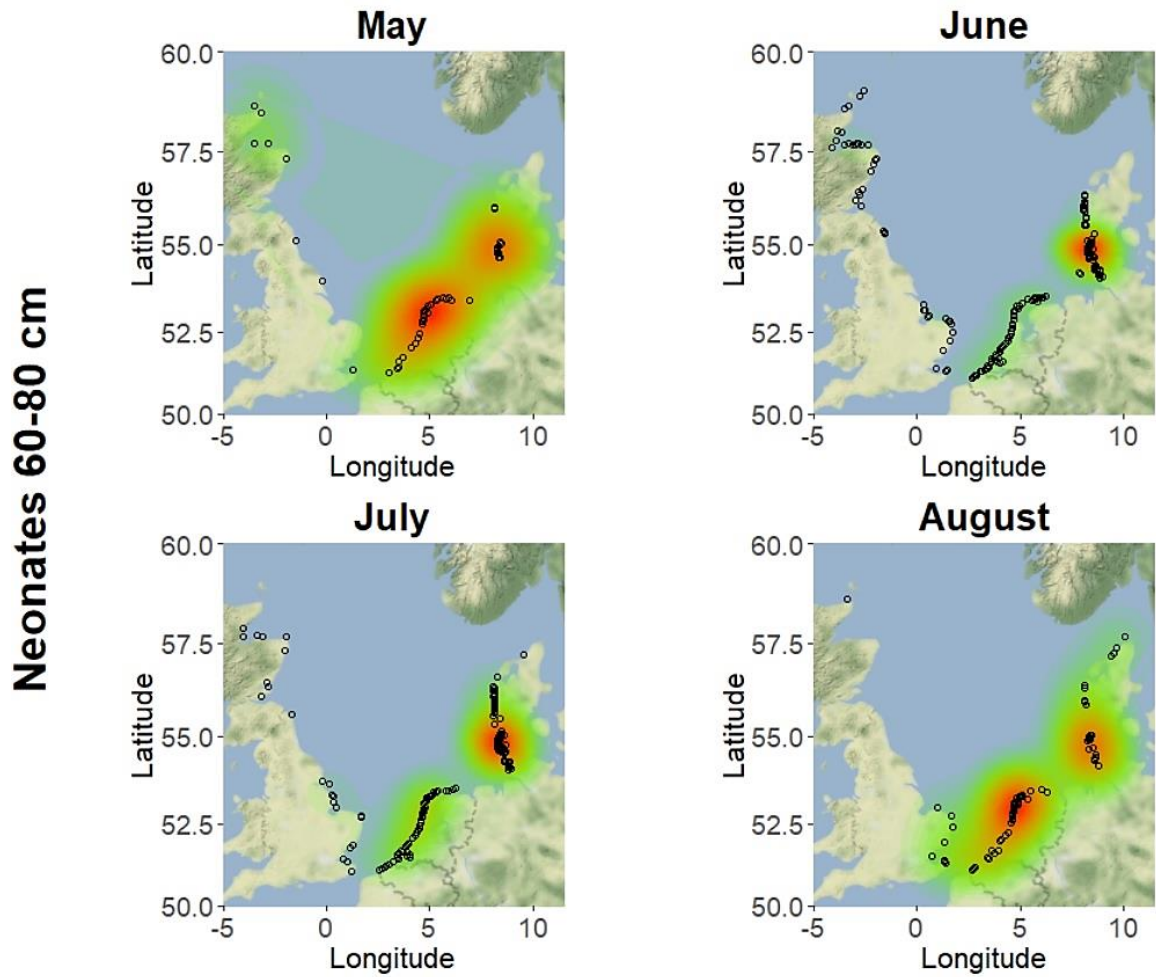
Neonates 60-80 cm

Figure 11: Harbour porpoise neonate (with a length of 60-80 cm) stranding frequencies in the study area in May – August (1990-2017). High densities are visible in May in most regions (except B and C), in June and July in mainly region F and in August in region E.

Table 3: Male to female numbers for neonates which had a sex determined (n=684).

Region	Males		Females		Total
	n	%	n	%	
A	10	45	12	55	22
B	5	45	6	55	11
C	10	67	5	33	15
D	54	66	28	34	82
E	64	57	49	43	113
F	236	54	205	46	441
Total	379		305		684

General Linear Model of biological parameters

The composition of the stranded population in terms of sex ratio per region in relation to length, as a proxy for age, was examined to explore whether there was heterogeneity in biological parameters possibly indicative of stratification of the harbour porpoise population of the North sea. The number of cases included in each analysis varied between models according to variables included and data availability and completeness. The optimal model included length as a proxy for age and an interaction of length with region, providing evidence of a significant relationship between sex ratio and age and heterogeneity of this relationship between regions. Model validation showed no evidence for violation of the underlying model assumptions. Plotted graphs show that the sex ratio for regions A and B is 0.5 and approximately stable with increasing total length, suggesting equal distribution of males and females in all age classes. For region C-F, the probability of a harbour porpoise stranded on the coast being a male drops with increasing length from an initiate 0.6-0.7, revealing higher probability of males for juveniles, towards 0.2 – 0.1 in larger, or older individuals, revealing that the larger adult individuals have a higher probability of being female in these areas (Figure 12).
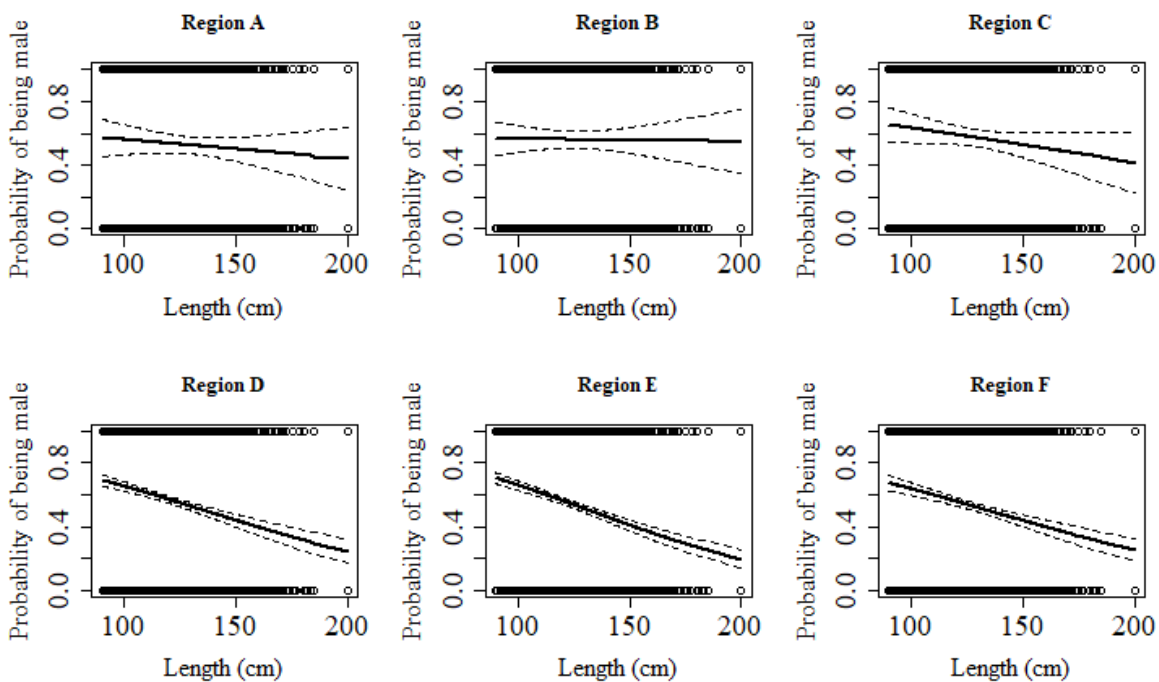

Figure 12: Model output of the optimal model representing the probability of a stranded harbour porpoise being male in relation to total body length (cm) plotted per region. Dotted lines representing 95% confidence intervals.

4   Discussion

This study utilised harbour porpoise strandings data to investigate spatial and temporal patterns of occurrence in the last 28 years. This is the first time these data from the individual national strandings surveillance schemes are combined for analyses at a spatial scale that is ecologically relevant, and provides a unique insight into the population of harbour porpoises in the North sea. A total number of 16247 harbour porpoises strandings along the North sea coastline were recorded from 1990 – 2017. Strandings were relatively equally distributed around the Scottish, English, Dutch, and Belgian coastlines at the beginning of the study period, with slightly higher numbers being recorded around the German and Danish coastlines. For all areas, the number of strandings increased annually yet particularly started to rise since 2004. This was especially the case in the more southern regions, including the Dutch Delta area and Belgium, where numbers increased exponentially to the extent that those areas now receive the majority of all harbour porpoise strandings in the North Sea annually.

Although an increase in stranding numbers in the southern regions was apparent, absolute numbers in the other regions remained stable. Our findings are not in complete agreement with the population estimates derived through the large scale decadal surveys by Hammond et al (2002; 2013; 2017). In those surveys no changes in overall abundance were found, a marked difference in harbour porpoise distribution was reported between 1994 and 2005, where the main concentration in the North Sea had shifted from the northwest in 1994 to the southwest in 2005, and the high densities around coastal Denmark in 1994 had dissipated in 2005 (Hammond et al. 2013), with similar findings for SCANS III (Hammond et al. 2017). Assessing the abundance estimates for the individual survey blocks in relation to observations in the similar regions used here, our findings correspond and reflect a marked increase in strandings in the southern regions observed from 2004 onwards. However stranding numbers in the more northern regions did not decrease, providing no evidence for reduced abundance or density in these areas throughout the period of our study in contrast to Hammond et al. (2013). Additionally, the most recent SCANS results for the regions corresponding to our regions B and C (Scotland and part of England) are still higher than those for the southern regions corresponding to our regions D and E. This supports the hypothesis that the higher stranding frequencies observed for regions D and E are more likely explained by an increase in mortality rate, rather than simply a recently higher abundance in these regions. The information on smaller-scale distributional variation such as stranding analysis could have significant management consequences particularly when aiming to mitigate local impacts of disturbance. The results of our study present a strong regional seasonality in strandings: an indication of season specific habitat use or season specific mortality. This is essential information that should be taken into account when e.g. planning offshore activities, aiming at reducing the negative impact on populations in particular areas at particular times or on particular vulnerable population groups.

Baseline spatiotemporal variation in stranding frequency

Modelling patterns in stranding frequencies as done here is a robust means to assess baseline variation, and identify significant deviations from expected stranding numbers in time and space. The GAM model permits for any change in the incidence of strandings to be detected and quantified at a regional scale, providing a framework for monitoring unusual mortality that can be used for future reference. By evaluating the normalised model residuals, deviations from the norm can be observed whilst taking into account the baseline heterogeneity between regions and years. This makes it possible to identify periods of unusual mortality, and assess the order of magnitude of these events compared to previous years as well as pre- and post-event periods. Being able to detect an elevation in stranding rates is however just the first step, but the interpretation of the detected unusual variation in stranding frequencies at particular times and in particular areas should be done with caution.

In our analyses, a clear seasonality was detected which was not homogenous across regions. Yet, regions A-E showed high stranding numbers in the months March and April. This apparent peak was found to be dominated by juvenile individuals for all these regions, and could therefore most likely be explained by juvenile mortality. Lockyer (2003) reported dependency on their mother of calves with a total length of <115 cm and presumable age of up to ten months for harbour porpoises. With calving occurring in spring and summer months, this means that animals should become independent February to April. Mortality at this life stage is reported to be highest in many mammal species (e.g. Barlow & Boveng 1991), and this additionally coincides with the period at which sea surface

temperatures are at their lowest in the North sea (Vishnyakova & Gol'din 2014). Long-term insufficient feeding can lead to dramatic loss of body condition, which is particularly ominous for harbour porpoises given their large body surface to body volume ratio and accompanied energetic requirements (Kastelein et al. 1997; Lockyer 2007). Juveniles have to forage independently for the first time in February-April, and combined with the low water temperature this can rapidly result in high nutritional and physiological stress, eventually leading to mortality due to hypothermia. Further investigation incorporating measures of nutritional condition of stranded animals and sources of mortality could provide valuable insight into whether this observed peak in the months March and April could indeed be explained by juvenile mortality following starvation, and whether the high density of juvenile mortality in particularly regions D and E can potentially be attributed to this process.

Neonatal porpoises

Profiling strandings at a spatial scale that makes ecological sense can reveal vital clues about the possible processes underlying the demographics of a population. In addition to spatiotemporal analysis, we also investigated age class and sex distributions of porpoises in the North Sea. Porpoises are born at a length of 65-75 cm (Lockyer 2003). Parturition is reported to occur from mid-May to August in the North Sea (Sørensen & Kinze 1994; Addink et al. 1995; Lockyer 2003). Mapping stranded porpoises with length of 60-80 cm and in the months May-August showed that higher density of neonatal strandings occurred in region D and E in May (Dutch coastline mainly), but centred around region F (Schleswig-Holstein, Germany and west Denmark), mainly in the month June. This corresponds to the reported peak birth period in the Danish area (Lockyer & Kinze 2003). Previously, Sonntag et al. (1999) suggested that the area off the islands of Sylt, Amrum and southern Rømø is an important calving ground for porpoises. Our findings correspond with this observation, and additionally show that also the coastal Dutch waters are presumable an area of importance at the start of the calving season. Given the lower density of recorded neonatal strandings in the other regions from May-August, it can even be suggested that regions E and F can be seen as areas of special importance for neonates from the entire North Sea Harbour porpoise population.

Biological parameters

The GLM model showed a higher probability of males for regions C-F for juvenile porpoises, with a decreasing probability with increasing total length. This pattern was not apparent in regions A and B and only slightly in region C, revealing heterogeneity in the age specific sex ratio of porpoises across the North sea. Sex ratio at time of birth for harbour porpoises is reported to be biased towards males: 1.1-1.2 males : 1 females in the foetal stage, and 1.1-1.7 males : 1 females in the post-natal stage (Lockyer 2003). For other odontocetes, like striped dolphins (*Stenella coeruleoalba*) male ratios in especially the foetus stage are higher, with 1.4 males : 1 females in the foetal stage, and 1.03 males : 1 females in the post-natal stage (Aguilar 1991). Although total numbers for which a sex was recorded was relatively small, the male to female ratios for the neonates in our study were 1.2:1 male to female in correspondence with Lockyer (2003). Ratios however differed for juveniles at 1.4:1 male to female. Strikingly though, especially the more south-eastern regions of the study area (regions D and E) presented proportionally higher numbers of juvenile male strandings than the other regions, and compared to juvenile females. An explanation for the difference seen in juvenile male strandings across the regions is yet to be established. The region specific finding is probably not explained by environmental biases, like wind or tides favouring juvenile males to strand, and this is therefore more likely explained by a difference in age- to sex specific habitat use. Sexual segregation, although known for other odontocetes like the sperm whale (*Physeter macrocephalus*) (Lyrholm et al. 1999), is not reported to occur in porpoises.

In mammals it is not uncommon to find higher mortality in juvenile males than females (e.g. Clutton-Brock et al. 1985a,b). This has previously been attributed to differences in the expression of X chromosomes; adaptive manipulation of postnatal sex ratio by mothers; or greater susceptibility of males to food shortage (Clutton-Brock et al. 1985a). Our study is the first to report upon a potential sex difference in mortality for harbour porpoises. Factors to explain this warrants further investigation, especially in regards to the observed spatial heterogeneity. One explanation for this observation could be that the southern North Sea reflects an area of less optimal habitat, and is therefore inhabited by the weakest population group: juvenile males. This could mean that the southern North Sea acts as a

sink for the entire North Sea harbour porpoise population; an ecological phenomenon known to occur in other taxa (Swennen 1983; Pulliam 1988; Mosser et al. 2009). Given their small size and limited ability to store energy, as well as their previously mentioned high energetic requirements, harbour porpoises have a strong dependency on food availability (Leopold 2015) and one would expect demographics to be mainly driven by prey dynamics and competition pressures. The southern North Sea therefore may represent a habitat of lower quality when it comes to prey abundance. Although causality will be difficult to determine, additional data on causes of mortalities and health parameters such as nutritional condition would be essential to further profile the stranded population and additionally assess the overall health status of individuals and compare these across regions.

The use of strandings as population indicator

A study by Pyenson (2011) using records from stranding and sighting databases from around the globe concluded that most strandings recorded the same ranked relative abundance as living communities and that strandings almost always provided better diversity information about cetacean communities than live surveys do. Strandings provide a unique sample of the living population that is difficult to obtain by most other means of surveillance (Pyenson 2010; 2011). It should however be emphasized that there is uncertainty around the extent to which stranding investigation can inform on the at-sea population. Strandings are a complex function of physical, social and biological processes (ten Doeschate et al. 2017) and whilst an unusual increase or decrease in strandings could indicate increased or decreased mortality, it may as well be a function of unusual variation in environmental conditions, or an increase in observer effort. It is therefore vital to characterise unusual deviations, which would require the identification and integration of multiple data sources informing on a number of biological, physical and social factors that can affect the observed strandings rate.

Oceanographic processes highly contribute to variation in stranding numbers and the probability of a carcass making landfall is dependent on a wide variety of physical static and dynamic variables (e.g. Peltier et al. 2012), as well as coastal bathymetry (Longhurst 2010). Efforts have been made previously to estimate the contribution of seasonal oceanographic climatology to temporal variability in stranding probabilities, where carcass drift was modelled through integration of a physical model that predicts trajectories of floating objects (Peltier et al. 2012; 2013). This was an important first step in delineating the complexity of carcase drift, yet a number of assumptions had to be made and further work would benefit from updating this model with prior information on biological parameters such as drift properties of individuals and density and distribution of the population. Making the model more specific incorporating regional hydrodynamic tidal models would additionally add to our understanding of the contribution of climatic and oceanographic variability to the seasonality observed in strandings, and has the potential to identify offshore mortality hotspots, which is useful to incorporate with future stranding monitoring efforts.

Given the robust signal of the region specific seasonal pattern throughout the study period, it is unlikely that observer bias has had a strong influence on the results of the stranding data analysis done here. Nevertheless, there is uncertainty around the efficiency with which strandings are reported and it remains probable that low- or zero values can be attributed to undetected or unrecorded strandings. It is not impossible that a higher number of strandings occurred annually in earlier years, but this is confounded by factors like development and growth of coastal communities, increased awareness of the scheme, or easier access to technologies with which strandings can be reported

The added value of investigating mortality trends for conservation purposes

To date, several spatiotemporal analysis have been conducted on longer-term cetacean stranding patterns (e.g. Hart et al. 2006; Pikesley et al. 2011; Barbieri et al. 2013; Huggins et al. 2015; McGovern et al. 2016; Saavedra et al. 2017; ten Doeschate et al. 2017; IJsseldijk et al. 2018b) but only few have incorporated the result of mortality investigations. Mortality patterns have been examined for certain regions previously for e.g. assessment of trends in relation to fisheries (e.g. López et al. 2002; Silva & Sequeira 2003; Leeney et al. 2008) or climatic variability (e.g. Truchon et al. 2013). Causes of cetacean mortality reflect the threats affecting a population, like (changes in) prey availability, predator presence, fisheries, disease and contaminant levels. Studying causes of death is the main metric to assess threats and pressures to cetacean populations (IJsseldijk et al. 2018a). There are key examples where underlying causes of unusual mortality event (UME) were

unrevealed through dedicated investigations: bottlenose dolphin UME's in Mexico, where high numbers of cases with infectious disease were detected, resulted from pollution following the Deepwater Horizon oil spill (Litz et al. 2014; Venn-Watson et al. 2015); striped dolphin UME's in Italy were an effect of morbillivirus outbreaks (e.g. Casalone et al. 2014); mass strandings of beaked whales in the Canary islands resulted from military noise (Fernández et al. 2005) and harmful algae blooms were held responsible for bottlenose dolphin strandings in Texas USA (Fire et al. 2011). Only through having the ability to compare cases prior, during and after an event will allow proper assessment of cause~effect relationships with UME's or other changes in stranding patterns over time and space.

There is a perennial need to monitor and detect changes to marine populations, which becomes ever more pressing with an increased requirement for offshore renewable energy developments and lack of knowledge regarding their effect on the marine ecosystem. Stranding data can be collected at fine spatial and temporal resolutions and despite all levels of complexity offer a way of surveillance that is able to detect change at a relatively early stage, and can additionally yield substantial information about the characteristics of individuals and the population. As with other opportunistic wildlife data, information derived from strandings usually cannot be gathered by other means, thus tools to improve and expand the utility of these data will be of significant benefit. Further improvements in the methodological approach, refinements of sampling strategies, and integration of multiple data sources such as environmental datasets would provide methods to quantify and further reduce biases associated with the strandings process. Furthermore, incorporation of metadata collected at post mortem investigation of individuals would facilitate the assessment of health status at a relevant spatial scale, as well as characterisation of threats and pressures to the harbour porpoise in the North Sea, adding value and improving the qualitative and quantitative applicability of strandings as a population indicator for monitoring.

5 Conclusions

What is the spatiotemporal variation in stranding frequencies of harbour porpoises in terms of biological parameters? A total number of 16247 harbour porpoises strandings along the North sea coastline were recorded from 1990 – 2017. Stranding numbers increased annually in all regions, with a sharp increase in especially the southern region since 2004. After comparison with the abundance estimates from the SCANS surveys, we conclude that the rise in stranding numbers in the southern areas cannot be explained solely by a shift in distribution of or increase in abundance, thus seem to reflect an increase in mortality. A consistent regional specific seasonal pattern in stranding frequencies was also evident throughout the study period. In two regions (E and F), the majority of neonatal porpoise strandings were recorded during the calving season, with very low numbers elsewhere. This could indicate that these regions are areas of special importance for calving. In addition, the GLM model showed a higher probability of males for regions C-F for juvenile porpoises, and this has not changed significantly during the study period. This pattern was not- or less apparent in regions A-C, revealing heterogeneity in age specific sex ratio across the North sea.

Can these biological parameters than be used to infer whether or not there are sub-populations or how harbour porpoises are distributed across the area? Yes, this can be used as an indication of population structure and on how certain populations groups use the North Sea habitat, e.g. we have suggested potential areas of importance for calving and neonates. We present evidence of high male juvenile mortality in specific areas, which can indicate that these areas are of lesser optimum for harbour porpoises, therefore a potential population sink. However, these findings need to be interpreted with caution, as without data on environmental and physical variables as well as health parameters and causes of death of the animals, we can only speculate about underlying causes of the observed heterogeneity in the composition of the stranded population. Determination of sub-population based on genetic variance can only be done through genomic studies (as described previously by Fontaine et al. 2007).

Is it possible to develop a model that is able to detect changes in mortality at a relevant spatial and/or ecological level? Have such changes in mortality frequency been present in the past decade? Yes, we demonstrated that it is indeed possible to develop such a model and presented regional and seasonal differences in spatiotemporal stranding frequencies. In addition we showed that the long term trend in annual stranding frequencies has not been homogenous across regions. Profiling spatiotemporal variation this way facilitates detection of unusual variation in stranding frequencies and permits for any change these to be quantified by evaluation of the normalised model residuals. The model detected particular periods per region which presented stranding rates of higher magnitude than expected. This can be used as a reference framework for future monitoring.

What would the cause of death results add to the model? In which way could cause of death information be used to derive information about anthropogenic influences on the population? Studying causes of death is the main metric to assess threats and pressures to cetacean populations. Although causes of death can vary widely between individuals, previous studies demonstrated that categories can be assigned making spatiotemporal analyses worthwhile. Key examples have been the increase in mortality after the Deepwater Horizon oil spill in Mexico, or the mass mortality following epizootic disease outbreaks in the Mediterranean. In these studies, researchers have been able to assess UME's by comparing cases prior, during and after an event. This is the only way to proper assess cause~effect and put changes in trends into context. Our results demonstrated that it is possible to establish a baseline in stranding frequencies and profile seasonality and biological parameters. It was also possible to detect elevations in stranding rates: a first step, but following this process there is a unique opportunity to assess changes in mortality, including those of anthropogenic origin. This could be done by setting a baseline for mortality causes and assessing spatiotemporal variance within. Additionally, metrics collected at post mortem investigation, including data on nutritional condition, parasitism, and other health indicators, would allow for profiling the health status of individuals and spatiotemporal variation in this, facilitating assessment of general population health and potential region specific issues. Only through assessment on when, where and to what extent threats and pressure occur will allow assessment of future population impacts, especially taken into account the predicted increase in offshore wind industries and other anthropogenic activities at sea; this seems a vital step in effectively monitoring of the species.

6 Recommendations

As mentioned in the discussion of this report, factors influencing where and when an animal strands include, but are not limited to, ocean and geographic conditions, prey availability, abundance of sympatric species, susceptibility to disease, and changes in species range, but also observer efforts (e.g. Brabyn & McLean 1992; Hunt et al. 2006; Warlick et al. 2018). After completion of the analyses as presented in this report and several rounds of discussion with international experts working on marine mammal strandings across the North Sea region, the following future research focus is recommended:

Improve understanding of underlying causes of observed changes in stranding rates

Adding of environmental data, including wind (speed, direction) and sea surface temperature is recommended as a minimum to prove or disprove the potential environmental factors influencing (increases in) stranding frequencies. This could be done by focussing upon changes in environmental factors prior or during periods of higher stranding elevation (e.g. August 2011 in region D) compared to period in which numbers were as expected based on the GAM model.

Cause of death, to prove or disprove whether higher stranding numbers have been an influence of higher population numbers in the southern North Sea, which we deem incorrect based on the SCANS surveys, or a result of (differences in or cumulation of) threats and pressures that the individual porpoises suffered of. Health assessment is key here: through investigation of spatiotemporal changes in e.g. nutritional condition or disease susceptibility will we be able to better assess individuals as well as population resilience.

Drift modelling as described in the discussion of this report, for which oceanographic factors are deemed necessary. These oceanographic features would be useful to assess the factors influential on carcase drift, addressing an important bias associated with the stranding process (ten Doeschate et al. 2017).

Assessment of habitat characteristics, including bathymetry, to understand potential effects of differences across the study areas. This would also shed more light into specific areas of importance for e.g. neonates or juvenile males. Habitat characteristics also include prey abundance.

Improve understanding of biological parameters and mortality in porpoises

Cause of death, to prove or disprove whether higher stranding numbers have been an influence of higher population numbers in the southern North Sea, which we deem unlikely based on the SCANS surveys, or a result of (differences in or cumulation of) threats and pressures resulting in higher mortality. Besides health metrics that are collected during necropsies (which includes e.g. nutritional condition), also important causes of mortality across the North Sea habitat can be appointed so a complete picture on threats and pressures the porpoise population in facing can be drawn, also in light of cumulative effects of multiple stressors.

Life history parameters, to be able to determine or detect changes in population size and demographics, establishing (spatiotemporal changes in) age at sexual maturity; pregnancy rate; maximum age etc.. We strongly recommend to update the currently available information on life history as it is outdated and based on low numbers (e.g. Lockyer 2003), also to incorporation this data in models as the PCOD model.

To further investigate whether region E and F are special areas of importance for neonatal porpoises, it needs to be confirmed that density of neonate is higher in these areas compared to other areas of the North Sea. It is therefore recommended to assess mother-calf presence from the live survey data and compare those with the results of this study.

Prey preference, Leopold (2015) described age specific prey preference in porpoises stranded in the Netherlands, but also that porpoises have a high demand for nutritional intake. It is recommend to review currently available information in regards to prey preference of porpoises throughout the North Sea. This is needed to be able to compare prey preference with availability; contributing to our understanding of habitat use and optimal areas.

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7 Supplementary files

7.1 Additional maps

All strandings (1990-2017)
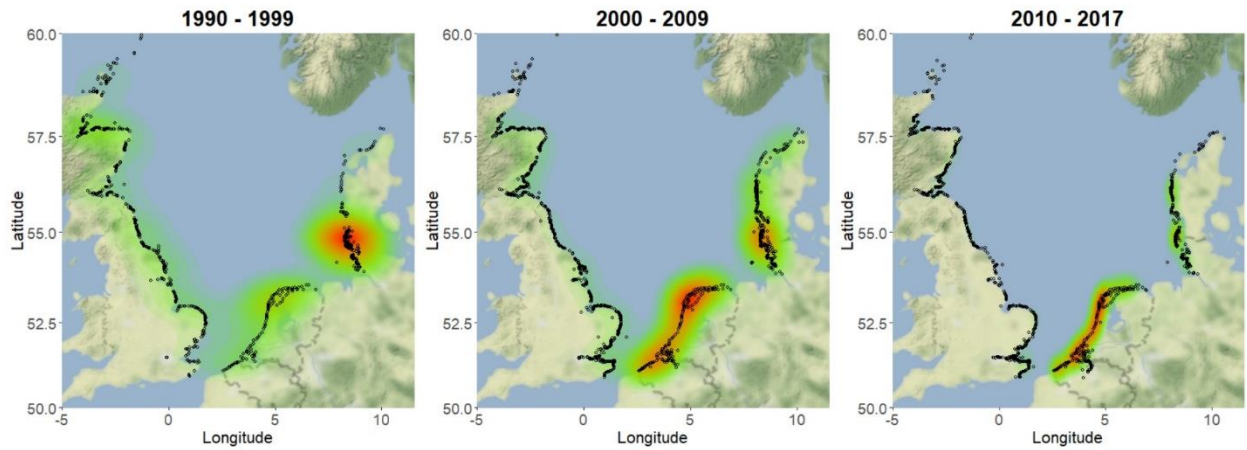
Supplementary figure 1: Harbour porpoise stranding frequencies in the study area overtime. Study area showing the density of all harbour porpoise strandings over three time periods (1990-1999; 2000-2009; 2010-2017).
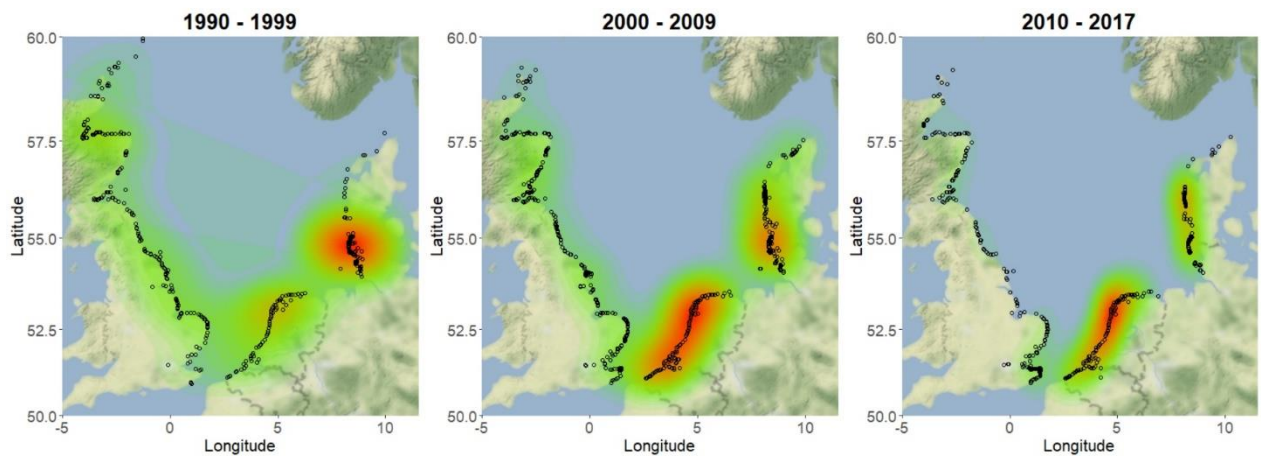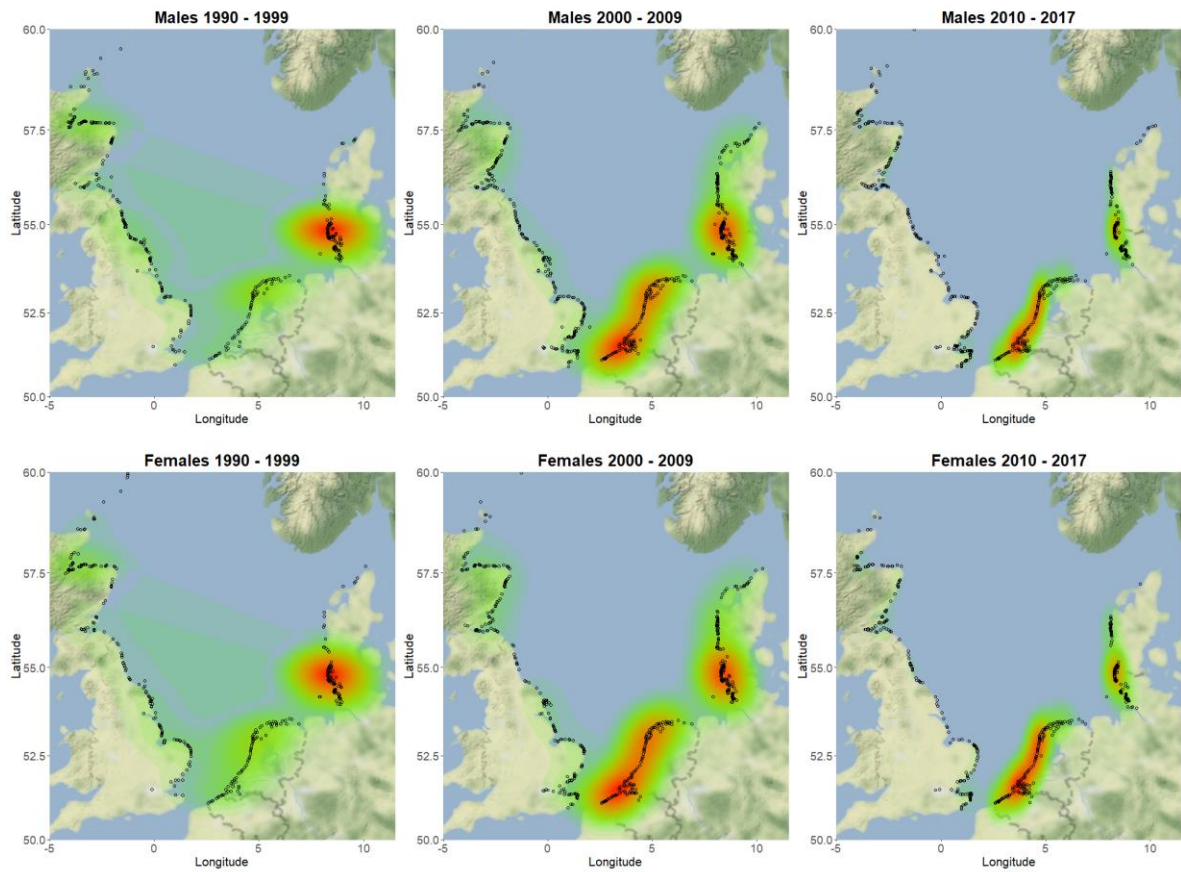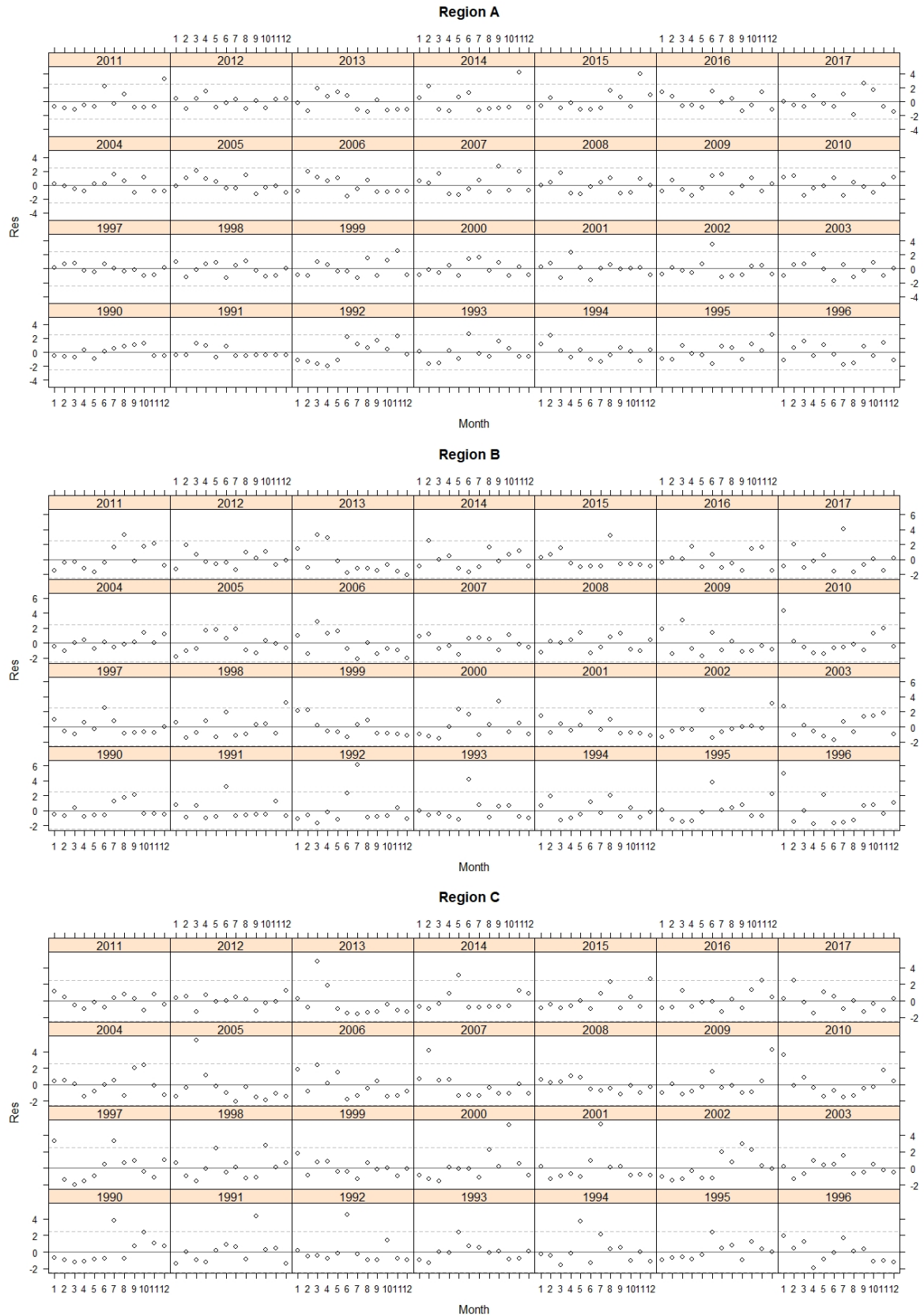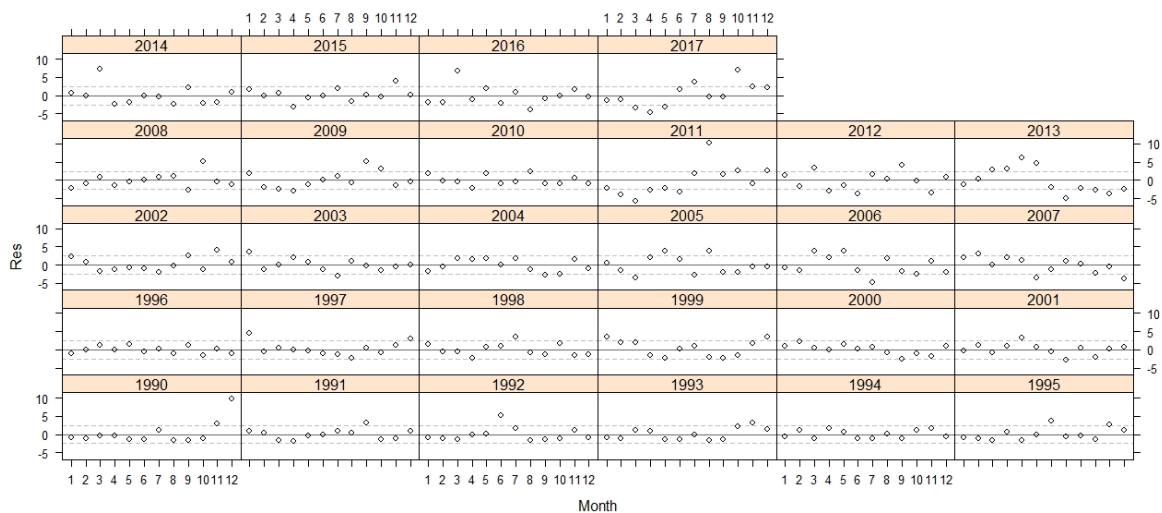
Neonates (1990-2017)
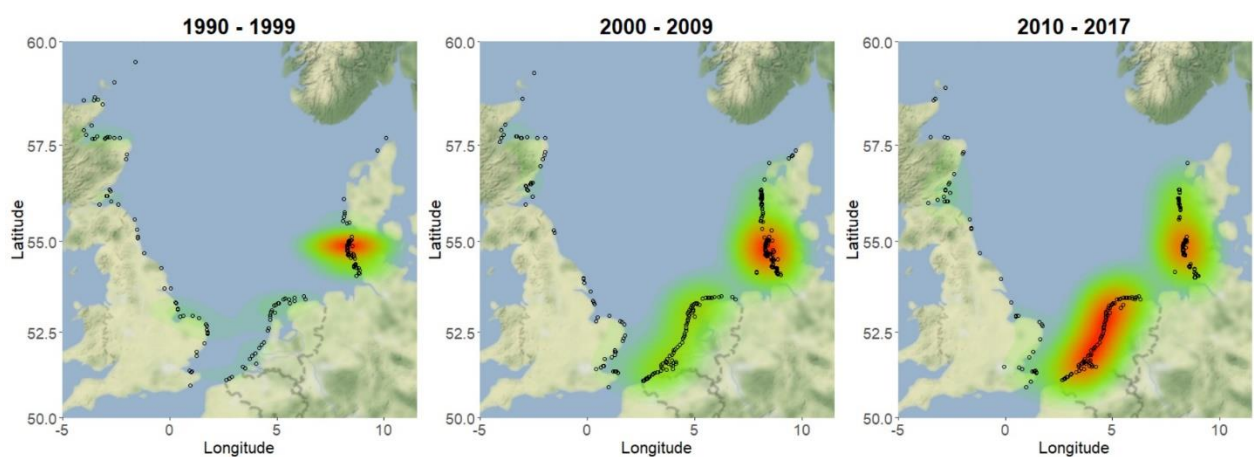
Supplementary figure 2: Neonate harbour porpoise stranding frequencies in the study area overtime. Study area showing the density of all harbour porpoises <90cm over three time periods (1990-1999; 2000-2009; 2010-2017).

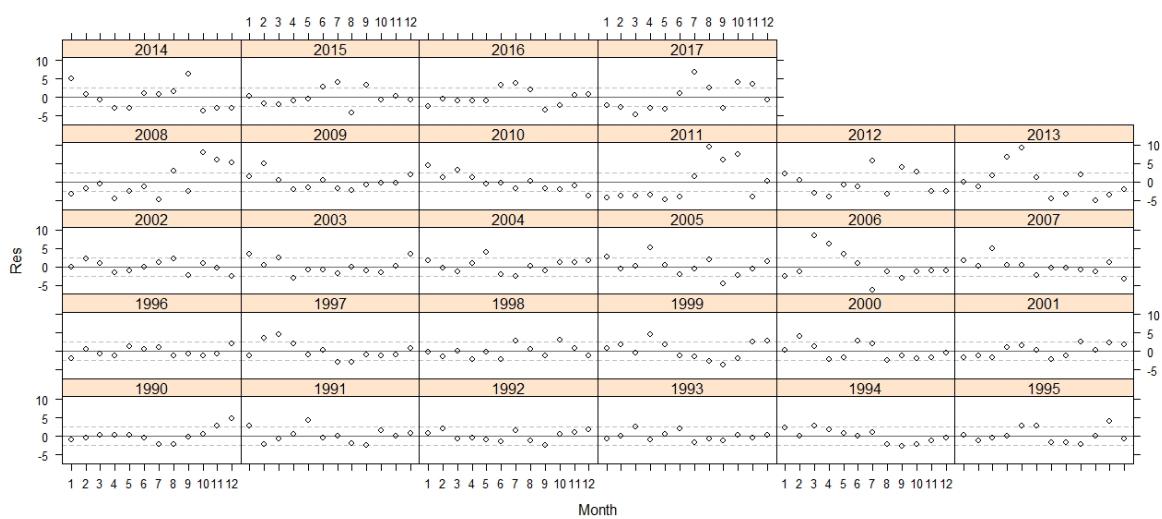**Juveniles (1990-2017)**
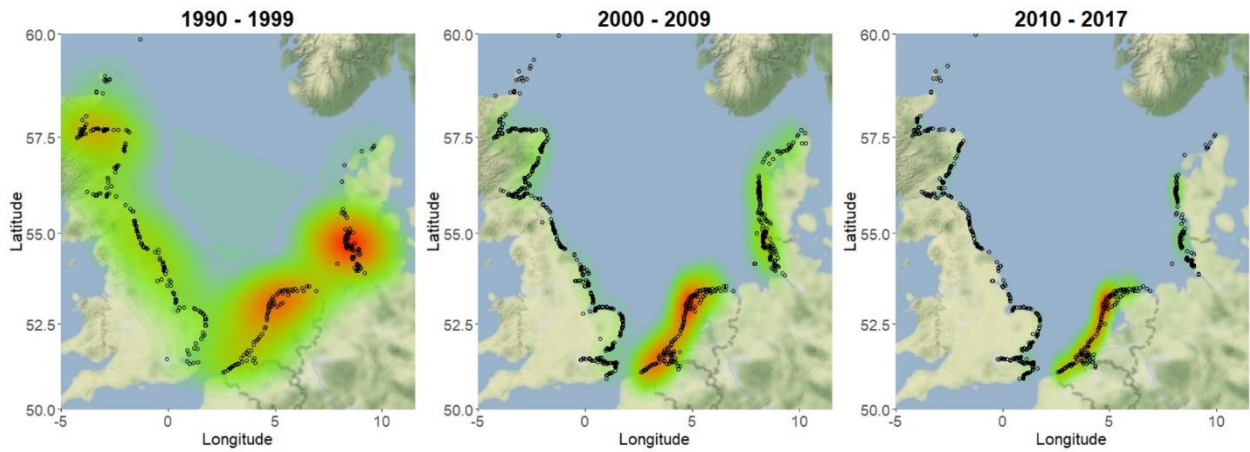
Supplementary figure 3: Juvenile harbour porpoise stranding frequencies in the study area overtime. Study area showing the density of all harbour porpoises 90-130 cm over three time periods (1990-1999; 2000-2009; 2010-2017).

Adults (1990-2017)

Supplementary figure 4: Adult harbour porpoise stranding frequencies in the study area overtime. Study area showing the density of all harbour porpoises >130 cm over three time periods (1990-1999; 2000-2009; 2010-2017).

Supplementary figure 5: Males (top) and females (down) harbour porpoise stranding frequencies in the study area overtime. Study area showing the density of all harbour porpoise stranding per sex over three time periods (1990-1999; 2000-2009; 2010-2017).

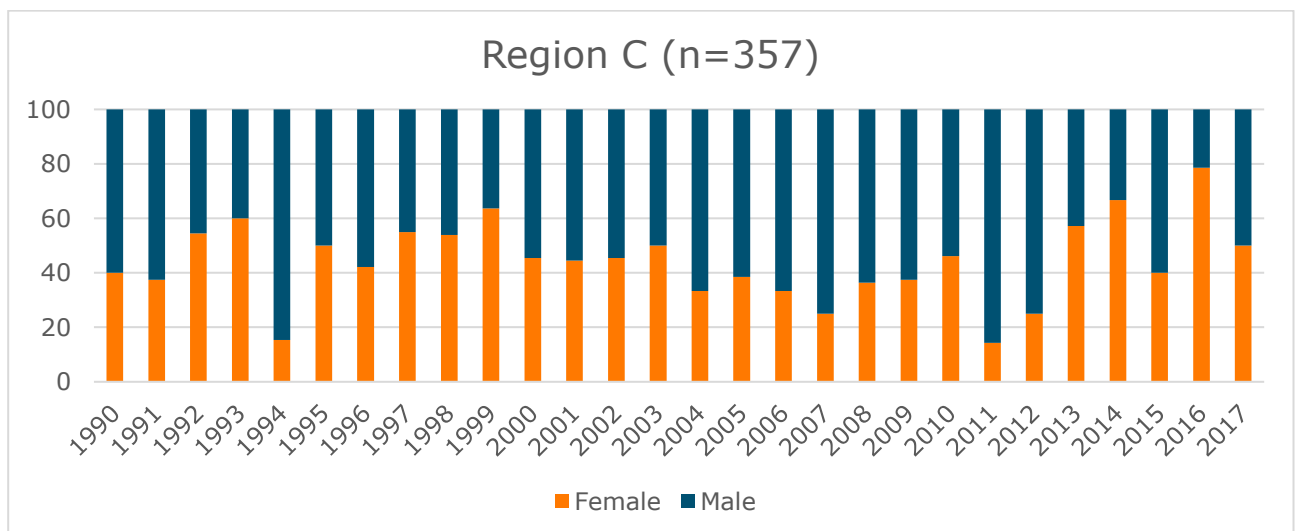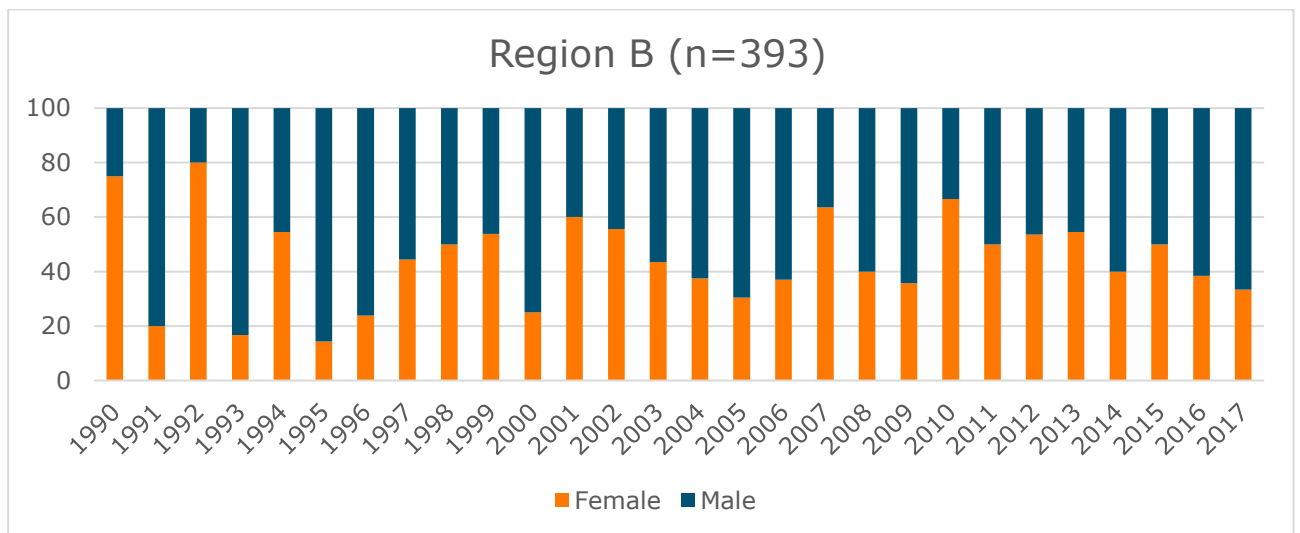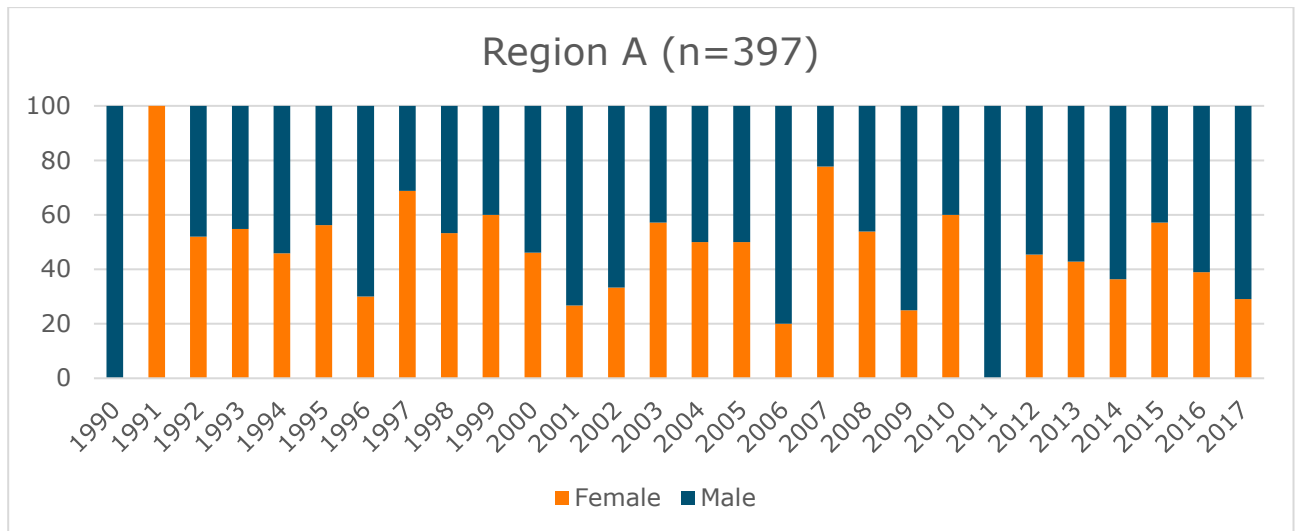## 7.2 Pearson residuals from the spatiotemporal GAMM

Region A

Region B

Region C

Region D

Region E

Region F
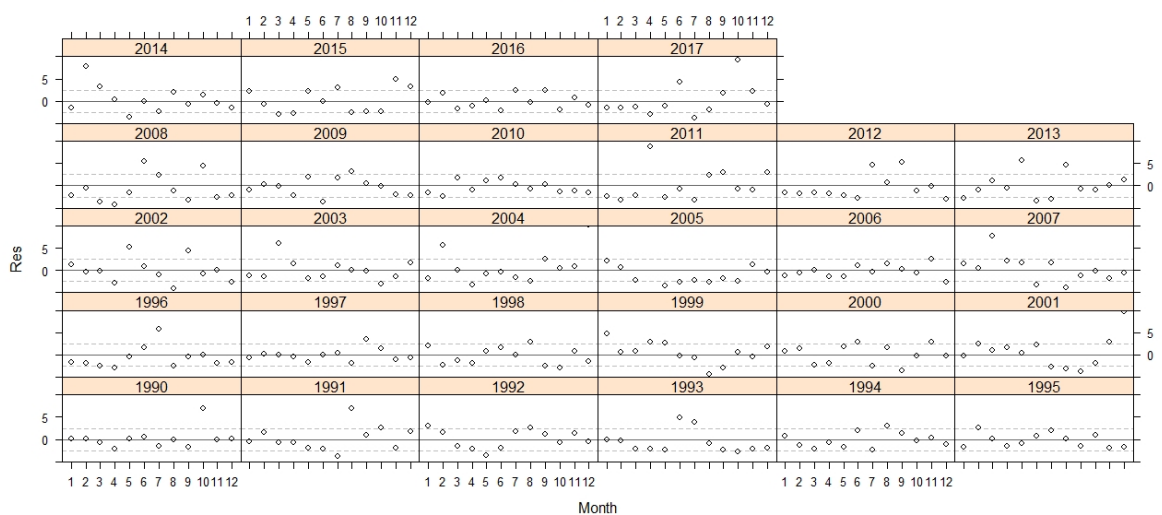
7.3 Proportions of males versus females per region

Region D (n=2833)

Region E (n=2803)

Region F (n=2763)

Faculty of Veterinary Medicine, Utrecht University
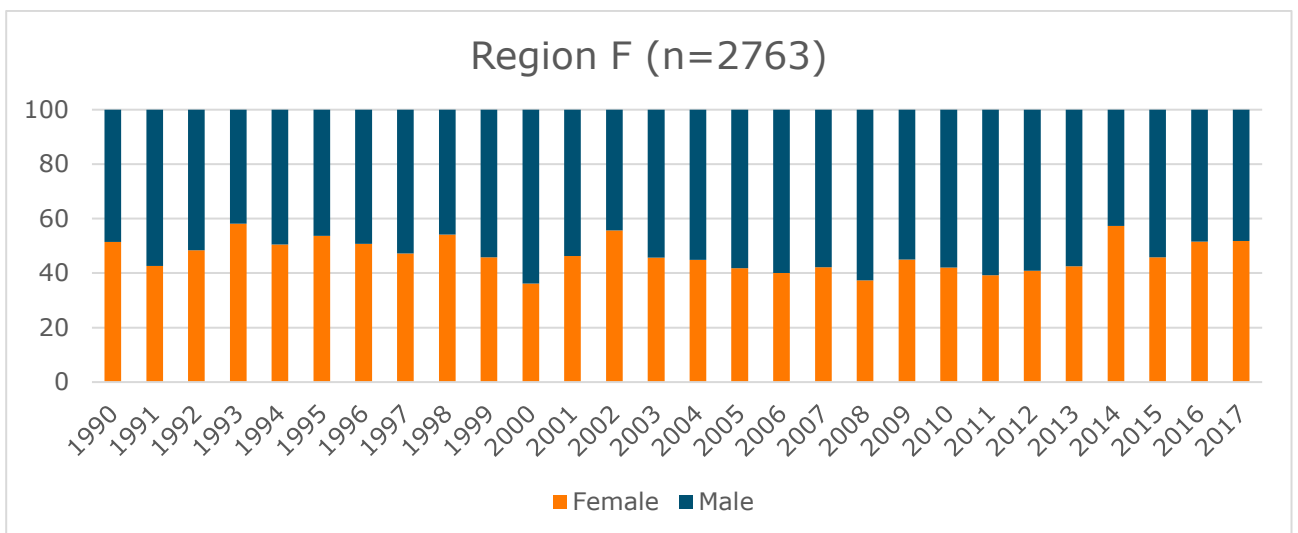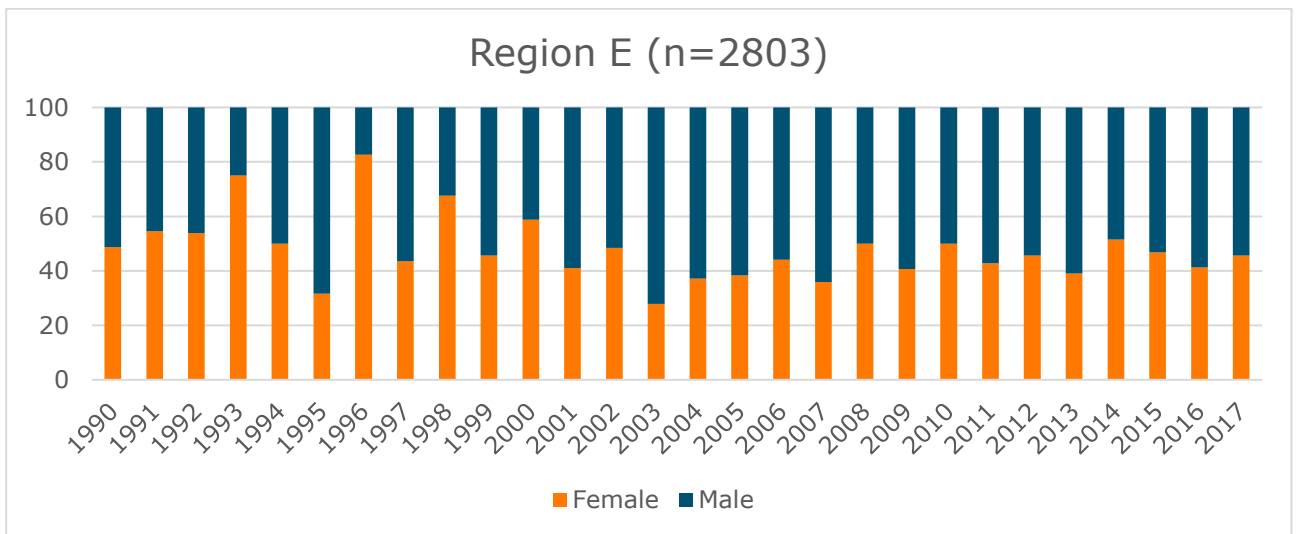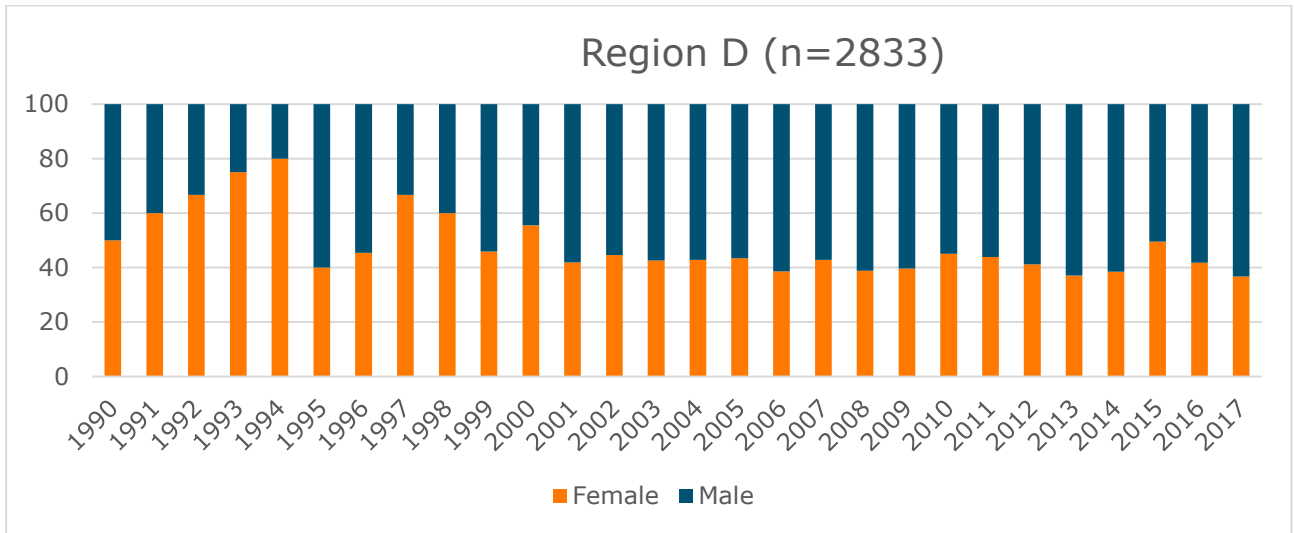
7.4 Proportions of age classes per region

Region A (n=511)

Region B (n=610)

Region C (n=554)

Region D (n=2703)

Region E (n=3846)

Region F (n=2696)