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Spatiotemporal mortality and demographic trends in a small cetacean: Strandings to inform conservation management

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ABSTRACT

With global increases in anthropogenic pressures on wildlife populations comes a responsibility to manage them effectively. The assessment of marine ecosystem health is challenging and often relies on monitoring indicator species, such as cetaceans. Most cetaceans are however highly mobile and spend the majority of their time hidden from direct view, resulting in uncertainty on even the most basic population metrics. Here, we discuss the value of long-term and internationally combined stranding records as a valuable source of information on the demographic and mortality trends of the harbour porpoise (*Phocoena phocoena*) in the North Sea. We analysed stranding records ($n = 16{,}181$) from 1990 to 2017 and demonstrate a strong heterogeneous seasonal pattern of strandings throughout the North Sea, indicative of season-specific distribution or habitat use, and season-specific mortality. The annual incidence of strandings has increased since 1990, with a notable steeper rise particularly in the southern North Sea since 2005. A high density of neonatal strandings occurred specifically in the eastern North Sea, indicative of areas important for calving, and large numbers of juvenile males stranded in the southern parts, indicative of a population sink or reflecting higher male dispersion. These findings highlight the power of stranding records to detect potentially vulnerable population groups in time and space. This knowledge is vital for managers and can guide, for example, conservation measures such as the establishment of time-area-specific limits to potentially harmful human activities, aiming to reduce the number and intensity of human-wildlife conflicts.

1. Introduction

As the pace of environmental change quickens, the need to monitor its impacts on wildlife populations becomes ever more pressing. Growth of the human population and the increase in global anthropogenic activities leads to increasing encroachment on ecosystems and wildlife communities (Tyne et al., 2016; Nickel et al., 2020). Surveillance or monitoring studies designed to quantify these pressures incorporate the ability to collect and analyse (repeated) observations or measurements, aiming at the detection of changes over time and space (Elzinga et al., 2009; Peltier et al., 2012). The efficiency of a monitoring plan relies on its ecological relevance, statistical credibility and cost-effectiveness;

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three aspects challenging to optimally achieve in wildlife studies (Hinds, 1984; Caughlan and Oakley, 2001; Tyne et al., 2016). The use of population indices and indicator species, particularly those that can inform on wider environmental health, are increasingly supported and included in the implementation of legislation (Carignan and Villard, 2002; Roberge and Angelstam, 2006; Moore, 2008; Bossart, 2011; Peltier et al., 2012, 2013).

The conservation and management of the marine environment is particularly challenging, as these habitats are difficult to monitor and often data-poor (Hiscock et al., 2003). Marine mammals, especially species which are long-lived and feed in the higher tropic levels, can be used as sentinels for monitoring of aquatic ecosystems (Moore, 2008; Bossart, 2011), but not without its complications. Marine mammals, and cetaceans specifically, are highly mobile animals that spend the majority of their time hidden from direct view. Therefore, even the most basic population metrics, such as abundance and life history parameters, remain mostly unknown for the majority of these species. Anthropogenic activities in the marine environment are increasing and this has raised significant concerns among conservationists (Aguirre and Tabor, 2004; Moore, 2008; Wassmann et al., 2011; Halpern et al., 2015). Without knowledge on population demographics and distribution, it is almost impossible to understand the severity of anthropogenic impacts on populations, and consequently how to effectively mitigate anthropogenic activities (National Academies of Sciences, Engineering, and Medicine, 2017; IJsseldijk et al., 2018a).

There are four fundamental population demographic metrics: reproduction, mortality, immigration and emigration. Declines in reproduction and/or immigration, or increases in emigration and mortality, will prevent population growth or may cause population declines. Monitoring changes in population dynamics is thereby most effective when demographic parameters can be measured at the scale of these four metrics directly, rather than focussing solely upon detecting changes in abundance, which is often the norm (National Academies of Sciences, Engineering, and Medicine, 2017). Although demographic parameters for marine mammals can in some cases be estimated from capture-recapture methods such as photo-identification, these methods come with a range of uncertainties and logistical restrictions (Evans and Hammond, 2004; Urian et al., 2015; Tyne et al., 2016) and are not applicable for all species. Population diversity, richness, and important metrics like age-specific mortality and age at sexual maturity, can be derived from analysis of stranded individuals, especially in areas where stranded marine mammal carcasses are found in sufficient numbers, and dedicated long-term data series are available (Pyenson, 2011; Peltier et al., 2012; National Academies of Sciences, Engineering, and Medicine, 2017; Saavedra et al., 2017).

Located in North-western Europe and adjacent to the North Atlantic Ocean, the North Sea basin is bordered by the United Kingdom, Belgium, the Netherlands, Germany and Denmark, in its western, southern and eastern parts, respectively. In these countries, systems for reporting, documenting and retrieving of stranded and bycaught marine mammals are well established and in most countries have been in place for decades. These systems were initiated due to the statutory requirement of several national, regional and international agreements and directives aiming at the protection of small cetaceans in these waters (such as ASCOBANS, 1992, European Habitat Directive 92/43/EEC, the European Marine Strategy Framework Directive (2008/56/EC), and Regional Sea Conventions, such as the Oslo-Paris Convention (OSPAR) and The Baltic Marine Environment Protection Commission (Helsinki Commission - HELCOM)). In the North Sea, this particularly involves a small, elusive yet abundant whale: the harbour porpoise (*Phocoena phocoena*) (Hammond et al., 2002, 2013; IJsseldijk et al., 2018a).

European stranding schemes have focussed mainly on reporting local stranding frequencies and seasonality within administrative management units (Jepson, 2005; Siebert et al., 2006; Keijl et al., 2016; Haelters et al., 2018; Kinze et al., 2018). However, to effectively investigate population dynamics among stranded individuals, assessments should be conducted at a relevant ecological and biological scale, independent of national borders. The objectives of this study were to assess the spatiotemporal stranding frequencies of harbour porpoises throughout the North Sea coastal area and to determine whether significant differences exist in the biological characteristics of the stranded specimens, using data spanning 28 years (1990–2017). The analysis conducted may serve as an example showing how long-term mortality data of a protected species can be used to assess demographic trends; a similar approach can be useful for wildlife conservation across different environments and taxa.

2. Methods

2.1. Stranding networks and study area

Harbour porpoise strandings data were collated from national stranding networks. These included records from the Dutch and Belgian coastlines, the North Sea coastlines of Denmark and Schleswig-Holstein (SH) in Germany, as well as the east coast of the United Kingdom (UK), starting at Romney Marsh (Kent) in the south, to Skerray (Sutherland) on the north coast of Scotland, including the Orkney Islands but excluding Shetland. Extensive descriptions on the history and procedures of these stranding networks can be found in Peltier et al. (2013).

2.2. Data collection and preparation

Stranding records from 1 January 1990 to 31 December 2017 (28 years) were selected, as the majority of the participating national stranding networks were initiated in 1990 (except for the Danish network, where quantitative stranding data was collected since 2008, see Kinze et al., 2018). Data submitted by each stranding network included as a minimum stranding month and year, and spatial location. Harbour porpoises floating or bycaught at sea were excluded. Animals that live stranded and died on the beach or were euthanised, without further rehabilitation or medical treatments, were included. The data comprised of 16,181 stranding records, all of which were single animal stranding events (Supplementary Table 1).

For the purpose of this analysis, the North Sea coastline was partitioned into six regions (A–F) of roughly equal coastal length and water depth. These regions closely follow the borders of the survey blocks as assigned by Hammond et al. (2017) to allow regional comparison with the results of a similar time-series of large-scale cetacean population abundance surveys (Small Cetacean Abundance in the North Sea and Adjacent waters; SCANS). Region A comprised of the Northeast of Scotland from Thurso to St Fergus, including Orkney. Region B followed the UK coastline southwards to Newcastle. Region C followed the UK coastline further south to Great Yarmouth. Region D included the rest of the English coast, the Belgian coastline, and the Delta area of the Netherlands. Region E included the rest of the Netherlands, and region F included the North Sea coastlines of Germany (SH) and Denmark (Fig. 1).

All animals were assigned to an age class based on body length, with animals < 91 cm classified as neonate, 91 cm to 130 cm as juvenile, and > 130 cm as adult (following Lockyer, 2003).

Due to differences in operational, logistical and financial capacity between stranding networks, two assumptions had to be adopted to allow for data comparison (also see Discussion). Effort and reporting is assumed to have been improved over time, likely attributable in part to increasing public awareness, technological developments facilitating submission of stranding reports, and an increased role of citizen science in marine conservation. This bias is unquantified for all stranding networks contributing to this study, but temporal variation in effort was assumed to be homogenous across the study area. The impact of carcass drift is considered important, although at the scale of this analysis we assume that animals stranded within a particular region, had died in

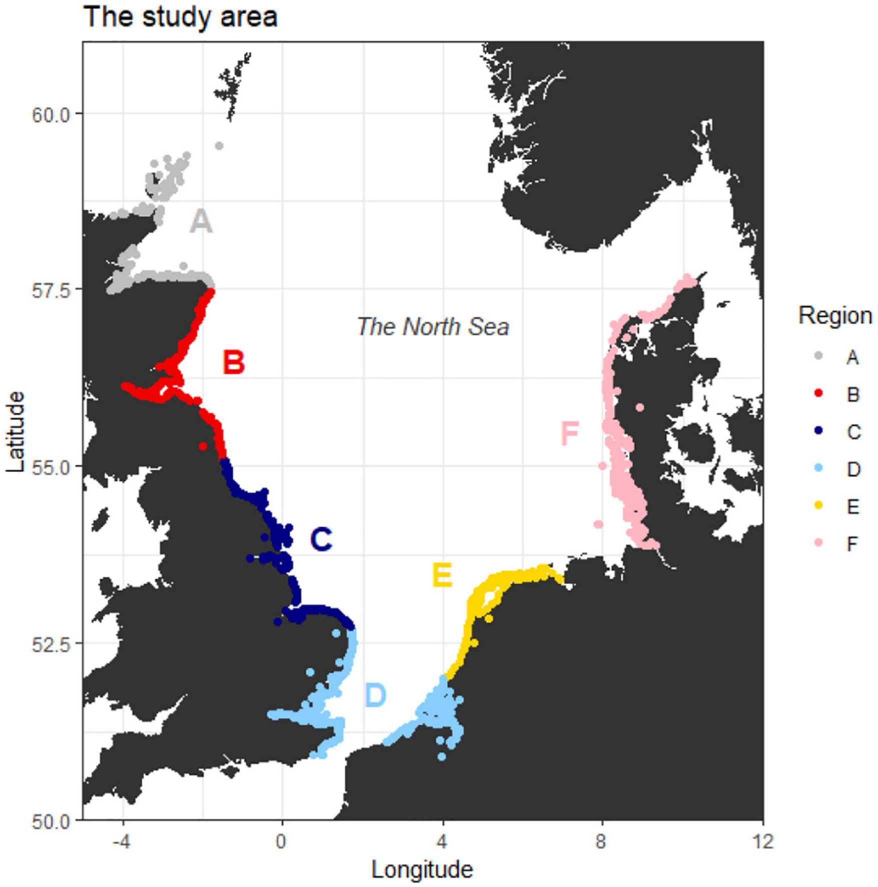

Fig. 1. The study area: the North Sea. The colours represent the six regions as assigned in this study, with: region A (in grey) comprised of the Northeast of Scotland from Thurso to St Fergus, including Orkney; region B (in red) from St Fergus, Scotland to Newcastle, England; region C (in dark-blue) from Newcastle, England to Great Yarmouth, England; region D (in light-blue) the rest of the English coast, the Belgian coastline, and the Delta area of the Netherlands; region E (in yellow) the mainland and Wadden area of the Netherlands; and region F (in pink) the North Sea coastlines of Schleswig-Holstein (Germany) and Denmark. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

that region (i.e. on that coastline or in the adjacent waters of that region).

2.3. Data exploration and analyses

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

2.3.1. Spatiotemporal variation and seasonality

Maps of harbour porpoise strandings were created using the ggplot2 version 3.1.1 (Wickham, 2016) and ggmap version 3.0.0 (Kahle and Wickham, 2013) libraries. Kernel densities were estimated to visualise point density and potential shifts in distribution across the study area and study period.

A Generalised Additive Mixed Model (GAMM) was implemented using the nlme version 3.1-140 (Pinheiro et al., 2018) and mgcv version 1.8-28 (Wood et al., 2016) packages. The number of strandings was modelled as a function of month to capture a potential seasonal effect, of year to examine long-term trends, and of region. 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. As autocorrelation can be expected in timeseries data, this was assessed following each model fit and appropriate correlation structures were fitted where necessary. Model selection was carried out through backwards elimination of variables. Data exploration indicated potential seasonality in all regions, but patterns were not identical and interactions between the three variables were therefore considered in the model selection. The model best describing the data was identified by examining the scaled residuals, parameter estimates, and the Akaike Information Criterion (AIC, Akaike, 1974). Model validation was done by evaluating diagnostic plots and residual variance using normalised Pearson residuals. The ratio of residual scaled deviance to residual degrees of freedom was calculated to examine over- or under-dispersion.

Additionally, it was investigated whether observed increases in stranding frequencies were related to regions. For this, the number of strandings was modelled as a dependent timeseries per region. A non-homogeneous birth process in discrete time was used following methods described in van den Broek and Heesterbeek (2007) and van den Broek (2020), with a negative binomial distribution for the observed strandings. The non-homogeneous birth process is a Markov model that is able to deal with the dependence in the data in time. Using this, we estimate the reproductive power directly from the data using the (log-)likelihood. This is a measure for the occurrence of the event ‘stranding’, and allowed to depend on age class, region and year. From this model, power odds ratios per region were calculated with region A as baseline.

2.3.2. Biological characteristics

The distribution of the biological characteristics (sex, body length, age class) in the set of stranded animals was examined to gain insight into population structure. Harbour porpoises are born at a length of 65–75 cm and in the North Sea parturition occurs between May and August (Sørensen and Kinze, 1994; Lockyer, 2003). Records with an unknown length/age class were excluded. We investigated whether areas important for calving could be identified, therefore neonates with body lengths between 60 and 80 cm, stranded in the period May to August (hereafter referred to as ‘new-borns’) were used to assess those areas with a high density of stranded new-borns. Additionally, sex ratios per region were assessed.

Strandings of juvenile and adult porpoises (> 90 cm) were analysed using Generalised Linear Models (GLM) fitted with a binomial error distribution and logit link. Sex (indicated as 1 for males and 0 for females) was modelled as a function of body length as a proxy of age, of month to examine seasonal differences, of year to assess potential long-term changes over time, and of region to evaluate potential heterogeneity between regions. Model selection was carried out by backwards elimination of variables and interaction, using the AIC to identify the optimal model. Model validation was done by evaluating calculated dispersion parameters and diagnostic plots using Pearson residuals.

3. Results

3.1. Spatiotemporal analysis

Annual stranding frequency varied greatly over the study period, with annual totals gradually increasing from around 150 in 1990 to almost 500 in 2004. After 2004, the density of strandings changed spatially and strandings started to concentrate more along the southern North Sea, with a steep increase in annual stranding numbers from 2004 until 2013. From 2009, the largest proportion of the total annual strandings was consistently observed in region D (southern England, Belgium and the south of the Netherlands). In contrast, absolute stranding numbers along the coastlines of regions A, B, C and F remained at levels similar to earlier years. Overall, years with the highest number of strandings within the dataset were 2011 and 2013, with 1313 and 1374 stranded harbour porpoises respectively (Figs. 2–3, Supplementary Fig. 1).

The spatiotemporal model best describing the data incorporated a smooth seasonal effect per region and a long-term trend per region (Supplementary Tables 2–3). There was a significant difference in seasonality in stranding frequency between regions, confirming that the long-term trend in annual stranding frequencies varied across the study area. This model was preferred over a model incorporating an interaction between month and year, suggesting that the observed seasonality in 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. Plotting model residuals versus fitted values showed patterns indicative of heterogeneity in the variance between regions, with the spread being much larger for regions D, E and F (south-western North Sea) than for regions A, B and C (northern UK coastline). Adding a variance structure to a GAMM is computationally highly intensive (Zuur et al., 2007), and there were convergence issues with a model allowing for a different variance in each region. Due to spatiotemporal similarities, it was decided to group regions A, B and C (northern-mid UK coastline), and regions D, E and F (south-western North Sea), and to incorporate a variance structure allowing for heterogeneity between the two groups only, which removed the majority of the heterogeneity in the residuals. The ratio of residual scaled deviance to residual degrees of freedom was 0.99, meaning the model was not under- or over-dispersed.

Seasonality in the regions A, B and C showed a similar pattern with a single peak in March (region B and C) and in May and June (region A) (Fig. 4). These single peaks were followed by a slow decrease and low stranding numbers throughout winter. Regions D and E were characterised by a bimodal pattern: one peak in March and April and a second peak in August. Region F was unimodal and only showed a clear peak from June to August with low numbers throughout the rest of the year (Supplementary Fig. 2).

The non-homogeneous birth model best describing the data incorporated a two-way interaction with year-region. Fig. 5 shows the odds of the regions B—F compared to the models' baseline region (A). Regions B, C and F had limited deviations from region A, but there were large effects in region D around 2004/2005 and again in 2011/2012, with much higher predicted strandings in these years. Additionally, region E presented a markedly high stranding rate in 2011compared to region A.

3.2. Biological characteristics

Sex was recorded for 58.7% of the individuals (n = 9496) and there were 5292 males and 4204 females. Body length was measured or estimated for 67.1% of the individuals (n = 10,863) and there were 1438 neonates, 6310 juveniles and 3115 adults (male/female-ratios given below). The distribution of lengths varied across the regions. In most regions but especially in regions D and E, the majority of animals were juveniles. Regions A, B and C showed a relatively even distribution of porpoises with lengths of 90–160 cm, with a slightly higher proportion of juveniles in region B. Proportionally fewer neonates were found in these regions. Regions D and E were dominated by juveniles, whilst region F was characterised by a proportionally higher number of neonates. Female harbour porpoises grow larger than males (Lockyer, 2003), explaining why the majority of individuals > 150 cm were females. Adult males were less commonly found in regions D, E and F compared to regions A, B and C (Supplementary Figs. 3–5).

New-borns (n = 963) were found in all regions, however, numbers in regions A, B and C were lowest (n = 30, n = 27 and n = 28, respectively), numbers in regions D and E intermediate (n = 122 and

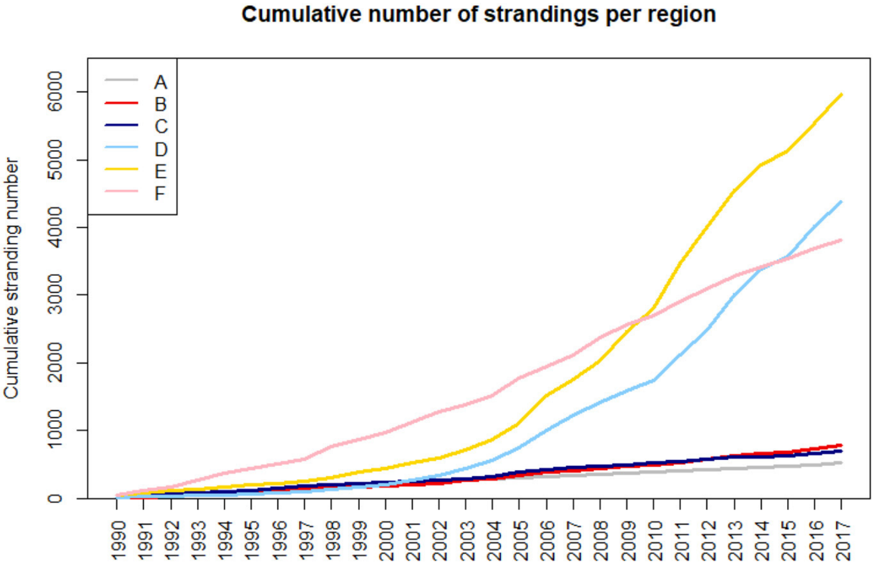

Fig. 2. Cumulative number of recorded stranded harbour porpoises per region over the study period (1990–2017).

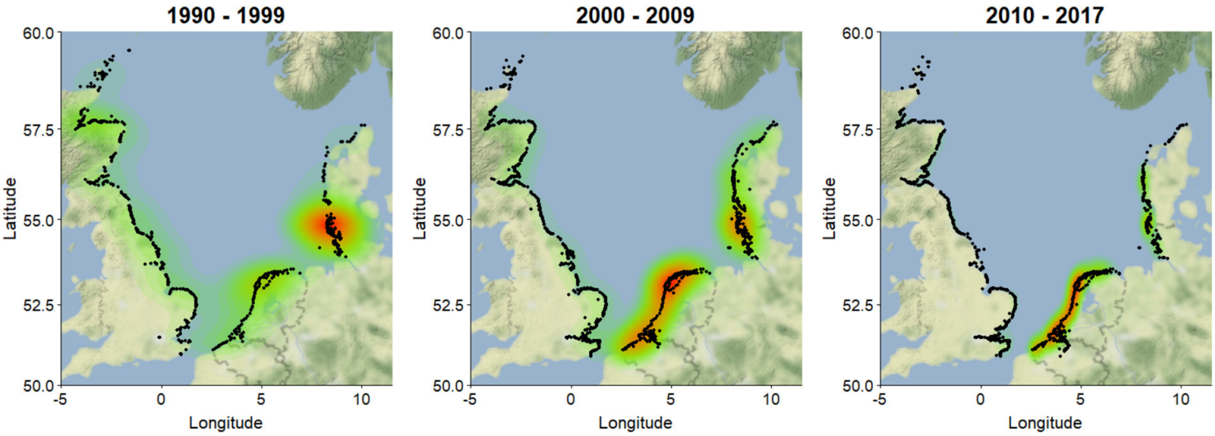

Fig. 3. Study area showing the density of all recorded harbour porpoise strandings over three time periods.

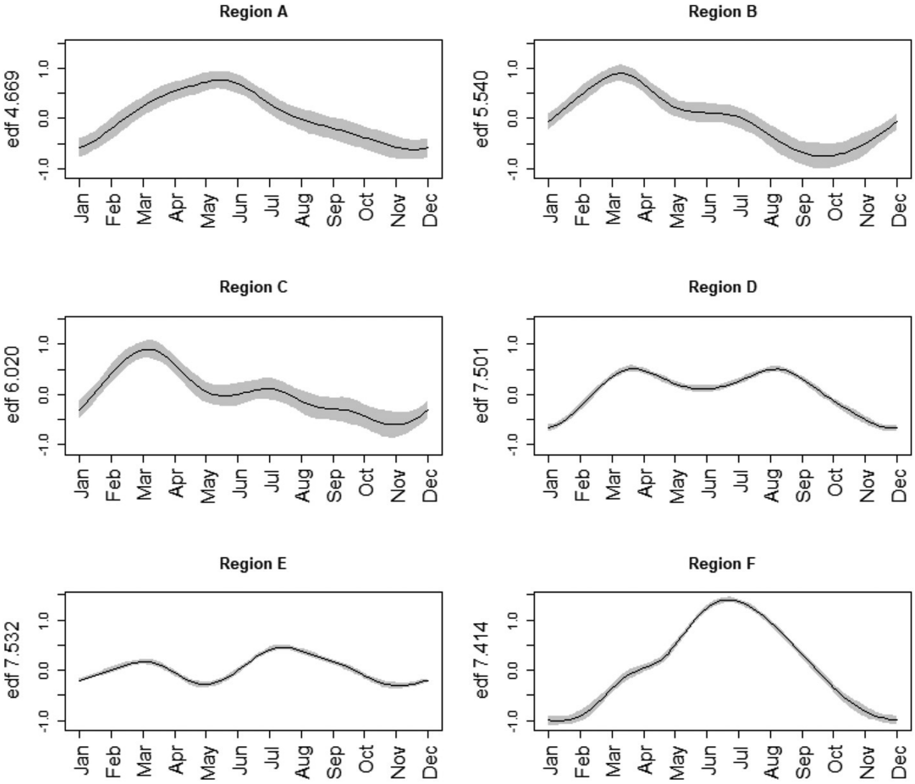

Fig. 4. Estimated smoothing curves showing seasonal patterns in the number of recorded strandings per region for the most parsimonious model, which incorporated a smoother for the month predictor for each region. Grey shaded areas represent 95% confidence intervals.

n = 260, respectively) and numbers in region F highest (n = 496) (Supplementary Fig. 6). From the new-borns where sex was known (n = 683), 378 were male and 305 were female (Fig. 6). Sex-ratio was skewed towards males in the neonate and juvenile age classes, with a male to female (M:F) ratio of 1:0.81 and 1:0.71, respectively. For adults in the regions D, E and F, the M:F ratios were equal; 1:1.05. Overall, the adult M:F ratio was 1:1.09. The largest difference in M:F ratio was found for juveniles in regions D and E, with a ratio of 1:0.68 (Supplementary Table 4).

The regional heterogeneity in sex- and age class was analysed for juveniles and adults. The optimal model included body length and an interaction of body length with region, providing further evidence of a significant relationship between sex-ratio and age class, and heterogeneity of this relationship between regions (Supplementary Table 5). Month was not incorporated in the final model, indicating that there was no significant seasonal variation in M:F ratio. Model results showed that the probability of a stranded porpoise being a male in regions A and B was 0.5, and that this was approximately stable with increasing length, suggesting more or less equal distribution of males and females across age classes within these regions. For regions C to F, however, the probability of a stranded porpoise being a male was 0.7, with a clearly decreasing relationship with increasing length (Fig. 7), i.e. in those regions sex ratio seems skewed towards males for shorter animals. Model validation showed no evidence for violation of the underlying model assumptions.

4. Discussion

Our study assessed population demographics and spatiotemporal trends of harbour porpoise based on data derived from an existing and continuous surveillance tool: stranded animals. Analysis demonstrated clear seasonality of strandings throughout the study area, indicative of

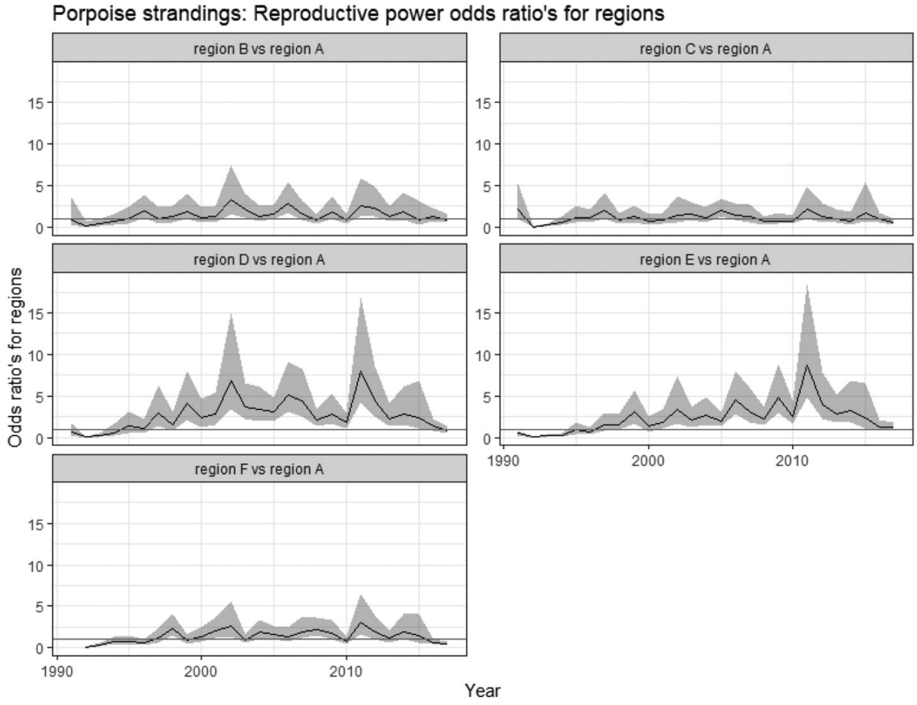

Fig. 5. Harbour porpoise stranding frequencies output from the non-homogeneous birth model presenting the reproductive power odds ratios for region B (2), region C (3), region D (4), region E (5) and region F (6) as a function of the baseline region A. Grey shaded areas represent 95% confidence intervals. The horizontal line represents the odds ratio of 1.

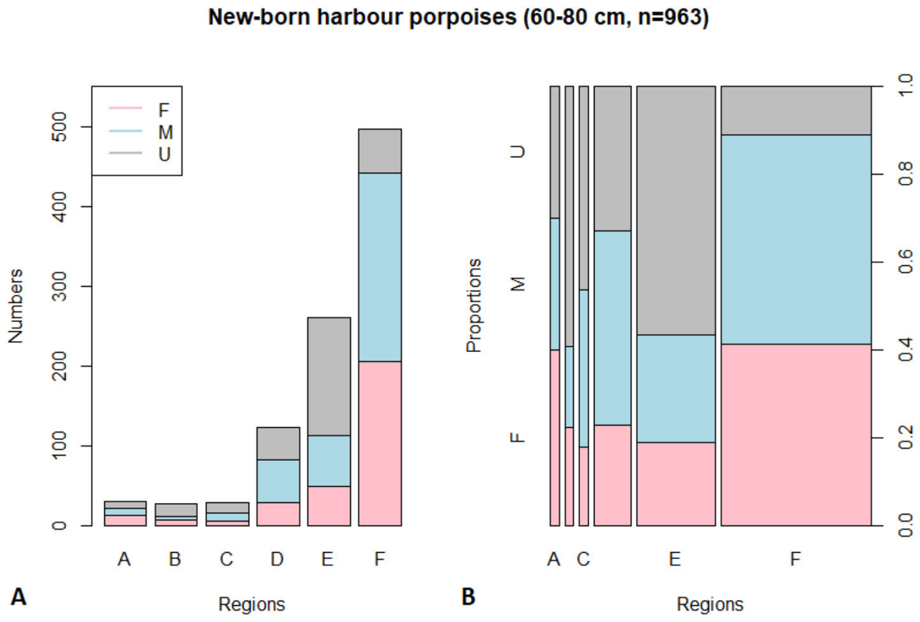

Fig. 6. Stranded new-born porpoises (60–80 cm). A: absolute numbers per region. B: proportions of sex per region, with bar widths reflecting the sample size. Pink blocks are females, blue blocks are males, grey blocks are those records with unknown sex. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

both season-specific abundance or habitat use, and season-specific or age-specific mortality. The high density of new-born strandings in certain regions is suggestive of areas important for calving, and the higher juvenile male mortality in the southern North Sea could indicate a possible population sink or reflect higher dispersion of males (further discussed below). It is essential to minimise disturbance and negative impacts on protected species when granting permits to proposed anthropogenic activities. To be able to do this, managers need to consider the nature and extent of impacts on vulnerable population groups, and thus information on spatiotemporal variation in population distribution is needed. With marine mammals being difficult to monitor in situ, stranding records provide a unique and cost-effective opportunity for surveillance purposes (Peltier et al., 2012, 2013; ten Doeschate et al., 2017; IJsseldijk et al., 2018b). Our results present key examples of potential vulnerable population groups in time and space and we therefore provide vital knowledge for managers, who can impose time-area closures as a management tool for specific human activities, aiming to reduce the number and intensity of human-wildlife interactions.

4.1. Spatiotemporal variation

Seasonality in strandings occurs as a result of variation in abundance, distribution or mortality of animals, as well as the non-biological components of the stranding process including oceanographic and effort factors (which are further discussed in Section 4.3). Understanding baseline variation in stranding rates is an essential first step in detecting unusual stranding events and requires a good knowledge of the existing natural variation at a relevant spatial scale. Clear seasonal patterns in stranding frequency were detected, consistent throughout the study

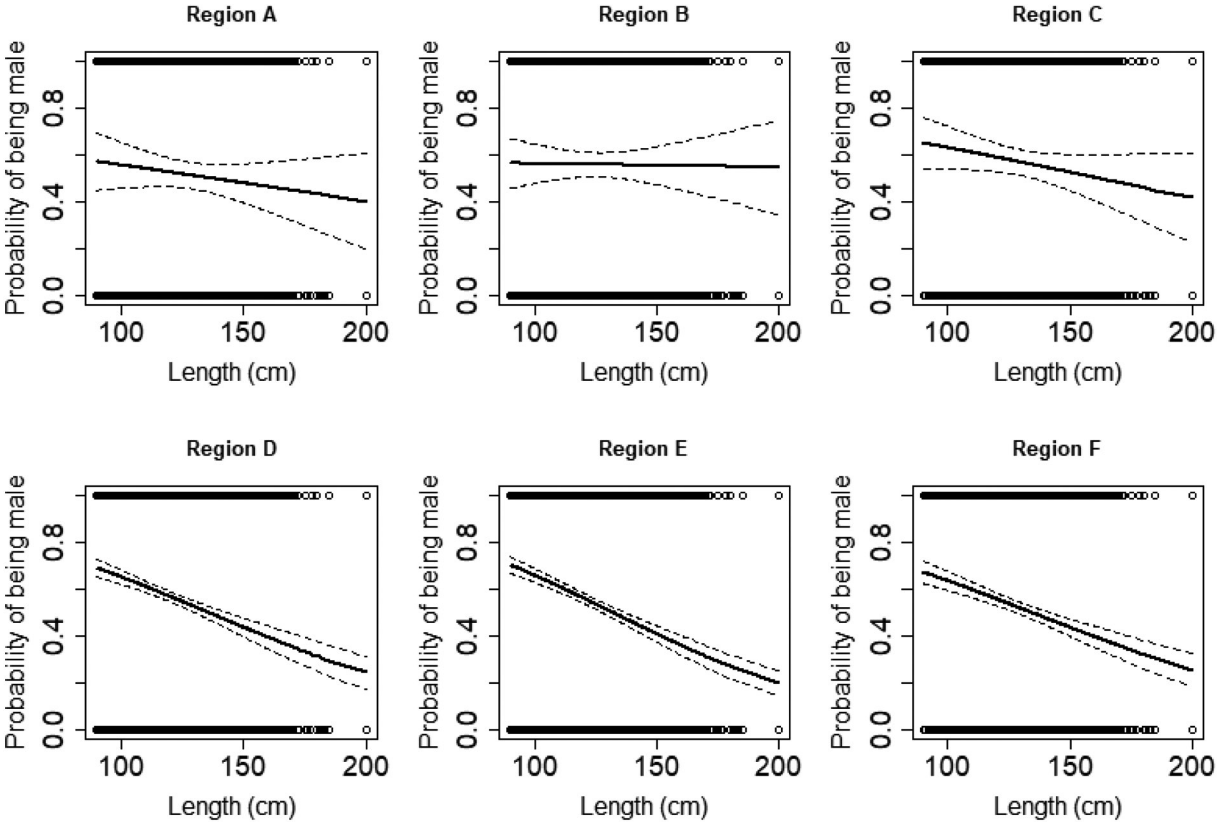

Fig. 7. Output of the optimal model representing the probability of a stranded harbour porpoise being male in relation to total body length (cm) plotted per region. The dots represent the raw data (being either 0 for the females, or 1 for the males). Solid line represents the predicted probability of being a male, with dotted lines representing the 95% confidence intervals.

period, with patterns differing between North Sea regions.

High stranding numbers in early spring were apparent in five regions (A to E), matching the high porpoise densities in spring in the southern and south-western region of the North Sea estimated through local abundance surveys and fine-scale model predictions (e.g. Siebert et al., 2006; Gilles et al., 2009, 2011, 2016; Geelhoed and Scheidat, 2018). The majority of stranded animals in March/April were juveniles. Harbour porpoises of < 115 cm and a presumable age of up to ten months may be maternally dependent (Lockyer, 2003). With calving occurring from May to August, this means that animals should become independent in February to April of the following year. This also coincides with the lowest sea surface temperatures in the North Sea (Høyer and Karagali, 2016). In marine mammal species, post-weaning mortality is reported to be highest (Barlow and Boveng, 1991). Long-term unsuccessful foraging can lead to dramatic loss of body condition, which is particularly ominous for smaller cetaceans such as harbour porpoises given their large body surface to body volume ratio and concomitant high and constant energetic requirements (Kastelein et al., 1997; Lockyer, 2007). Foraging independently for the first time combined with cold water temperatures can rapidly result in nutritional and physiological stress, eventually leading to hypothermia and death. The observed peak in March and April could potentially be explained by high juvenile mortality following emaciation and/or starvation. However, seasonal differences in both abundance and anthropogenic pressures, e.g. following spatiotemporal differences in fishery intensity and risk of bycatch mortality (Leeney et al., 2008), could also contribute to the observed pattern. Such increases in strandings should further be investigated incorporating data collected during post-mortem investigations, including information on causes of death and nutritional condition (further discussed in Section 4.3).

4.2. Age- and sex-specific variation

Information on the increases in mortality of particular age groups can act as early warning signals for population declines (National Academies of Sciences, Engineering, and Medicine, 2017). Assessing demographic parameters of stranded animals provides knowledge on distributional variation, regions of importance for reproduction, and age-specific mortality. A higher number of new-born animals were found in region F, corresponding to the coastline of Denmark and SH, Germany. The area around the islands of Sylt, Amrum, and southern Rømø, and the region of the Sylt Outer Reef have previously been identified as important calving grounds for the harbour porpoise (Sonntag et al., 1999; Siebert et al., 2006; Gilles et al., 2009). Our findings are in agreement with this and additionally add the northern Dutch coastal waters as a potentially important area for calving. Other areas important for calving may exist, but remain undetected where drift conditions or discovery conditions are less favourable.

A higher proportion of males was observed among the juveniles stranded in regions D, E and F. This was not apparent in regions A and B and only marginally in region C, revealing a difference in the age-specific sex ratio of porpoises across the North Sea. Relatively more adult females compared to adult males stranded in regions D, E and F and given that these latter areas were also suggested to be important calving grounds, this might be explained by mortality following calving and reproductive stress or by a higher density of adult females. It should be emphasised that the M:F ratio of neonates was also skewed towards males (1.24:1) and that a higher M:F ratio at birth was previously suggested by others (Lockyer and Kinze, 2003; Ólafsdóttir et al., 2003).

In mammals, it is not uncommon to find higher mortality in juvenile males compared to juvenile females (Clutton-Brock et al., 1985a,b; Clutton-Brock and Isvaran, 2007). The region-specific difference in sex ratio warrants further investigation and only allows for speculation at this stage. The most optimal habitat for harbour porpoises is yet to be defined. Due to their relatively small size, limited ability to store energy, and high energetic requirement, harbour porpoises are sensitive to even short-term decreases in food availability. In addition, prey quality rather than quantity is suggested to be an important determinant of foraging strategies (Spitz et al., 2012). Energy-budget population models for pilot whales (*Globicephala melas*) suggest that vulnerability to disturbance increases in areas, or during periods, with lower resource availability and strongly depends on population density (Hin et al., 2019). This is likely also the case for other cetacean species, including the harbour porpoise. Human activities are highly concentrated in the North Sea, where nearly all known anthropogenic stressors to marine mammals occur and overlap. There are indications that the southern North Sea specifically is an area of higher disturbance compared to the more northern areas (Halpern et al., 2008, 2015). Von Benda-Beckmann et al. (2015) reported on the impact of underwater clearance of unexploded ordnance on harbour porpoises in the Dutch sector of the North Sea, and indicated that detonation events occurred only in the most southern part. The English Channel is an area with higher marine traffic densities than other North Sea areas (NorthSee, 2016; Wisniewska et al., 2016, 2018). This could result in a higher mortality rate in this area or reflect a less optimal habitat compared to other North Sea regions. Consequently, the southern North Sea may be inhabited by the weaker population groups, i.e. juvenile males or compromised individuals, and reflects a possible population sink; a phenomenon described for other species and taxa (Swennen, 1984; Clutton-Brock et al., 1985a,b; Pulliam, 1988; Mosser et al., 2009). Another hypothesis is that this finding reflects higher dispersion of males. Sex-specific dispersal is known to occur in other odontocetes like the sperm whale (*Physeter macrocephalus*) (Lyrholm et al., 1999) and bottlenose dolphin (*Tursiops truncatus*) (Connor et al., 2000). To assess this further, additional data on causes of mortality and health parameters such as nutritional condition, incorporated with data on prey abundance and anthropogenic activities, would be essential, although causality would be difficult to determine. An assessment of genetic variation of stranded animals along the North Sea coastline, as well as the more southern areas of the harbour porpoise range (the French, Spanish and Portuguese coastlines) could additionally provide valuable insights into such hypotheses (Manlik et al., 2019).

4.3. Strandings as a surveillance tool

Population abundance surveys are mostly used as a monitoring tool for wildlife species. However, the timely detection of declines in marine mammal abundance requires intense levels of survey effort and currently there is fundamentally no reliable method to detect precipitous declines in most whales, dolphins and porpoises populations (Taylor et al., 2007; Tyne et al., 2016). Increasing the extent and frequency of surveys would improve the chances of detecting declines, but surveys are limited by the resources made available for them (Tyne et al., 2016). Three large-scale multinational abundance estimate surveys (SCANS) targeting harbour porpoises among other cetaceans have been conducted in European Atlantic waters, including the North Sea (Hammond et al., 2002, 2013, 2017). The dedicated SCANS surveys were run along particular transects during summer months at decadal intervals. Due to this temporal restriction, seasonal differences in distribution are not captured and precipitous changes would likely go unnoticed. Differences in seasonal distribution of harbour porpoises in the North Sea occur (Gilles et al., 2011, 2016; Geelhoed and Scheidat, 2018). Without the ability to quantify these, significant consequences for species conservation can be expected, specifically when assigning protected areas or aiming at minimising disturbance from anthropogenic activities.

Strandings data, which are continuously recorded, have a high temporal resolution and cover areas that cannot easily be surveyed through other monitoring strategies. The strandings data, however, have innate biases, as is the case with many wildlife population monitoring methods. A stranding event is a result of physical, social and biological processes (Peltier et al., 2013; Saavedra et al., 2017; ten Doeschate et al., 2017) and whilst an unusual increase or decrease in strandings could reflect a change in abundance and mortality, it may also be a function of variations in environmental, sea and climatic conditions, observer effort or a combination of these factors. Despite robust signals arising from our analyses, it should be emphasised that there is uncertainty regarding the extent to which strandings are representative of the at-sea populations and their distribution. In our study, the majority of the strandings were recorded on beaches facing west, which could be a result of the prevailing westerly winds that are apparent in the North Sea. Variation in coastal geomorphology also likely has profound impact on the rates of retention on the coast and the detection of carcasses. Additionally, it is possible that more strandings occurred than were recorded in earlier years, with the increase in records being a result of development and growth of coastal communities, increased awareness of the stranding schemes, or easier access to technologies to report and record strandings. Reporting biases could exist, either in protocols or in coverage. For example, in the Danish data a reporting bias is likely due to the absence of a dedicated stranding scheme prior to 2008 (Kinze et al., 2018), with effort likely to be higher in summer during the years where a systematic strandings network was not in place. In other North Sea areas, like Lower Saxony (Germany) or Norway, no long-term, dedicated stranding network exists. Reporting effort is additionally prone to fine-scale variation, for example when local awareness increases following targeted knowledge exchange efforts, or after a particular stranding event resulting in significant publicity and subsequent engagement. This can cause spikes in reporting effort, but the potential effect of finer-scale influences is difficult to quantify. Despite these biases affecting the data, the use of long-term large-scale datasets, and analytical treatment of these data as undertaken in this study, results in a robust baseline pattern of spatiotemporal variation, resilient to small or short-term variations in mortality, distribution, effort or oceanographic factors.

When we compare the observed trends in stranding numbers with the outcomes of the abundance estimates of harbour porpoises in the North Sea (Hammond et al., 2002, 2013, 2017), they both suggest a population shift from north to south. However, this change in distribution does not fully explain the high stranding numbers in the most southerly part of the North Sea (our regions D and E) since 2005. This may reflect a higher mortality rate, although a higher probability of deceased animals that wash ashore cannot be excluded. It is therefore strongly recommended to consider drift as part of further stranding investigations, as previously demonstrated by others (Peltier et al., 2012, 2013; Saavedra et al., 2017). If the increase in strandings in the southern North Sea reflects a larger per capita mortality at a given population size, changes in mortality due to changes in pressures (e.g. fishing or other anthropogenic activities or predatory presence) should be further investigated. Reducing the uncertainty around the use of information on stranded individuals when making population level inferences, e.g. by increasing the statistical credibility of this data, is a necessary next step. Including metrics collected at post-mortem investigations in future analyses on strandings, like information on causes of death, nutritional condition, parasitism, diseases, and immunology, would allow profiling of health status and spatiotemporal variation within these factors. This would facilitate the assessment of potential region-specific or local issues and possibly, the identification of high-risk areas of human-wildlife conflicts at sea.

4.4. Using mortality and citizen-science data to inform conservation management

The spatiotemporal scale at which information derived from stranded cetaceans is gathered is not easily recovered by other means of surveillance. When it comes to the conservation of protected species in cryptic habitats or those with low-resource allocation to wildlife monitoring, the assessment of trends in mortality could present a cost-effective alternative or supplement. This is especially true in habitats where animal carcasses are found in sufficient numbers and/or where data exist over a long period, as is the case for harbour porpoises in the North Sea. A similar example can be found in the assessment of the spatial and temporal distribution of three species of ziphiids (beaked whales) in New Zealand, where data and samples collected at stranding events provided new evidence for key habitat use of these otherwise rarely encountered and threatened odontocetes (Thompson et al., 2013). Important population demographic parameters as absolute or relative survival rates can also be estimated based on the recoveries of dead animals, like previously demonstrated in bird banding, where the subsequent recovery of the proportion of dead birds provided information on the survival rates over successive years (Manly, 1981). Data collected as part of ecotourism, e.g. by birdwatchers (Horns et al., 2018), or more dedicated citizen-science programmes on a range of taxa, like reptiles and amphibians (Tiago et al., 2017) and terrestrial wildlife (Paul et al., 2014) have been demonstrated to provide robust knowledge on species distribution that successfully informs conservation management. The approaches presented in our study provide a model for developing data collection and additional sampling strategies for deceased wildlife and additionally proves useful to provide a wider picture on mortality patterns and trends. Our analysis may therefore serve as a detailed example showing how long-term mortality data of a protected species could be used to assess demographic trends, applicable for wildlife conservation across different environments and taxa.

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Author statement

Lonneke IJsseldijk: Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Visualization, Writing - original draft preparation. Mariel ten Doeschate: Conceptualization, Formal analysis, Investigation, Methodology, Visualization, Writing - original draft preparation. Jan van den Broek: Formal analysis. Andrea Gröne & Hans Heesterbeek: Supervision, Writing – review and editing. All other authors: Data curation, Writing – review and editing.

Declaration of competing interest

This manuscript is original work carried out by the authors. This work has not been published previously and is not under consideration for publication elsewhere. The author declares that there are no conflicts of interest (NO copyright, financial or ethical issues) with our work and the subject matter or materials discussed in this manuscript.

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Appendix A. Supplementary data

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