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Original research article

Spatiotemporal and demographic variability in body condition of North Sea harbour porpoises

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A R T I C L E I N F O

Dataset link: Research data and scripts

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A B S T R A C T

Bioenergetic models play an important role in assessing effects of anthropogenic disturbance on a marine mammal population. However, model application is hindered by knowledge gaps, including population composition, demographics and body condition. The latter can be used as a health and fitness indicator. Body condition, measured by body mass index (BMI), was analysed for 1700 stranded or bycaught harbour porpoises (*Phocoena phocoena*) from five countries around the North Sea between 1990 and 2023. Variation in body condition was examined across regions, seasons, age classes, sexes, and mortality categories. Mortality categories, based on necropsies, were: 'acute' (including bycatch, trauma and predation), 'non-acute' (including infectious diseases or other prolonged processes), and 'other' (including live stranding and unknown). All regions experienced seasonal variation in body condition. Juvenile harbour porpoises had the lowest BMI in summer, especially in the southern regions. Adults showed higher regional variability, with the lowest BMI occurring from late summer to early autumn. BMI also differed across

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mortality categories: individuals classified as 'acute' had significantly higher BMI than those in the 'non-acute' and 'other' categories. For adults, BMI varied by sex, with females in mortality categories 'non-acute' and 'other' showing lower values than males. These results provide reference values for harbour porpoise body condition in the North Sea, indicating spatiotemporal heterogeneity in body condition. This variability should be considered when assessing the effect of anthropogenic disturbance and informing marine mammal management and conservation in the Anthropocene.

1. Introduction

Over the last three centuries, anthropogenic activities have increasingly impacted the Earth's ecosystems, a period widely referred to as the Anthropocene (Crutzen, 2002). In marine environments these human influences are widespread, and understanding the impact and consequences of anthropogenic activities on marine mammal populations is both important and challenging. Disturbance from activities such as shipping, fisheries, and chemical and noise pollution can cause direct and indirect behavioural, physiological, and health changes in individuals and species (Avila et al., 2018; Bedriñana-Romano et al., 2021; Williams et al., 2020; Wisniewska et al., 2018). However, a lack of fundamental knowledge of marine mammal demographics and distribution hinders the assessment of the disturbance effects (McHuron et al., 2023, 2022).

The North Sea is one of the world's most intensively used marine environments (Halpern et al., 2015, 2008). Here, marine mammals face numerous anthropogenic stressors, including intensive shipping traffic and fisheries (Chirosca et al., 2022; Emeis et al., 2015; Madsen et al., 2006). More recently, the construction of offshore wind farms and the broadscale effects of climate change raise concerns about habitat alteration and changes in prey availability, and the subsequent cumulative effects on marine mammal populations (Chambault et al., 2018; Chirosca et al., 2022; Heide-Jørgensen et al., 2011; Kebke et al., 2022; Teilmann and Carstensen, 2012).

With an estimated population size of around 339,000 individuals, the harbour porpoise (*Phocoena phocoena*) is the most abundant marine mammal in the Greater North Sea (Gilles et al., 2023; Hammond et al., 2017). Harbour porpoises are protected by national, regional and international legislation and agreements, including the European Habitats Directive, the UK Habitats Regulation, the Marine Strategy Framework Directive, the UK Marine Strategy, the Common Fisheries Policy, and the Agreement on the Conservation of Small Cetaceans of the Baltic, Northeast Atlantic, Irish and North Seas (ASCOBANS) (ASCOBANS, 2020; Council of the European Communities, 1992; European Parliament and Council of the European Union, 2013, 2008; UK Parliament, 2017, 2010). Several European countries translated these legal obligations into national legislation and implemented long-term harbour porpoise monitoring programmes. These programmes include using predictors or indicator metrics to assess harbour porpoise health.

Body condition is intricately linked to the survival and reproductive success of harbour porpoises, and has thus been used as a proxy for individual fitness (IJsseldijk et al., 2021; McHuron et al., 2023). Given the harbour porpoise's high metabolic rate and limited availability to store energy, together with the relatively cold environment it lives in, it must spend a lot of time foraging (IJsseldijk et al., 2021; Kastelein et al., 1997; Leopold, 2015; Rojano-Doñate et al., 2024, 2018). High energetic demands leave them with little ability to compensate for potential sudden environmental change (Wisniewska et al., 2016). Individuals in a better body condition may be able to adapt to or combat environmental disturbances more efficiently (Pirotta et al., 2018; Rojano-Doñate et al., 2018). Changes in prey- and habitat quality, and exposure to stressors could significantly impact their health and reproductive capacity, potentially altering population dynamics and making populations vulnerable to decline (IJsseldijk et al., 2021; McHuron et al., 2023, 2022; Pirotta et al., 2018; Wisniewska et al., 2016).

Bioenergetic models and other predictive frameworks can provide valuable insights on how disturbances affect harbour porpoises, informing management and conservation decisions (McHuron et al., 2022; National Academies, 2017; New et al., 2014; Pirotta et al., 2018). However, applying these models requires demographic and other data of the targeted population, which for most marine mammal species is not available. For example, how body condition affects health and reproduction is an important aspect of bioenergetics (McHuron et al., 2022). Due to the lack of empirical data, researchers either use data from other species or assume theoretical relations based on expert elicitation, both introducing uncertainty (Pirotta et al., 2018). Providing data on harbour porpoise body condition, including spatial, temporal and individual variation by age, sex and health state, will result in more accurate information for management and conservation. Consequently, these models can help develop time- and area-based measures.

The goal of the present study was to investigate spatiotemporal variation in body condition, measured by body mass index (BMI), of stranded and incidentally bycaught North Sea harbour porpoises from 1990 to 2023, aiming at addressing knowledge gaps in bioenergetic models. The present study provides new empirical data on spatiotemporal and demographic variation in harbour porpoise body condition, emphasising that BMI varies across regions, seasons, age classes, sexes, and causes of death (subdivided into mortality categories). Accounting for this variance when assessing population consequences of disturbance will allow for species-specific evaluations of resilience to additional stressors and marine mammal management and conservation efforts in the Anthropocene.

2. Methods

2.1. Data collection

For the present study, data was used from harbour porpoises that were stranded or bycaught and were collected for post-mortem investigation from North Sea coasts of the United Kingdom, France, Belgium, the Netherlands and Denmark. Not all post-mortem programmes started in the same year. From the UK, data came from the Cetacean Strandings Investigation Programme and the Scottish Marine Animal Stranding Scheme from 1990 onwards. Data from northern France came from Observatoire PELAGIS, part of the University of La Rochelle, in cooperation with the Belgian University of Liège, from 1999 onwards. From Belgium, data were made available by the Royal Belgian Institute of Natural Sciences in cooperation with the University of Liège, from 1990 onwards. From the Netherlands, data came from the Faculty of Veterinary Medicine, Utrecht University from 2005 onwards. For the Danish North Sea coast, data were provided by the Fisheries and Maritime Museum of Esbjerg and the Natural History Museum of Denmark from 1995 onwards. Further details on the stranding schemes and procedures can be found in Peltier et al. (2013).

Necropsies were performed according to international guidelines (IJsseldijk et al., 2019; based on Kuiken and Hartmann, 1991). The main aim was to determine the cause of death and health status of each individual. For each case the stranding date, location (latitude and longitude), body mass (kg), body length (cm), sex, decomposition condition code (DCC, from 1 = very fresh to 5 = skeletal remains), and age class (<90 cm categorised as neonates, 91–130 cm categorised as juveniles, and >130 cm as adults, with the inspection of the reproductive organs to make a final differentiation, following Lockyer (2003). For the present study, juvenile and adult harbour porpoises (>91 cm) were selected. Neonates were excluded due to their reliance on maternal nutrition.

To reduce the potential bias in body mass measurements due to post-mortem changes, as blubber lipid content is known to decrease with advancing decomposition (Borrell and Aguilar, 1990), only DCC 1–2 cases were selected. To ensure carcass completeness, necropsy reports and photos were checked. Where this was not available (see Supplemental File 1 for a detailed description), it was assumed that by selecting DCC 1–2 animals, only primarily intact carcasses with minimal predator, scavenging or post-mortem tissue loss were included. A total of 1700 harbour porpoises matched the inclusion criteria.

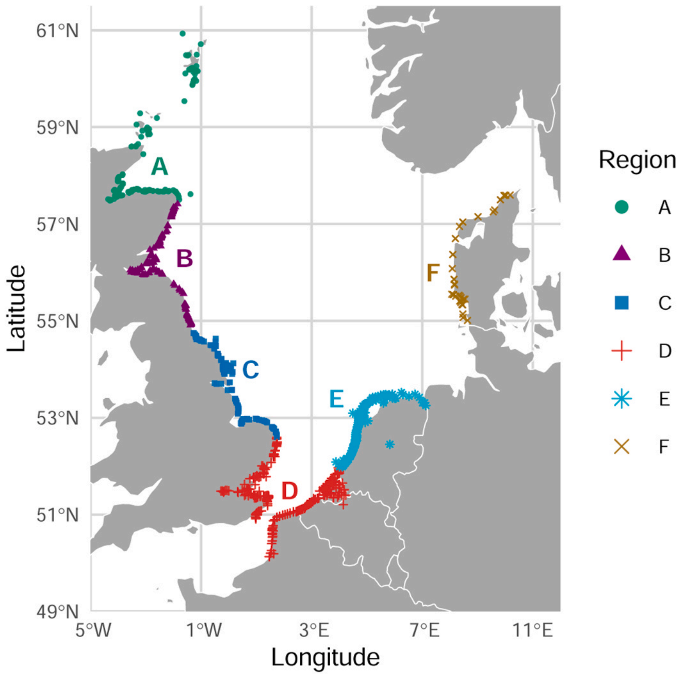

Fig. 1. The study area: the North Sea, with plotted harbour porpoise cases included in the present study. The six regions follow IJsseldijk et al. (2020), which was based on Hammond et al. (2017). Region A (green circles) comprised of the Northeast of Scotland from Thurso to St Fergus, including Orkney and Shetland. Region B (purple triangles), from St. Fergus, Scotland to Newcastle, England. Region C (blue squares), from Newcastle, England to Great Yarmouth, England. Region D (red plusses), the rest of the English North Sea coast, the French side of the eastern English Channel, the Belgian coastline and the Delta area of the Netherlands. Region E (cyan asterisks), the mainland and Wadden area of the Netherlands. Region F (brown crosses) comprised of the North Sea coast of Denmark. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

2.2. Data preparation

2.2.1. Study area

The area was divided into six regions (A-F), following IJsseldijk et al. (2020), which was based on Hammond et al. (2017). There were two notable changes: region D was expanded with the French coastline of the eastern English Channel, and region F only included data from Denmark (Fig. 1).

The distribution of the 1700 harbour porpoises per region was as follows: region A (N = 233), region B (N = 209), region C (N = 165), region D (N = 628), region E (N = 408) and region F (N = 57).

2.2.2. Mortality categories

The harbour porpoises were subdivided into three mortality categories. These categories were: 'acute', 'non-acute' and 'other', following previously established subdivisions (Albrecht et al., 2024; IJsseldijk et al., 2021; Kershaw et al., 2017; van den Heuvel-Greve et al., 2021). In short: the category 'acute' consisted of harbour porpoises that most likely died suddenly from acute causes, such as bycatch, attacks from grey seals (*Halichoerus grypus*) (Leopold et al., 2015; van Neer et al., 2020) or bottlenose dolphins (*Tursiops truncatus*) (Ross and Wilson, 1996), and those that died due to other blunt or sharp trauma, or dystocia (problems surrounding birth) (IJsseldijk et al., 2022). The category 'non-acute' included harbour porpoises that most likely died following a more prolonged (series of) event(s), such as infectious diseases (parasitic, bacterial, viral or mycotic, or a combination thereof) (IJsseldijk et al., 2022; Kapetanou et al., 2020), some of which resulted from previous grey seal or bottlenose dolphin attacks (escaped after attack, but later succumbed to injuries) (Gilbert et al., 2020; IJsseldijk et al., 2022; Leopold et al., 2015). The final category, 'other', consisted of harbour porpoises that could not be placed in the two former categories. This included animals with a cause of death related to live stranding and animals that were euthanised and could not clearly be divided into 'acute' or 'non-acute'. Definition differences among the post-mortem programmes for the effects of long-term and short-term serious food shortage, in cases where no other significant pathological findings helped in the diagnosis of another cause of death, made it impossible to assign these animals to the other two categories and therefore these were also placed in 'other'. Finally, this category also included those cases where the cause of death could not be established.

2.2.3. Body condition proxy

Numerous indicators for body condition have been proposed for marine mammals, but there is not one single indicator that can be applied to all species (Castrillon and Bengtson Nash, 2020). For harbour porpoises Kershaw et al. (2017) and Stepien et al. (2023) demonstrated that BMI was the most useful proxy for body condition, as it was the metric that best captured the variation in body condition. In addition, acquiring length and mass was consistently conducted across the stranding schemes included in the present study. Therefore, BMI was used in the present study, which was calculated using the body mass (kg) divided by the square length (m) of the harbour porpoises: $BMI = Body\ mass\ /\ Length^2$.

2.3. Data exploration and analyses

The data was explored following Zuur et al. (2010), (2007). Data exploration and analyses were performed using R, version 4.3.3 (R Core Team, 2024). Graphs and maps were created using the ggplot2, version 3.5.1 (Wickham, 2016), gratia, version 0.10.0 (Simpson, 2024) and rnaturalearth, version 1.0.1 (Massicotte and South, 2023) libraries. Extensive data exploration was performed to assess data composition in order to ensure a reliable comparison between regions in relation to the other independent variables: month, age class, sex and mortality category.

Due to the differences in the establishment of the different stranding schemes and the associated data quantity and quality, it was not possible to reliably model annual and decadal trends in BMI across the full study area. Although these trends were thoroughly explored, the patterns reflected scheme-specific data availability rather than real temporal changes; see Discussion 4.3 for further clarification.

A Shapiro-Wilk test for normality ($p = 0.05$) was conducted on the dependent variable BMI. Spatial differences in BMI between age class, sex and mortality categories were tested using the non-parametric Kruskal-Wallis test ($p = 0.05$). A Dunn's post hoc test was performed to compute pairwise comparisons between BMI and the categorical variables that were significant according to the Kruskal-Wallis test with a Bonferroni correction for multiple comparisons ($p = 0.05/2$).

Data exploration indicated non-linear relationships between the dependent variable, BMI, and the independent variables (region, month, age class, sex and mortality category). A Generalised Additive Model (GAM) was chosen to investigate the variation and test for significant differences ($p = 0.05$), using the mgcv package, version 1.9.1 (Wood et al., 2016). Region F was excluded from GAM analyses as the sample size was considered too small (N = 57) compared to the sample size of the other regions. Since the age class of harbour porpoises is mainly based on length, and BMI is calculated using length, juvenile and adult harbour porpoises were modelled separately to prevent collinearity confounding the results. BMI was modelled to the independent variables to explore relationships and assess spatiotemporal variability, which included month, region, sex and mortality category. Models were constructed incorporating various smooth factors and interactions, and model selection was done by backwards elimination of the variables. The models were fitted using a Gamma distribution with an identity link to account for the positively skewed BMI. The model with the lowest Akaike Information Criterion (AIC) was selected as the model that best described the data, with a cutoff difference of two (Akaike, 1974). Assumptions were inspected through graphical checks of the model residuals and tested with mgcv's gam.check.

3. Results

3.1. Spatial differences in body condition

BMI varied across regions, age classes, sexes, and particularly mortality categories, suggesting differences in average body condition of harbour porpoises across the North Sea (Table 1, Supplemental Table 1). Individuals in regions A and C had significantly higher BMI than those in regions B, D, and E (Table 1, Supplemental Figure 1, details in Supplemental File 2). Both the lowest and the highest BMI values were found in region D (Supplemental Figure 1, Supplemental Table 1).

Regional differences were also significant for juveniles and adults for BMI per age class (details in Supplemental File 2). Juvenile harbour porpoises in regions A and C had significantly higher BMI than juvenile harbour porpoises in regions D and E (Table 1, Supplemental Figure 2). The BMI of adult harbour porpoises in region A was significantly higher than the BMI of adult harbour porpoises in regions B, D, and E (Table 1, Supplemental Figure 2, details in Supplemental File 2).

While at large there were no significant differences found between sexes (Table 1, exact values in Supplemental File 2), female BMI did vary significantly across regions, with female BMI being significantly higher in regions A and C compared to regions B and D (Table 1, Supplemental Figure 3, details in Supplemental File 2). Male BMI also varied significantly across regions, with the BMI of male harbour porpoises from regions A and C being higher than male harbour porpoises from regions D and E (Table 1, Supplemental Figure 3, details in Supplemental File 2).

As expected, overall BMI differed significantly across mortality categories, with harbour porpoises from the mortality category ‘acute’ presenting significantly higher BMI than those from the mortality categories ‘non-acute’ and ‘other’ (Table 1, Fig. 2, details in Supplemental File 2). For harbour porpoises in the mortality category ‘acute’, BMI was significantly higher in regions A and C compared to regions B and D. There were no significant regional differences found for harbour porpoises in the mortality category ‘non-acute’, but BMI varied significantly for harbour porpoises in the mortality category ‘other’, with harbour porpoises in region D showing lower BMI than harbour porpoises from regions C and F (Table 1, Fig. 2, details in Supplemental File 2).

3.2. Juvenile harbour porpoise model

The model best describing the BMI of juvenile harbour porpoises included factor-smooth effects for month and region and a fixed effect for the mortality category (details in Supplemental File 2). Juvenile harbour porpoises that were in the mortality category ‘non-acute’ and ‘other’ had significantly lower BMI, with −2.18 BMI points ($SE = 0.24$, $p < 0.001$) and −2.99 BMI points ($SE = 0.23$, $p < 0.001$) respectively, as compared to the reference level (mortality category ‘acute’), independent of month of stranding.

The factor smooth function for month by region showed non-linear relations between BMI and month across regions ($p < 0.001$), suggesting that the shape of the seasonal variation differs per region (Fig. 3). There was a clear seasonal variation in BMI of juvenile harbour porpoises in the regions D and E, with the lowest BMI in the months of July and August. The lowest BMI in regions B and C was in June, with a less distinct variation compared to regions D and E. There was a strong increase in the BMI of juvenile harbour porpoises in region A, D and E in the last months of the year (October to December) (Fig. 3).

Table 1
Average BMI and total number of harbour porpoises per investigated region, age class, sex and mortality category. The table includes the average BMI values and the corresponding sample sizes (N) and standard deviation (±) for each category across different regions.

		Region A	Region B	Region C	Region D	Region E	Region F	Average overall
Average overall		19.1 ± 3.6 (N = 233)	17.6 ± 3.1 (N = 209)	19.0 ± 3.2 (N = 165)	17.7 ± 4.2 (N = 628)	17.8 ± 3.4 (N = 408)	18.5 ± 3.3 (N = 57)	18.1 ± 3.8 (N = 1700)
Age class								
	Juvenile	17.7 ± 3.3 (N = 138)	16.8 ± 2.9 (N = 134)	18.0 ± 3.1 (N = 91)	16.7 ± 4.2 (N = 436)	16.8 ± 3.2 (N = 256)	18.1 ± 3.3 (N = 42)	17.0 ± 3.6 (N = 1097)
	Adult	21.2 ± 3 (N = 95)	19.2 ± 3 (N = 75)	20.2 ± 3 (N = 74)	19.8 ± 3.6 (N = 192)	19.5 ± 3.1 (N = 152)	19.5 ± 3.3 (N = 15)	19.9 ± 3.3 (N = 603)
Sex*								
	Female	19.2 ± 3.9 (N = 111)	17.2 ± 3.4 (N = 90)	18.9 ± 3.4 (N = 79)	17.7 ± 4.4 (N = 297)	18.0 ± 3.6 (N = 169)	18.4 ± 3.3 (N = 19)	18.1 ± 4 (N = 765)
	Male	19.2 ± 3.2 (N = 121)	18.0 ± 2.8 (N = 118)	19.0 ± 3 (N = 86)	17.6 ± 4.1 (N = 330)	17.6 ± 3.2 (N = 238)	18.7 ± 3.4 (N = 31)	18.1 ± 3.6 (N = 924)
Mortality category								
	Acute	20.2 ± 3.4 (N = 126)	18.3 ± 3.1 (N = 88)	20.3 ± 3.1 (N = 77)	19.0 ± 4.3 (N = 219)	18.9 ± 3.2 (N = 115)	18.9 ± 3.4 (N = 24)	19.3 ± 3.7 (N = 649)
	Non-acute	18.7 ± 3.1 (N = 57)	18.0 ± 2.5 (N = 58)	18.0 ± 2.8 (N = 40)	17.4 ± 3.8 (N = 231)	17.8 ± 3.3 (N = 213)	17.6 ± 4.1 (N = 6)	17.8 ± 3.4 (N = 605)
	Other	17.0 ± 3.7 (N = 50)	16.4 ± 3.3 (N = 63)	17.7 ± 3.1 (N = 48)	16.3 ± 4.4 (N = 178)	16.1 ± 3.3 (N = 80)	18.3 ± 3.2 (N = 27)	16.7 ± 3.8 (N = 446)

* There were 11 harbour porpoises where sex could not be determined: 1 each in regions A, B, D, and E and 7 in region F. They were subsequently removed before any further analyses.

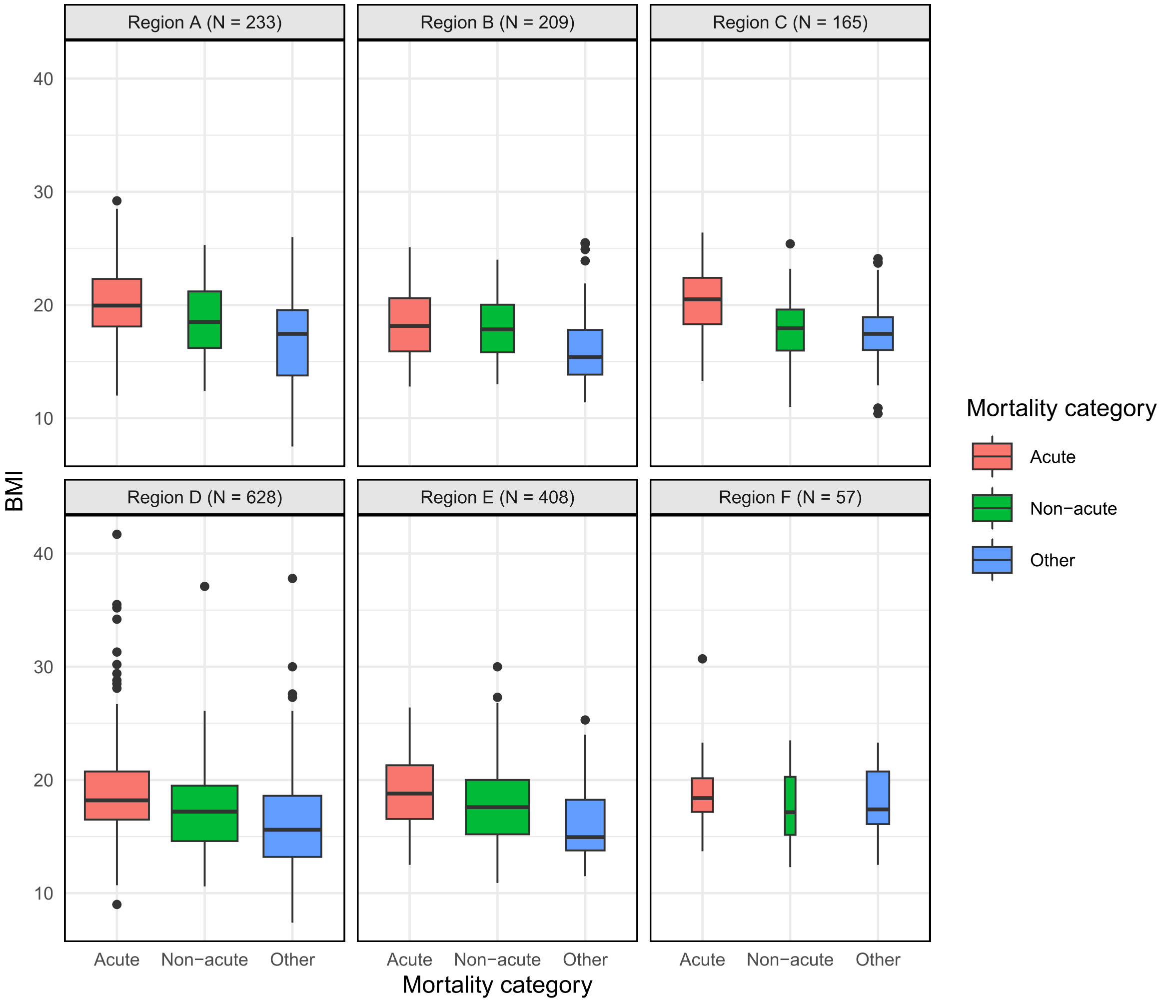

Fig. 2. Boxplot of median harbour porpoise BMI across the six regions and mortality category. See Fig. 1 for regional boundaries. In short, North Sea coasts of: A: NE Scotland; B: E Scotland, NE England; C: NE–E England; D: SE England, France, Belgium, Dutch Delta; E: Dutch mainland/Wadden area; F: Denmark. The number of observations is displayed per region, and the width of each boxplot is proportional to the sample size distribution.

3.3. Adult harbour porpoise model

The model best describing the BMI of adult harbour porpoises included a factor-smooth effect for month and region and fixed effects for mortality category and sex, as well as an interaction between mortality category and sex (details in Supplemental File 2). There was a significant difference in BMI between mortality categories, with adult harbour porpoises in the mortality category 'non-acute' ($SE = 0.47$, $p < 0.001$) and 'other' ($SE = 0.56$, $p < 0.001$) having significantly lower BMI by -2.88 and -3.14 points, respectively, as compared to the reference level (mortality category 'acute'). Adult male harbour porpoises had a significantly lower BMI with -1.52 points than adult female harbour porpoises ($SE = 0.51$, $p = 0.003$). The interaction of mortality category and sex showed that adult males in the mortality categories 'non-acute' and 'other' had higher BMI, with 1.42 ($SE = 0.61$, $p = 0.019$) and 1.55 ($SE = 0.74$, $p = 0.036$), respectively, than adult female harbour porpoises from the same mortality categories.

The factor smooth function for month by region showed non-linear relations between BMI and month across regions ($p < 0.001$) suggesting that the seasonal patterns in BMI varied per region (Fig. 4). The pattern in the BMI of adult harbour porpoises was most distinct for regions D and E, similar to the BMI pattern of juvenile harbour porpoises, with the lowest BMI in August and September and an increase in the last months of the year (October to December). The variation in BMI of adult harbour porpoises in regions B and C was less pronounced, and region A (the reference level) showed minimal variation.

4. Discussion

The present study provides the first exploration of spatiotemporal differences and demographic variation in body condition of harbour porpoises across the North Sea, based on data from 1700 deceased individuals necropsied between 1990 and 2023. The results

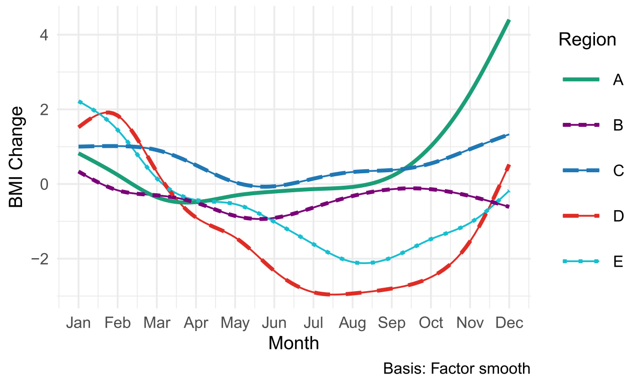

Fig. 3. Factor-smooth output of GAM model for juvenile harbour porpoises per region, showing monthly variance in BMI. See Fig. 1 for regional boundaries. In short, North Sea coasts of: A: NE Scotland; B: E Scotland, NE England; C: NE–E England; D: SE England, France, Belgium, Dutch Delta; E: Dutch mainland/Wadden area.

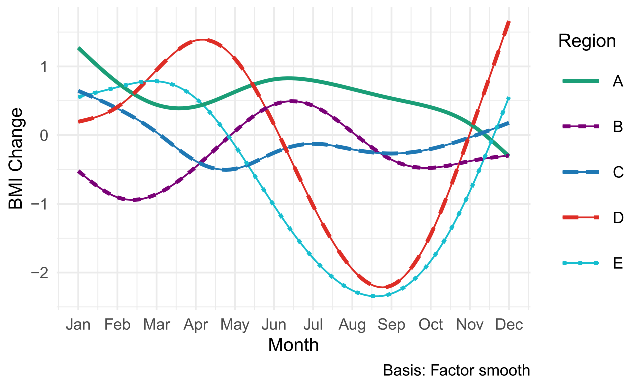

Fig. 4. Factor-smooth output of GAM model for adult harbour porpoises per region, showing monthly variance in BMI. See Fig. 1 for regional boundaries. In short, North Sea coasts of: A: NE Scotland; B: E Scotland, NE England; C: NE–E England; D: SE England, France, Belgium, Dutch Delta; E: Dutch mainland/Wadden area.

demonstrate strong variance in BMI of harbour porpoises across regions, season, age class, sex, and mortality category, indicating that body condition in this population is regionally potentially less homogeneous than previously assumed, which challenges the assessment of the Greater North Sea harbour porpoise population as a single unit.

4.1. Spatial and seasonal variation in BMI

The results show spatial and seasonal variation in harbour porpoise BMI. Seasonal variation occurred across all regions, with harbour porpoises from the southern regions exhibiting more pronounced fluctuations, reaching their lowest BMI between July and September. Animals from the northwestern and western North Sea regions had higher BMI than those from the southern regions. These differences in BMI across months and regions could, either fully or in part, be attributed to seasonal variation in water temperature. Seasonal variation in body condition has been reported in both free-roaming and captive harbour porpoises, indicating that this variation occurs regardless of available resources (Kastelein et al., 2018; Leopold, 2015; Lockyer et al., 2003; Stepien et al., 2023). The seasonal variations in body mass and subsequently BMI, are likely mainly caused by changes in blubber thickness (Lockyer, 2007). A decrease in BMI during the summer (June to August), can be considered normal and is probably beneficial for harbour porpoises, as less insulation is needed when water temperatures are generally at their highest. The more fluctuating seasonal variation in BMI in the southern regions could be related to the local bathymetry, with shallow parts of the North Sea showing greater fluctuations in sea temperature (Mathis et al., 2015), which could influence seasonal cycles in harbour porpoise blubber and BMI.

Differences in food intake and diet composition may provide another potential explanation for the variation in body condition of harbour porpoises. In the present study, BMI was generally lowest during the summer, corresponding to the period when lower prey numbers were found in harbour porpoise stomachs from the southern North Sea (Leopold, 2015). The diet composition of North Sea harbour porpoises largely consists of gobies, gadoids, clupeids and sandeels (Haelters et al., 2012; Leopold, 2015; Ransijn et al., 2019; Santos et al., 2004; Santos and Pierce, 2003). A previous study investigating the mean prey energy density in North Sea harbour porpoises from stomach content analysis showed no clear regional differences (IJsseldijk et al., 2021). This suggests that not regional but seasonal shifts in prey availability or quality may drive variations in body condition. However, assessing these relationships remains challenging. Fishery surveys provide limited insights in key prey species of harbour porpoises, such as gobies and sandeels, because of their small size and low catchability (Ransijn et al., 2021, 2019). To better evaluate the relation between regional harbour porpoise body condition and prey, area-wide seasonal information on prey abundance, distributions, and quality are required.

While the seasonal variations in body condition may be a response to either water temperatures or prey availability, or both, it may also point to region-specific stressors, such as exposure to chemical pollutants. Pollutants are a well-established threat to marine mammal health and are intrinsically linked to body condition, with animals exposed to higher pollutant levels often exhibiting lower body condition (Williams et al., 2020). A possible explanation for the observed heterogeneity in BMI in the present study, where for example adult male harbour porpoises from southern regions have lower BMI than those in northern regions, may partly result from differences in pollutant exposure. This hypothesis fits with previous findings where pollutants like polychlorinated biphenyls or heavy metals that are known to be detrimental to harbour porpoise health, occur in higher concentrations in the southern North Sea than in the northern North Sea (Williams et al., 2025, 2023). However, the relationship between pollutant burden and body condition may not be causal. Nutritional stress in southern regions could plausibly be driven by higher pollutant burdens (e.g., via impaired physiological function (Desforges et al., 2018)), but it is also possible that nutritional stress is primarily caused by other factors (e.g., a poor prey base, disease, or other stressors). Reduced blubber mass may subsequently result in higher measured contaminant concentrations because pollutants are distributed across a smaller lipid pool (i.e., concentration via lipid loss). In other words, elevated concentrations could reflect increased exposure and/or toxicological impact, but they could also partly reflect redistribution and concentration effects during periods of reduced condition. Although the present study did not assess the influence of contaminants on body condition, it is recommended to further investigate the spatiotemporal variation of pollution and its link to and effect on harbour porpoise body condition.

4.2. Age class, sex and mortality category

Initial descriptive analyses showed no significant differences in BMI between male and female harbour porpoises. Accounting for age class changed that outcome. The BMI of juvenile male and female harbour porpoises did not differ significantly, but adult females generally presented higher BMI than adult males. The lack of significant sex-based differences in juvenile harbour porpoise BMI can be explained by the sexual dimorphism that develops in adulthood, when the female harbour porpoises outgrow the males (Lockyer, 2003). In contrast to adult female harbour porpoises in the mortality category 'acute', those in the mortality categories 'non-acute' and 'other' had lower BMI than adult males in these categories. This suggests a sex-specific difference when health conditions become unfavourable. Both male and female harbour porpoises live on an energetic knife edge, making them vulnerable to disturbances (Murphy et al., 2015; Wisniewska et al., 2016). Adult female harbour porpoises, however, have a higher energetic demand, mainly during lactation (Kastelein et al., 1993). This may result in overall reduced energy reserves and consequently, a lower tolerance to prolonged illness or disturbances, which could ultimately affect their survival.

Regional differences in the mortality categories point to differences in micro-habitats or exposure to threats, that may also result in the observed BMI variation. In the present study, the northern regions had a larger proportion of harbour porpoises in the mortality category 'acute', whereas the southern regions had a larger proportion of harbour porpoises in the mortality category 'non-acute' (Table 1). Infectious disease is more frequently reported as a cause of death for adult harbour porpoises, while acute causes such as bycatch, predation and trauma are more often diagnosed in juveniles (IJsseldijk et al., 2022; Lennon et al., 2025a). Regional differences in mortality could reflect regional differences in exposure to stressors. In the southern North Sea, shipping activity is more intense than further north, and has also increased significantly over the years, especially in the Belgian and Dutch exclusive economic zones (Robbins et al., 2022). Additionally, harbour porpoises in those regions are at a higher risk of bycatch, due to the overlap in harbour porpoise density and static net fisheries, especially in summer (Irvine et al., 2024). There is also variation in predator pressure, with bottlenose dolphin attacks occurring mainly in the northern North Sea, while harbour porpoises in the southern North Sea more frequently face grey seal predation (Leopold et al., 2015; Ross and Wilson, 1996). These regional differences may influence the behaviour of the harbour porpoise, potentially affecting their movements, foraging strategies and stress levels, and ultimately their body condition.

4.3. Use of stranded animals to assess BMI

As with many wildlife population monitoring methods, the assessment of stranded marine mammals is subject to biases, which have been extensively discussed elsewhere (IJsseldijk et al., 2020; Lennon et al., 2025b, 2025a; Peltier et al., 2013, 2012; ten Doeschate et al., 2018). The present study includes a subset of stranded and bycaught harbour porpoises: those that were collected for post-mortem investigation. How well the BMI of these animals represent the body condition of the living population remains uncertain. Besides, not all stranding schemes bordering the North Sea have had the ability to perform post-mortem investigations throughout the years included in the present study, due to financial or other constraints, including different starting years, the Covid−19 pandemic or highly pathogenic avian influenza outbreaks (Supplemental Figure 4). Given these variations, it was not possible to reliably assess annual or decadal trends for the whole North Sea. In addition, a limited sample size restricted some regional analyses, e.g., for the northeast North Sea, which resulted in the exclusion of that region from the GAM analyses. Finally, the present study identified a lack of a common indicator that reflects carcass completeness, to be assigned during necropsies. Multiple approaches were used to ensure carcass completeness, including selecting only fresh harbour porpoises and by reviewing necropsy reports and photographs where available (Supplemental File 1). It is recommended to agree upon a completeness category for future studies.

Despite the constraints, the present study demonstrates key strengths of using data from deceased harbour porpoises from combined national databases to assess body condition. Previous studies focused on seasonal body condition in either captive porpoises, or from stranded animals from subareas within the North Sea (IJsseldijk et al., 2021; Leopold, 2015; Lockyer et al., 2003; Siebert et al., 2022; Stepien et al., 2023), while here a much broader spatiotemporal scale was applied. This shows that routine post-mortem investigations can supply predictive models with relevant and long-term information. Therefore, the establishment of a regional-wide common database on strandings is strongly recommended as such a standardised resource currently does not exist (ASCOBANS, 2024). This unified database should include, at a minimum, species, date, location, carcass completeness, length, weight and cause of death.

4.4. Implications and future directives for management and conservation

Although the large population of harbour porpoises in the Greater North Sea is reported as stable (Gilles et al., 2023), the cumulative threats of increasing levels of anthropogenic disturbances is putting the population under pressure (Halpern et al., 2015; Hammond et al., 2017). Region-specific exposure to shipping, fisheries, pollution and predation may in part explain differences in harbour porpoise BMI across regions, seasons, age classes, sexes and mortality categories. Harbour porpoises in the Greater North Sea are considered as one population in the assessment units of the OSPAR Quality Status Report (Geelhoed et al., 2022). However, assumed resilience is likely not equal across this area. Improved models assessing disturbance consequences should be able to consider when and where harbour porpoises are in lower body condition and thus potentially more vulnerable to disturbance, which would support effective and region-specific conservation and management measures.

While the present study focused on BMI, future studies should also assess heterogeneity in other harbour porpoise parameters, including reproduction parameters. The lower BMI observed in adult female harbour porpoises in the mortality categories 'non-acute' and 'other' suggests a potential link between reproduction, health status and body condition. It is recommended that future studies investigate the sex-specific differences in body condition of harbour porpoises and the link between reproductive states and spatiotemporal variation, particularly because the survival of adult female harbour porpoises strongly affects long-term population trajectories (Castrillon and Bengtson Nash, 2020; IJsseldijk et al., 2021; Kershaw et al., 2017; Vermeulen et al., 2023; Wisniewska et al., 2016).

Yearly trends could not be assessed, though it is recommended that future studies explore this, especially as climate change will likely influence harbour porpoise body condition as a result of changes in prey availability, distribution and quality (Bossart, 2011; Leopold, 2015; Rojano-Doñate et al., 2018; Simmonds and Isaac, 2007; Wisniewska et al., 2018). This could potentially make harbour porpoises more susceptible to a sudden lack of food, hypothermia, or diseases (Castrillon and Bengtson Nash, 2020). Understanding the connection between ocean temperature changes and harbour porpoise body condition is therefore a crucial research priority.

5. Conclusion

Understanding spatial and temporal variation in body condition of wild animals is increasingly important in the Anthropocene, as climate change and human activities alter ecosystems and put marine mammal populations under pressure. The present study aimed to assess spatiotemporal and demographic variation in the BMI of stranded and bycaught North Sea harbour porpoises. The findings demonstrate that harbour porpoise BMI is not uniform across space and time, but varies significantly between regions and seasons, as well as age classes, sexes and mortality categories. Harbour porpoises from the southern regions generally had lower and more fluctuating BMI than those from more northern regions, and seasonal declines in BMI were most pronounced during summer months. Additionally, harbour porpoises from the 'acute' mortality category generally had higher BMI than those in the 'non-acute' or 'other' mortality categories. Differences in BMI were also found across demographic groups. While juvenile female and male harbour porpoises had similar BMI, adult female harbour porpoises generally had a higher BMI than adult males. However, adult females showed a lower BMI under less favourable health conditions than adult males. These findings indicate that certain demographic groups, notably adult female harbour porpoises, may respond differentially to cumulative pressures, with potential consequences for reproduction and long-term population dynamics. Bioenergetic models should account for this variation to allow for effective and more accurate predictions to inform the conservation and management of the harbour porpoise population in the Greater North Sea.

CRediT authorship contribution statement

Eva T. Schotanus: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Mariel T.I. ten Doeschate:** Writing – review & editing, Writing – original draft, Validation, Resources, Methodology, Investigation, Formal analysis, Conceptualization. **Andrew C. Brownlow:** Writing – review & editing, Resources, Investigation. **Willy Dabin:** Writing – review & editing, Resources, Investigation. **Rob Deaville:** Writing – review & editing, Resources, Investigation. **Andrea Gröne:** Writing – review & editing, Supervision, Resources, Investigation. **Jan Haelters:** Writing – review & editing, Resources, Investigation. **Hans Heesterbeek:** Writing – review & editing, Supervision. **Thierry Jauniaux:**

Writing – review & editing, Resources, Investigation. **Tim K. Jensen:** Writing – review & editing, Resources, Investigation. **Natacha M. Kristensen:** Writing – review & editing, Resources, Investigation. **Rachel L. Lennon:** Writing – review & editing, Resources, Investigation. **Mardik F. Leopold:** Writing – review & editing, Resources, Investigation. **Hélène Peltier:** Writing – review & editing, Resources, Investigation. **Charlotte B. Thøstesen:** Writing – review & editing, Resources, Investigation. **Rosie S. Williams:** Writing – review & editing, Resources, Investigation. **Lonneke L. IJsseldijk:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Ethics statement

Ethical review and approval were not required for the animal study because the animals described in this study were free living harbour porpoises which died of natural causes or were euthanised on welfare grounds and not for the purpose of this, or other, studies. No consent from an Animal Use Committee is required, as the animals described in this study were not used for scientific or commercial testing. Consequently, animal ethics committee approval was not applicable to this work.

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Data on English stranded harbour porpoises was collated by the Cetacean Strandings Investigation Programme (CSIP), a collaborative partnership tasked with the investigation of strandings of vulnerable marine species in England and Wales, under contract to Defra and the Welsh Government.

The Scottish Marine Animal Stranding Scheme, currently part of the University of Glasgow, conducts the investigation of strandings of cetacean, seals, basking shark and marine turtles under contract to Marine Directorate and Scottish Ministers. Extraction of necropsy data from stranded harbour porpoise in the Scottish Marine Animal Stranding Scheme database was funded by Sea-Changers small grants.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2026.e04275.

Data Availability

Research data and scripts (Zenodo)

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