ARTICLE
NAMMCO Scientific Publications

BOWHEAD WHALES SPEND MORE TIME IN WATERS WITH COLDER SEA SURFACE TEMPERATURES

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ABSTRACT

Marine mammals are under potential threats due to rapid ocean warming. Such threats may be especially challenging for the bowhead whale (*Balaena mysticetus*), an endemic arctic cetacean, because it is limited in how much further north it can go. To explore the effects of global warming on this species, data from 84 bowhead whales in Baffin Bay – West Greenland tagged with satellite linked radio transmitters during the 11 years between 2001 and 2011 were analysed. With this time series, it is possible to investigate the effect of increasing temperature of preferred water mass temperature and temperature at depth where most bowhead feeding occurs through sea surface temperature (SST) on bowhead whale behaviour. We used daily positions and daily SST to develop seasonal Tweedie generalised linear mixed models to model the duration that bowhead whales spend in 20 x 20 km cells as a function of SST. The model was fitted on a much finer spatial and temporal scale than in previous studies, thus enabling a more detailed understanding of behaviour relative to water temperature. Our study demonstrates that bowhead whales spend more time in water with colder surface temperatures, suggesting that as waters continue to warm, bowheads may move further north, potentially reducing their overall available habitat.

Keywords: Argos data, bowhead whales (Balaena mysticetus), East Canada-West Greenland stock, Tweedie distribution, generalised linear mixed models

INTRODUCTION

The bowhead whale (*Balaena mysticetus*), also called the Greenland right whale, is a baleen whale endemic to Arctic and sub-Arctic waters. It has several features that make it well adapted to a life in cold and ice-covered waters, e.g., extremely thick blubber layer exceeding 40 cm in adult whales, a thick epidermis or skin, and a low body core temperature of 33.8 °C (George et al., 1994; Haldiman & Tarpley, 1993). It reaches body lengths of up to 17 m, with an estimated body mass of up to 70,000 kg (George et al., 2021). Bowhead whales reach sexual maturity at >18 years for females and >25 for males (Tarpley et al., 2021), with three-year intervals between pregnancies, and are believed to live longer (>200 yrs) than any other mammal (George et al., 2021). It is mainly distributed in the high Arctic with three stocks known as Bering-Chukchi-Beaufort Seas, East Canada-West Greenland (ECWG), and the East Greenland-Svalbard-Barents Sea stocks. A small relict stock persists in the Okhotsk Sea (Givens & Heide-Jørgensen, 2021). Due to its distribution in the Arctic, it is believed to be sensitive to the ongoing warming that is amplified in the Arctic with rapid reduction in sea ice and increasing sea surface temperatures (Alexander et al. 2018; IPCC 2013). Recent climate changes have impacted the movements and habitats of many species endemic to the Arctic, especially 11 species of marine mammals, including the bowhead whale (Perrin et al., 2009; Kovacs et al., 2011; Laidre et al., 2015). Unlike seals and walruses, cetaceans are not directly dependent on sea ice. However, sea ice may be involved in governing trophic processes that create and concentrate their zooplankton prey.

Bowhead whales feed on zooplankton, and *Calanus* species seem to be an especially important prey item for the ECWG stock (Fortune et al., 2020; Heide-Jørgensen et al., 2012; Pomerleau et al., 2017). Climate warming of Arctic waters and the subsequent loss of sea ice may change the availability and location of prey. Some prey species may move north in response to ocean warming or competition from more southern species entering the Arctic (Michel et al., 2012). Also, the timing of the pelagic phase of zooplankton may change with reduction of sea ice changing the onset of primary production that the zooplankton depends on, which may affect the abundance of prey (Hansen et al., 2003).

Bowhead whales are physiologically adapted to year-round presence in cold water and their thick blubber and lack of a dorsal fin limits their ability to dump heat during exertion the way many cetaceans can. Bowheads may, however, cool by circulating water past their highly vascularised palate while they are swimming (George et al., 2021). Bowhead whales are among the slowest of the baleen whales, possibly to reduce heat generation. With continued climate warming, bowheads may have limited capacity to respond to increased water temperatures, new predators, and anthropogenic activities that may arrive in Arctic waters.

The seasonal movements of bowhead whales in Baffin Bay and the Canadian Arctic Archipelago are influenced by two currents: the warm West Greenland current (WGC) of Atlantic origin and the cold Baffin Bay current (BC) of polar origin (Hansen et al., 2020; Heide-Jørgensen et al., 2021). The WGC is a mixed current

Ngo, M.C., Ditlevsen, S. & Heide-Jørgensen, M.P. (2019). Bowhead whales spend more time in waters with colder sea surface temperatures. *NAMMCO Scientific Publications 13*. https://doi.org/ 10.7557/3.7372

that includes the medium deep (200–1,000 m) and warm water of the Irminger Current, and the shallow and cold East Greenland current (ECG). At the Davis Strait, WGC divides into two branches. The first branch turns west to join the Outer Labrador Current that flows to the south. The second branch continues flowing to the north until ~75° N, where it turns west. Here, it joins the current from the polar basin that is flowing south through Nares Strait and the other channels in the Canadian Arctic Archipelago, to create the south-going Baffin Bay current (Figure 1).

It is notoriously difficult to study how sea temperatures affect the trophic cascade in remote Arctic waters and bowhead whales may be a better indicator of the underlying processes. A full mechanistic understanding behind the trophic processes requires more targeted studies. Here we analysed the behaviour and movements of bowhead whales relative to changes in sea surface temperatures in order to understand their sensitivity to changes in oceanic conditions. We used a large time series of satellite tracking of bowhead whales in West Greenland and Canada, collected between 2001 to 2011 and applied Tweedie generalised linear mixed models (GLMMs) (Dunn & Smyth, 2018; Jørgensen, 1987). Our hypothesis was that the more time whales spent in a cell, the greater the probability that the whale had encountered suitable environmental conditions (i.e., preferred SST). We fitted the model on a finer temporal (5 min) and spatial (20 x 20 km) scale than in a previous study (Chambault et al., 2018).

MATERIALS AND METHODS

Whale tagging data

We analysed a data set collected from 84 bowhead whales in Disko Bay, Greenland, that were tagged with ARGOS satellite transmitters during 2001-2011. All the tags were made by Wildlife Computers (https://wildlifecomputers.com), in which most tags were of the fully implantable C-type (Andrews et al., 2019). Details of the tagging methods are provided in Heide-Jørgensen et al. (2003, 2006). Briefly, to tag the whales, small boats with a length of ~6 m were deployed on days with good weather (calm sea and good visibility). Once the whales were spotted, the boats approached close enough to attach an implantable tag to the whale to tag them using an 8-m long fiberglass pole or a pneumatic gun (Heide-Jørgensen et al., 2001). Tag models can be found as a supplementary excel file. If the tagging failed because the whales started diving, the boats spread out and searched for the whales again, then the procedure was repeated until the whales were tagged. Skin samples were also collected for genetic studies and sex identification (Heide-Jørgensen et al., 2013). The length of the whales was estimated by comparing its length to the size of the boat. The duration of tagging across years varied between years, from a couple of months to a couple of years: May–June 2001, May–November 2002, May–December 2003, April–October 2005, April–September 2006, April–November 2008, April 2009–July 2011 (Figure 1).

Location filtering

Whale location data were collected through the ARGOS system. However, non-Gaussian errors occur in these data sets (Jonsen et al., 2015; Patterson et al., 2008). The method of Albertsen et al*.* (2015) was applied to correct these errors. Whale locations were often scarce (approximately 131 min between each location on average), so we interpolated locations at 5-min intervals from the linear trajectory between corrected locations to estimate the duration the whales spent in each cell. Whale locations and interpolated locations were assigned to 20 x 20 km cells (see Environmental data below). Locations that fell on land were removed based on the General Bathymetric Chart of the Oceans (GEBCO) database (http://www.gebco.net/).

Environmental data

Our study focused on the association of temperature on the behaviour of bowhead whales, so we used sea surface temperature (SST). These remote sensed environmental data were measured by the satellite system of Copernicus Climate Change Service (https://climate.copernicus.eu/). All temperatures below -1.7 °C were replaced by random values uniformly drawn between -1.7 °C and -1.8 °C, because the freezing temperature of sea water in the Arctic is within this range and the temperature below -1.7°C should be disregarded because it is essentially ice (Overland, 1990; Overland et al., 1986). The daily SST data were overlain on the whale location within the geographic grid system made of meridians and lines of latitude to create a grid of squares, denoted cells, of size 0.166° x 0.166°, or roughly 20 x 20 km.

Habitat modelling

We modelled time spent by the whales in each cell per day. Our hypothesis was that the more time whales spent in a cell, the greater the probability that the whale had encountered suitable environmental conditions (i.e., preferred SST). We only included cells where at least one whale was located during the 10 years of data, and we considered a global spatio-temporal model to capture the preferable SST for a 10-year period. We fitted four different seasonal models to the four seasons: spring (January–March), summer (April–June), autumn (July–September), and winter (October-December) to avoid the inter-season effect of seasonal migrations. We used a compound Poisson-gamma distribution, which is a special case of a Tweedie distribution, to model the continuous positive duration by summing all 5-minute durations of bowhead whales in each cell when they appeared there, and with zero observations at the days they did not. The compound Poisson-gamma distribution allows for exact zeros but is otherwise continuous. Let Y be a response variable following a compound Poisson-gamma distribution. Assume that the mean $E(Y) = \mu > 0$, and the variance $Var(Y) = \varphi\mu^p$, then $Y \sim Tweedie_p(\varphi,\mu)$ where p and $\varphi > 0$ are variance power and dispersion parameters, respectively. The compound Poisson-gamma distribution has $1 < p < 2$.

The response variable was the time the whales spent in each cell in each day, regressed on SST within each cell, and an offset with the total number of whales at the given time point. The model furthermore corrected for the time that the whales spent in the same cell as well as neighbouring cells the day before to take into account the autocorrelation in the data. A random effect of cells was included on the intercept and on SST, such that each cell is assumed to have values of the intercept and of the slope that are normally distributed around a common population value of all cells. These random effects correct for all time-invariant unmeasured confounders at each cell, such as depth, distance to coast, or bowhead whale–specific site-fidelities. We included an offset with the number of tagged whales n_t at day t, because the number of tagged whales was not constant over time.

The regression model provided population estimates of the intercept and the temperature effect (the slope), as well as the random effects of each cell. The population estimates of the slope and intercept reveal the overall effect of temperature on the choice of locations of the whales. In the generalised linear mixed regression, the log-link was used. The model can be written in R as

glmmTMB(formula = $duration_t \sim SST + cell_{t-1} + cells^n_{t-1} + SST|cell,$ *family = tweedie(link.power = 0), offset =* n_t*)*

using the packages statmod (Giner & Smyth, 2016), tweedie (Dunn, 2017), and glmmTMB (Brooks et al., 2017). Here, $cell_{t-1}$ is the total time the whales spend in the same cell at day *t-1*, $cells^n_{t-1}$ is the total time the whales appeared in any of the eight neighbouring cells at day *t-1*. These are included to correct for autoregressive effects.

The common way to fit the model is with maximum likelihood estimation (MLE) for a series of fixed values of the variance power parameter *p*, and the AICs (Akaike information criterion) are extracted to choose the optimal *p*. However, glmmTMB incorporates the estimation of *p* directly. The values of *p* of our spring, summer, autumn, and winter models were estimated to 1.38, 1.35, 1.34, and 1.34, respectively (Table 1). All values satisfy the assumption of a Poisson-gamma model, $1 < p < 2$, and are impressively close to one another, suggesting that *p* is the same for all seasons, and that the estimation is robust.

To test the goodness of fit, we created new datasets by simulating data from each of the fitted models. We then refitted

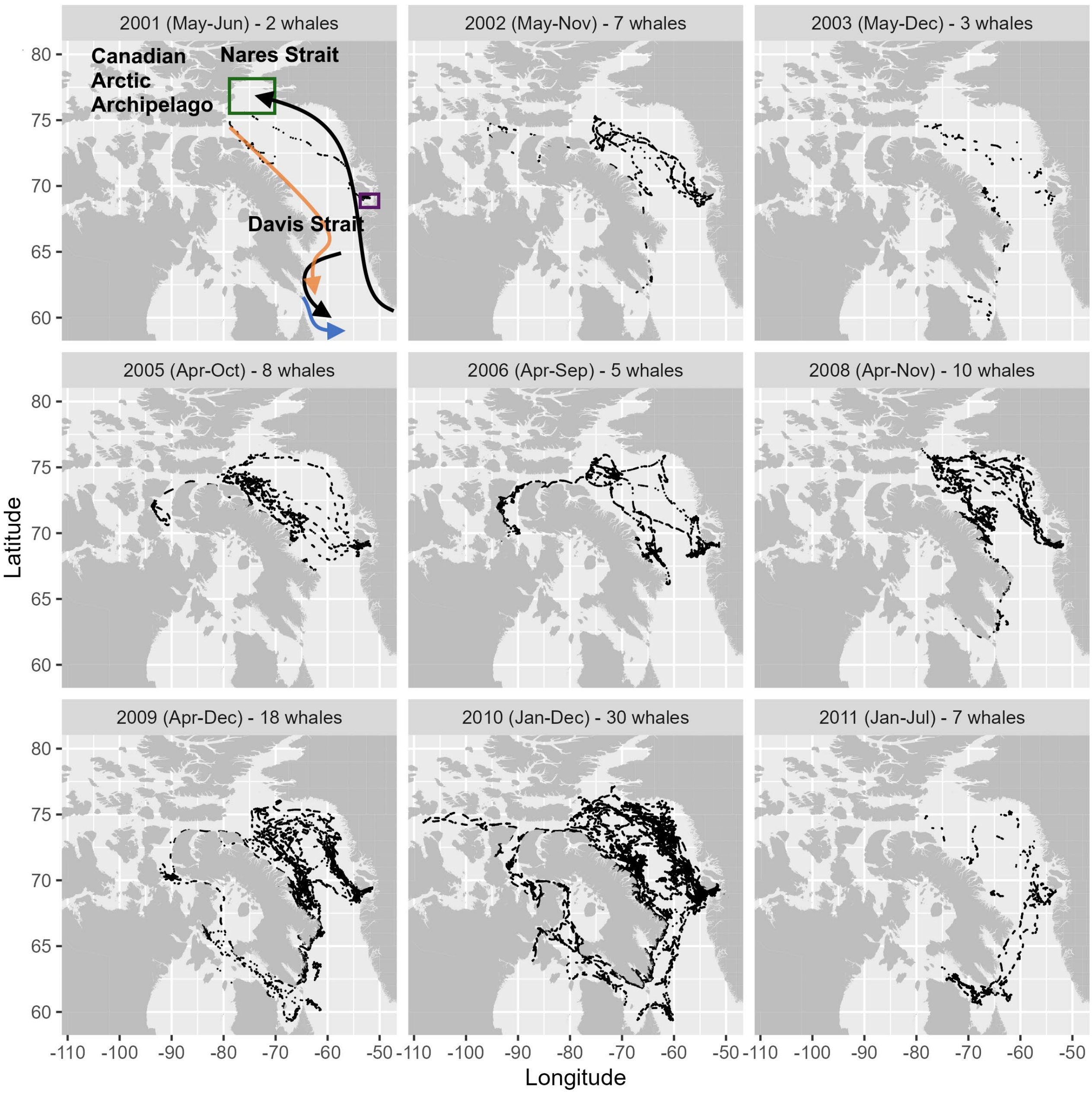

Figure 1. Locations of tagged bowhead whales over the years: 2001–2003, 2005, 2006, 2008–2011. The black curves represent the West Greenland Currents, the orange curves represent the Baffin Current, and the blue curve represents the Outer Labrador Current (adapted from Figure 1, Hansen et al., 2020). The violet box shows the location of Disko Bay, and the green box shows the location of the North Water Polynya.

Table 1. Estimated coefficients (95% confidence intervals), regression coefficients of the same and neighbouring cells the day before (95% confidence intervals), values of the power parameter *p*, and standard deviation of the random effect on the intercepts of the four seasonal models. The intercepts indicate the log of the average durations per day in each cell at 0 °C. Negative SST coefficients imply that the whales prefer colder waters.

Season	Intercept (95% CI)	SST (95% CI)	Same cell (95% CI)	Neighbouring cells (95% CI)	*p*	Standard deviation of the random effect
Spring	-6.17 (-6.21, -6.13)	0.005 (-0.02, 0.03)	2.06 (1.99, 2.13)	1.16 (1.13, 1.18)	1.38	0.19
Summer	-6.13 (-6.18, -6.08)	-0.19 (-0.21, -0.17)	3.01 (2.90, 3.12)	1.79 (1.75, 1.83)	1.35	0.28
Autumn	-5.61 (-5.67, -5.55)	-0.19 (-0.14, -0.23)	5.24 (5.06, 5.43)	3.89 (3.80, 3.99)	1.34	0.26
Winter	-6.97 (-7.45, -6.48)	-1.52 (-1.83, -1.22)	4.28 (4.03, 4.53)	3.44 (3.31, 3.57)	1.34	0.50

the models to each data set and calculated the deviance residuals. This is an important step for the Tweedie models, because the distribution of residuals under the correct model is unknown. The simulations from the fitted model will show how residuals should look, if the model is correct. If the residuals look similar to the simulated residuals, the model is a good fit.

RESULTS

There were 29–5466 locations per whale, with tracking durations ranging from four to 489 days. Figure 1 shows the locations of all whales per year. The total linear travelling distance estimated from the corrected Argos's data ranged from 179 to 16,581 km. In 2001, only two months of data were collected but more data were collected in the subsequent years, including the whole period between April 2009 and July 2011.

The average SST for June in the study area showed a general spatial pattern during 2001–2011 (Figure 2). Warm water was found in Davis Strait, along West Greenland up to Disko Bay, and in the North Water Polynya (Figure 1). Cold water was found throughout the Canadian Arctic Archipelago and Baffin Bay was dominated by a large pool of cold water. Compared to 2001, the warm water from the south was found increasingly further north between 2002 and 2010.

To assess the temperature trend in bowhead whale habitat, we estimated the slope of each cell using linear regression (Figure 3). Positive slopes, i.e., increasing trends, were detected in most cells (more than 95% of slopes > 0.01), except some small areas outside Disko Bay and north of Baffin Bay. The largest increases were observed in Disko Bay, the north and the south of Baffin Bay and along its east coast. The water in the central part of Baffin Bay had the lowest temperature increases, partly because of the mixing of warm water from Southwest Greenland and the cold polar water from the north. The average slope was 0.04 (Figure 3B). This corresponds to an average increase of 0.44 degrees over the 11-year study period, and an increase of more than one degree in the most affected areas. We also randomly selected 10 cells where whales were located and noticed a slow increasing trend in all 10 cells (Figure 3C).

We ran the Poisson-gamma model including all the cells where the bowhead whales appeared at some point. The estimated population coefficients of the effect of SST were between -1.52 and 0.005 and the intercepts were between -10.15 and -8.79 in the four seasonal models. The effect of SST was negative in all seasonal models, except in spring where it was close to zero and not statistically significant, implying that in general the whales prefer colder waters (Figure 4 and Table 1). The model estimates that the whales spent from 4.6 (in winter) to 1.2 times (in summer and autumn) longer in a cell for every decrease of 1 °C (Table 1). The positive effect of SST in spring may be due to

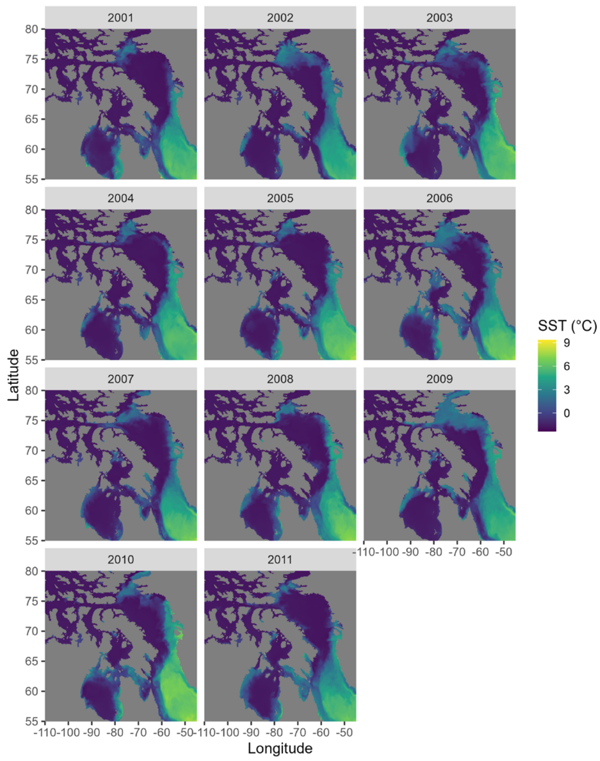

Figure 2. Average sea surface temperature (° C) of June during 2001–2011 in Baffin Bay and the Canadian Arctic Archipelago.

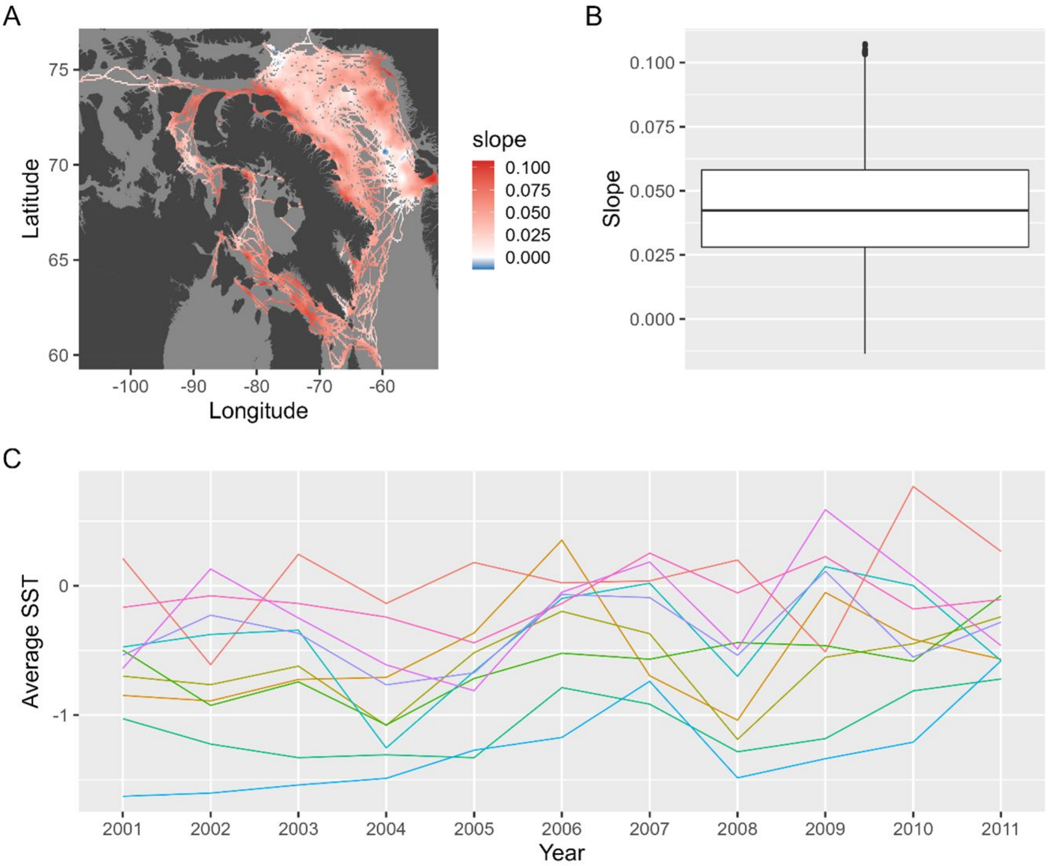

Figure 3. Changes in sea surface temperature in the study area from 2001 to 2011. A) Spatial distribution of slopes, B) Boxplot of slopes: centreline indicates 50th quantile; the bottom and the top of box indicate 25th and 75th quantiles respectively; and dots represent outliers, and C) Yearly average temperature of 10 randomly selected cells in which whales visited.

the specific behaviour of bowhead whales during the spring migration, which includes mating and calving. However, this effect is small and not statistically significant (Table 1).

The regression coefficients of the effect of neighbouring cells the day before were positive for all four seasons and varied between 1.16 and 3.44, as were the regression coefficients for the same cell the day before, with values between 2.06 and 4.28 (Table 1), as expected. The intercepts indicate the log of the average duration per day in each cell at 0 °C. The estimated values of p were similar in all seasonal models (between 1.34 and 1.38), stating that the relationships between mean and variance were stable between seasons (Table 1). The random effects standard deviations were smallest in spring, and highest in winter (Table 1), probably due to less mobility in spring, where activities such as intensive feeding, mating, and calving may keep them in these preferred habitats.

In Figure 5 and Figure 6, deviance residual plots show similar patterns in the models fitted to the original data and to the simulated data, suggesting all the models provide good fits to the data.

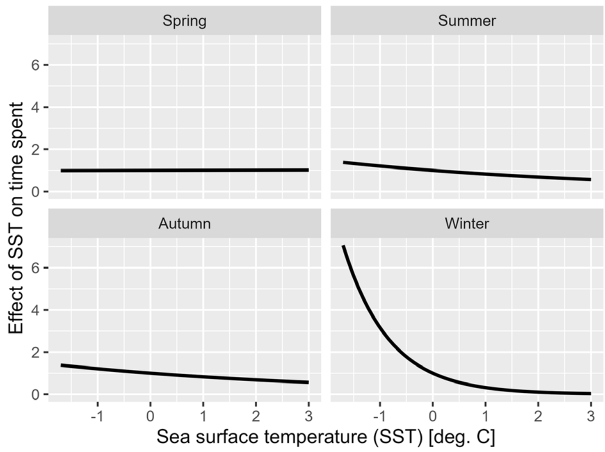

Figure 4. The population estimate of the effect of SST on the time bowhead whales spent in different cells. The value of the curve at a given temperature provides the factor with which the proportion of time spent at a given temperature changes compared to time spent at 0 degrees. Negative trends imply that the whales prefer colder waters.

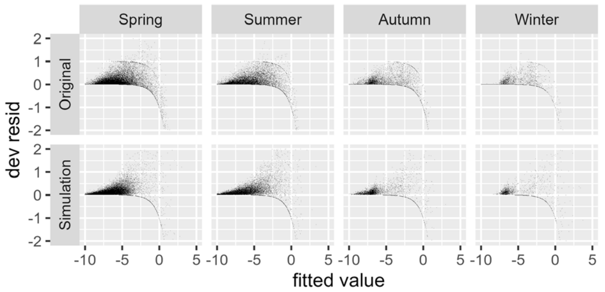

Figure 5. Deviance residuals plotted against fitted values for the four seasonal models: with original data (upper panel), and with simulated data (lower panel).

DISCUSSION AND CONCLUSIONS

In this study, we investigated the relationship between SST and behaviour of bowhead whales. The study was based on a large dataset with up to three million observed and imputed datapoints from the bowhead whale locations. We showed that a GLMM can be suitable for such large data sets without the need to deploy more complex models. To deal with a large number of zeros, Poisson-gamma models were used, which are special cases of Tweedie GLMMs that are not as well-known models as Poisson GLMM or Gamma GLMM. Sea ice concentration was not included in our analysis due to the high correlation between sea ice and SST, and also because Chambault et al. (2018) found SST to be a more important predictor of bowhead whale distribution, partly because of lack of sea ice during the summer months.

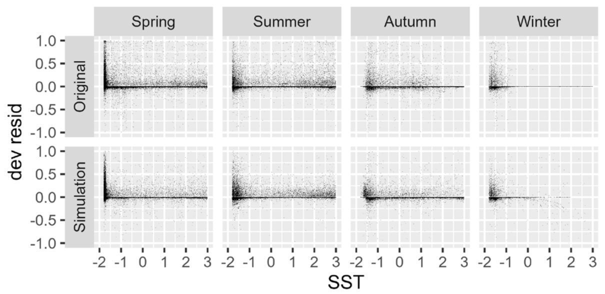

Figure 6. Deviance residuals plotted against SST for the four seasonal models: with original data (upper panel), and with simulated data (lower panel).

The mixed effect population estimates of the effect of SST were negative in all seasons, except for spring when the effect was weak but positive, indicating that the bowhead whales generally preferred colder water masses, possibly due to the effect of SST on copepod distribution. The contrary behaviour of bowhead whales in spring suggests that other fundamental activities, like intensive feeding, mating, and calving, may require them to use areas of warmer water. The population effect of SST was stronger in winter than in other seasons. This suggests that colder water in winter is more important or more available when the bowheads are in West Greenland, which is more influenced by warm Atlantic water, compared to the other seasons.

The telemetry data showed that at the end of spring, the whales started migrating along West Greenland to northern Baffin Bay, the east coast of Baffin Island and inside the Canadian Arctic Archipelago (Heide-Jørgensen et al., 2003; Laidre & Heide-Jørgensen, 2012). What triggers the departure from Disko Bay remains unknown, but the spring influx of warm water to Disko Bay could be involved, because during cold conditions in winter and spring bowhead whales are feeding actively in Disko Bay (Heide-Jørgensen et al., 2012; Laidre et al. 2007,). This influx of warm water in spring occurs at 300–400m depth. It is, however, not possible to assess the temperature at these depths at the seasonal resolution of cells applied to this study (Madsen et al., 2001). Only remotely sensed surface temperature was available at the necessary resolution, but bowheads are not likely responding to SST directly. However, warmer SST usually represents warmer water in general, except when stratification occurs and warmer water overlays colder water.

In general, our study confirmed that bowhead whales preferentially avoid areas with higher SSTs. This generally agrees with the findings of Citta et al. (2018, 2021) that bowhead whales target colder, saltier water and, more specifically, with Chambault et al. (2018), where bowhead whales targeted a narrow range of SSTs from -0.5 to 2 °C. Chambault et al., however, used a much larger grid, 0.5° x 0.5° (approximately 60 x 60 km) and monthly data instead of daily data for predicting habitat suitability. The larger dataset applied in this study captured more of the variance, and our model also included the interaction term between SST and cell, allowing the correction for all time-invariant unmeasured confounders at each cell, such as depth, distance to coast, or bowhead whale–specific site–fidelities. Our results show that in all seasons except spring, bowhead whales are more likely to be found in waters with lower SST. Bowheads may not move to colder areas in spring because of site fidelity to areas important for feeding, calving, or mating. The SST data showed that the temperature of sea water has increased slowly in most of the area in our study during 2001–2011 (more than 95% of the cell temperature increases exceeded 0.01 °C /year). It also confirmed the finding of Alexander et al. (2018), based on simulations, that strong warming has been happening in the Arctic. This change in temperature could be related to changes in the temporal migration patterns of bowhead whales. Based on reports from the whaling stations, the mean departure date for bowhead whales in Disko Bay was around 5 June (interquartile range 20 May – 14 June) during 1780–1837 (Eschricht & Reinhardt, 1861). The whales tracked in the present study departed 1.5–3 weeks earlier than some centuries ago (Laidre & Heide-Jørgensen, 2012), and it is likely due to the waters warming earlier in spring compared to the earlier period that coincided with the little ice age (Mann, 2003).

Data availability

The tagging data have been archived in the Dryad Digital Repository (https://doi.org/10.5061/dryad.tqjq2bw2c).

ADHERENCE TO ANIMAL WELFARE PROTOCOLS

The research presented in this article has been done in accordance with the institutional and national animal welfare laws and protocols applicable in the jurisdictions in which the work was conducted.

AUTHOR CONTRIBUTION STATEMENT

Manh Cuong Ngo: Methodology, Visualization, Formal analysis, Software, Writing – original draft; **Susanne Ditlevsen:**

Supervision, Validation, Writing – review & editing; **Mads Peter Heide-Jørgensen:** Data curation, Supervision, Validation, Writing – review & editing. This article is the peer-reviewed version of Chapter 8 of the first author's PhD thesis (Ngo, 2022). Any textual overlap between the two documents is a form of text recycling approved by this journal.

ACKNOWLEDGEMENTS

We would like to thank Helle Sørensen and Jonas Peters for fruitful discussions. This study was funded by the Greenland Institute of Natural Resources. The study was conducted under the general permission from the Greenland Government to the Greenland Institute of Natural Resources for tagging baleen whales. SD was supported by Independent Research Fund Denmark, case: 9040-00215B and the Novo Nordisk Foundation NNF20OC0062958, MCN was funded by Greenland Research Council and MPHJ was funded by the Greenland Institute of Natural Resources.

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