Habitat preference and trend in relative abundance of common minke whales (*Balaenoptera acutorostrata*) in Skjálfandi Bay, Iceland

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ABSTRACT

Anthropogenic activity has contributed to increased extinction rates, creating a need to monitor and conserve vulnerable species. Understanding the distribution and habitat preferences of threatened species can help identify crucial habitats, for which protection can improve population size numbers. This paper investigates habitat preferences of the common minke whale, a species reported to be declining in Icelandic waters. We analyse minke whale sightings over time and in relation to environmental factors (depth, sea surface temperature, sediment, chlorophyll), based on long-term monitoring data from Skjálfandi Bay in the northeast of Iceland. We find that minke whales have a preference for water depth between 9–70m. Shallow depth was a strong predictor of minke whale presence, which matched sandeel habitat preference. Although the relationship between minke whale presence and sea surface temperature is weak, it also matched sandeel preference. We also detect a decline in the number of minke whale sightings over the study period (2009–2018), which is consistent with the estimated trend for the Icelandic population. We suggest the habitat preferences identified in this and other studies should be considered for conservation recommendations and minimising disturbance in the crucial feeding areas.

KEYWORDS: COMMON MINKE WHALE; TRENDS; FEEDING GROUNDS; DISTRIBUTION; HABITAT; CONSERVATION; ICELAND

INTRODUCTION

Past and present threats to the common minke whale

Human-driven activities such as habitat loss, overexploitation, climate change and pollution have been changing our planet since the 18th Century (Halpern *et al*., 2008; Geldmann *et al*., 2014; IPCC, 2014; Halpern *et al*., 2015). The unprecedented speed of these changes can outstrip some populations' ability to adapt, which is the basis for growing concerns over a sixth global mass extinction event (Barnosky *et al*., 2011; Cote *et al*., 2016). Many cetacean species were previously brought to the brink of extinction by commercial whaling (Tulloch *et al*., 2019). Since the International Whaling Commission (IWC) introduced the whaling ban in the 1980s, some species have shown steady improvement in population size (e.g., humpback whale *Megaptera novaeangliae*). Others have shown marginal improvement (e.g., blue *Balaenoptera musculus* and fin whales *Balaenoptera physalus*). Some are still in decline (e.g., vaquita porpoise *Phocoena sinus* and North Atlantic right whale *Eubalaena glacialis*) (Stevick *et al*., 2003; Jaramillo-Legorreta *et al*., 2017; Tulloch *et al*., 2018; Tulloch *et al*., 2019).

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Despite this reduction in the extent of whaling, cetaceans still face other anthropogenically-driven pressures, such as changing climate, noise pollution and entanglement. Anthropogenic activity has contributed to ocean warming, loss of ice from polar regions, acidification and oxygen loss (Halpern *et al*., 2008; IPCC, 2019). Chronic human-generated noise can mask up to 97% of cetacean communication signals in the noisiest sites, causing disturbance to survival, reproduction and feeding activity (Dunlop *et al*., 2010; Holt *et al*., 2011; Williams *et al*., 2014; Parks *et al*., 2016). Bycatch/entanglement in fishing gear and vessel collisions can contribute between 19–49% of cetacean mortality depending on location (Kirkwood *et al*., 1997; Arbelo *et al*., 2013; Diaz-Delgado *et al*., 2018). Though there is growing evidence that close proximity of vessels disrupts cetacean feeding (Williams *et al*., 2006; Christiansen *et al*., 2013; Ovide, 2017; Vatcher, 2020), whale-watching is rapidly expanding, with some countries, including Iceland, having little or no regulation (O'Connor *et al*., 2009; Martin, 2012). Despite a long list of known and potential threats, the life history and population trends of many cetaceans are still poorly understood due to a lack of research and difficulties in collecting data. Reduced whale population sizes and rapidly changing oceans, which can contribute to distribution shifts (Hazen *et al*., 2013), create the need to understand key links between environmental factors and whale habitat preference in order to assess and mitigate potential threats to contemporary whale populations.

Common minke whale

The common minke whale (*Balaenoptera acutorostrata*) is one of the most widely distributed cetaceans in the world and present throughout the Northern Hemisphere (Arnold *et al*., 2005; Cooke, 2018).

Despite its wide range, the current global population size and trend for the common minke whale are unknown due to patchy distribution, pelagic lifestyle and cryptic behaviour (including short surface time and lack of surface behaviour) (Stockin *et al*., 2001; Arnold *et al*., 2005; Cooke, 2018). The Convention on International Trade in Endangered Species (CITES) classifies all but the Greenland stock of common minke whales as threatened with extinction (CITES, 2021). In contrast, the International Union for Conservation of Nature (IUCN) lists them as Least Concern, primarily because they were less targeted by commercial whaling than other cetaceans, rather than based on population data (Cooke, 2018; Rocha *et al*., 2015). Due to small size and fast movement, minke whales only became the target of excessive whaling when other species' numbers were severely reduced (Heide-Jorgensen *et al*., 2001; Rocha *et al*., 2015). Recent studies on minke whale population trends suggest ongoing declines, at least in local populations. The Icelandic population has been decreasing since 2001 and is currently estimated at one quarter of the historic population (Borchers *et al.*, 2009; Pike *et al*., 2011; Pike *et al*., 2020). The current minke whale population in Central North Atlantic (including Iceland) is estimated to be between 30,000–83,000 individuals (best estimate 50,000) (Sigurjónsson, 1995; IWC, 2021a). Despite suggestions of rapid population decline, minke whales are one of the few cetacean species still being hunted today due to this 'Least Concern' status (Cooke, 2018). This includes Iceland, where the last hunting season was 2018 (IWC, 2021b), even though demand for whale meat is declining. Between 100–900 minke whales are hunted annually in Norway and Greenland (IWC, 2021b) and it is unknown how this impacts the population structure. Future studies are needed to confirm how modern whaling contributes to population decline.

The growing popularity of whale-watching has led to a significant increase in the number of vessels directly interacting with whales, with little or no regulation (Martin, 2012; O'Connor *et al*., 2009). Although the impacts of whale-watching on whales are not currently clear, studies suggest the presence of boats disrupts whale feeding behaviour (Christiansen *et al*., 2013; Ovide, 2017; Vatcher, 2020; Williams *et al*., 2006). Entanglement in fishing gear was documented as the cause of death of 56% stranded minke whales in Scotland between 1990 and 2010 (Northridge *et al*., 2010). Chronic human-generated noise can mask up to 97% of cetacean communication signals in the noisiest sites, causing disturbance to survival, reproduction and feeding activity (Dunlop *et al*., 2010; Holt *et al*., 2011; Parks *et al*., 2016; Williams *et al*., 2014). Despite all the known threats, the life history and population trends of many cetaceans are still poorly understood and in need of assessment.

Linking diet and habitat preference

Common minke whales undergo an annual migration between high-latitude summer feeding grounds and low-latitude winter breeding grounds (Risch *et al*., 2014). As little or no feeding occurs at the winter breeding grounds, minke whale survival and reproduction depends on energy stores obtained during the summer months (Stephens *et al*., 2009). The minke whale's diet is highly variable and consists of many species, including capelin (*Mallotus villosus*), herring (*Clupea harengus*), cod (*Gadus morhua*), sandeel (*Ammodytes sp*), haddock (*Malanogrammus aeglefinus*) and euphausiids (Haug, 1995; Sigurjónsson *et al*., 1997; Folkow *et al*., 2000; Olsen *et al*., 2001; Astthorsson *et al*., 2007; Smout *et al*., 2007; Víkingsson *et al*., 2014).

Cetaceans are attracted to high-latitude grounds by high prey abundance. Previously identified factors associated with cetacean distribution in feeding grounds include depth, sea surface temperature (SST), chlorophyll-a concentration and sediment type (Hoelzel *et al*., 1989; Kasamatsu *et al*., 2000; Naud *et al*., 2003; Macleod *et al*., 2004; Tetley *et al*., 2008; Robinson *et al*., 2009; Anderwald *et al*., 2012; Vallejo, 2013a). This combination of constant (depth and sediment type) and dynamic (SST and chlorophyll) variables produces the most accurate results, avoiding temporal and spatial displacements between physical and biological responses (Stanton *et al*., 2012). Because the minke whale diet is highly variable, monitoring a single prey species is unlikely to yield effective results. Instead, metrics that use environmental variables associated with the physical, chemical and resource environments of a wide range of prey have the potential to capture overall prey availability and better explain cetacean habitat selection (Torres *et al*., 2008). Understanding the relationship between minke whale habitat preference and their prey can help identify potential Important Marine Mammal Areas (IMMA) (Hoyt *et al*., 2021) and Marine Protected Areas (Hoyt, 2012). In this study, we focus on depth, SST, chlorophyll and sediment types as potential environmental variables for explaining minke whale distributions on the spatial scale of Skjálfandi Bay (approximately 500 km^2). Our rationale for choosing each one of these variables is outlined below.

Bathymetry can influence prey distribution indirectly by increasing primary productivity. Shallow coastal waters experience nutrient inflow from land and rivers (Gíslason, 2004). Complex bathymetry such as steep slopes or canyons promote upwellings and eddies cycles, which encourage nutrient cycling in the water column (Cecchetti, 2006). Spawning grounds of some prey species are depth limited and occur at certain species-specific depths (Reay, 1970; Maravelias *et al*., 2000; González-Irusta *et al*., 2015). The preferred depth range of minke whales has been shown to be between 20–250m, depending on the location and prey availability (Hoelzel *et al*., 1989; Hooker *et al*., 1999; Naud *et al*., 2003; Macleod *et al*., 2004; Ingram *et al*., 2007; Robinson *et al*., 2009; Vallejo, 2013a).

Previous studies indicate minke whale preference for certain SSTs, but the relationship was often weak or better explained by other factors (Kasamatsu *et al*., 2000; Anderwald *et al*., 2012; Vallejo, 2013a). Prey species require certain SST ranges for survival and reproduction, but minke whale diet is highly variable and opportunistic. SST preference is unique for each prey species and does not follow a common pattern, as different species have different thermal affinities (Lavender *et al*., 2021). On the contrary, depth, sediment type and chlorophyll seem to influence prey distribution in a similar fashion regardless of prey species. Therefore, whale distribution is often not strongly associated with SST because of a wide variety of prey.

Areas with higher primary productivity support higher biomass of all organisms up the food web (Smith *et al*., 1986; Huot *et al*., 2007). In marine ecosystems, primary productivity is dependent on phytoplankton, which means chlorophyll concentration is often used as a proxy to assess the biomass of potential minke whale prey (Smith *et al*., 1986; Huot *et al*., 2007). Furthermore, chlorophyll allows a more accurate representation of the ecosystem biomass as it accounts for rapid temporal and spatial nutrient variation (Joint *et al*., 2000). Previous studies report an increase in minke whale abundance with an increase in chlorophyll concentration (between 0.5–3 mg/m^3), which was attributed to higher prey biomass (Tetley *et al*., 2008; Anderwald *et al*., 2012; Vallejo, 2013a).

Some prey species distribution is restricted to specific sediment type which they rely on both for overwintering settlement grounds and burrowing for protection (Reay, 1970; Scott, 1982; Carscadden *et al*., 1989). The presence of certain sediments can be used to predict high abundance of certain prey species and thus minke whales. In Scotland, sediment type is widely used to predict the presence of minke whales and closely matches sandeel distribution in the region (Macleod *et al*., 2004). In Canada, more minke whales are observed in the dune habitat which was reported to have a higher abundance of capelin (Naud *et al*., 2003).

This study aims to identify habitat preferences of common minke whales using environmental variables and changes in the relative abundance of common minke whales in Skjálfandi Bay over the 10-year study period.

Ultimately, these associations can be used to inform management and protection decisions about marine habitats, as protecting key cetacean habitats can help prevent or mitigate minke whale population decline (Borchers *et al*., 2009; Pike *et al*., 2011). Protection may include fishing limits in certain areas and time periods, or creating additional guidance for tourist vessels, given the popularity of whale-watching in this location. ICEWHALE (the Icelandic whale watching association) currently provides guidelines, but these are voluntary and not always followed. Extra guidance for boats could be especially beneficial as previous studies have shown how whale-watching can disturb the feeding activity of minke whales (Christiansen *et al*., 2013).

METHODS

Study site and data collection

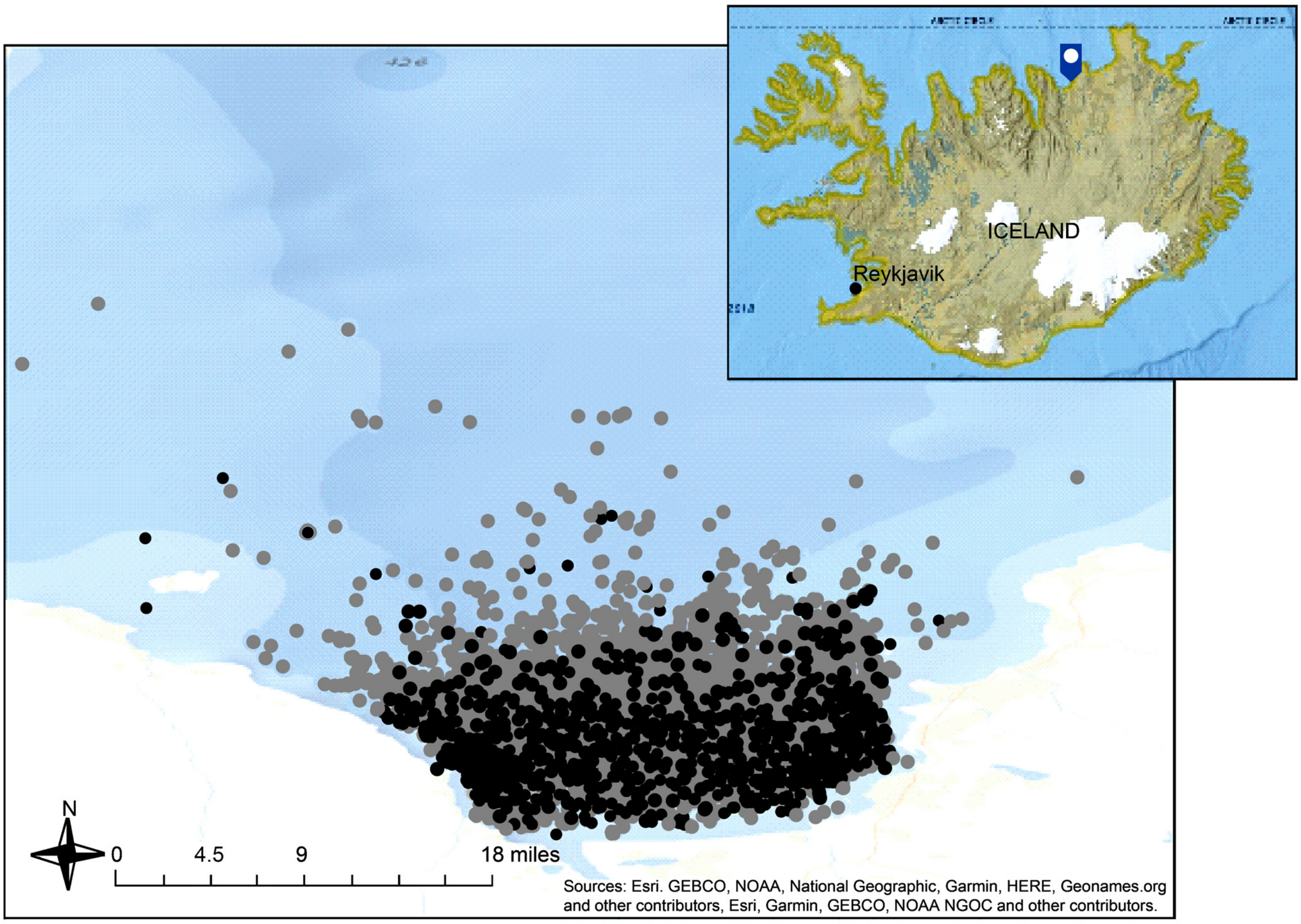
The study was conducted in Skjálfandi Bay, Iceland (Fig. 1), between April and November 2009–2018. This period coincides with the summer season when migratory species such as minke whales appear in the feeding grounds (Rasmussen, 2009). Skjálfandi Bay, which has been named the whale-watching capital of Iceland, is famous for high cetacean activity (Borchers *et al*., 2009; Gunnlaugsson *et al*., 1990; Rasmussen, 2009). Rivers (Skjálfandafljót and Laxá) and snowmelt bring nutrients to the bay while bathymetry, frequent earthquakes and influence of four major currents (East Greenland Current, Atlantic water, East Icelandic Current and Icelandic Coastal Current) promote upwellings (Stefánnson, 1962; Stefánsson *et al*., 1991; Gíslason, 2004). The biological importance of the bay, combined with a long-running cetacean sightings dataset from whale-watching vessels, creates a unique opportunity to study Icelandic cetaceans. Data collection was conducted by trained volunteers at the University of Iceland's Húsavík Research Centre on commercial whale-watching oak boats (Bertulli *et al.*, 2013).

Boats searched the bay without a consistent pattern. Different vessels were in communication and would often head to the same spots where cetaceans were spotted. Surveys were conducted usually twice per day, once in the morning and once in the afternoon. All cetacean species and other marine animals (sharks, seals, etc.) were recorded. The boats were only able to leave the dock in calm conditions; the boats rarely leave when the waves are more than 2m and the wind is stronger than 10m/s. This means no data were collected when the sea state was higher than 3m. Each survey took three hours and was conducted by two trained volunteers simultaneously searching for whales. Environmental data (Beaufort Sea state, precipitation, wind direction, strength and visibility) were collected every 30 minutes, unless there was a sudden change in weather conditions. Whales were located using visual cues, such as a blow, dorsal fin or water splashes (Anderwald *et al*., 2011). Since 2014, sighting data were recorded on SpotterPro (created by conserve.io) (Bingham, 2014). Before 2014, paper and voice recorder logs were taken. The data includes: date, time, observer ID, vessel position (GPS coordinates, latitude and longitude) and whale species. The final dataset includes 10 years, 66 months, 2,002 trips, 5,466 cetacean sightings, with 1,515 minke whale sightings. Data is available here: *https://github.com/ALechwar/JCRM_2021*.

Habitat preference

Spatial analysis

Habitat preference is defined as the proportion of the use of habitat relative to its availability in the environment (Aarts *et al*., 2008). In this study we focus on the proportion of the area identified as important for minke whales. Information on habitat availability therefore needs to be incorporated into the model (Peterson *et al*., 2011). Because surveys do not follow a set route, survey effort is not distributed equally across the bay. Thus, using habitat availability data from the whole area was not appropriate as certain areas are surveyed less or not at all, giving incomplete sighting data. To avoid this, background data (in the form of randomly selected absence points along the survey route) can be collected on each survey to reflect spatial survey effort. However, randomly selected points along the survey route have been shown to introduce selection sample bias, as sightings usually occur in more accessible areas (depending on visibility, glare and sea conditions) (Phillips *et al*., 2009). We therefore used sightings of other marine mammals and birds as pseudo-absence points (background data) (Phillips *et al*., 2009; Peterson *et al*., 2011; González García *et al*., 2018). At these locations, environmental factors (e.g., sea state and visibility) allowed successful sightings of other animals but minke whales were not present.



Sources: Esri. GEBCO, NOAA, National Geographic, Garmin, HERE, Geonames.org and other contributors, Esri, Garmin, GEBCO, NOAA NGOC and other contributors.

Fig. 1. Map of the study area with all minke whale sightings during the study period. Black dots represent minke whale sightings, grey dots represent sightings of other whale species.

We downloaded SST (°C) and chlorophyll (mg/m^3) data from Giovanni satellite data (MODIS-Aqua MODISA_L3m_SST_Monthly_4km vR2019.0; MODIS-Aqua MODISA_L3m_CHL v2018) (Giovanni, 2021). Both variables came as monthly average packages, displayed as a 4km resolution grid. We downloaded depth data from the EMODnet DTM (EMODnet, 2021a). We downloaded sediment data from EMODnet Geology (Seabed substrate (coarse sediment, hard bottom, mud, sand, sandy mud); 1:1,000,000 (1 M)) (EMODnet, 2021b). Sighting data were aggregated per month to match SST and chlorophyll data before performing statistical analysis.

We used ArcMap 10.6.1 for spatial analysis (Minami *et al.*, 1999). We assigned values for these environmental parameters (SST, chlorophyll concentration, depth and sediment type) to each presence and absence point, based on GPS coordinates. Occasionally estimates of SST and chlorophyll were not available for some areas due to cloud cover and proximity to the coast. Those datapoints were not included in our final analysis. Ultimately, 4,564 sightings with environmental data were included in the final dataset.

Statistical analysis

Previous studies have shown habitat preference is not likely to be linear (Guisan *et al*., 2000; Oksanen *et al*., 2002). Generalised Additive Models (GAMs) can identify non-linear relationships between explanatory and response variables (Hastie *et al*., 2017). Therefore, GAM is an appropriate technique for identifying habitat preference and has been widely used in cetacean habitat preference research (Panigada *et al*., 2008; Torres *et al*., 2008; Marubini *et al*., 2009; Spyrakos *et al*., 2011; Vallejo, 2013a; Esteban *et al*., 2014; Correia *et al*., 2015; Lambert *et al*., 2017; González García *et al*., 2018).

Statistical analysis was conducted in RStudio 4.0.2 (R Core Team, 2017) using the mgcv package (version 1.8-40) (Wood *et al*., 2015). We used a GAM with a binomial distribution and logit link function. The response variable was minke whale presence/absence. Explanatory variables were depth, sea surface temperature, chlorophyll concentration and sediment type. We applied the smoothing function, which allows identification of non-linear relationships, to all continuous variables (depth, sea surface temperature, chlorophyll concentration). The K value (number of knots) which describes the complexity of the fitted non-linear curve, was set to five to avoid unrealistically complex trendlines (Spyrakos *et al*., 2011; González García *et al*., 2018). We checked for collinearity and concurvity between explanatory variables to avoid biases introduced by two explanatory variables being dependent on each other (Næs *et al*., 2001). No relationships were identified between our explanatory variables ($p > 0.8$) (Vallejo, 2013a), and all explanatory variables remain in the model. Background variable selection was used to identify the best-fitted model. First, a complete model was produced with all explanatory variables, then the least significant one (with the highest p-value) was deleted. This was repeated until all explanatory variables in the model were significant. All produced models were checked for overall goodness of fit measure by the Akaike Information Criterion (AIC) test (Sakamoto *et al*., 1986). The model with the lowest AIC value (representing the best fit) was used as the final model, even if it contained non-significant ($p > 0.05$) explanatory variables (González García *et al*., 2018). The residual plots of the final model were investigated using the DHARMa package to check whether the model met the assumptions (Hartig, 2019).

Change in the relative abundance

To assess change in relative abundance, we investigated the change in monthly minke whale sightings per unit effort (SPUE) over the study period of 10 years. We defined unit effort as the number of surveys in a given month (each survey is equivalent to three hours). Number of surveys was used because neither distance travelled nor accurate measure of search time was recorded during the surveys. Final SPUE values were calculated by dividing the total number of minke whale sightings in a given month by the total number of surveys within the same month (number of unique trip IDs). The final sample size was 66 months.

Statistical analysis was performed in RStudio 4.0.2 (R Core Team, 2017). We conducted a Generalised Linear Model (GLM) (Poisson distribution) using the lme4 package (Bates *et al*., 2015). We used the offset function due to the inclusion of rare data (sightings divided by effort). Monthly SPUE was used as a response variable. Month (April–November) and year (2009–2018) were used as explanatory variables. Months were binned into groups of two (April–May; June–July; August–September; October–November) to better represent seasonality. As most surveys were done in summer, we did not use traditional season definition (summer: June to August; autumn: September to November; etc.), as it would result in an uneven number of months per category and would reduce the number of groups in the analysis. Although some individuals are year-round residents, the majority migrate to the breeding grounds during winter, which means their abundance may change with the season (Rasmussen, 2009; Vikingsson *et al*., 2015). Since some months were not sampled in some years, we added months to the analysis in order to verify seasonal variation and account for potential bias in the missing data. After running the model, the summary showed overdispersion in the data, so the quasipoisson model was therefore used to best fit the data.

RESULTS

Habitat preference

The best fit model explained 11.7% of the deviance. It included depth, sea surface temperature, chlorophyll concentration and sediment type (Table 1). Proportion of presence/absence data for each predictor is shown in Figure 2. The sampled available depth ranged from 3–232m. Minke whales were observed at depths between 9–214m. We found a preference for shallow waters, between 9–70m (Fig. 3a). The sampled available sea surface temperature ranged from 2.3–13.87°C. Minke whales were observed throughout the entire SST range. We found a preference for water colder than 6°C and warmer than 9°C (Fig. 3b). The sampled available chlorophyll concentration ranged from 0.34–10.27mg/m^3. Minke whales were observed between 0.34–8.99mg/m^3. Chlorophyll improved the model, but there was no strong relationship between chlorophyll values and minke whale sightings (Table 1; Fig. 3c). Figure 3c suggests minke whales may prefer higher concentrations of

Table 1

Generalised additive model (GAM) output showing the relationship between minke whale sighting and explanatory variables: depth (m); sea surface temperature (°C); chlorophyll concentration (mg/m^3); sediment type.
Values in **bold** represent a significant relationship ($p < 0.05$). *N* = 4,564.

Parametric coefficients	Estimate	Standard Error	Z value	P-value
Intercept	–0.9342	0.3622	–2.579	**0.0099**
Hard bottom	0.3093	0.4923	0.628	0.5299
Mud	–0.2049	0.3665	–0.559	0.5761
Sand	–0.2314	0.3644	–0.635	0.5255
Sandy mud	0.1913	0.3864	0.495	0.6206
Approximate coefficients of smooth terms	**Effective degrees of freedom**	**Reference degrees of freedom**	**Chi-square**	**P-value**
Depth	3.848	3.986	348.4	**< 0.001**
Sea Surface Temperature	3.872	3.989	45.4	**< 0.001**
Chlorophyll	2.337	2.838	4.6	0.134

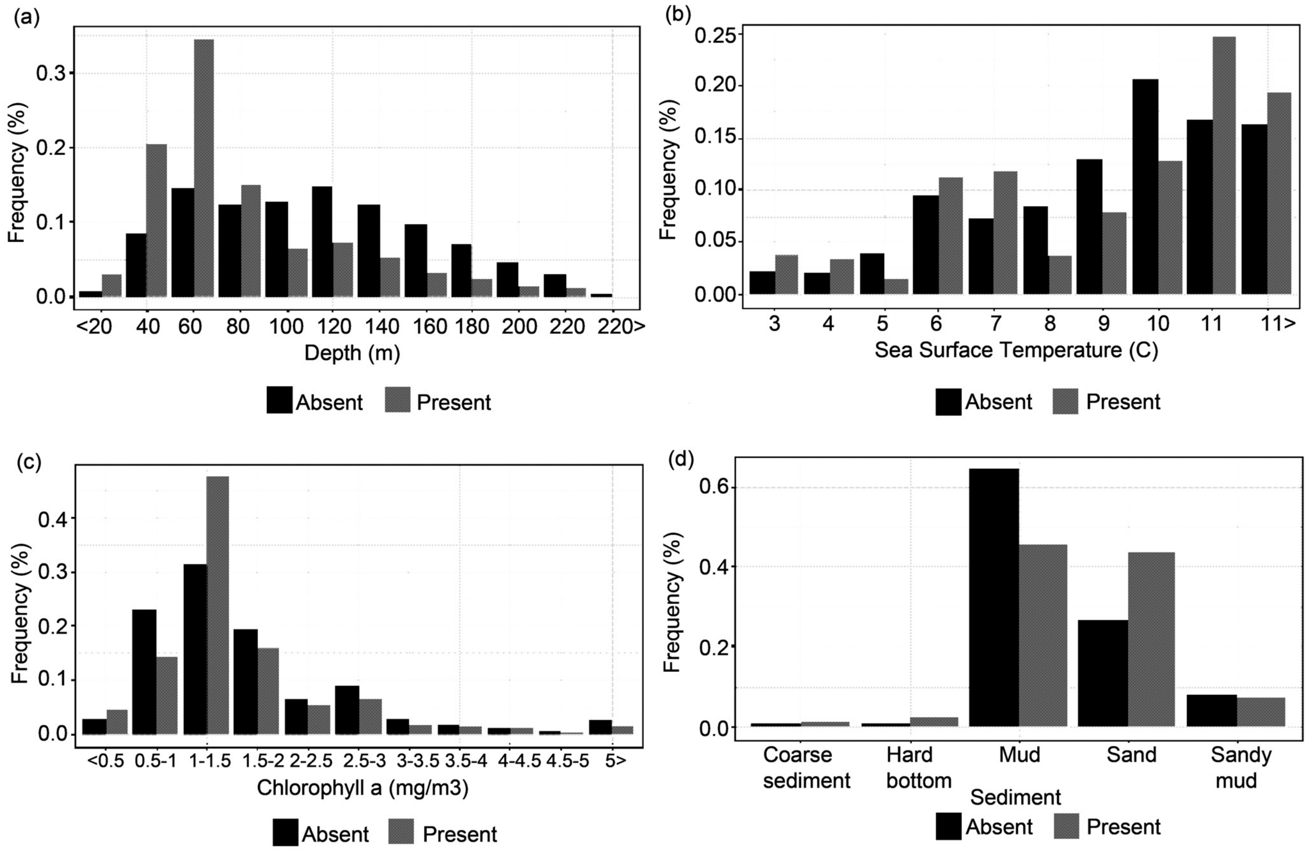


Fig. 2. Histogram of environmental variables recorded for minke whale presence/absence data points: a) depth (m); b) sea surface temperature (°C); c) chlorophyll-a concentration (mg/m^3); d) sediment type. N = 4,564.

chlorophyll, but wide confidence intervals, caused by small numbers of samples between 4–10mg/m^3, prevent us from drawing statistically supported conclusions here. Including information on sediment type improved the overall model, but minke whales had no significant preference towards any of the sediment types in the study area (Table 1; Fig. 3d).

Change in relative abundance

We found a decline in the number of minke whales sighted over the study period (2009–2018) (Table 2; Fig. 4). We did not find a significant influence of season (between April–November) on minke whale abundance. We consider the p-value of 0.049367 for months August–September too close to the threshold of $p < 0.05$ to be considered significant. However, the data do suggest that a seasonal trend should not be discounted, as the

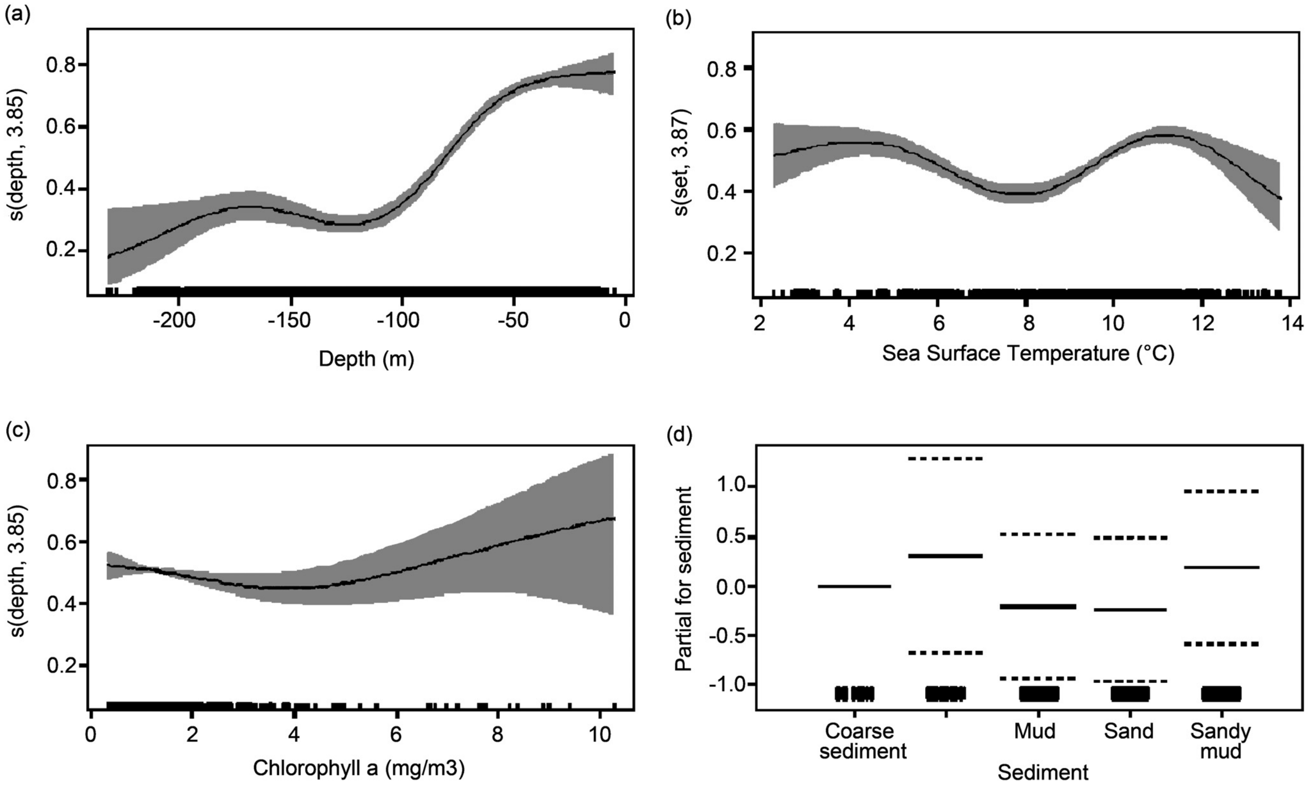


Fig. 3. Generalised additive model (GAM) plots showing the relationship between minke whale sightings and explanatory variables: a) depth (m); b) sea surface temperature (°C); c) chlorophyll concentration (mg/m^3); d) sediment type. The y-axis represents the probability of a minke whale sighting, assuming other variables are at their average value. Black marks on the x-axis represent the total distribution of data. Black line represents the best-fitted trend line. Grey area represents 95% confidence intervals of the trend line. N = 4,564.

Table 2

Output from a Generalised Linear Model (Poisson distribution) testing the effects of year and month on the monthly number of minke whale sightings per unit effort (SPUE). April–May is the reference season and does not appear in the table. Values in **bold** represent significant effect ($p < 0.05$). *N* = 35.

Coefficients	Estimate	Standard Error	Z value	P-value
Intercept	0.87302	0.25006	3.491	**0.001512**
Year	–0.11981	0.03085	–3.884	**0.000525**
Month (June–July)	–0.10876	0.22212	–0.490	0.627956
Month (August–September)	–0.54539	0.26626	–2.048	0.049367
Month (October–November)	–0.41090	0.39106	–1.051	0.301770

p-value for months August–September was marginally significant at a 0.05 threshold (Table 2; Fig. 4). This could be because either the effect size is relatively small or inter-annual variability in the data was too large to make a robust inference on seasonality.

DISCUSSION

Using survey data collected over 10 years in Skjálfandi Bay, Iceland, we assessed the local habitat preferences and change in relative abundance of the common minke whale. Overall, we found that minke whales show significant preference for certain water depths and sea surface temperatures, but no preference for certain sediment types or chlorophyll concentrations. Secondly, we found a decline in minke whale sightings per unit effort over the study period. The minke whale habitat preference patterns identified in this study are best explained by prey habitat preferences (as the whale habitat preference and main prey type preference overlap). Therefore, our study suggests that monitoring minke whale prey species and gaining a better understanding of how their distributions affect minke whale habitat choice could be an important future step in understanding minke whale population distributions and trends.

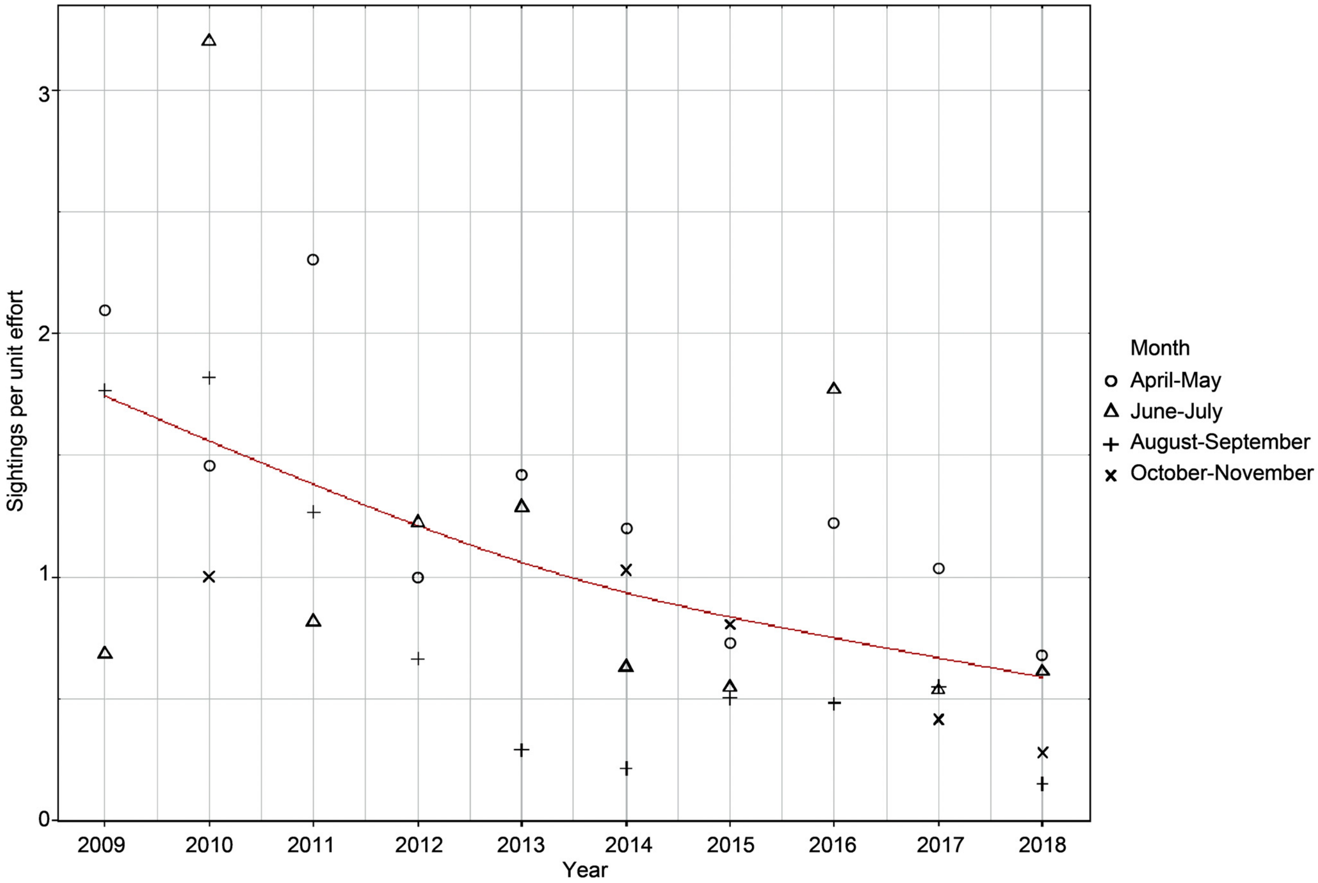


Fig. 4. Monthly and annual variation in minke whale sightings per unit of effort (SPUE). Each dot represents the SPUE value for a single month. The dotted line represents the best-fitted trendline. N = 66.

Habitat preference based on depth

We found that minke whales showed a preference for shallow water, between 9–70m. The most consistent explanation for this preference is the spatial distribution of prey species. Different prey species use different depths for spawning and feeding habitat. For example, sandeel is most abundant at depths between 20–40m; herring 100–150m; and cod below 125m (Maravelias *et al*., 2000; Reay, 1970; Wright *et al*., 2000; González-Irusta *et al*., 2015). The observed minke whale depth preference of 9–70m corresponds to depths with the highest sandeel abundance (20–40m), suggesting that sandeel might be targeted by minke whales. Stomach content analysis has also shown that sandeels are one of the main minke whale prey items in northern Iceland (along with capelin and gadoids) (Víkingsson *et al*., 2014). Furthermore, previous studies report a direct relationship between the two species, where an increase in sandeel abundance was followed by an increase in minke whale sightings (Macleod *et al*., 2004; Tetley *et al*., 2008; Anderwald *et al*., 2012). This study does not directly measure local sandeel abundance. Future studies are needed to confirm the influence of sandeel abundance on minke whale presence in the study area. Behaviour data was not collected, which means we cannot verify how many individuals were feeding during sightings. Despite the lack of feeding data, it is relevant to link habitat preference with feeding preference. The study site is a feeding ground and individuals are likely to spend most of the time foraging, but behavioural data should be included in future studies.

An alternative explanation for the observed depth preference is that shallow areas may result in minke whales taking shorter dives and thus more sightings are recorded at the surface. But studies using recording tags attached to whales suggest that long deep dives are infrequent, even when water depth allows them, and that minke whales tend to use short shallow dives (under 3–4min) regardless of depth (Stockin *et al.*, 2001; Friedlaender *et al*., 2014). Changes in diving behaviour due to the available depth are therefore unlikely to explain the results. In addition, the optimal diving depth increases with whale body size; minke whales, as one of the smallest baleen whales, are therefore expected to be successful in shallow waters (Noren *et al*., 2000). Numerous studies report minke whale preference for shallow waters between 0–100m (Hoelzel *et al*., 1989; Naud *et al*., 2003; Macleod *et al.*, 2004; Robinson *et al*., 2009; Vallejo, 2013a). But there are contrasting reports from some locations where whale abundance is higher in deeper areas (150+ m) (Hooker *et al*., 1999; Ingram *et al*., 2007; Vallejo, 2013a).

Finally, there might be increased minke whale presence in shallow waters due to increased primary productivity in coastal areas. Shallow coastal waters experience nutrient inflow from the land and rivers (Gíslason, 2004). Complex bathymetry such as steep slopes or canyons promotes upwellings and eddies cycles, which encourages nutrient cycling in the water column (Cecchetti, 2006). Skjálfandi Bay has a wide area of steep slope along the coast and previous studies identified a positive relationship between presence of dolphin species and slope steepness (Vallejo, 2013b). But productivity is unlikely to explain minke whale abundance here (see Habitat preference based on chlorophyll).

Habitat preference based on sea surface temperature

We found that minke whales prefer waters colder than 6°C and warmer than 9°C. The survey effort was not uniform throughout the year; in particular, early spring and late autumn were surveyed less due to extreme weather and the reduced whale-watching schedule. These were often the same months where environmental data was limited due to cloud cover. As a result, low temperatures, especially below 6°C, might be misrepresented due to the small sample size in this temperature range, which means we do not consider the preference for waters colder than 6°C to be significant. June–September had the highest survey effort, with the majority of datapoints being in the 8–11°C range. The small sample size is not relevant to the water temperature preference warmer than 9°C, but the relationship in this range is not strong. Considering that we observed a marginal influence of season (August–September), seasonal variation and SST preference should not be discounted and would be a valuable future study focus. But we do not identify a conclusive influence of season or SST.

Previous studies report a correlation between minke whale abundance and SST, but it is often weak and better explained by other factors (Kasamatsu *et al*., 2000; Tetley *et al*., 2008; Anderwald *et al*., 2012; Vallejo, 2013a). Documented relationships are often explained by prey species SST preference and requirements for spawning. For example, an increased abundance of sandeels is often observed at around 11°C, capelin at 5–7°C, herring at 4–18°C, krill at 0–4°C, and cod at 3–7°C (Thors, 1981; Rajasilta, 1993; Drinkwater, 2005; Tetley *et al.*, 2008; Anderwald *et al*., 2012; Perry *et al.*, 2019). Whereas depth, sediment type and chlorophyll have a similar influence on the distribution of prey species, SST prey preference is species-specific. Minke whales are opportunistic feeders and switch between prey species based on their availability (Haug *et al*., 1995; Folkow *et al*., 2000). Although minke whales show preference toward certain species (Víkingsson *et al*., 2014), the ability to adapt current prey composition means some prey were available at all temperatures where minke whales were observed.

The indicated minke whale preference for waters warmer than 9°C may indicate the main minke prey species in Skjálfandi Bay, as it is consistent with the distribution of sandeels. Sandeel swimming activity increases with an increase in water temperature (from 5–10°C), meaning they are more available to minke whales in warmer waters (Winslade, 1974). Peak sandeel abundance is estimated to occur at water temperatures around 9°C (van der Kooij *et al*., 2008). Sandeels may therefore be an important prey item for minke whales. This is further supported by depth preference results and stomach content analysis (Víkingsson *et al.*, 2014). But the SST preference identified here is weak and requires further research.

Habitat preference based on chlorophyll

Previous studies report an increase in minke whale abundance in areas with between 0.5–3 mg/m^3 of chlorophyll (Tetley *et al.*, 2008; Anderwald *et al.*, 2012; Vallejo, 2013a). We found no relationship between chlorophyll concentration and minke whale sightings. Wide confidence intervals, due to few datapoints at high chlorophyll concentrations, do not allow a final trend identification. To improve the model and verify the trend, future studies could use higher resolution concentration maps (for example 1km resolution grid) to represent spatial variation. In this study chlorophyll concentration was illustrated as monthly average values in a 4km resolution grid, which may not have been detailed enough to capture the relationship.

Although minke whales are known for varied diets, there is evidence to suggest that some prey species are favoured above others. This is indicated by stomach content analysis (Víkingsson *et al.*, 2014) and further supported by the results of this study. Therefore, the overall prey biomass, regardless of species (indicated by chlorophyll), might be a poor indicator of minke whale abundance. Furthermore, studies suggest that minke whales might not be influenced by the productivity of the area as they use distinctive hunting techniques that rely on features such as bathymetry (Hoelzel *et al.*, 1989), but more studies on hunting techniques are needed to verify this theory. Thus, other variables such as bathymetry, sediment or SST might be better minke whale presence predictors (Tetley *et al.*, 2008; Anderwald *et al.*, 2012; Vallejo, 2013a).

Habitat preference based on sediment type

Previous studies report the association between substrate type and minke whales (Naud *et al.*, 2003; Macleod *et al.*, 2004; Robinson *et al.*, 2009). Many minke whale prey species rely on sediment for overwinter burrowing, spawning and protection (Macer, 1966; Reay, 1970; Scott, 1982; Carscadden *et al.*, 1989; Wright *et al.*, 2000). Macleod *et al.* (2004) reported that sediment type was the main predictor of minke whale presence, where coarse sand indicates high sandeel abundance as the fish burrow into the sand for protection (Reay, 1970; Wright *et al.*, 2000; Macleod *et al.*, 2004). Furthermore, capelin and sand lance abundance are higher in sandy substrate, which closely matches minke whale distribution in areas where capelin is the main prey item (Scott, 1982; Carscadden *et al.*, 1989; Naud *et al.*, 2003). Given the growing evidence of the importance of sandy sediment for minke whale prey, we expected to observe a preference for sandy sediment, but found no preference for any sediment type.

This lack of preference for sediment type may be explained by the limited sediment variety at the study site. According to seabed substrate data from EMODnet Geology, 99% of the Skjálfandi Bay area consists of mud, sand or a mixture of both (EMODnet, 2021), which means there might not be sufficient variation to detect a preference. In this study we used a map illustrating sediment at a scale 1:1,000,000. The lack of variance could therefore be attributed to an insufficiently detailed map. Because sediment type has been documented as important for minke whale distribution, future studies should repeat the model using higher-resolution data (for example 1:1,000) to confirm this lack of variance and preference.

Alternatively, the prey species might be distributed uniformly across Skjálfandi Bay. Previous studies emphasise the importance of coarse sand or fine gravel for sandeel and capelin distribution, both of which were identified as main components of northern minke whales' diet (Víkingsson *et al.*, 2014). But according to EMODnet Geology, the study area has little or no coarse sediment available (EMODnet, 2021). Although sandeels prefer coarse sand with low gravel fraction, they are present across all sediment types apart from sediments with silt or clay content greater than 10% (Wright *et al.*, 2000). Because the preferred sandeel sediment type is not present in the study site, other factors such as depth and SST might therefore be better predictors for both sandeel and minke whale distribution.

Change in relative abundance in Skjálfandi Bay

We found that the minke whale sightings per unit effort in Skjálfandi Bay declined between 2009–2018. This timescale is limited by data availability. Although it is a short timescale relative to the estimated minke whale lifespan of at least 50 years (Carwardine, 2019), our assessment is consistent with other observations of this population. Local communities have reported visible declines in Skjálfandi Bay minke whale abundance over the last 10 years (Stoller, 2020), and other studies have shown the Icelandic population of minke whales in decline over recent decades (Borchers *et al.*, 2009; Pike *et al.*, 2011).

Population declines due to shift in prey distribution

Prey type might be important for Icelandic minke whales based on stomach content analysis (Víkingsson *et al.*, 2014). For example, sandeel, krill, capelin, large fish (gadoids), and to a lesser extent herring, have been identified as the main prey items of minke whales in northern Iceland (Víkingsson *et al.*, 2014). The diet of minke whales between 2003–2007 differed from the 1977–1984 period. In recent periods, less krill and capelin, and more sandeel, have been observed in the diet, which could be attributed to recent environmental changes in Icelandic waters: the water temperature and salinity were higher during the last decade, which led to changes in the abundance and distribution of some fish species (Víkingsson *et al*., 2014). The abundance of krill, the biggest component of minke whales' diet in 1977–1984, was observed to be in decline between 1995–2007, which to some extent was consistent with a shift in other krill-eating cetaceans' abundance and distribution (Paxton *et al*., 2009; Skúladóttir *et al*., 2009; Víkingsson *et al*., 2014). The distribution of blue and fin whales was observed to shift northwards; it has been suggested this is due to the northward shift of krill (Víkingsson *et al.*, 2014). Coldwater species such as capelin have been observed to be retreating from the Icelandic coast towards colder water around East Greenland (Astthorsson *et al*., 2007; Pálsson *et al*., 2012; Víkingsson *et al*., 2014). A similar pattern is believed to occur in sandeel distribution. Unfortunately, monitoring of Icelandic sandeel stock only started in 2006, which means historic records come from indirect evidence, such as fish stomach samples or bird breeding success (Víkingsson *et al*., 2014).

Given the northward shift of some prey species, whales may follow these species and retreat from the Icelandic shelf area (Víkingsson *et al*., 2014). The northward shift is further supported by the fact that body examination of individuals between 2003–2007 shows no evidence of malnutrition, which would be expected if the population was declining due to lack of food (Christiansen *et al*., 2013). The population is therefore more likely to be shifting distribution rather than going extinct due to food shortage. The most recent survey records high minke whale densities in East Greenland (Pike *et al*., 2020), but this area was poorly covered in previous studies, which means it is difficult to estimate the change over time (Pike *et al*., 2009). A study in Jan Mayen (Norway) recorded a recent increase in minke whale abundance in the area (Solvang *et al*., 2017). In contrast, there are some indications of distribution change of southern Europe minke whale populations (Hammond *et al*., 2017). It is therefore suggested that Icelandic minke whales might be moving northwards following their main prey species.

Study limitations

In this study we used data collected by trained volunteers on whale-watching vessels. This is a collaborative and cost-effective method of creating long-term datasets. Numerous previous studies have successfully used datasets gathered on whale watching vessels (e.g., Gill *et al*., 1995; Macleod *et al*., 2004; Bartha *et al*., 2011; Spyrakos *et al*., 2011; Anderwald *et al*., 2012; Bertulli *et al*., 2013; Vallejo, 2013a; Esteban *et al*., 2014; Bertulli *et al*., 2016; González García *et al*., 2018). The main advantage of our dataset is the long timeframe and number of encounters: sightings have been consistently collected for 10 years resulting in over 5,000 datapoints, which means it is a valuable long-term dataset taking advantage of pre-existing infrastructure (whale-watching vessels) without introducing more marine traffic to the area.

But the number of surveys, time spent at sea and survey routes were more inconsistent than they would have been in a dedicated survey due to the nature of whale-watching tours. Although we controlled for some inconsistencies by using SPUE and pseudo-absence points, our results may still be influenced by existing biases. Whale-watching tours do not follow a specific route and can be biased towards known hotspots. However, whale-watching in Skjálfandi Bay is focused on humpback whales as they are bigger and easier to follow than minke whales. Humpback whales are widely distributed through the bay with hotspots on the western part of the bay (Klotz *et al*., 2017), which means the survey is unlikely to be biased towards areas where minke whale sightings were either more or less common. Although the focus is on humpback whales, trained observers are instructed to record all whale sightings enroute, even if whale watching boats do not stop to follow the animal. Secondly, around 60% of the minke whales in the area are sighted only once, which suggests observed animals are a random sample of a larger population (Bertulli *et al*., 2018).

In this study we used sightings of other marine animals as pseudo-absence points (background data). This method may not be representative of available habitat as other species are likely to have their own habitat preference which can overlap between species. However, we use a variety of species as pseudo-absence points: 10 cetacean species, pinnipeds, basking shark (*Cetorhinus maximus*), sunfish (*Mola mola*) and sea birds. Based on the variety of species surveyed, we chose to use background data as it introduces less bias than using random habitat points in the area, when spatial survey effort is unknown. Logistically, using whale-watching ships and reducing bias using pseudo-absence points allows these surveys to be informative even in the absence of opportunities for dedicated sampling programmes, which is valuable for generating hypotheses and assessing whether diverting resources towards dedicated sampling is the best course of action.

We assumed each sighting was of a unique whale, but it is likely that many individuals were reencountered at the study site (Dorsey *et al*., 1990; Gill *et al*., 1995; Gill *et al*., 2000; Bartha *et al*., 2011; Bertulli *et al*., 2016). Some individuals often return to the same area over multiple years (16.4% of identified whales) (Bertulli *et al*., 2013). Dorsey (1983) proposed evidence of territoriality, as exclusive minke whale ranges were observed with little individual crossovers between them. Thus, omitting individual ID might have introduced bias as some individuals and their territories might have been oversampled. Future studies should identify individuals based on unique features via photo identification (Dorsey *et al*., 1990; Gill *et al*., 1995; Gill *et al*., 2000; Bartha *et al*., 2011; Bertulli *et al*., 2016) and include whale ID as a random effect in the analysis.

In this study we use pseudo-absence points to assess habitat availability. We chose this approach because surveys do not follow a set route, meaning survey effort is not distributed equally across the bay. It wasn't appropriate to use habitat availability data from the whole area as certain areas are surveyed less or not at all. Ideally, we would use points collected during surveys at constant time intervals which also take into consideration survey effort, but such data were not possible to obtain at this scale. Our pseudo-absence points include 10 cetacean species, pinnipeds, basking shark, sunfish and sea birds. This variety of species should ensure random distribution of data points because different species have different habitat requirements (Phillips *et al*., 2009; Peterson *et al*., 2011; González García *et al*., 2018). However, sightings of other animals may not be representative of habitat availability as they can also have habitat preferences. In future this should be mitigated by including a wide range of species with different ecologies. It is important to consider how other marine mammals can co-exist in food-rich areas, leading to overlap between species preference regardless of the diversity of pseudo-absence points. Future studies could assess the accuracy of pseudo-absence points by randomly choosing habitat points within the whole area and comparing them with background data.

In this study we analysed all sightings together, regardless of time. But minke whale habitat preference is likely to change across seasons (Macleod *et al*., 2004; Anderwald *et al*., 2012). Macleod *et al.* (2004) report that sediment type is a strong minke whale presence predictor in the spring, as it closely matches sandeel abundance in the sandy sediment, but this relationship becomes weaker towards the end of the summer, as the fish move northwards (Macleod *et al.*, 2004). Similarly, the relationship between depth and sandeel abundance is strongest between April–July when sandeels emerge from overwinter burrows (Macleod *et al.*, 2004). Anderwald *et al.* (2012) report that chlorophyll is a strong predictor of minke whale presence in late summer when sprat aggregates in highly productive areas. As we analysed all minke whale sightings regardless of time, the seasonal variation was not captured. Future studies should conduct a separate habitat preference analysis for each season to further verify the suggested habitat preference.

CONCLUSIONS

This study identifies depth as minke whale presence predictors. Results also suggest that time of the year and sea surface temperature are important, though this needs further investigation. These results can be considered for making conservation recommendations used to form hypotheses that will improve the design of future surveys or models. In line with other studies, we suggest that the Icelandic minke whale population might be declining due to potential population distribution shift. Based on depth preference, vital feeding areas can be identified and disturbance within them can be limited. Skjálfandi Bay is a popular whale-watching location with multiple vessels interacting with whales on a daily basis. There is growing evidence of the negative impact of whale-watching boats on cetaceans (Williams *et al*., 2006; Christiansen *et al*., 2013; Christiansen *et al*., 2014; Ovide, 2017; Vatcher, 2020). Minke whales were reported to increase energy expenditure during interactions with boats, which was attributed to stress and attempts to outpace the vessel (Christiansen *et al*., 2014). Furthermore, they performed shorter dives, more sinuous movement and less frequent surface feeding when boats were present, indicating that whale-watching disturbs their feeding activity (Christiansen *et al*., 2013).

Minke whales build up energy stores for reproduction during the summer months; disrupted feeding success can therefore have negative effects on foetus development and nursing, ultimately resulting in reduced calving success (Costa, 1993; Stephens *et al*., 2009). However, when including photo-identification data, Christensen *et al*. (2015) concluded that the overall disturbance for individual whales in Faxaflói Bay was very low because different minke whales were always observed. Similar studies are recommended in Skjálfandi Bay to verify impact of whale-watching in the area and implement effective conservation strategies, such as more distance between vessels and whales in crucial feeding locations. In line with previous studies, our data also suggest that minke whales have a preference for sandeel, which would support ongoing assessment and monitoring of local sandeel populations. Prolonged minke whale migration induced by prey migration north may still be a threat to the species as it decreases feeding time. Since minke whale survival and reproduction depends on summer energy stores, reduced feeding time can negatively impact reproductive success.

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