



The acoustic presence and migration timing of subarctic baleen whales in the Bering Strait in relation to environmental factors

Erica D. Escajeda^{1,4} · Kathleen M. Stafford² · Rebecca A. Woodgate³ · Kristin L. Laidre³

Received: 9 May 2024 / Revised: 4 September 2024 / Accepted: 26 September 2024

© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2024

Abstract

Subarctic baleen whales, including humpback (*Megaptera novaeangliae*), fin (*Balaenoptera physalus*), and gray whales (*Eschrichtius robustus*), migrate through the Bering Strait every summer to feed in the Chukchi Sea. When and where the whales are found in the region likely reflects environmental conditions. Using recordings collected between 2009 and 2018 from a hydrophone ~ 35 km north of the strait, we identified whale calls during the open-water season (May–December), examined migration timing, and investigated potential drivers of whale presence. The acoustic presence of fin and humpback whales varied across the years, while gray whales were consistently detected each year. We compared detection rates for October and November since these months had recordings each year. We observed the highest proportion of recordings with humpback whale calls for October–November in 2009, 2017, and 2018 (66–80% of recordings); the highest proportion of recordings with fin whale calls in 2015, 2017, and 2018 (75–79% of recordings); and the highest proportion of recordings with gray whale calls in 2013 and 2015 (46 and 51% of recordings, respectively). Fin and humpback whales departed the Bering Strait ~ 3 and 2 days later per year over the study period ($p < 0.04$). Both fin and humpback whales delayed their southward migration in years with warmer water temperatures (Pearson $r \geq 0.73$, $p < 0.02$). Generalized additive models of location, shape, and scale identified day of the year, water temperatures, and the lagged presence of a thermal front the previous month as drivers of acoustic presence for all three species during the open-water season.

Keywords Subarctic · Baleen whales · Bioacoustics · Water temperature

Introduction

Understanding the connection between species occurrence and environmental factors is crucial for predicting the effects of habitat shifts on recovering populations of marine mammals. Climate change in combination with other anthropogenic stressors—such as fishing gear entanglements, ship collisions, and increased ocean noise—may impact the recovery of baleen whale populations from commercial

whaling that took place throughout the twentieth century (Clapham 2016; Tulloch et al. 2019; Nelms et al. 2021). Moreover, changes in ocean conditions related to climate change and masking of calls from conspecifics (individuals from the same species) by ocean noise may obscure the cues whales use to facilitate their migrations (Clark et al. 2009; Torres 2017). Identifying the drivers of baleen whale migration and distribution, therefore, is essential for understanding how baleen whales will respond to habitat shifts associated with climate change (Hazen et al. 2013; Abrahms et al. 2019; Meynecke et al. 2021). The present study seeks to characterize the occurrence of subarctic baleen whales in the Bering Strait and Chukchi Sea, including identifying migration timing and the factors that influence whale presence during the open-water season.

The Chukchi Sea is a shallow continental shelf sea that owes its productivity to the influx of nutrient-rich Pacific waters that are advected northward by currents through the Bering Strait (Grebmeier et al. 2006; Fig. 1). The combination of abundant daylight during the polar summer along

✉ Erica D. Escajeda
ericaescajeda@gmail.com

¹ School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA, USA

² Marine Mammal Institute, Oregon State University, Newport, OR, USA

³ Applied Physics Laboratory, University of Washington, Seattle, WA, USA

⁴ H.T. Harvey & Associates, Los Gatos, CA, USA

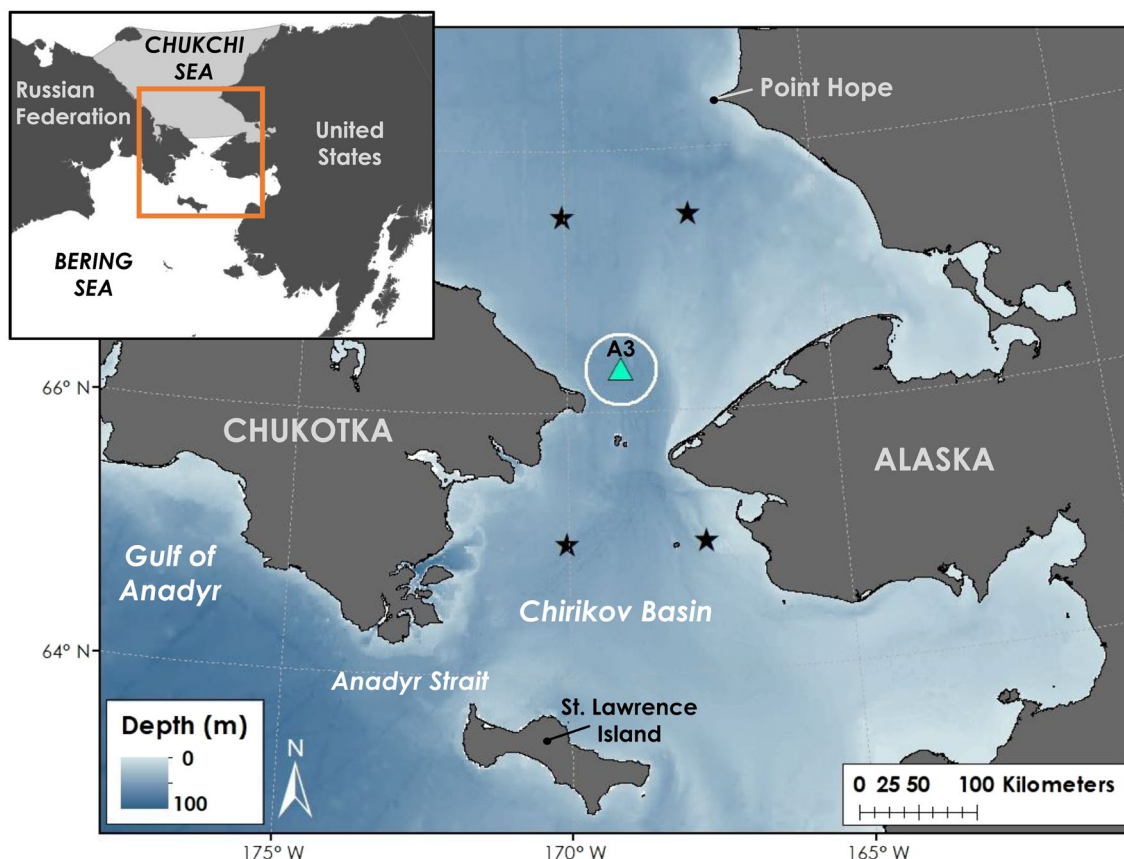


Fig. 1 Map of the study area, the mooring site (A3), and the Bering Strait region. The white circle around A3 indicates the extent of the assumed detection range of the hydrophone (radius of 30 km from the mooring). The 30-km region was then used to calculate the sea-surface temperature (SST) gradient. The magnitude of the SST gradient was used as a proxy for thermal front strength. The four wind data points from the National Oceanic and Atmospheric Administration's

(NOAA) National Center for Atmospheric Prediction (NCEP) North American Regional Reanalysis (NARR) dataset used to calculate mean wind speeds are included (stars). The inset map shows the study area along with the boundaries of the Chukchi Sea as defined by the International Hydrographic Organization (gray shading; <http://www.marinerregions.org/gazetteer.php?p=details&id=4257>)

with a steady supply of advected nutrients make the Chukchi Sea one of the world's most productive marine ecosystems (Grebmeier et al. 2006; Zerbini et al. 2016). In addition to nutrients, Pacific water masses also transport zooplankton, including large copepods (Eisner et al. 2013; Ershova et al. 2015; Pinchuk and Eisner 2017; Spear et al. 2020) and euphausiids (Berline et al. 2008), as well as juvenile forage fish species (Levine et al. 2021) into the Chukchi Sea. Three dominant water masses flow through the Bering Strait and into the Chukchi Sea. The cold, salty, and productive Anadyr Water flows on the western side of the Bering Strait, the warmer and less salty Bering Sea Water flows through the center of the strait, while the still warmer and fresher Alaskan Coastal Current flows along the eastern side against the Alaskan coast in summer to early winter (Coachman et al. 1975; Grebmeier et al. 1989; Weingartner et al. 2005; Woodgate et al. 2005). Fronts form where these water masses meet (Coachman et al. 1975; Bluhm et al. 2007; Danielson

et al. 2017), trapping zooplankton and small fish. Additionally, eddies form in the wake of the Diomed Islands north of the strait (Woodgate et al. 2015), vertically mixing the water column and creating isolated water zones, fronts, and upwelling. The replenishment of nutrients to the surface by mixing promotes phytoplankton blooms (Hasegawa et al. 2009), which in turn create feeding opportunities for upper trophic levels, including baleen whales.

Subarctic baleen whales—specifically humpback (*Megaptera novaeangliae*), fin (*Balaenoptera physalus*), and gray whales (*Eschrichtius robustus*)—migrate into the Chukchi Sea during the late spring and summer months to take advantage of the seasonal abundance of prey (Brower et al. 2017, 2018; Stafford et al. 2023). Previous studies have found interannual variation in the presence of fin and humpback whales in the Chukchi Sea during the open-water season. More fin whale calls were recorded in the northeast Chukchi Sea in 2007 than in 2009 and

2010 by Delarue et al. (2013) while a study by Woodgate et al. (2015) observed higher detection rates of fin whales in the southern Chukchi Sea in 2009 and 2012 than in 2010 and 2011. Similarly, more humpback whale calls were recorded in the southern Chukchi Sea in 2009 and 2012 than in 2010 and 2011 (Woodgate et al. 2015). Both studies attribute the increased presence of the two species to warmer conditions, earlier sea-ice retreat coupled with low sea-ice extent, higher transport through the Bering Strait, and shifts in the distribution of the productive Anadyr Water mass (Delarue et al. 2013; Woodgate et al. 2015). While the presence of fin and humpback whales in the Chukchi Sea varies from year to year, gray whales are reliably observed in the region each summer (Clarke et al. 1989, 2016; Moore et al. 2000, 2022; Clarke and Moore 2002; Brower et al. 2017). Declining sea ice may benefit gray whales in the short term since earlier ice melt in the spring allows them to enter their foraging grounds earlier and delays in ice formation in the fall allows them to graze for longer (Perryman et al. 2002; Stewart et al. 2023). However, few observations have been collected on the timing of the gray whale southward migration out of the Chukchi Sea, so it is unclear if gray whales are extending their residence time in the Pacific Arctic.

Any variation in the presence of the three whale species is likely dependent on prey availability, which in turn, is dependent on environmental conditions in the Chukchi Sea. Environmental variability in the Chukchi Sea is driven by the presence and distribution of the major water masses, as well as changes in the Bering Strait through-flow, which in turn is dependent on local and far-field wind stress and ocean pressure gradients (Aagaard et al. 1985; Woodgate et al. 2012; Danielson et al. 2014; Peralta-Ferriz and Woodgate 2017, 2023; Woodgate 2018; Nguyen et al. 2020). Previous studies examining environmental influences on the presence of baleen whales found that primary production rates, and in turn, prey abundance, along with sea surface temperatures, bathymetry, and sea surface height influenced the acoustic presence of baleen whales (Širović and Hildebrand 2011; Shabangu et al. 2017; Ryan et al. 2019; Szesciorka et al. 2020). In the northern Chukchi Sea, Ashjian et al. (2010) found that interannual variability in the distribution of bowhead whales (*Balaena mysticetus*) corresponded to both short-term (i.e., changes in wind speed and direction) and long-term environmental variability (i.e., sea ice and water mass distribution). What cues subarctic baleen whales use for finding their prey in the Pacific Arctic, however, remain unclear.

Using passive acoustic data along with in situ and satellite-derived environmental variables collected over nine years in the Bering Strait region (2009–2018), we examined whether fin, humpback, and gray whales shifted their migration timing in response to environmental conditions,

and explored potential environmental influences on the presence of these species during the open-water season (May through early December).

Methods

Acoustic data collection

Passive acoustic data were collected using an AURAL-M2 hydrophone (Autonomous Underwater Recorder for Acoustic Listening-Model 2, Multi-Électronique, Inc.) attached to a mooring (A3) positioned ~35 km north of the Bering Strait (Fig. 1; Woodgate et al. 2015). The hydrophone was first installed on the mooring in September 2009 and was serviced annually, yielding a recording time series from September 2009 through December 2018. Data gaps indicate periods when the hydrophone's batteries were depleted, or when the hydrophone was serviced. The hydrophone failed to record in 2016, resulting in a loss of data for fall 2016 through spring 2017. The hydrophone was set to record the first 10–20 min of every hour at a sampling rate of 8 kHz or 16 kHz depending on the year (16-bit resolution) and a gain of 16 dB (2009–2016) or 22 dB (2017 and 2018). The hydrophone was positioned 4–8 m above the seafloor (depth at the A3 mooring site ~56 m). See Table 1 for recording start/end dates, and the duty cycles for each year.

Spectrograms of the acoustic data were visualized in the software *Ishmael* (2014 version; Mellinger 2002), and recordings with whale calls were identified by visually inspecting the spectrograms. For each calendar year, we scanned recordings from May, when sea ice typically retreats in the study area (Stroeve et al. 2014; Serreze et al. 2016; Grebmeier et al. 2018), through to freeze-up when sea ice concentration in the Chukchi Sea first rose above 80% (typically late November to mid-December; see next section for sea ice methods). If a call from any of the three study species was captured by a recording, we counted that species as present for that hour. Note that we could not assume the physical absence of whales since we were only able to detect calling individuals (i.e., we can only assume 'acoustic absence').

Environmental data collection

We quantified sea ice melt and formation dates in the Chukchi Sea to compare with the migration timing of whales in and out of the region. We defined the Chukchi Sea using boundaries defined by the International Hydrographic Organization (<http://www.marineregions.org/gazetteer.php?p=details&id=4257>; Fig. 1). Daily sea ice

Table 1 Hydrophone deployment data, positions, and recording settings (duty cycle refers to the recording time per hour)

Deployment year	Latitude N	Latitude W	Record start date	Record end date	Sampling rate (kHz)	Hourly duty cycle
2009	66.33°	168.97°	2009–09-01	2010–03-03	16	12 min
2010	66.33°	168.97°	2010–08-11	2011–02-19	16	15 min
2011	66.33°	168.97°	2011–10-01	2012–05-25	8	10 min
2012	66.33°	168.97°	2012–09-01	2013–05-17	16	10 min
2013	66.33°	168.97°	2013–07-15	2014–07-02	8	20 min
2014	66.33°	168.97°	2014–07-10	2015–07-02	8	20 min
2015	66.33°	168.97°	2015–07-05	2016–07-08	8	20 min
2017	66.33°	168.95°	2017–08-17	2018–07-25	8	20 min
2018	66.33°	168.95°	2018–08-12	2019–09-07	8	20 min

Dates are in the format ‘YYYY-MM-DD.’ The ‘Record Start/End’ dates indicate when the hydrophone started and stopped recording, however we only analyzed recordings for the open-water season (May through freeze-up in November/December of each year) when the three whale species are present in the region

concentrations were obtained from the Special Scanning Microwave/Imager (SSM/I) dataset (25 km resolution; Cavalieri 1996). We defined the initiation of sea ice melt-out as the day when the average sea ice concentration in the Chukchi Sea dropped below 80% for the last time that calendar year, while freeze-up onset was defined as the day when the average ice concentration first rose above 80%. We defined an area as ‘ice-free’ if the average sea ice concentration was $\leq 15\%$, a threshold commonly used to indicate the initiation of the open-water period (Serreze et al. 2009; Stroeve et al. 2012).

Environmental predictors were selected based on their hypothesized potential to influence the presence of baleen whales. In-situ environmental predictors were recorded by other sensors on the mooring and included near-bottom temperature and salinity (40–55 m depth) measured by Sea-Bird Electronics (SBE) sensors (model #16), and water velocity (cm s^{-1}) measured by Teledyne Workhorse Acoustic Doppler Current Profilers (ADCP; Woodgate 2018). We analyzed ADCP water velocities from the bin closest to ~30 m depth to measure mid-water column velocities while avoiding contamination by waves and other surface activity. Note that at this mooring site, the water velocity is dominantly barotropic (Woodgate et al. 2015; Woodgate 2018). Boxplots and Cleveland dot plots (Cleveland 1993) were generated for each environmental covariate to identify outliers and violations of homogeneity. We removed any outliers before we calculated daily averages.

In addition to the in-situ mooring data, we also examined wind speed and direction, as well as satellite-derived sea-surface temperatures (SST). Daily mean wind speed (m s^{-1}) and direction were calculated from the National Centers for Environmental Prediction (NCEP) North American Regional Reanalysis 2 (NARR 2) 6-hourly wind data product (grid size of ~32 km; Mesinger et al. 2006). We calculated daily mean wind speed by taking the average of the northward

(v) and eastward components (u) for the four NCEP-NARR 2 grid points nearest to the mooring site (Fig. 1). We then averaged the vectors across the four grid points, and used the mean vectors ($\bar{u}$ and $\bar{v}$) to calculate mean wind speed for a given day (i) using the following equation:

$$\overline{\text{wind speed}}_i = \sqrt{(\bar{u}_i^2 + \bar{v}_i^2)}$$

Daily mean SST were calculated for the grid point closest to the mooring site using the National Oceanic and Atmospheric Administration (NOAA) Optimum Interpolation Sea Surface Temperature (OISST) gridded dataset (0.25° resolution; Reynolds et al. 2007). All satellite-derived data were visualized in ArcMap (v. 10.8; ESRI 2019).

Migration timing

We estimated the arrival of whales into the study region by calculating the 5% quantile of the cumulative distribution of days with whale calls after May 1 of each year, and departure dates were estimated using the 95% quantile of the cumulative distribution of days with whale calls after October 1 of each year, similar to Hauser et al. (2017). We restricted the range for calculating the departure dates with a set start date since the recording start dates differed amongst the years and we did not want this difference to affect the calculation of the departure dates. October 1 was chosen as the starting point of the range for calculating departure dates since it was the latest recording start date (Table 1). We only had recordings in the spring for four years (2014–2016, and 2018), whereas we had nine years of fall recordings (2009–2015, 2017–2018). Therefore, we focused our statistical analyses on the fall departure dates.

We tested the departure dates for annual trends using linear regressions, for correlations to freeze-up in the Chukchi

Sea using Pearson correlation tests, and for correlations and linear relationships to seasonal environmental conditions. We used a significance level of 0.05 for determining the significance of all statistical tests. We defined the four seasons using the solstices and equinoxes as the boundaries: winter was defined as 21 December of previous year through 20 March, spring was defined as 21 March through 20 June, summer was defined as 21 June through 20 September, and fall was defined as 21 September through 20 December. Seasonal means were calculated for near-bottom temperatures and salinities ('SBE Temp' and 'SBE Salt'), SST, water speeds, and wind speeds. Due to correlations between multiple seasonal means (Online Resource Table S1), we built separate linear models for each species and predictor with departure dates ($n=9$) as the response variable. For example, we tested for a linear relationship between departure dates for fin whales and a predictor (e.g., the spring mean of near-bottom temperatures for the corresponding year), by fitting the following equation to the data, using least squares to obtain the constants β_0 and β_1 :

Fin Whale Departure Dates

$$= \beta_0 + \beta_1(\text{Spring Mean SBE Temp})$$

Modeling the relationship between whale presence and environmental covariates

We conducted an exploratory modeling analysis to determine potential temporal and environmental covariates associated with the probability of observing whale calls (p) during the open-water season. Our analyses included examining the influence of time of year, quantified as day of the year (DOY), and environmental conditions at the mooring site on the acoustic presence of each whale species.

Conditions measured at or near the mooring site included daily means for: temperature and salinity near the bottom ('SBE Temp' and 'SBE Salt'), SST, water speed (cm s^{-1}), wind speed (m s^{-1}), and wind direction (included as a categorical variable). Sea ice extent for the Chukchi Sea was considered for the models, however preliminary correlation tests found that sea ice extent was highly correlated with both SST and near-bottom temperatures. Since all three whale species are typically in the study region when it is ice-free, we omitted sea ice extent as an explanatory variable, and retained SST and near-bottom water temperatures. Ocean-basin scale indices such as the Arctic Oscillation Index, Pacific Decadal Oscillation Index, and the North Pacific Gyre Oscillation Index were also considered for the models, however preliminary tests with these covariates resulted in large models that were likely overfitting the data. Moreover, factors relevant to the indices, such as SST,

were already included in the models. Therefore, ocean-scale indices were excluded from our models.

Fronts form important feeding habitats for baleen whales (Bluhm et al. 2007; Bost et al. 2009; Scales et al. 2014; Bassoi et al. 2020), and can be identified using horizontal gradients in water temperature, salinity, chlorophyll concentration, and sea surface height (Bluhm et al. 2007). We used high-resolution SST data from the Group for High Resolution Sea Surface Temperature (GHRSSST) Level 4 sea surface temperature analysis product (0.054° resolution) to calculate the maximum gradient in SST in any direction within 30 km of the mooring site, taking the magnitude of this maximum as a proxy of the strength of any thermal fronts within this region (see Fig. 1). A 30 km radius was chosen since fin whale calls were previously detected at two hydrophones spaced 28 km apart in the northeast Chukchi Sea (Delarue et al. 2013). Fin whales produce the lowest frequency calls of the three species at ~ 20 Hz (Watkins 1981; Watkins et al. 1987) and lower frequency calls travel farther underwater than higher frequency calls. Therefore the 30 km radius likely captures the maximum detection ranges for all three species in the shallow Chukchi Sea. In addition to the daily value for the 30 km SST gradient, we also included a one-month lagged version of the SST gradient in our model (i.e., the SST gradient one month prior to the day when calls were recorded) to test for a delay between the presence of a front and the presence of a calling whale(s).

For the response variable, the acoustic data were converted into counts of hourly recordings with calls present ("Detected") along with the number of recordings that did not have calls present ("Not Detected") for each day. Thus, our response variable consisted of a Bernoulli outcome for each day where the 'successes' were the number of hourly recordings when whale calls were detected, and the 'failures' were the number of hourly recordings when whale calls were not detected. The ratio of successes to the total number of available Bernoulli trials per day (24 hourly recordings per day) represents the probability of a calling whale being present on any given day. Given that the probability of a calling whale being present during a given hour was likely influenced by the presence/absence of a calling whale the previous hour, our model choice was driven by the need to account for the fact that the Bernoulli outcomes in our response variable were not independent of each other. Also, our data had more hourly recordings with zero calls than expected, therefore our data were zero-inflated. The beta-binomial distribution does not assume independent Bernoulli outcomes and is a good choice when zero-inflation is a concern (Hisakado et al. 2006; Martin et al. 2011). We did not know a priori the functional form of the relationship between whale presence and the predictors; therefore we also required a non-parametric model fitting algorithm

that could accommodate a beta-binomial distribution. Generalized additive models for location, shape, and scale (GAMLSS) are robust to more complex distributions, such as beta-binomial, and allow for nonparametric predictors (Monnahan et al. 2014).

We generated our beta-binomial GAMLSS models using the *gamlss* package (Rigby and Stasinopoulos 2005) in *R* (R Core Team 2021), and ran separate models for each species with all years combined (2009–2018, excluding 2016 due to recorder failure). Following Monnahan et al. (2014), we fit the same predictors for both the probability of observing whale calls on a given day (p) and the over-dispersion parameter (σ). We used cubic splines (cs) for the environmental variables, and penalized b-spline smoothers (pb) for DOY:

$$\begin{aligned}\text{logit}(\hat{p}) = & \text{pb}(\text{DOY}) + \text{cs}(\text{SBE Temp}) + \text{cs}(\text{SBE Salt}) \\ & + \text{cs}(\text{SST}) + \text{cs}(\text{Water Speed}) + \text{cs}(\text{Wind Speed}) \\ & + \text{factor}(\text{Wind Direction}) + \text{cs}(\text{SST Gradient}) \\ & + \text{cs}(\text{Lagged SST Gradient})\end{aligned}$$

$$\begin{aligned}\log(\hat{\sigma}) = & \text{pb}(\text{DOY}) + \text{cs}(\text{SBE Temp}) + \text{cs}(\text{SBE Salt}) \\ & + \text{cs}(\text{SST}) + \text{cs}(\text{Water Speed}) + \text{cs}(\text{Wind Speed}) \\ & + \text{factor}(\text{Wind Direction}) + \text{cs}(\text{SST Gradient}) \\ & + \text{cs}(\text{Lagged SST Gradient})\end{aligned}$$

Note that all variables except for wind direction were continuous; wind direction was included as a categorical variable (noted in the equations above as a “factor”), and thus, does not have a smoother. The type of smoother used as well as model selection were based on the Akaike information criterion score (AIC) with a correction for small sample sizes (AICc; Akaike 1973). To avoid multicollinearity among the model parameters, we tested pairs of variables using Pearson’s correlation tests and eliminated any predictor variables with a correlation factor >0.7 —signifying a moderately strong correlation (explains more than half the variance between the two variables)—and $p < 0.05$, following Širović and Hildebrand (2011). Predictors were selected using the *stepAIC* function (Rigby and Stasinopoulos 2005) applied to the full model in *R*, which performed backwards stepwise selection using Generalized AIC (GAIC) as the model selection criterion. Next, we applied the *drop1* function from the *stats* package in *R* to the final model for each species to check for any spurious covariates. The *drop1* function systematically removes one variable at a time and compares the AIC score of the reduced model to that of the full model. Any variables that did not significantly decrease the likelihood relative to the full model ($p > 0.05$) were removed. Finally, we assessed the relative importance of each predictor variable in the final model using an incremental R^2 test where the incremental R^2 for a predictor variable

equals the increase in the value of the model’s R^2 when the predictor is the last variable added to the model (Cohen et al. 2003). For the incremental R^2 tests, we calculated the Cox and Snell R^2 (Cox and Snell 1989) for each model using the *Rsquared* function from the *gamlss* package.

When fitting a smoothed nonparametric term, the effect of the predictor variable on the response variable cannot be interpreted using the coefficients. Instead, the influence of a predictor variable must be interpreted using the whole smoothing function (Stasinopoulos et al. 2017). We used the *term.plot* function in *gamlss* to plot the additive smoothing fits to evaluate the influence of each predictor on the probability of acoustic occurrence (p). The relative direction of the curve for a predictor represents the effect of the variable on p . The y-axis is unitless and we used different scales for the y-axis to aid in the legibility of each explanatory variable’s effect. Increasing trends represent a positive effect of the explanatory variable on p , while declining trends signify a negative effect.

Results

Acoustic detections

We scanned a total of 33,371 audio files recorded at the A3 mooring site from 1 May to freeze-up in November and December 2009–2018 (see Table 2 for freeze-up dates). Humpback whales were the most commonly detected species across the nine years of our study (2009–2018) with 20% of all recordings containing humpback whale calls. Fin whales were detected in 12% of all recordings,

Table 2 Melt-out (sea ice concentration $<80\%$) and freeze-up (sea ice concentration $\geq 80\%$) initiation dates along with the start and end dates and length of the open-water period for the Chukchi Sea (see boundaries of Chukchi Sea in Fig. 1)

Year	Melt-out initiation date	Open-water start date	Open-water end date	Freeze-up initiation date	Open-water period length (days)
2009	21 May	3 Jul	14 Nov	28 Nov	134
2010	20 May	16 Jul	7 Nov	13 Dec	114
2011	18 May	25 Jun	16 Nov	2 Dec	144
2012	3 Jun	22 Jul	29 Oct	25 Nov	99
2013	6 Jun	10 Jul	12 Nov	17 Dec	125
2014	11 May	2 Jul	1 Dec	15 Dec	152
2015	13 May	22 Jun	17 Nov	7 Dec	148
2016	17 May	6 Jul	21 Nov	28 Dec	138
2017	2 May	23 Jun	22 Nov	2 Jan	152
2018	23 Apr	27 Jun	25 Nov	14 Dec	151

and gray whales were detected in 7% of all recordings. Detection of humpback and fin whale calls peaked in October whereas gray whale calls were detected throughout

the open-water season at low levels with a peak in June–August (Fig. 2).

We calculated the proportion of recordings with whale calls for October through November for each year to

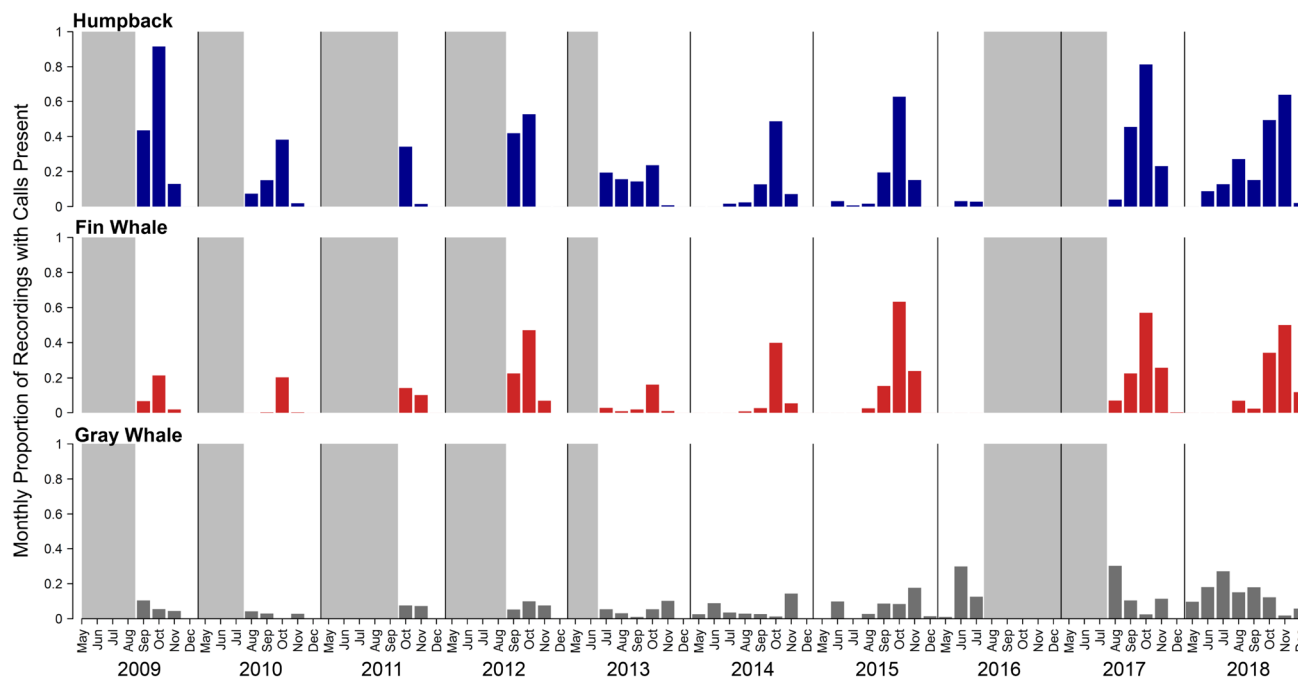


Fig. 2 Proportion of hourly recordings with whale calls by month during the open-water season for humpback whales (top plot), fin whales (middle plot), and gray whales (bottom plot) at the A3 moor-

ing site. Vertical lines separate each year while the gray shaded areas indicate periods with no recordings

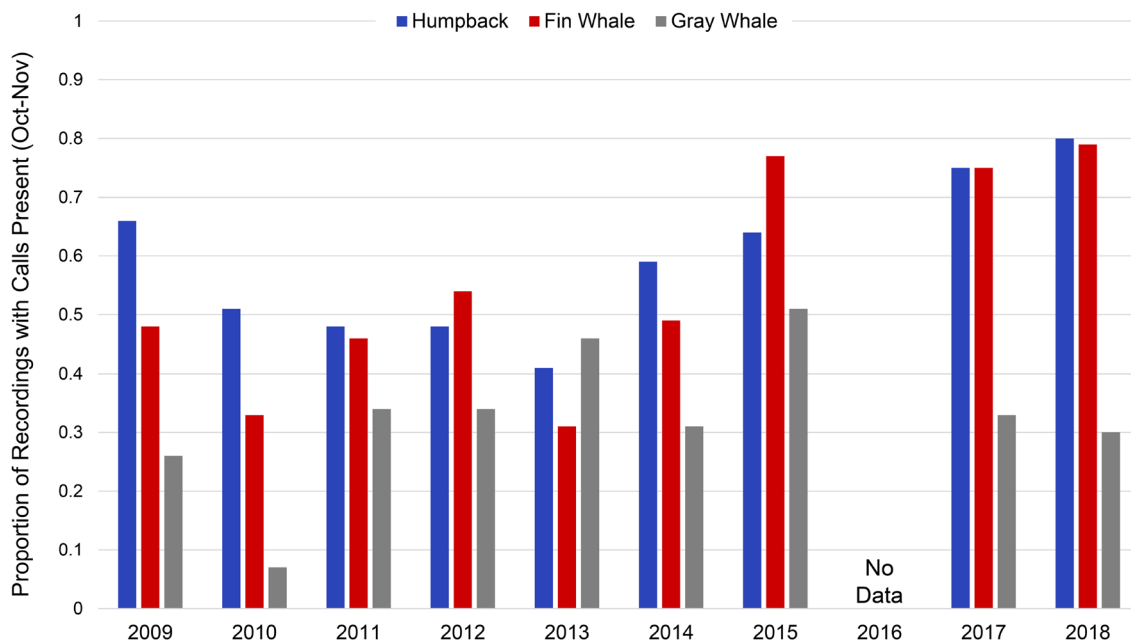


Fig. 3 Proportion of October–November recordings with whale calls by year for each species

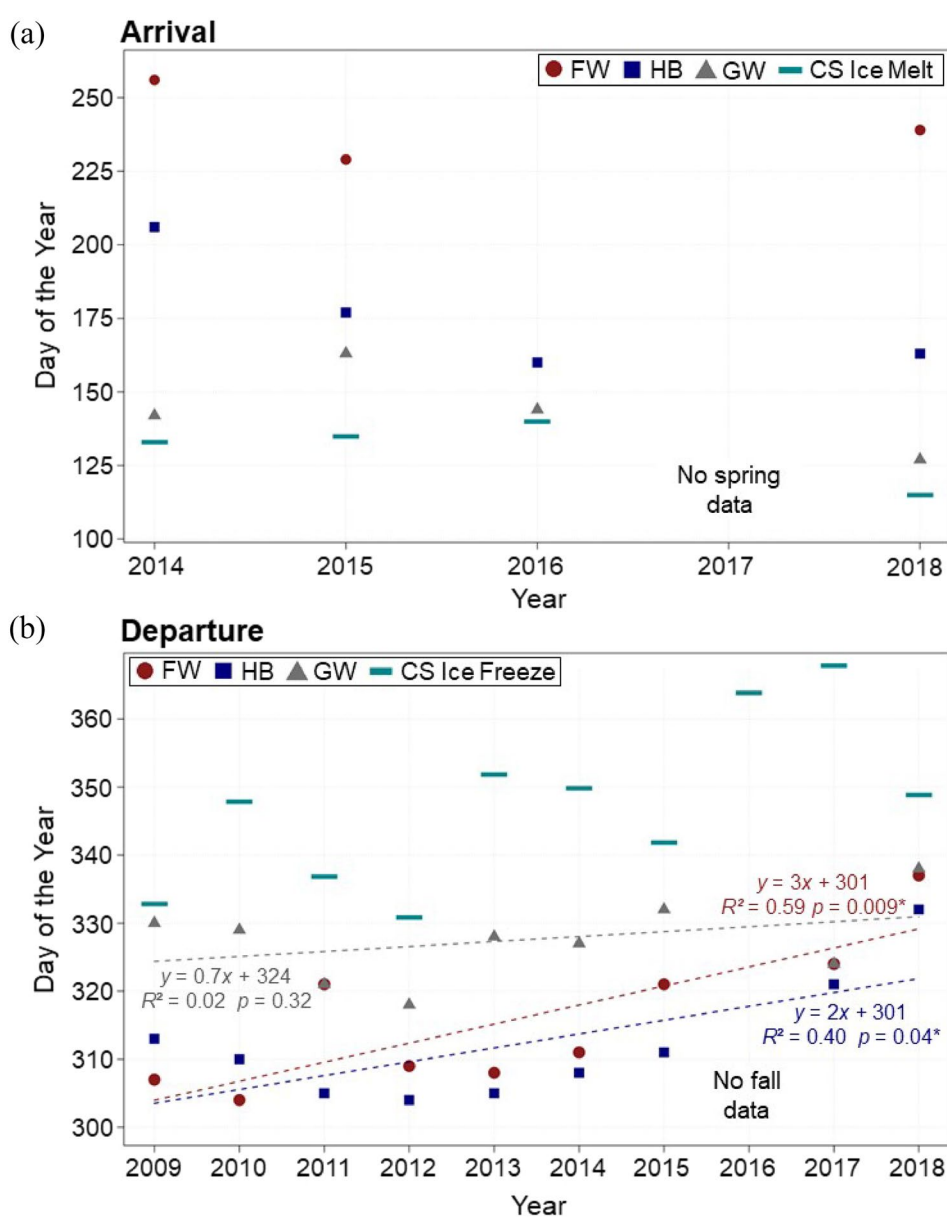
compare acoustic occurrence across the years. October and November were chosen since all years had recordings for these two months (Fig. 2). The years 2009, 2017, and 2018 had the highest proportion of recordings with humpback vocalizations with 66%, 75%, and 80% of the total recordings for October–November containing humpback whale calls, respectively (Fig. 3). For fin whales, 2015, 2017, and 2018 had the highest proportion of recordings with fin whale vocalizations, with 77%, 75%, and 79% of the total recordings for October–November containing fin whale calls, respectively. We observed the highest proportion of recordings with gray whale calls for October–November in 2015 (51%) followed by 2013 (46%; Fig. 3).

Migration timing

Gray whales had the earliest arrival dates of the three species, with arrival dates ranging from 7 May to 12 June for the years that had spring data available (2014–2016 and 2018; Fig. 4a). Humpback whale calls were typically detected starting in early June with arrival dates ranging from 8 June to 25 July. Fin whales were first detected in late summer with arrival dates ranging from 17 August to 13 September.

All three species typically began to depart the Bering Strait region in late October according to our analysis of the fall recordings (2009–2018, excluding 2016). Humpback whales were usually the first to leave the study area, with departure dates starting in late October (mean departure date = 8 November; Fig. 4b). Fin whales typically

Fig. 4 (a) Arrival and (b) departure days of the year for fin whales (FW; circles), humpback whales (HB; squares), and gray whales (GW; triangles). Arrival dates shown for the years that had recordings available in spring ($n = 4$; 2014–2016, 2018). Note that fin whale calls were not detected in spring 2016 (hydrophone stopped recording on 8 July 2016). Departure dates are shown for the years that had recordings available in fall ($n = 9$; 2009–2015, 2017–2018). Linear regressions are shown as dotted lines. The days of the year when sea ice concentrations reached $< 80\%$ ('CS Ice Melt') and $\geq 80\%$ ('CS Ice Freeze') in the Chukchi Sea are included with the arrival and departure dates for illustrative purposes (dashed points)



left the region in early to mid-November (mean departure date = 12 November), and gray whales were the last to leave with departure dates ranging from mid to late November (mean departure date = 23 November; Fig. 4b). Fin whales departed the Bering Strait 3 days later over the study period (standard error = ± 1 day, $R^2 = 0.59$, $p = 0.009$; Fig. 4b) while humpback whales departed 2 days later (standard error = ± 1 day, $R^2 = 0.40$, $p = 0.04$; Fig. 4b), and the trend for gray whales was non-significant. Also, there were no significant correlations between the

departure dates for the three species and freeze-up dates for the Chukchi Sea (all Pearson $r \leq 0.45$, $p \geq 0.23$). We found significant positive relationships between departure dates for fin whales and seasonal mean near-bottom temperatures for all four seasons (all Pearson $r \geq 0.8$, all $p < 0.02$; Fig. 5). Humpback whale departure dates were significantly correlated with seasonal mean near-bottom temperatures for winter, spring, and fall (all Pearson $r \geq 0.73$). We also found significant positive correlations between departure dates for fin and humpback whales

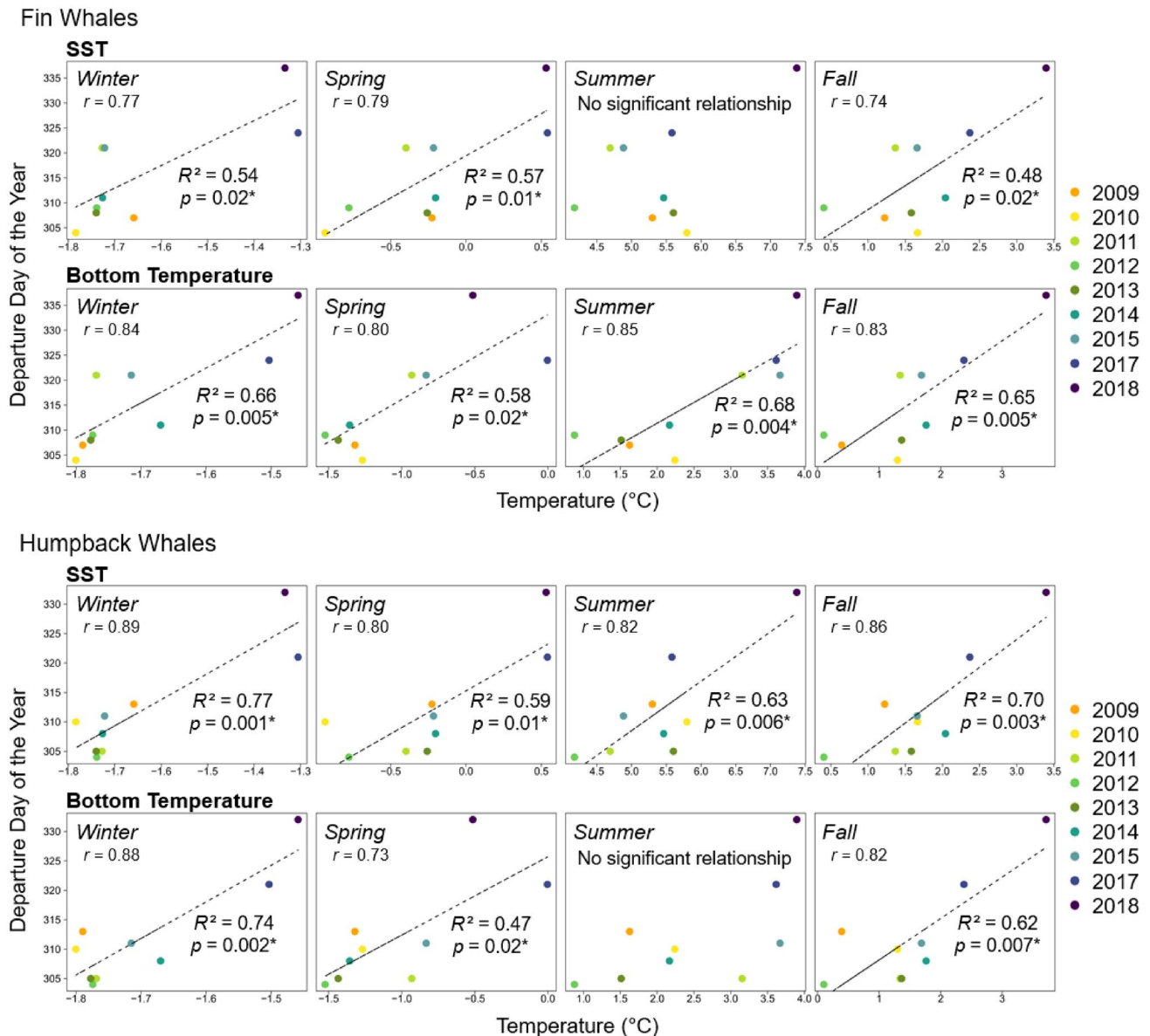


Fig. 5 Results from the Pearson correlation tests (r) and linear regression between departure days for fin whales (top plot) and humpback whales (bottom plot) and seasonal mean sea-surface temperatures (SST; NOAA Optimum Interpolation Sea Surface Temperature [OISST] dataset; $^{\circ}\text{C}$), and near-bottom temperatures (SBE-16 temper-

ature data; $^{\circ}\text{C}$). Seasons were defined as follows: winter = 21 December–20 March, spring = 21 March–20 June, summer = 21 June–20 September, and fall = 21 September–20 December. See Online Resource Table S2 for the linear equations. The asterisk indicates a significant p -value

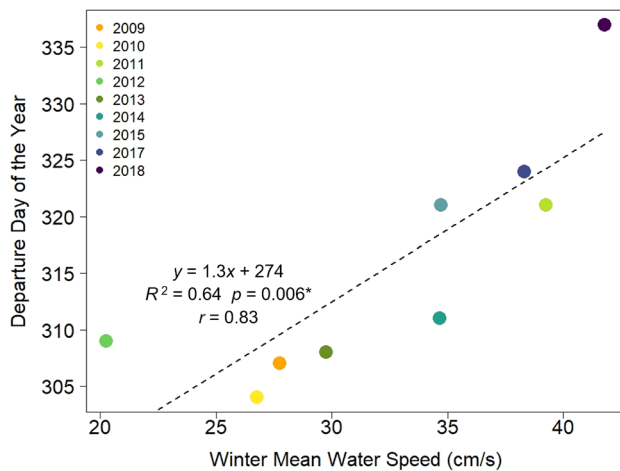


Fig. 6 Results of the Pearson correlation test (r) and linear regression between fin whale departure days and winter mean water speeds (ADCP data; cm s^{-1}). Winter was defined by the period 21 December–20 March. The asterisk indicates a significant p -value

and seasonal mean SST for all four seasons (all Pearson $r \geq 0.77$, all $p < 0.02$; Fig. 5), except between fin whale departure dates and summer SST ($p = 0.15$). Departure dates for fin whales were positively correlated to higher water speeds in the previous winter ($r = 0.83$, $p = 0.006$; Fig. 6). Gray whale departure dates had a positive significant relationship to summer and fall mean SST (all Pearson $r \geq 0.72$, $p < 0.3$; Fig. 7).

Modeling results

Six models were within 10 AICc units of the best model for each species (Online Resource Table S3). Among these models, day of the year (DOY), daily mean near-bottom temperatures ('SBE Temp'), SST, water speed, and the lagged SST gradient ('Lagged SST Gradient,' lagged by one month) were included in all three species models (Table 3).

The probability (p) of observing fin whale calls increased with DOY, peaking between early September (DOY 250) and mid-November (~DOY 325; Fig. 8). The probability of calling fin whales being present increased with increasing near-bottom temperatures with a peak between 4 and 5 °C, and calling fin whales were more likely to be present on days with SST ranging from 1 to 4 °C. Water speed was the most important predictor for the fin whale model with a 15% decrease in R^2 when the variable was removed from the model (Table 4). The probability of a calling fin whale being present decreased with faster water speeds ($> 30 \text{ cm s}^{-1}$). The relationship between the probability of calling fin whales being present and SST Gradient was negative, with the probability decreasing as the SST Gradient increased. In contrast, more recordings with fin whale calls occurred when the SST Gradient was within 2–4 °C the previous month.

Like with fin whales, the probability of observing humpback whale calls increased with day of the year (DOY), particularly between early September (DOY 250) and early November (~DOY 305; Fig. 9). DOY was the most important predictor for the humpback model, with a 12% decrease in the R^2 value according to the incremental R^2 test (Table 4). There was a bimodal relationship between near-bottom temperature and humpback calls, with a peak between 0 and

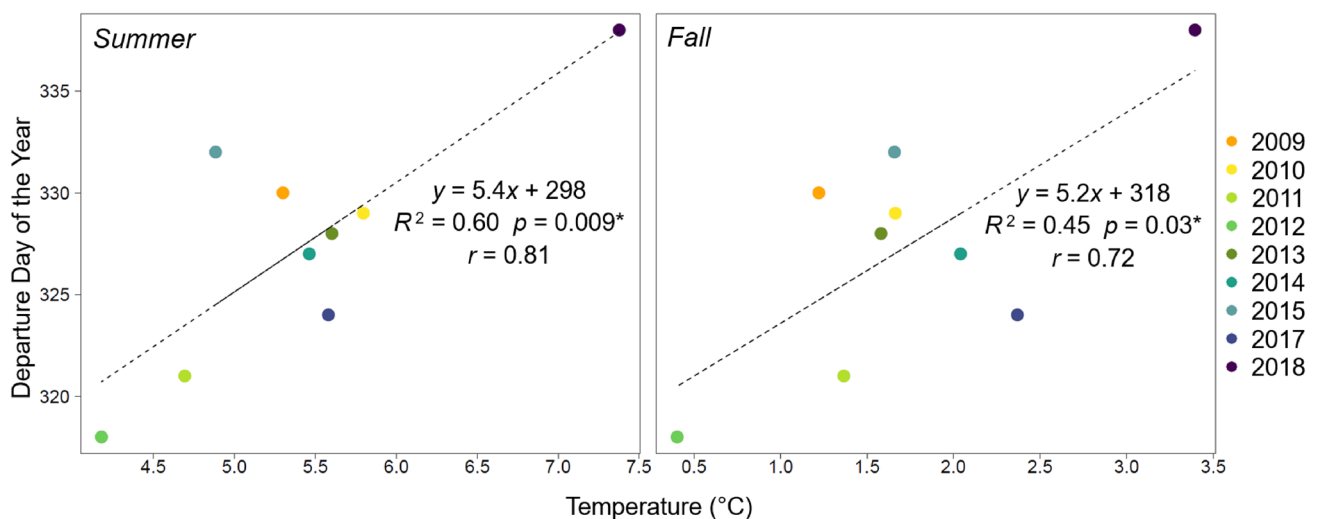


Fig. 7 Results of the Pearson correlation test (r) and linear regression between gray whale departure days and summer (left plot) and fall (right plot) mean sea-surface temperatures (SST). Summer was

defined as the period between 21 June and 20 September and fall was defined as 21 September–20 December. The asterisk indicates a significant p -value

Table 3 List of variables included in the best model for each species (i.e., the model with lowest AICc score)

Variable	Fin whales	Humpback whales	Gray whales
pb(DOY)	✓	✓	✓
cs(SBE Temp)	✓	✓	✓
cs(SBE Salt)		✓	✓
cs(SST)	✓	✓	✓
cs(Water Speed)	✓	✓	✓
cs(Wind Speed)		✓	✓
cs(SST Gradient)	✓	✓	
cs(Lagged SST Gradient)	✓	✓	✓

A check mark (✓) indicates that the variable was included in the model. Smoothers are: cs=cubic spline, pb=penalized b-spline smoothers. Variables in **bold** text were included in all three species' models

2 °C and another between 4 and 5 °C. Calling humpback whales were more likely to be present on days with warmer SST (> 2 °C). The probability of calling humpback whales being present decreased with increasing near-bottom salinity with a slight peak between 32 and 32.5 psu. Similar to fin

whales, humpback whale calls were less likely to be detected on days with high winds and water speeds. The plot for SST Gradient shows a mostly negative relationship between the probability of calling humpbacks being present and the daily maximum SST gradient, similar to fin whales. However, the probability of a calling humpback being present increased with lagged SST gradients between 2 and 4 °C, with greater uncertainty towards higher gradients.

There were two best gray whale models according to AICc (with equal R^2), therefore we chose the model with fewer predictors (Online Resource Table S3). The probability of a calling gray whale being present had a negative relationship with DOY whereas it had a positive relationship with increasing near-bottom temperatures (Fig. 10). The relationship with SST was bimodal with a slight peak in probability at ~1 °C and another around 7 °C. The probability of calling gray whales being present slightly decreased with increasing near-bottom salinities with higher probabilities around 31–32 psu (Fig. 10). Lagged SST Gradient was included in the gray whale model with a higher probability of calling gray whales being present when the lagged SST gradient was low (0–1 °C). Calling gray whales were more likely to be detected on days with slower water and wind speeds (Fig. 10), though water

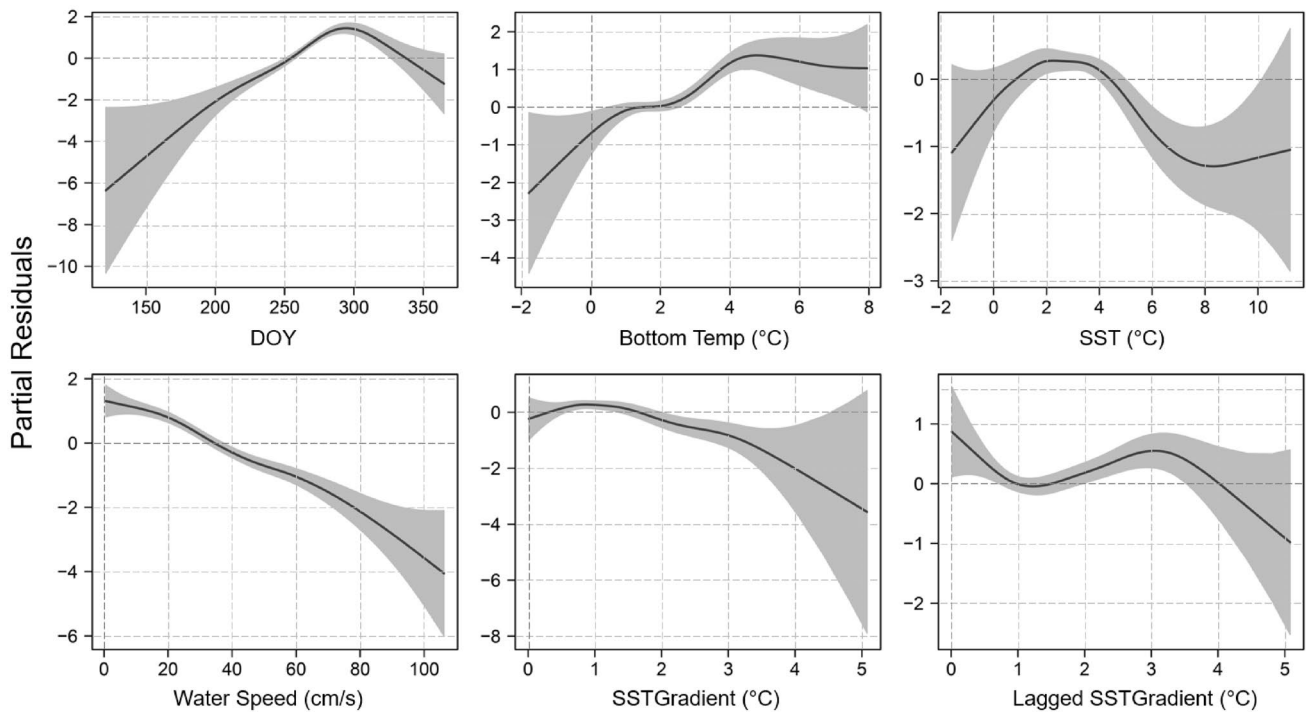


Fig. 8 Plots of the additive smoothing fits for the best fin whale model with the smoothed functions for the daily probability of a calling fin whale being present in relation to day of the year (DOY), and environmental conditions. Daily means were used for the environmental covariates, including near-bottom temperature, sea surface temperatures (SST), and water speed. The ‘SST Gradient’ represents

the maximum difference in daily mean SST between grid cells within a 30-km radius around the mooring site, which was then lagged by one month (‘Lagged SST Gradient’). The lines indicate the effect of the covariate on the probability and the gray areas represent the standard errors for the effect of the smoothed term

Table 4 Results of the incremental R^2 test on the final models for each species

Fin whale final model $R^2=0.51$			
Variable	R^2	ΔR^2	% change
Water Speed	0.44	− 0.08	15
DOY	0.44	− 0.07	13
SBE Temp	0.49	− 0.03	6
Lagged SST Gradient	0.5	− 0.02	4
Humpback whale final model $R^2=0.60$			
Variable	R^2	ΔR^2	% change
DOY	0.53	− 0.07	12
Water Speed	0.57	− 0.03	5
SBE Temp	0.58	− 0.02	3
SST	0.58	− 0.02	3
Wind Speed	0.58	− 0.02	3
SBE Salt	0.59	− 0.01	2
SST Gradient	0.59	− 0.01	2
Lagged SST Gradient lagged	0.59	− 0.01	2
Gray whale final model $R^2=0.45$			
Variable	R^2	ΔR^2	% change
Water speed	0.15	− 0.3	67
DOY	0.44	− 0.01	2
SBE Temp	0.44	− 0.01	2
SBE Salt	0.44	− 0.01	2
SST	0.44	− 0.01	2
Wind Speed	0.44	− 0.01	2
Lagged SST Gradient	0.44	− 0.01	2

The R^2 value listed for each predictor variable is the R^2 value for the full model with that variable removed. The ΔR^2 indicates the change in R^2 from that of the full model, and the percent (%) change indicates how much the full-model's R^2 value changed with that variable removed. The R^2 values were calculated using the Cox-Snell equation (Cox and Snell 1989)

speed was the far more important variable with a 67% decrease in R^2 compared to a 2% decrease for wind speed (Table 4).

Discussion

Acoustic presence

We found that the presence of fin and humpback whales varied from year to year in the Bering Strait, similar to previous visual and acoustic studies (Sleptsov 1961; Clarke et al. 2013; Delarue et al. 2013; Woodgate et al. 2015; Melnikov 2019). Both fin and humpback whales had a pronounced peak in their calls around late September to October which likely corresponds with increased vocal activity amongst males in association with the approaching breeding season (Winn and Winn 1978; Tyack 1981; Watkins et al. 2000; Darling and Bérubé 2001; Stafford et al. 2007). Additionally,

feeding fin and humpback whales are commonly observed in the southern Chukchi Sea during the late summer to early fall months (August to October; Clarke et al. 2013; Brower et al. 2018; Melnikov 2019). High zooplankton biomass in the southern Chukchi Sea in late summer to early fall (August to November; Tsujii et al. 2016) could also explain the peaks in acoustic presence for both species during this period (Fig. 2).

In comparison to fin and humpback whales, the acoustic presence of gray whales was relatively consistent across the years, except for 2010 when gray whale calls were only detected in 7% of recordings for October–November (compared to 26–51% in other years). The year 2010 had the second shortest open-water season (114 days) due to a long melt-out period (Table 2), which could explain why gray whale detections were relatively low. Also of note, Moore et al. (2022) report that 2010 had the lowest number of gray whale sightings in the south and northeast Chukchi Sea during the 2009–2019 Aerial Surveys of Arctic Marine

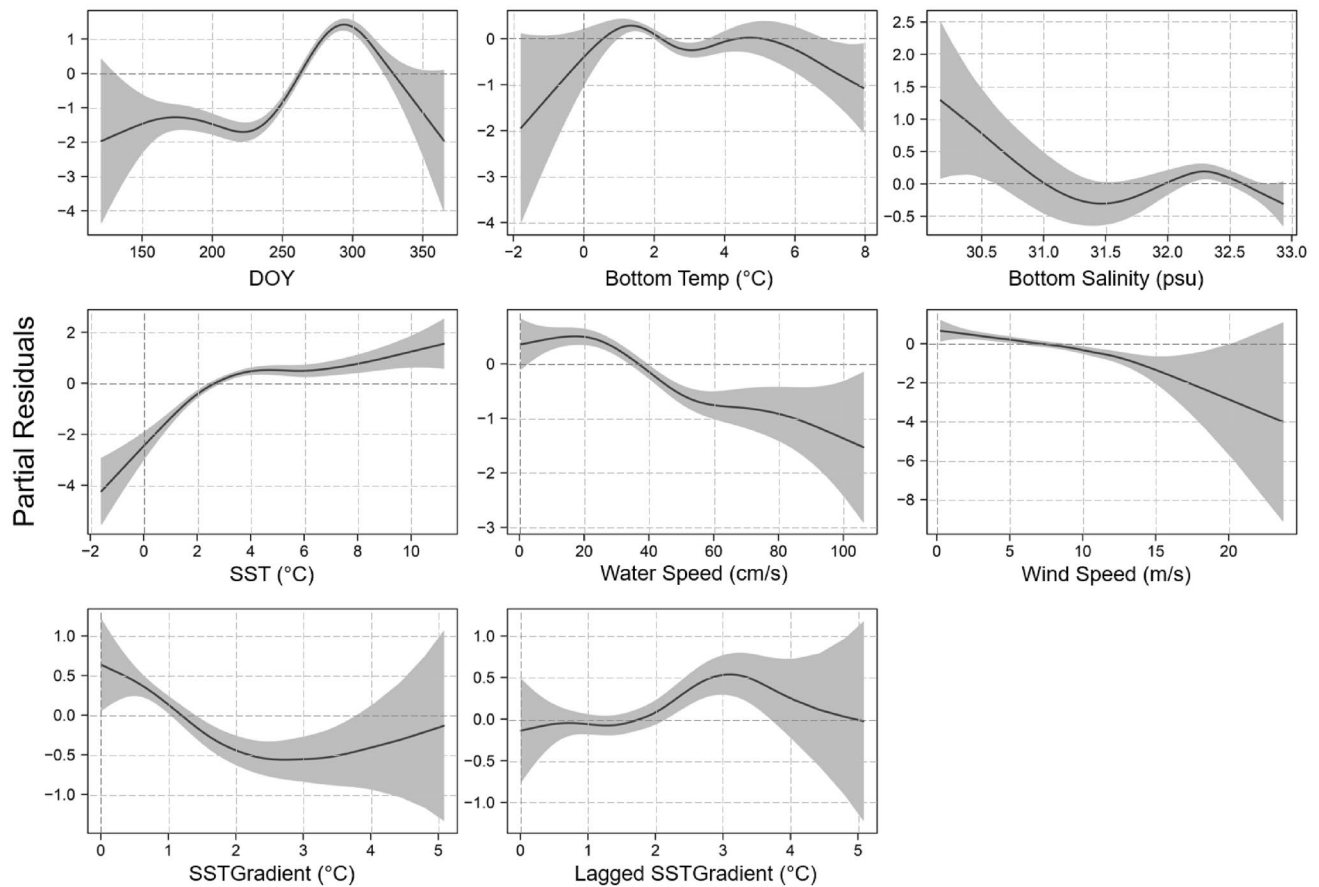


Fig. 9 Plots of the additive smoothing fits for the best humpback whale model with the smoothed functions for the daily probability of a calling humpback whale being present in relation to day of the year (DOY) and environmental conditions. Daily means were used for the environmental covariates, including near-bottom temperature and salinity, sea-surface temperatures (SST), water speed, and

wind speed. The ‘SST Gradient’ represents the maximum difference in daily mean SST between grid cells within a 30-km radius around the mooring site, which was then lagged by one month (‘Lagged SST Gradient’). The lines indicate the effect of the covariate on the probability and the gray areas represent the standard errors for the effect of the smoothed term

Mammals (ASAMM) project. Unlike fin and humpback whales, the pattern in the acoustic occurrence of gray whales during the open-water season was more pulsed. In years with both spring and fall recordings (2013–2015, 2018), there is a clear spring peak in recordings with gray whale calls (~ June–July) and a clear fall peak (~ November; Online Resource Fig. S1). This pattern likely reflects the migration of gray whales in and out of the study area given that the most common gray whale call we saw, the ‘M3’ call, has been associated with migration (Crane and Lashkari 1996; Guazzo et al. 2017).

Migration timing

Gray whales were the first of the three species to arrive in the study area (calls detected starting in early May), which aligns well with observations by Urbán et al. (2021) of tagged gray whales arriving in the Chirikov Basin in May, as

well as historical eyewitness accounts of gray whales entering the Bering Strait as early as late April (Sleptsov 1961). Humpback whales were the second species detected at our mooring site with the earliest humpback whale vocalizations recorded at the start of June. Fin whales were the last to arrive at the Bering Strait with the earliest fin whale calls detected in July. While observations of fin and humpback whales north of the Bering Strait in the spring months are lacking, land-based surveys conducted along the Chukotka Peninsula have observed humpback whales in the Gulf of Anadyr as early as the end of April (Melnikov 2019). By June, small pods of humpback whales can be seen along the east coast of the Chukotka Peninsula, including the Bering Strait area (Melnikov 2019). Soviet whalers regularly observed fin whales in the Chukchi Sea starting in mid-June in the mid-twentieth century (Nikulin 1946). More contemporary observations indicate that fin whales are typically in

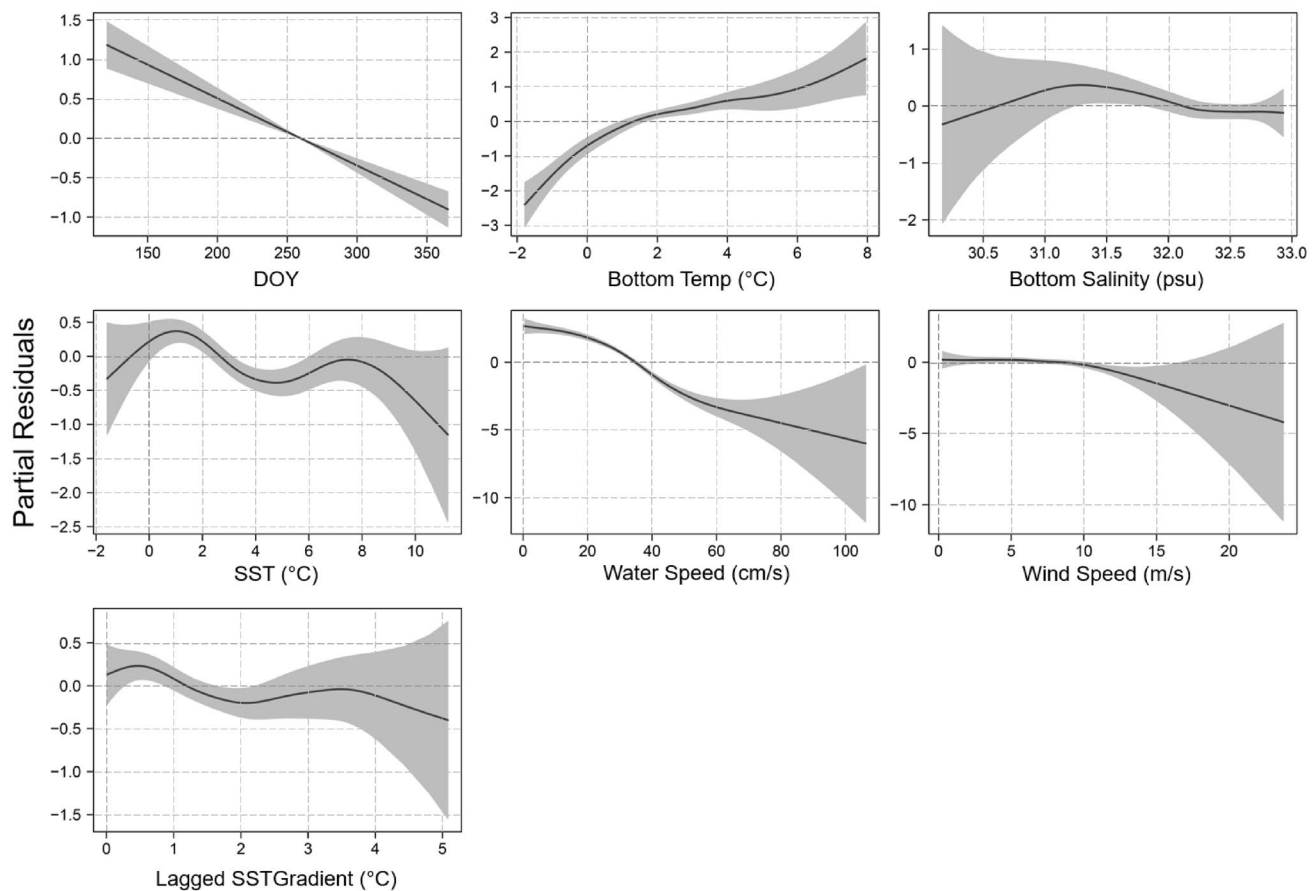


Fig. 10 Plots of the additive smoothing fits for the best gray whale model with the smoothed functions for the daily probability of a calling gray whale being present in relation to day of the year (DOY), and environmental conditions. Daily means were used for the environmental covariates including near-bottom temperature and salinity, sea-surface temperatures (SST), water speed, and wind speed.

The ‘Lagged SST Gradient’ represents the maximum difference in daily mean SST between grid cells within a 30-km radius around the mooring site lagged by one month. The lines indicate the effect of the covariate on the probability and the gray areas represent the standard errors for the effect of the smoothed term

the Chukchi Sea region by July (Clarke et al. 2013; Delarue et al. 2013).

Historical observations for the Chukchi Sea indicate that all three species typically departed the Chukchi Sea in October with gray whales sometimes leaving in November (Nikulin 1946; Berzin 1984; Sleptsov 1961) although the accuracy of these historical observations was restricted by sea ice, weather, and reduced daylight. In the present study, fin whale departure dates for 2009–2017 ranged from the end of October to mid-November, however in 2018, fin whale calls were detected well into early December (departure date = 3 December 2018). Humpback whales similarly were last detected in the study region in late October and early November, with the latest departure date on 28 November 2018. Gray whales were typically the last to leave the study area with departure dates ranging from mid-November to early December (latest departure date = 4 December 2018). The departure dates for gray whales calculated here

are 1–2 months later than those observed by Moore et al. (2022) using acoustic data recorded at a point ~78 km southwest of Point Hope in the Chukchi Sea (~179 km north of our mooring site). The difference in departure dates could be due to the gradual movement of gray whales southward during their fall migration. Additionally, fewer gray whale calls were recorded at the Point Hope location in 2018 than in 2012–2017 (Moore et al. 2022), whereas 2018 was a good year for gray whale detections at the A3 mooring site (Online Resource Fig. S1). Possible explanations for this discrepancy include the limited spatial coverage of hydrophones in the Chukchi Sea and/or imperfect detection associated with acoustic data (Moore et al. 2022). Whales must vocalize to be detected using passive acoustics, and it is possible that calling gray whales could have been out of range of either hydrophone during the fall migration period.

Fin whales left the study region an average of 3 days later each year and humpback whales departed an average

of 2 days later. Gray whales departed the study region around the same time each year, except for 2018 which had a departure date in early December (4 December 2018). We did not find a significant correlation between the departure dates and sea ice freeze-up dates (when sea-ice concentration > 80%). Instead, the departure of fin, humpback, and gray whales from the study region appears to be influenced by water temperature. Note that fin whale departure dates were also significantly correlated with mean water speeds from the previous winter. Examination of the plots of departure dates as a function of water temperature (Figs. 5 and 7) show that the significant correlations are likely driven by 2017 and 2018 which had abnormally high water temperatures throughout the year and high water speeds in winter (See the Online Resources for a discussion of the environmental conditions observed at the A3 site). Strong northward water speeds coupled with warmer temperatures in summer and fall 2017 delayed sea ice formation in the Chukchi Sea (Wang et al. 2021), allowing whales to stay for longer in the region that fall. Similarly, strong water speeds along with warmer temperatures during the winter of 2017–2018 likely prevented sea ice from forming as far south as in previous years, reducing total sea-ice extent for the region, and allowing whales to remain in the Chukchi Sea for longer in fall 2018.

Tsujii et al. (2016) found that the departure of fin whales from the southern Chukchi Sea corresponded to a decrease in water temperatures and salinities, implying that changes in temperature may trigger the southward migration of fin whales. It is possible, then, that the lack of such a cold-water signal in 2017 and 2018 in the Chukchi Sea resulted in later departure dates for fin whales. However, whether the connection between fin whale departure dates and temperature is determined by thermal tolerances, decreased feeding opportunities in the fall, or other environmental conditions associated with temperature is unclear. Given that fin whales were regularly observed swimming close to sea ice in the Pacific Arctic in the past (Sleptsov 1961), it is likely that other changes in the environment related to warmer temperatures affected the whales' migration timing rather than any physiological limitations.

Instead, warmer temperatures could extend the ice-free period in areas where subarctic whales feed in the fall. Both the Bering and Chukchi shelves have experienced rapid warming over the past decade, which in turn, has affected ice patterns in the region. Danielson et al. (2020) found that the warming rate for the Chukchi Sea tripled from 0.14 ± 0.07 °C decade⁻¹ to 0.43 ± 0.35 °C decade⁻¹ from 1990 to 2018. Warmer ocean temperatures impact the formation of sea ice in winter and the retention of sea ice in spring (Serreze et al. 2019; Kodaira et al. 2020), leading to unprecedented low winter and spring ice cover in the Pacific Arctic (Danielson et al.

2020). The Bering Strait inflow has also warmed over 1990–2018 (0.05 ± 0.02 °C year⁻¹) with longer durations of the warm-water period (from 5.5 months in the 1990s to > 7 months in 2017) on account of earlier warming (1.3 ± 0.7 days year⁻¹; Woodgate 2018; Woodgate and Peralta-Ferriz 2021). Warmer seasonal temperatures are extending the ice-free period in the Chukchi Sea, potentially allowing whales to delay their southward migration.

Alternatively, and perhaps concurrently, warmer conditions throughout the Pacific could mean reduced quality and quantity of prey for fin and humpback whales (Arimitsu et al. 2021). The occurrence of an unusual mortality event (UME) for fin whales in 2015 following a heatwave in the North Pacific (2014–2016) suggests that warmer conditions are leading to poorer feeding conditions elsewhere in their range, leading to starvation (Savage 2017). Humpback whales in the Hawaii Distinct Population Segment exhibited declines in reproductive rates between 2013 and 2018, possibly in connection to the North Pacific heatwave (Cartwright et al. 2019). Therefore, both species may be staying longer in the Chukchi Sea to acquire greater fat reserves before migrating south.

Environmental influence on whale presence

The importance of day of the year (DOY) in the fin and humpback models suggests that time of the year is highly influential in determining the probability of a calling whale being present for both species. Peaks in fall detections coincide with increased vocalization rates amongst male fin and humpback whales (Stafford et al. 2007; Kowarski et al. 2019), as well as the timing of the fall outmigration (Sleptsov 1961; Melnikov et al. 2019). In contrast, DOY had low importance in the gray whale model, suggesting that time of the year has little effect on the probability of a calling gray whale being present during the open-water season. Gray whales have low vocalization rates (0.74 calls hr⁻¹; Cummings et al. 1968), which likely contributed to low rates of detection throughout the open-water season.

Near-bottom temperature was included in all three species' models, while near-bottom salinity was only included in the humpback and gray whale models. The range of near-bottom water temperatures and salinities identified by models as contributing to higher probability of calling whales align with typical temperatures and salinities observed at A3 during the open water season (Woodgate 2018; Online Resource Fig. S4). Similarly, the range of SST that had the highest probabilities of a calling fin whale being present match the range of fall mean SST at the mooring site (Woodgate 2018; Online Resource Fig. S4a). Therefore, it is unclear if the models identified preferred temperature and salinity ranges for whales, or simply reflect seasonal conditions at the mooring site. The effect of SST on the acoustic

occurrence of humpback and gray whales exhibited divergent patterns, likely due to the difference in detection densities for the two species. Unlike fin whales who were mostly detected in fall, humpback whales were detected throughout the summer when SST are higher on average (Online Resource Fig. S4a). Therefore, the probability of calling humpback whales being present increased with increasing SST. The effect of SST on gray whale acoustic occurrence had a somewhat bimodal shape (Fig. 10). The first peak associated with colder SST could reflect the increase in gray whale detections in spring when colder temperatures prevail (Woodgate 2018; Online Resource Fig. S4a), while the second peak was likely driven by warmer SST in summer. Additionally, 2017 and 2018 had high SST throughout the open-water period (Online Resource Fig. S4a) and higher abundances of recordings with whale calls (Fig. 3), likely driving the relationship between water temperature and the presence of calling whales.

Along with day of the year, water speed was among the most important variables with calling whales more likely to be present at the mooring site when water speeds were low to moderate ($< 20 \text{ cm s}^{-1}$). The most likely explanation is that instrument strumming noise caused by water flowing past the mooring could have obscured calls in the spectrograms (Online Resource Fig. S2), leading to lower detection rates when water speeds were high. Though we scanned the spectrograms to identify calls rather than using an automated detector, missed detections are a factor when recording in the Bering Strait due to the presence of strong northward currents throughout the open-water season (Woodgate et al. 2005; Woodgate 2018). Also, singing fin and humpback whales are known to swim more slowly than non-singing whales (Frankel et al. 1995; McDonald et al. 1995; Soule and Wilcock 2013; Varga et al. 2018; Clark et al. 2019; Guazzo et al. 2021), therefore whales may choose to cease vocalizing when water speeds are strong to conserve energy.

Whale acoustic presence was also impacted by wind speeds according to the humpback and gray models, with low to moderate wind speeds ($\leq 10 \text{ m s}^{-1}$) more favorable for detection of calls. Wind and water speeds in the Bering Strait are highly correlated, with faster flow speeds caused by stronger wind speeds, although the relationship is asymmetric due to the background northward flow at zero wind (Woodgate et al. 2005). It is no surprise then that slower wind speeds increased the probability of detection. Also, most days during the study period had wind speeds $\leq 10 \text{ m s}^{-1}$, indicating that low wind speeds are more common in the strait during the open-water season.

The presence of calling fin and humpback whales had a negative relationship with the presence and strength of a front near the A3 mooring site (indicated by the SST gradient) on the day that the whale calls were detected. This result was likely driven by the lack of strong fronts during

the fall season when most fin and humpback whale calls were detected (Online Resource Figs. S8–S9). The presence and strength of a thermal front in the previous month ('Lagged SST Gradient') was included in all three species' models, though the relationship between the gradient and the probability of a calling whale being present varied for the three species. A stronger gradient the previous month resulted in a higher probability of calling fin and humpback whales being present. Though its intensity and presence changes over the season, a front reliably forms off the coast of Point Hope, Alaska, ($\sim 179 \text{ km}$ north of A3) at the boundary of the Alaskan Coastal Current, and fin, humpback, and gray whales are often seen feeding there (Bluhm et al. 2007; Clarke et al. 2013, 2016; Brower et al. 2018; Moore et al. 2022). The location and intensity of fronts created by water masses in the Chukchi Sea are likely important habitat features that drive patterns in subarctic baleen whale occurrence, and should be explored in future research.

Conclusions

Our goal for this study was to better understand the connection between the presence of subarctic whales and environmental factors in the Pacific Arctic. Though the occurrence and abundance of the three species seems to vary year to year, as estimated by their vocal activity, all three species regularly travel through the Bering Strait and thus, are an important part of the Chukchi Sea ecosystem during the open-water period. More research is needed to see if the trends of later departure dates continue for fin and humpback whales as the Pacific Arctic continues to change.

Our study was conducted over a period of intense warming for the Arctic; the ten warmest years on record for the entire Arctic all occurred after 2011 (Ballinger et al. 2022). From 2014 to 2018, the Pacific Arctic experienced increasingly warmer temperatures with increased heat flux into the Bering and Chukchi seas (Danielson et al. 2020) which coincided with a strong El Niño event and heatwave in the North Pacific in 2015–2016 (Joh and Di Lorenzo 2017). Despite warmer conditions, portions of the northern Bering Sea still had spring sea ice prior to 2018 (Stabeno and Bell 2019), allowing for the formation of both an ice-edge bloom and an open-water bloom in the Bering Strait (Kikuchi et al. 2020). However, that all changed with the winter of 2017–2018 which had the lowest sea-ice extent on record in the northern Bering Sea (Stabeno and Bell 2019). Reduced ice cover in winter 2018 led to a contraction in the areal extent of the ice-edge bloom and delayed the open-water bloom (Duffy-Anderson et al. 2019; Kikuchi et al. 2020), which likely had cascading impacts on the food web. The loss of springtime ice in 2018 followed by another ice-free spring in 2019 added further evidence that a hypothesized regime change

is underway in the Pacific Arctic (Huntington et al. 2020; Ballinger and Overland 2022). Whether the changes in sea ice and warmer temperatures will lead to better conditions for subarctic baleen whales in this region, however, remains to be seen (Moore and Huntington 2008; Moore 2016). Our results suggest that subarctic baleen whales are already modifying their behavior in response to changes in the Pacific Arctic and are delaying their fall migrations.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00300-024-03314-0>.

Acknowledgements This study is based upon work supported by the National Science Foundation (NSF) Graduate Research Fellowship Program under grant number DGE-1256082. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of NSF. We also thank the University of Washington School of Aquatic and Fishery Sciences for providing funding for the primary author. Additional funding for this study was provided to K. Stafford from the North Pacific Research Board Arctic IERP (A94-00), the Office of Naval Research Marine Mammals and Biology Program N000141712274, and the National Science Foundation Polar Programs ARC-1107106; and to R. Woodgate from the NSF Arctic Observing Network PLR-1304052, 1758565 and 2153942. We would like to thank the crew of the R/V Norseman II for their support in retrieving and deploying the moorings. Many thanks to Alex Hornof, Trevor Branch, and Lisa Eisner whose feedback greatly improved earlier versions of this manuscript.

Author contributions All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by E.D.E. The first draft of the manuscript was written by E.D.E and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding University of Washington; National Science Foundation Graduate Research Fellowship Program, DGE-1256082; North Pacific Research Board, A94-00; National Science Foundation Polar Programs, ARC-1107106; Office of Naval Research Marine Mammals and Biology Program, N000141712274; National Science Foundation Arctic Observing Network, PLR-1304052

Data availability The Bering Strait mooring data can be accessed from the permanent archives of the U.S. National Centers for Environmental Information/National Oceanographic Data Center (www.ncei.noaa.gov), and from: psc.apl.washington.edu/BeringStrait.html.

Declarations

Competing interests The authors declare no competing interests.

References

- Aagaard K, Roach AT, Schumacher JD (1985) On the wind-driven variability of the flow through bering strait. *J Geophys Res* 90:7213. <https://doi.org/10.1029/JC090iC04p07213>
- Abrahms B, Hazen EL, Aikens EO et al (2019) Memory and resource tracking drive blue whale migrations. *PNAS* 116:5582–5587. <https://doi.org/10.1073/pnas.1819031116>
- Akaike H (1973) Maximum likelihood identification of Gaussian autoregressive moving average models. *Biometrika* 60:255–265. <https://doi.org/10.1093/biomet/60.2.255>
- Arimitsu ML, Piatt JF, Hatch S et al (2021) Heatwave-induced synchrony within forage fish portfolio disrupts energy flow to top pelagic predators. *Glob Change Biol* 27:1859–1878. <https://doi.org/10.1111/gcb.15556>
- Ashjian CJ, Braund SR, Campbell RG et al (2010) Climate variability, oceanography, bowhead whale distribution, and Iñupiat subsistence whaling near Barrow, Alaska. *Arctic* 63:179–194
- Ballinger TJ, Overland JE, Wang M, et al (2022) Surface air temperature. Arctic report card 2022, In: Druckenmiller ML, Thoman RL, Moon TA (eds) <https://doi.org/10.25923/13qm-2576>
- Ballinger TJ, Overland JE (2022) The Alaskan Arctic regime shift since 2017: a harbinger of years to come? *Polar Sci* 32:100841. <https://doi.org/10.1016/j.polar.2022.100841>
- Basso M, Acevedo J, Secchi ER et al (2020) Cetacean distribution in relation to environmental parameters between Drake Passage and northern Antarctic Peninsula. *Polar Biol* 43:1–15. <https://doi.org/10.1007/s00300-019-02607-z>
- Berline L, Spitz YH, Ashjian CJ et al (2008) Euphausiid transport in the Western Arctic Ocean. *Mar Ecol Prog Ser* 360:163–178
- Berzin AA (1984) Soviet studies on the distribution and numbers of the gray whale in the Bering and Chukchi Seas from 1968 to 1982. In: Jones ML, Swartz SL, Leatherwood S (eds) *The gray whale: Eschrichtius robustus*. Academic Press, Massachusetts, pp 409–419
- Bluhm BA, Coyle KO, Konar B, Highsmith R (2007) High gray whale relative abundances associated with an oceanographic front in the south-central Chukchi Sea. *Deep Sea Res Part II Top Stud Oceanogr* 54:2919–2933. <https://doi.org/10.1016/j.dsr2.2007.08.015>
- Bost CA, Cotté C, Bailleul F et al (2009) The importance of oceanographic fronts to marine birds and mammals of the southern oceans. *J Mar Syst* 78:363–376. <https://doi.org/10.1016/j.jmarsys.2008.11.022>
- Brower AA, Ferguson MC, Schonberg SV et al (2017) Gray whale distribution relative to benthic invertebrate biomass and abundance: Northeastern Chukchi Sea 2009–2012. *Deep Sea Res Part II Top Stud Oceanogr* 144:156–174. <https://doi.org/10.1016/j.dsr2.2016.12.007>
- Brower AA, Clarke JT, Ferguson MC (2018) Increased sightings of subArctic cetaceans in the eastern Chukchi Sea, 2008–2016: population recovery, response to climate change, or increased survey effort? *Polar Biol* 41:1033–1039. <https://doi.org/10.1007/s00300-018-2257-x>
- Cartwright R, Venema A, Hernandez V et al (2019) Fluctuating reproductive rates in Hawaii’s humpback whales, *Megaptera novaeangliae*, reflect recent climate anomalies in the North Pacific. *R Soc Open Sci* 6:181463. <https://doi.org/10.1098/rsos.181463>
- Cavalieri DJ, Parkinson CL, Gloersen P, Zwally, HJ. (1996). Sea Ice Concentrations from Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Data, Version 1. Boulder, Colorado USA. NASA National Snow and Ice Data Center Distributed Active Archive Center. <https://doi.org/10.5067/8GQ8LZQVL0VL>. [Accessed 25 April 2017].
- Clapham P (2016) Managing leviathan: conservation challenges for the great whales in a post-whaling world. *Oceanography* 29:214–225. <https://doi.org/10.5670/oceanog.2016.70>
- Clark C, Ellison W, Southall B et al (2009) Acoustic masking in marine ecosystems: intuitions, analysis, and implication. *Mar Ecol Prog Ser* 395:201–222. <https://doi.org/10.3354/meps08402>
- Clark CW, Gagnon GJ, Frankel AS (2019) Fin whale singing decreases with increased swimming speed. *R Soc Open Sci* 6:180525. <https://doi.org/10.1098/rsos.180525>

- Clarke J, Moore S (2002) A note on observations of gray whales in the southern Chukchi and northern Bering Seas, August–November, 1980–89. *J Cetacean Res Manage* 4:283–288
- Clarke JT, Moore SE, Ljungblad DK (1989) Observations on gray whale (*Eschrichtius robustus*) utilization patterns in the north-eastern Chukchi Sea, July–October 1982–1987. *Can J Zool* 67:2646–2654
- Clarke J, Stafford K, Moore S et al (2013) Subarctic cetaceans in the southern Chukchi Sea: evidence of recovery or response to a changing ecosystem. *Oceanography* 26:136–149. <https://doi.org/10.5670/oceanog.2013.81>
- Clarke JT, Kennedy AS, Ferguson MC (2016) Bowhead and gray whale distributions, sighting rates, and habitat associations in the Eastern Chukchi Sea, summer and fall 2009–15, with a retrospective comparison to 1982–91. *Arctic*. <https://doi.org/10.14430/arctic4597>
- Cleveland W (1993) Visualizing data. Hobart Press, Summit
- Coachman LK, Aagaard K, Tripp RB (1975) Bering Strait: the regional physical oceanography. University of Washington Press, Seattle
- Cohen J, Cohen J, West SG, Aiken LS (2003) Applied multiple regression/correlation analysis for the behavioral sciences, 3rd edn. Erlbaum, Mahwah
- Cox DR, Snell EJ (1989) Analysis of binary data, 2nd edn. Chapman & Hall, Boca Raton
- Crane NL, Lashkari K (1996) Sound production of gray whales *Eschrichtius robustus* along their migration route: A new approach to signal analysis. *J Acoust Soc Am* 100:1878–1886
- Cummings WC, Thompson PO, Cook R (1968) Underwater sounds of migrating gray whales, *Eschrichtius glaucus*. *J Acoust Soc Am* 44:1278–1281
- Danielson SL, Weingartner TJ, Hedstrom KS et al (2014) Coupled wind-forced controls of the Bering–Chukchi shelf circulation and the Bering Strait throughflow: Ekman transport, continental shelf waves, and variations of the Pacific–Arctic sea surface height gradient. *Prog Oceanogr* 125:40–61. <https://doi.org/10.1016/j.pocean.2014.04.006>
- Danielson SL, Eisner L, Ladd C et al (2017) A comparison between late summer 2012 and 2013 water masses, macronutrients, and phytoplankton standing crops in the northern Bering and Chukchi Seas. *Deep Sea Res Part II Top Stud Oceanogr* 135:7–26. <https://doi.org/10.1016/j.dsr2.2016.05.024>
- Danielson SL, Ahkinga O, Ashjian C et al (2020) Manifestation and consequences of warming and altered heat fluxes over the Bering and Chukchi Sea continental shelves. *Deep Sea Res Part II Top Stud Oceanogr* 177:104781. <https://doi.org/10.1016/j.dsr2.2020.104781>
- Darling JD, Berube M (2001) Interactions of singing humpback whales with other males. *Mar Mamm Sci* 17:570–584. <https://doi.org/10.1111/j.1748-7692.2001.tb01005.x>
- Delarue J, Martin B, Hannay D, Berchok CL (2013) Acoustic occurrence and affiliation of fin whales detected in the northeastern Chukchi Sea, July to October 2007–10. *Arctic* 66:159–172
- Duffy-Anderson JT, Stabeno P, Andrews AG et al (2019) Responses of the northern Bering Sea and southeastern Bering Sea pelagic ecosystems following record-breaking low winter sea ice. *Geophys Res Lett* 46:9833–9842. <https://doi.org/10.1029/2019GL083396>
- Eisner L, Hillgruber N, Martinson E, Maselko J (2013) Pelagic fish and zooplankton species assemblages in relation to water mass characteristics in the northern Bering and southeast Chukchi seas. *Polar Biol* 36:87–113. <https://doi.org/10.1007/s00300-012-1241-0>
- Environmental Systems Research Institute (2019) ArcGIS Desktop: release 10.8. Environmental Systems Research Institute, Redlands
- Ershova E, Hopcroft R, Kosobokova K et al (2015) Long-term changes in summer zooplankton communities of the Western Chukchi Sea, 1945–2012. *Oceanogr* 28:100–115. <https://doi.org/10.5670/oceanog.2015.60>
- Frankel AS, Clark CW, Herman LM, Gabriele CM (1995) Spatial distribution, habitat utilization, and social interactions of humpback whales, *Megaptera novaeangliae*, off Hawai'i, determined using acoustic and visual techniques. *Can J Zool* 73:1134–1146. <https://doi.org/10.1139/z95-135>
- Grebmeier JM, Feder HM, McRoy CP (1989) Pelagic-benthic coupling on the shelf of the northern Bering and Chukchi Seas. III. Benthic food supply and carbon cycling. *Mar Ecol Prog* 51:253–268
- Grebmeier JM, Overland JE, Moore SE et al (2006) A major ecosystem shift in the northern Bering Sea. *Science* 311:1461–1464
- Grebmeier JM, Frey K, Cooper L, Kędra M (2018) Trends in benthic macrofaunal populations, seasonal sea ice persistence, and bottom water temperatures in the Bering Strait region. *Oceanogr* 31:136–151. <https://doi.org/10.5670/oceanog.2018.224>
- Guazzo RA, Helble TA, D'Spain GL et al (2017) Migratory behavior of eastern North Pacific gray whales tracked using a hydrophone array. *PLoS ONE* 12:e0185585. <https://doi.org/10.1371/journal.pone.0185585>
- Guazzo RA, Durbach IN, Helble TA et al (2021) Singing fin whale swimming behavior in the Central North Pacific. *Front Mar Sci* 8:696002. <https://doi.org/10.3389/fmars.2021.696002>
- Hasegawa D, Lewis MR, Gangopadhyay A (2009) How islands cause phytoplankton to bloom in their wakes. *Geophys Res Lett* 36:L20605. <https://doi.org/10.1029/2009GL039743>
- Hauser DDW, Laidre KL, Stafford KM et al (2017) Decadal shifts in autumn migration timing by Pacific Arctic beluga whales are related to delayed annual sea ice formation. *Glob Change Biol* 23:2206–2217. <https://doi.org/10.1111/gcb.13564>
- Hazen EL, Jorgensen S, Rykaczewski RR et al (2013) Predicted habitat shifts of Pacific top predators in a changing climate. *Nat Clim Change* 3:234–238. <https://doi.org/10.1038/nclimate1686>
- Hisakado M, Kitsukawa K, Mori S (2006) Correlated binomial models and correlation structures. *J Phys A* 39:15365–15378. <https://doi.org/10.1088/0305-4470/39/50/005>
- Huntington HP, Danielson SL, Wiese FK et al (2020) Evidence suggests potential transformation of the Pacific Arctic ecosystem is underway. *Nat Clim Change* 10:342–348. <https://doi.org/10.1038/s41558-020-0695-2>
- Joh Y, Di Lorenzo E (2017) Increasing coupling between NPGO and PDO leads to prolonged marine heatwaves in the Northeast Pacific. *Geophys Res Lett* 44(11):663–711. <https://doi.org/10.1002/2017GL075930>
- Kikuchi G, Abe H, Hirawake T, Sampei M (2020) Distinctive spring phytoplankton bloom in the Bering Strait in 2018: a year of historically minimum sea ice extent. *Deep Sea Res Part II Top Stud Oceanogr* 181–182:104905. <https://doi.org/10.1016/j.dsr2.2020.104905>
- Kodaira T, Waseda T, Nose T, Inoue J (2020) Record high Pacific Arctic seawater temperatures and delayed sea ice advance in response to episodic atmospheric blocking. *Sci Rep* 10:20830. <https://doi.org/10.1038/s41598-020-77488-y>
- Kowarski K, Moors-Murphy H, Maxner E, Cerchio S (2019) Western North Atlantic humpback whale fall and spring acoustic repertoire: insight into onset and cessation of singing behavior. *J Acoust Soc Am* 145:2305–2316. <https://doi.org/10.1121/1.5095404>
- Levine RM, De Robertis A, Grünbaum D et al (2021) Autonomous vehicle surveys indicate that flow reversals retain juvenile fishes in a highly advective high-latitude ecosystem. *L&O* 66:1139–1154. <https://doi.org/10.1002/lno.11671>
- Martin J, Royle JA, Mackenzie DI et al (2011) Accounting for non-independent detection when estimating abundance of organisms

- with a Bayesian approach: Correlated behaviour and abundance. *MEE* 2:595–601. <https://doi.org/10.1111/j.2041-210X.2011.00113.x>
- McDonald MA, Hildebrand JA, Webb SC (1995) Blue and fin whales observed on a seafloor array in the northeast Pacific. *J Acoust Soc Am* 98:712–721
- Mellinger D (2002) Ishmael 1.0 User's Guide. NOAA Technical Memorandum OAR PMEL-120. <http://www.pmel.noaa.gov/pubs/PDF/mell2434/mell2434.pdf>
- Melnikov VV (2019) Observation of humpback whales (*Megaptera novaeangliae*) in the waters adjacent to the Chukotka Peninsula with comparisons to historical sighting data. *OALIB* 6:e5407
- Mesinger F, DiMego G, Kalnay E, Mitchell K, Shafran PC, Ebisuzaki W, Jović D, Woollen J, Rogers E, Berbery EH, Ek MB (2006) North American regional reanalysis. *Bull Am Meteorol Soc* 87(3):343–360
- Meynecke J-O, de Bie J, Barraqueta J-LM et al (2021) The role of environmental drivers in humpback whale distribution, movement and behavior: a review. *Front Mar Sci* 8:720774. <https://doi.org/10.3389/fmars.2021.720774>
- Monnahan CC, Branch TA, Stafford KM et al (2014) Estimating historical eastern North Pacific blue whale catches using spatial calling patterns. *PLoS ONE* 9:e98974. <https://doi.org/10.1371/journal.pone.0098974>
- Moore SE (2016) Is it 'boom times' for baleen whales in the Pacific Arctic region? *Biol Lett* 12:20160251. <https://doi.org/10.1098/rsbl.2016.0251>
- Moore SE, Huntington HP (2008) Arctic marine mammals and climate change: Impacts and resilience. *Ecol Appl* 18:S157–S165
- Moore SE, deMaster DP, Dayton PK (2000) Cetacean habitat selection in the Alaskan Arctic during summer and autumn. *Arctic* 53:432–447
- Moore SE, Clarke JT, Okkonen SR et al (2022) Changes in gray whale phenology and distribution related to prey variability and ocean biophysics in the northern Bering and eastern Chukchi seas. *PLoS ONE* 17:e0265934. <https://doi.org/10.1371/journal.pone.0265934>
- Nelms S, Alfaro-Shigueto J, Arnould J et al (2021) Marine mammal conservation: Over the horizon. *Endanger Species Res* 44:291–325. <https://doi.org/10.3354/esr01115>
- Nguyen AT, Woodgate RA, Heimbach P (2020) Elucidating large-scale atmospheric controls on Bering Strait throughflow variability using a data-constrained ocean model and its adjoint. *J Geophys Res.* <https://doi.org/10.1029/2020JC016213>
- Nikulin PG (1946) Distribution of cetaceans in the seas surrounding the Chukchi Peninsula. *Izv TINRO, Vladivostok*
- Peralta-Ferriz C, Woodgate RA (2017) The dominant role of the east Siberian Sea in driving the oceanic flow through the Bering Strait—conclusions from GRACE ocean mass satellite data and in situ mooring observations between 2002 and 2016. *Geophys Res Lett.* <https://doi.org/10.1002/2017GL075179>
- Peralta-Ferriz C, Woodgate RA (2023) Arctic and sub-Arctic mechanisms explaining observed increasing northward flow through the Bering Strait and why models may be getting it wrong. *Geophys Res Lett.* <https://doi.org/10.1029/2023GL104697>
- Perryman WL, Donahue MA, Perkins PC, Reilly SB (2002) Gray whale calf production 1994–2000: Are observed fluctuations related to changes in seasonal ice cover? *Mar Mamm Sci* 18:121–144. <https://doi.org/10.1111/j.1748-7692.2002.tb01023.x>
- Pinchuk AI, Eisner LB (2017) Spatial heterogeneity in zooplankton summer distribution in the eastern Chukchi Sea in 2012–2013 as a result of large-scale interactions of water masses. *Deep Sea Res Part II Top Stud Oceanogr* 135:27–39. <https://doi.org/10.1016/j.dsr2.2016.11.003>
- R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Reynolds RW, Smith TM, Liu C et al (2007) Daily high-resolution-blended analyses for sea surface temperature. *J Clim* 20:5473–5496. <https://doi.org/10.1175/2007JCLI1824.1>
- Rigby RA, Stasinopoulos DM (2005) Generalized additive models for location, scale and shape. *J R Stat Soc Ser C Appl Stat* 54:507–544
- Ryan JP, Cline DE, Joseph JE et al (2019) Humpback whale song occurrence reflects ecosystem variability in feeding and migratory habitat of the northeast Pacific. *PLoS ONE* 14:e0222456. <https://doi.org/10.1371/journal.pone.0222456>
- Savage K (2017) Alaska and British Columbia large whale unusual mortality event summary report protected resources division. National Oceanic and Atmospheric Administration, Juneau
- Scales KL, Miller PI, Hawkes LA et al (2014) On the front line: Frontal zones as priority at-sea conservation areas for mobile marine vertebrates. *J Appl Ecol* 51:1575–1583. <https://doi.org/10.1111/1365-2664.12330>
- Serreze MC, Barrett AP, Stroeve JC et al (2009) The emergence of surface-based Arctic amplification. *Cryosphere* 3:11–19. <https://doi.org/10.5194/tc-3-11-2009>
- Serreze MC, Crawford AD, Stroeve JC et al (2016) Variability, trends, and predictability of seasonal sea ice retreat and advance in the Chukchi Sea. *J Geophys Res: Oceans* 121:7308–7325. <https://doi.org/10.1002/2016JC011977>
- Serreze MC, Barrett AP, Crawford AD, Woodgate RA (2019) Monthly variability in Bering Strait oceanic volume and heat transports, links to atmospheric circulation and ocean temperature, and implications for sea ice conditions. *J Geophys Res: Oceans* 124:9317–9337. <https://doi.org/10.1029/2019JC015422>
- Shabangu FW, Yemane D, Stafford KM et al (2017) Modelling the effects of environmental conditions on the acoustic occurrence and behaviour of Antarctic blue whales. *PLoS ONE* 12:e0172705. <https://doi.org/10.1371/journal.pone.0172705>
- Širović A, Hildebrand JA (2011) Using passive acoustics to model blue whale habitat off the Western Antarctic Peninsula. *Deep Sea Res Part II Top Stud Oceanogr* 58:1719–1728. <https://doi.org/10.1016/j.dsr2.2010.08.019>
- Sleptsov MM (1961) O kolebaniakh chislennosti kitov v Chukotskom more v raznye gody. (On fluctuations in the number of whales in the Chukchi Sea in different years). *Proceedings of the A.N. Severtsov Institute of Animal Morphology*. Nauka, Moscow, pp 54–64
- Soule DC, Wilcock WSD (2013) Fin whale tracks recorded by a seismic network on the Juan de Fuca Ridge, Northeast Pacific Ocean. *J Acoust Soc Am* 133:1751–1761. <https://doi.org/10.1121/1.4774275>
- Spear A, Napp J, Ferm N, Kimmel D (2020) Advection and in situ processes as drivers of change for the abundance of large zooplankton taxa in the Chukchi Sea. *Deep Sea Res Part II Top Stud Oceanogr* 177:104814. <https://doi.org/10.1016/j.dsr2.2020.104814>
- Stabeno PJ, Bell SW (2019) Extreme conditions in the Bering Sea (2017–2018): Record-breaking low sea-ice extent. *Geophys Res Lett* 46:8952–8959. <https://doi.org/10.1029/2019GL083816>
- Stafford KM, Mellinger DK, Moore SE, Fox CG (2007) Seasonal variability and detection range modeling of baleen whale calls in the Gulf of Alaska, 1999–2002. *J Acoust Soc Am* 122:3378–3390. <https://doi.org/10.1121/1.2799905>
- Stafford KM, George JC, Harcharek Q, Moore SE (2023) Humpback whale sightings in northern Arctic Alaska. *Mar Mamm Sci.* <https://doi.org/10.1111/mms.13051>

- Stasinopoulos D, Rigby RA, Heller G et al (2017) Flexible regression and smoothing: Using GAMLSS in R. Chapman and Hall, Boca Raton
- Stewart JD, Joyce TW, Durban JW et al (2023) Boom-bust cycles in gray whales associated with dynamic and changing Arctic conditions. *Science* 382:207–211. <https://doi.org/10.1126/science.adi1847>
- Stroeve JC, Serreze MC, Holland MM et al (2012) The Arctic's rapidly shrinking sea ice cover: A research synthesis. *Clim Change* 110:1005–1027. <https://doi.org/10.1007/s10584-011-0101-1>
- Stroeve JC, Markus T, Boisvert L et al (2014) Changes in Arctic melt season and implications for sea ice loss. *Geophys Res Lett* 41:1216–1225. <https://doi.org/10.1002/2013GL058951>
- Szesciorka AR, Ballance LT, Širović A et al (2020) Timing is everything: drivers of interannual variability in blue whale migration. *Sci Rep* 10:7710. <https://doi.org/10.1038/s41598-020-64855-y>
- Torres LG (2017) A sense of scale: Foraging cetaceans' use of scale-dependent multimodal sensory systems. *Mar Mamm Sci* 33:1170–1193. <https://doi.org/10.1111/mms.12426>
- Tsuji K, Otsuki M, Akamatsu T et al (2016) The migration of fin whales into the southern Chukchi Sea as monitored with passive acoustics. *ICES J Mar Sci: Journal Du Conseil* 73:2085–2092. <https://doi.org/10.1093/icesjms/fsv271>
- Tulloch VJD, Plagányi ÉE, Brown C et al (2019) Future recovery of baleen whales is imperiled by climate change. *Glob Change Biol* 25:1263–1281. <https://doi.org/10.1111/gcb.14573>
- Tyack P (1981) Interactions between singing Hawaiian humpback whales and conspecifics nearby. *Behav Ecol Sociobiol* 8:105–116
- Urbán RJ, Jiménez-López E, Guzmán HM, Vilorio-Gómora L (2021) Migratory behavior of an eastern North Pacific gray whale from Baja California Sur to Chirikov Basin. *Alaska Front Mar Sci* 8:619290. <https://doi.org/10.3389/fmars.2021.619290>
- Varga L, Wiggins S, Hildebrand J (2018) Behavior of singing fin whales *Balaenoptera physalus* tracked acoustically offshore of Southern California. *Endang Species Res* 35:113–124. <https://doi.org/10.3354/esr00881>
- Wang Y, Liu N, Zhang Z (2021) Sea ice reduction during winter of 2017 due to oceanic heat supplied by Pacific water in the Chukchi sea, west Arctic ocean. *Front Mar Sci* 8:650909. <https://doi.org/10.3389/fmars.2021.650909>
- Watkins WA (1981) Activities and underwater sounds of fin whales. *Sci Rep Whales Res Inst* 33:83–117
- Watkins WA, Tyack P, Moore KE, Bird JE (1987) The 20-Hz signals of finback whales (*Balaenoptera physalus*). *J Acoust Soc Am* 82:1901–1912
- Watkins WA, Daher MA, Repucci GM et al (2000) Seasonality and distribution of whale calls in the North Pacific. *Oceanogr* 13:62–67
- Weingartner T, Aagaard K, Woodgate R et al (2005) Circulation on the north central Chukchi Sea shelf. *Deep Sea Res Part II Top Stud Oceanogr* 52:3150–3174. <https://doi.org/10.1016/j.dsr2.2005.10.015>
- Winn HE, Winn LK (1978) The song of the humpback whale *Megaptera novaeangliae* in the West Indies. *Mar Biol* 47:97–114. <https://doi.org/10.1007/BF00395631>
- Woodgate RA (2018) Increases in the Pacific inflow to the Arctic from 1990 to 2015, and insights into seasonal trends and driving mechanisms from year-round Bering Strait mooring data. *Prog Oceanogr* 160:124–154. <https://doi.org/10.1016/j.pocean.2017.12.007>
- Woodgate RA, Peralta-Ferriz C (2021) Warming and freshening of the Pacific inflow to the Arctic from 1990–2019 implying dramatic shoaling in Pacific winter water ventilation of the Arctic water column. *Geophys Res Lett*. <https://doi.org/10.1029/2021GL092528>
- Woodgate RA, Aagaard K, Weingartner TJ (2005) A year in the physical oceanography of the Chukchi Sea: Moored measurements from autumn 1990–1991. *Deep Sea Res Part II Top Stud Oceanogr* 52:3116–3149. <https://doi.org/10.1016/j.dsr2.2005.10.016>
- Woodgate RA, Weingartner TJ, Lindsay R (2012) Observed increases in Bering Strait oceanic fluxes from the Pacific to the Arctic from 2001 to 2011 and their impacts on the Arctic Ocean water column. *Geophys Res Lett* 39:L24603. <https://doi.org/10.1029/2012GL054092>
- Woodgate RA, Stafford K, Prah F (2015) A synthesis of year-round interdisciplinary mooring measurements in the Bering Strait (1990–2014) and the RUSALCA years (2004–2011). *Oceanography* 28:46–67. <https://doi.org/10.5670/oceanog.2015.57>
- Zerbini AN, Friday NA, Palacios DM et al (2016) Baleen whale abundance and distribution in relation to environmental variables and prey density in the Eastern Bering Sea. *Deep Sea Res Part II Top Stud Oceanogr* 134:312–330. <https://doi.org/10.1016/j.dsr2.2015.11.002>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.