



The role of sea ice in the distribution, habitat use, and phenology of eastern North Pacific gray whales

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ABSTRACT: A strong negative relationship has been observed between calf production of eastern North Pacific gray whales *Eschrichtius robustus* and Pacific Arctic sea ice area with the exception of 2 potentially anomalous periods: 2013–2014 and 2017–2019. Sea ice may play a role in reproductive variability by blocking gray whale access to foraging hotspot habitats. We tested this ‘sea ice exclusion’ hypothesis using complementary aerial survey and moored hydrophone data sets that together provide broad spatial and temporal coverage. A negative relationship (generalized additive model, $p < 0.001$) was found between gray whale aerial counts and ice concentration in the northeast Chukchi Sea (2008–2019), with a nonlinear increase in negative slope above 45–55% concentration. A comparison of distribution patterns between years further indicated the absence of sightings within northern Bering and northeastern Chukchi foraging hotspots during years with delayed ice break-up versus years with an early-to-average ice retreat. Passive acoustic recordings likewise showed the near-absence of detections during periods of dense ice cover and indicated a strongly positive relationship between ice break-up dates and the timing of acoustic detection onset. Together, these analyses point to the important role of sea ice in gray whale distribution, habitat use, and phenology. However, a relatively consistent 10–15 d lag observed between ice break-up and acoustic onset dates suggested that the mechanism(s) underpinning gray whale interactions with sea ice may be more complex than simply ‘sea ice exclusion.’ Here, we propose ‘prey quality timing’ as a potential alternative hypothesis that warrants further investigation.

KEY WORDS: Gray whale · Sea ice · Distribution · Habitat use

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1. INTRODUCTION

The Arctic is experiencing one of the fastest rates of climatic change globally, with an Arctic-wide rate of warming nearly double the global mean (Screen &

Simmonds 2010, Cohen et al. 2014, Dai et al. 2019). Associated decreases in sea ice cover and thickness (Dai et al. 2019) represent one of the most prominent physical and ecological consequences of this ongoing warming, with the potential to alter the availability of

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key resources for a variety of polar predators, including human subsistence hunters (Kovacs & Lydersen 2008, Moore & Huntington 2008, Jay et al. 2012, Bromaghin et al. 2015, Laidre et al. 2015, Christie et al. 2018, Moore & Reeves 2018, Huntington et al. 2020). For eastern North Pacific (ENP) gray whales *Eschrichtius robustus* which seasonally forage in the Pacific Arctic, sea ice cover plays a number of important roles in the ecological processes supporting the rich macrofaunal assemblages exploited by this population (Sigler et al. 2011). Gray whale foraging distributions, where they have been extensively documented in the Pacific Arctic (Moore et al. 2003, 2022, Bluhm et al. 2007, Brower et al. 2017, Clarke et al. 2020), appear to focus primarily around a relatively small number of discrete and persistent hotspots associated with elevated benthic macrofaunal production, and potentially also with elevated biomasses of epibenthic and pelagic swarming prey (Schonberg et al. 2014, Grebmeier et al. 2015, 2018). These well-documented hotspots (see Fig. 1) include (1) the Chirikov Basin in the northern Bering Sea (Moore et al. 2003, 2022), (2) the southeastern Chukchi Sea south of Pt. Hope and extending westward into Russian waters north of the Chukotka Peninsula (Bluhm et al. 2007, Moore et al. 2022), and (3) the northeastern Chukchi Sea shelf surrounding Barrow Canyon and extending northwestward to Hanna Shoal (Schonberg et al. 2014, Brower et al. 2017).

The combination of inter-annually variable sea ice cover with relatively geographically fixed and persistent foraging hotspot locations is also hypothesized to play a more direct role in the high inter-annual and multi-year variability observed in ENP gray whale reproductive success. Over the period 1994–2016, Perryman et al. (2021) demonstrated a relatively strong negative relationship ($R^2 = 0.64$) between ENP gray whale calf production estimates and the amount of ocean surface area covered by sea ice during the previous spring and early summer (e.g. May, June, and July) in the Pacific Arctic sector, which includes the Bering and Chukchi seas. Perryman et al. (2021) hypothesized on the basis of this correlation that in years with extensive early season sea ice coverage, gestating female ENP gray whales may be delayed in accessing important benthic foraging hotspot habitats. This delay may be biologically important, occurring at an energetically demanding phase of gray whale reproductive phenology when gestating females are returning from long-distance migration in a relatively energetically depleted state and are simultaneously experiencing accelerated fetal growth. The mechanism underpinning this hypothe-

sized interaction, referred to herein as 'sea ice exclusion', could potentially relate to gray whales minimizing their risk of collision injuries while maneuvering in dense sea ice and/or minimizing the risk of being cut off from openings in the ice to breathe (Anonymous 1989, Kochnev 1998). This delay may in turn affect the rate at which pregnancies are carried to term and potentially also the survival of calves along the migration route and in the wintering lagoons, leading to the observed fluctuations in calf production estimates and body condition metrics during the following winter and spring. This correlation also closely aligns with a strong relationship ($R^2 = 0.77$) observed between western North Pacific (WNP) gray whale calf survival and the number of days of open water in 2 key foraging areas off northeast Sakhalin Island in the Sea of Okhotsk (Gailey et al. 2020). Gailey et al. (2020) defined 'open water' as sea ice concentrations below 40%. As an explanation for this positive relationship, Gailey et al. (2020) proposed an analogous mechanism whereby the duration of open water access to key WNP foraging habitats affected female body condition. Female body condition in turn affected the capacity for maternal investment, leading to downstream consequences for pre- and post-weaning calf survival.

The fact that analogous relationships have been documented in 2 distinct population segments (Gailey et al. 2020, Perryman et al. 2021) potentially lends credibility to the importance of changing sea ice conditions in gray whale population dynamics. This hypothesized relationship also potentially positions gray whales as possible climate change 'winners' among other prominent Arctic species with population dynamics influenced by changing Arctic sea ice conditions (e.g. polar bear *Ursus maritimus*, Bromaghin et al. 2015; Pacific walrus *Odobenus rosmarus*, Jay et al. 2012; spectacled eider *Somateria fischeri*, Christie et al. 2018). However, the evidence from both recent studies supporting the 'sea ice exclusion' mechanism is fundamentally correlative in nature. Moreover, within the ENP gray whale population, there have been 2 recent deviations that complicate this historic negative correlation between sea ice cover and calf production and potentially bring into question the long-term stationarity of this relationship during a period of rapidly changing Arctic conditions and ecological dynamics (e.g. Duffy-Anderson et al. 2019, Ardyna & Arrigo 2020). The first of these deviations occurred in 2013 and 2014, when calf production remained elevated above the time series mean despite relatively extensive Pacific Arctic sea ice cover during May, June, and July of the

preceding summers (2012 and 2013). This deviation was treated in part as an outlier event by Perryman et al. (2021) because calf production returned to historical expectations during the remainder of the time series considered in that study (i.e. in 2015 and 2016). However, during the most recent period, 2017–2019, which was not analyzed in Perryman et al. (2021), reproductive output dropped substantially below the historical average (Stewart & Weller 2021) despite record low sea ice cover. These reduced levels of reproductive success have also coincided with an ongoing unusual mortality event (UME) along the Pacific coast of North America from Alaska to Baja California from January 2019 through 2022, during which rates of ENP gray whale stranding mortalities were elevated 4–5 times above the long-term average (Raverty et al. 2020, Christiansen et al. 2021).

Together, these divergent data points suggest a need to better describe the relationship of gray whale distribution, habitat use, and phenology to sea ice conditions in the Pacific Arctic. Our overall goal, therefore, was to examine whether additional lines of evidence based on complementary aerial survey and moored hydrophone data sets showed patterns consistent with the ‘sea ice exclusion’ mechanisms hypothesized by Perryman et al. (2002, 2011, 2021) and Gailey et al. (2020). Our first objective was to evaluate whether intra- and inter-annual variation in gray whale distribution patterns across different seasons and years with divergent sea ice conditions qualitatively support the hypothesized mechanism of sea ice constraining access to foraging habitats. Second, we quantitatively examined the relationship of gray whale encounter rates with different spatial configurations and concentrations of sea ice. Finally, we evaluated whether the timing (or phenology) of gray whale arrival and occupation of different habitats across different years varied relative to the timing of sea ice retreat.

2. MATERIALS AND METHODS

2.1. Aerial surveys

To characterize overall gray whale distribution patterns and model the association between sea ice and gray whale habitat use, we extracted gray whale sightings data from the Aerial Surveys of Arctic Marine Mammals (ASAMM) database (<https://www.fisheries.noaa.gov/resource/data/1979-2019-aerial-surveys-arctic-marine-mammals-historical-database>; accessed 19 June 2020). The ASAMM database com-

prises marine mammal aerial surveys in the Northern Bering, Chukchi, and Beaufort seas conducted between 1979 and 2019. The aerial line-transect distance sampling methods used to record marine mammal sightings and effort are comprehensively described in Clarke et al. (2020).

Over 90% of this aerial transect survey effort occurred between mid-July and October, when sea ice had already retreated from gray whale foraging hotspot habitats within the ASAMM sampling domain in the vast majority of years and before the seasonal return of sea ice cover in late fall/early winter. However, within a subset of survey years there was sufficient aerial survey coverage within gray whale foraging habitats in late May (1980–1982), late June (2008–2011), and early July (2013) to qualitatively compare gray whale distribution patterns under divergent sea ice conditions.

In addition to marine mammal sightings, observers also recorded visual estimates of environmental conditions associated with transects of varying lengths, including percent sea ice cover in 5% increments. These *in situ* measurements of sea ice cover were estimated by each observer scanning their 180° field of view, from directly beneath the aircraft out to the limit of visibility. Since 2018, estimates of sea ice cover from observers on left and right sides of the plane have been recorded separately; however, prior to 2018, only a single estimate representing the average percent sea ice cover for both sides was recorded. For consistency with the earlier data, the separate left and right estimates since 2018 were averaged into a single, combined percent ice cover estimate.

Visibility used in calculating a survey effort offset term in the gray whale habitat use models was estimated based on the maximum distance that observers could reliably detect marine mammals within their field of view. Visibility was categorized into ordinal classes of unlimited, 5–10, 3–5, 2–3, 1–2, <1, and 0 km.

For the purposes of modeling, portions of the flight path during which observers were actively searching for marine mammals (i.e. effort types ‘transect’, ‘search’, and ‘cetacean aggregation protocol’ [CAP]) were subdivided into 5 km segments. The positions of smaller (<5 km) segments remaining after subdividing transects were randomized along the length of the original transect. Within each 5 km segment, ordinal visibility classes were converted to approximate continuous values based on the midpoint distance of each visibility bracket. Visibility distance estimates and sea ice estimates were then averaged

over all observations within each segment to obtain an overall segment mean visibility and segment mean sea ice concentration.

2.2. Passive acoustic monitoring

The phenology and distribution of marine mammal vocalizations within the Pacific Arctic was monitored via a network of autonomous passive acoustic recording units deployed on moorings in the Bering and Chukchi seas as part of the Arctic Long-Term Integrated Mooring Array (ALTIMA) program and provided nearly continuous coverage over the period 2013–2019. Data from 2 hydrophone recorders situated near gray whale foraging hotspots in the Chirikov Basin (NM1 mooring site; 64.849° N, 168.393° W) and in the southeast Chukchi Sea (PH1 mooring site; 67.907° N, 167.200° W) were used in our study (see Fig. 1). Technical specifications of recorder configuration and deployment details are summarized in Wright et al. (2019) and Crance et al. (2019). Sound files and corresponding spectrogram image files generated by the recorders were manually analyzed in 10 min increments by trained acousticians for the presence of positively identified gray whale vocalizations (Burnham et al. 2018). The percentage of 10 min increments containing positive detections was further summarized on a daily basis to normalize day-to-day variation in recording unit duty cycling. There was also a reasonable amount of vocal and frequency overlap between gray whales and humpback whales *Megaptera novaeangliae*, and both species were commonly detected during vessel and aerial surveys in the vicinity of both mooring sites (Clarke et al. 2013). Ambiguous vocalizations that could not be identified to species were excluded from the results presented here.

For analyses examining the timing of gray whale arrival and departure relative to sea ice retreat and advance, we calculated the numeric day of each year corresponding to the onset and cessation of gray whale acoustic detections. Following the approach of Szesciorka et al. (2020), periods of gray whale acoustic presence in the vicinities of the NM1 and PH1 moorings were identified such that 99% of the 10 min spectrogram periods containing positive detections fell between the acoustic onset and cessation dates. This approach intentionally excluded a small number of isolated, short-duration early- and late-season vocal bouts that likely represented single individuals or small groups, allowing onset and cessation dates to provide a clearer representation of the

arrival/departure timing of the bulk of the migratory ENP gray whale population.

2.3. Sea ice remote sensing

Remotely sensed sea ice concentration layers, based on satellite microwave radiometer measurements, were used to examine the responses of gray whale habitat use patterns to sea ice conditions over larger spatial scales compared to the localized estimates recorded by the aerial visual observers. High-resolution daily sea ice concentration estimates with a nominal resolution of 3.125 km at 70° N in polar stereographic projection (EPSG: 3411) were obtained over the period 2008–2019 (<https://seaice.uni-bremen.de/data/>; accessed 7 June 2020). These layers are based on brightness temperature differences in the 89 GHz channels of the Advanced Microwave Scanning Radiometer EOS (AMSR-E; 2002–2011) and Advanced Microwave Scanning Radiometer 2 (AMSR-2; 2012–present) instruments, and were processed using the Arctic Radiation and Turbulence Interaction Study Sea Ice algorithm (v.5.4; Spreen et al. 2008). To examine sea ice conditions and spatial configurations associated with some of the earliest ASAMM surveys in the early 1980s, we also retrieved Sea Ice Index (SII) concentration layers from the NOAA National Snow and Ice Data Center (NSIDC; <ftp://sidads.colorado.edu/DATASETS/NOAA/G02135/north/daily/geotiff/>; accessed 26 May 2021) that were available on either a daily or an alternating day schedule and provided information at a nominal resolution of 25 km at 70° N. Sea ice concentration contours, such as the 40% concentration level highlighted in the analysis of Gailey et al. (2020), were estimated using the 'contour' function in the 'raster' package (v.3.3-13; Hijmans 2020) within R (v.4.0.2; R Core Team 2020). Minimum distances of each sighting from the 40% sea ice concentration contour lines were calculated using the 'dist2line' function from the 'geosphere' package (v.1.5-10; Hijmans 2019). Mean sea ice concentration levels over the temporal periods specified (see Fig. 2) were calculated on the basis of daily or alternating day AMSR and SII sea ice concentration layers using the 'calc' function in the 'raster' package (Hijmans 2020).

For analyses comparing the timing of sea ice retreat and advance with the onset and cessation of gray whale acoustic activity in the vicinity of the NM1 and PH1 mooring sites, we estimated the numeric day-of-year break-up dates, denoting the last day of spring or summer with 40% sea ice cover,

and freeze-up dates, representing the first day of autumn or winter with 40% sea ice cover. Both metrics were based on time series of sea ice concentration values sampled from daily SII layers at the NM1 (64.849°N, 168.393°W) and PH1 (67.907°N, 167.200°W) mooring sites using the 'extract' function in the 'raster' package (v.3.3-13; Hijmans 2020).

2.4. Statistical analysis: aerial surveys

Spatio-temporal modeling was implemented in the generalized additive model (GAM) framework using the package 'mgcv' (v.1.8-31; Wood 2011). This framework allowed for flexible, non-linear relationships between gray whale aerial counts and *in situ* or remotely sensed sea ice smooth functions while accounting for sampling effort, gray whale habitat use patterns, and the potential for spatio-temporally autocorrelated residuals. The primary objective in fitting these models was ecological inference about the functional form, uncertainty, and strength of the relationship between the gray whale aerial encounter rate and sea ice concentration. To arrive at unbiased estimates of the sea ice concentration smooth terms, we used the spatio-temporal modeling approach outlined by Wikle et al. (2019), employing a tensor product spline term composed of easting, northing, and time (i.e. integer number of days since 1 January 2008) to account for temporally variable patterns of gray whale habitat use. In an initial Poisson specification of these GAMs, counts of the total number of gray whale individuals observed within each transect segment (≤ 5 km) were related to covariates via a natural logarithm link function. The models accounted for variation in sampling effort via an offset term based on transect segment length and visibility distance out to a maximum horizontal range of 5 km. This truncation of sampling area at 5 km corresponded to the horizontal range over which the vast majority of gray whale sightings were recorded. This simple encounter rate model was analogous to the approach employed by Brower et al. (2017) and could be justified in place of a more complex distance sampling detection function because the objective of our study was to estimate the effects of environmental conditions on gray whale counts rather than an attempt to estimate absolute abundance.

The study area for this analysis was the northeast Chukchi Sea from 169.1 to 154°W, and 69 to 72.1°N (see Fig. 1). This was the only portion of the ASAMM sampling domain where gray whale observations commonly intersected with retreating sea ice during the ASAMM seasonal sampling window (typically

late June/early July to October). To minimize the potential confounding influence of intra-seasonal shifts in gray whale habitat, such as those noted by Brower et al. (2017), survey effort used in the models was also restricted to the months of June and July, after which sea ice was generally no longer present in the habitats predominately used by gray whales.

Standardized scaled residuals were estimated from the initial Poisson configuration of spatial-temporal GAMs using the 'simulateResiduals' function from the 'dHARMA' package (v.0.3.3.0; Hartig 2020). This allowed for more readily interpretable validation of models in the generalized linear/GAM class using residual plots analogous to those from linear models. Standardized 'dHARMA'-simulated residuals from the Poisson model suggested heteroskedasticity, and the 'DispersionTest' function indicated that there was significant overdispersion even after accounting for spatial-temporal trends and sea ice effects. We therefore fitted negative binomial spatio-temporal GAMs that allowed for the variance of counts to exceed the mean. However, even after accounting for the overdispersion of counts, we noted that there remained significant spatial autocorrelation in the deviance residuals based on Moran's I statistic calculated in the 'ape' package (v.5.0; Paradis & Schliep 2019). Qualitative mapping of the deviance residuals showed that spatial autocorrelation was elevated in areas of high predicted encounter rates, where there were a small number of sizeable negative residuals corresponding to a few abnormally high counts surrounded by a large number of small positive residual values corresponding to a large number of zero counts. To better capture a portion of the count variance not accounted for by the spatio-temporal tensor product spline, and ultimately to allow for unbiased inference regarding the effects of sea ice, a residual autocovariate (RAC) term was included in the final models (Crane et al. 2012). This RAC term was calculated by rasterizing the residuals from the negative binomial specification of the spatio-temporal GAMs and applying a mean focal operation to the first-order neighborhood surrounding each cell (i.e. the focal cell plus the 8 surrounding cells). The RAC values at the segment midpoints were then included in the final models as an additional smooth term alongside the sea ice and spatio-temporal predictors.

2.5. Statistical analysis: passive acoustic monitoring

For analyses comparing the timing of gray whale arrival and departure in the Chirikov Basin and SE

Chukchi Sea with annual variation in the timing of sea ice retreat and advance, we fitted linear mixed effects models with fixed effects relating acoustic onset and cessation numeric day-of-year to break-up and freeze-up day-of-year, respectively. We also fitted a linear mixed effects model at a 1 yr time lag to assess whether gray whale acoustic onset at NM1 and PH1 reflected sea ice break-up timing during the current foraging season or potentially a prediction of sea ice break-up timing based on cues encountered during the prior foraging season (Szesciorka et al. 2020). Mixed effects models were fitted in R using the 'lme' function from the 'nlme' package (Pinheiro et al. 2020). Site was included as a random effect in these models to allow for intercept variation associated with the NM1 and PH1 mooring sites. Marginal and conditional coefficients of determination, representing the variance explained by the fixed effects and

overall mixed effects models, respectively, were estimated following the method of Nakagawa et al. (2017).

3. RESULTS

The ASAMM database consists of over 641 461 linear km of aerial survey effort during which observers actively recorded marine mammal observations (i.e. effort types 'transect', 'search', and 'CAP'). Over the period 1979–2019, there were a total of 4992 gray whale sightings, comprising an estimated total of 9410 individuals (Fig. 1). The ALTIMA data archive contains a total of 4845 d of passive acoustic recordings collected on the NM1 and PH1 moorings between 2012 and 2019, which were analyzed for the presence of various marine mammal vocalizations, including gray whales.

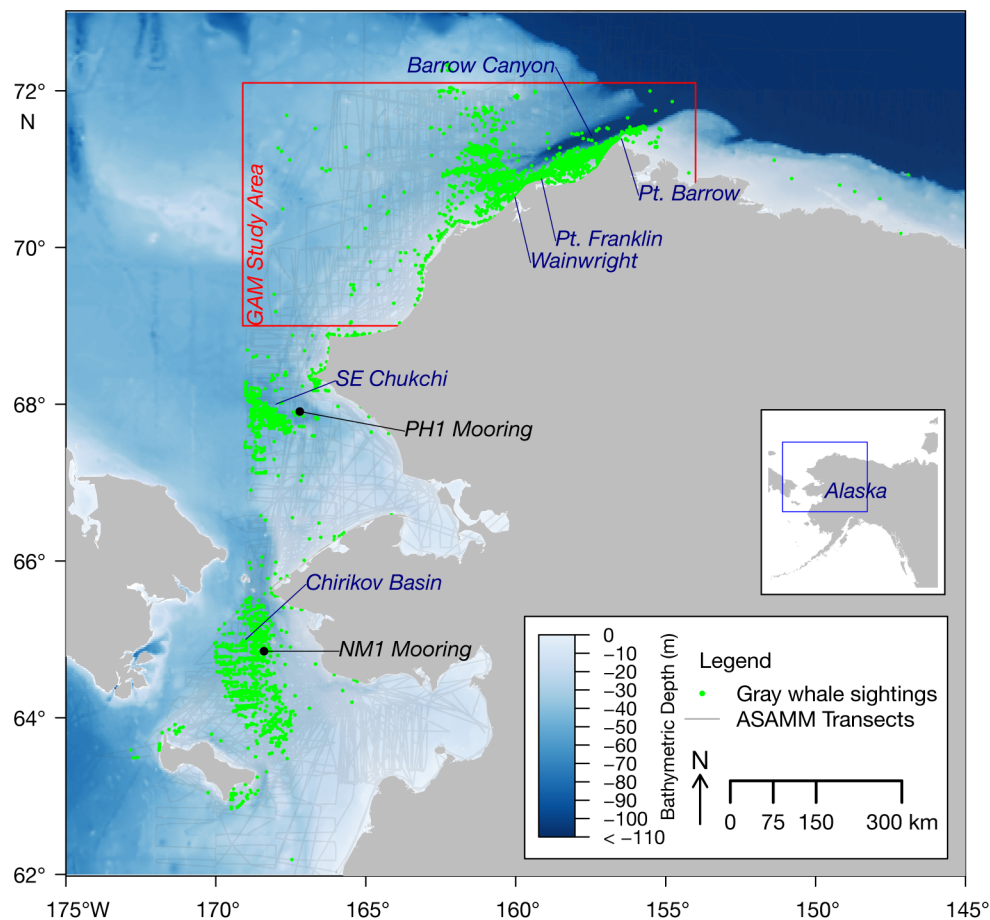


Fig. 1. Cumulative spatial distribution of all gray whale sightings recorded in the Aerial Surveys of Arctic Marine Mammals (ASAMM) sampling domain of the Bering, Chukchi, and western Beaufort seas between 1979 and 2019. Red box: spatial domain of spatio-temporal generalized additive model (GAM) analyses covering the northeastern Chukchi Sea from 169.1 to 154° W and 69 to 72.1° N. Locations of the Point Hope (PH1) and Nome (NM1) passive acoustic moorings are shown in black

3.1. Spatial distribution patterns relative to sea ice

Fig. 2 illustrates the overall distribution patterns of gray whale sightings under divergent sea ice conditions in the northern Bering and northeast Chukchi seas. Fig. 2d shows that despite extensive transect effort, gray whale observations were absent along

the southern edge of Barrow Canyon during late June 2008, when dense sea ice cover persisted between Wainwright and Pt. Barrow. This absence contrasts with numerous gray whale observations within these same habitats during comparable periods of late June in 2009 and 2011 (Fig. 2e,f), when open water stretched northward to Pt. Barrow.

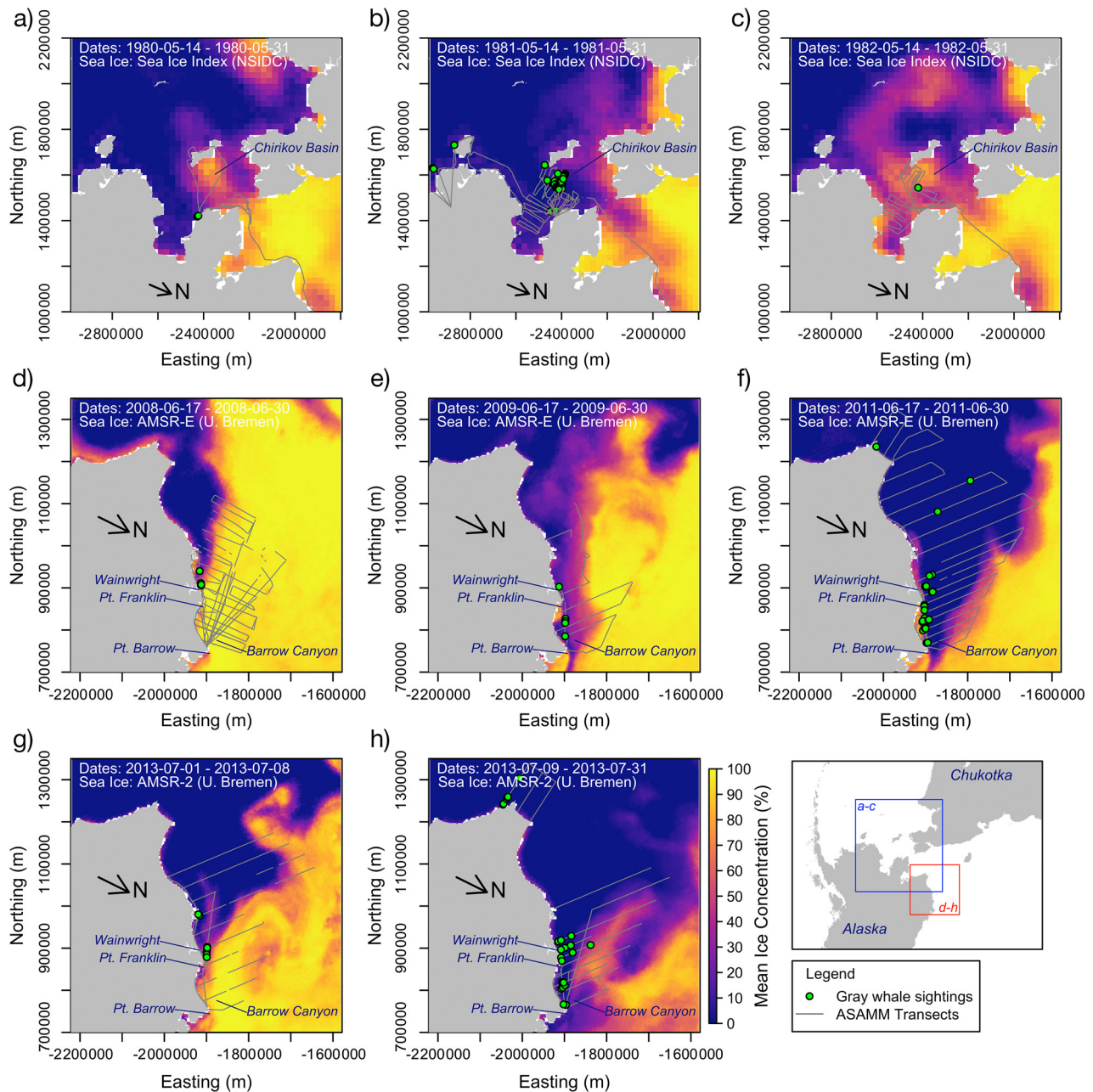


Fig. 2. Distribution of gray whale sightings during Aerial Surveys of Arctic Marine Mammals (ASAMM) surveys in the northern Bering and northeastern Chukchi seas during (a–c) late May, (d–f) late June, and (g,h) early July of different years. Background colors show contrasting mean sea ice spatial configurations and concentration values during the survey periods, indicated at the top of each map. Maps are displayed in the polar stereographic projection (EPSG: 3411) native to the National Snow and Ice Data Center (NSIDC) Sea Ice Index and Advanced Microwave Scanning Radiometer (AMSR) sea ice concentration layers

Although not shown in Fig. 2, the southern edge of Barrow Canyon between Wainwright and Pt. Barrow was also extensively utilized later in the summer of 2008 after sea ice had retreated. Analogous patterns of within-year variability were also apparent in the contrasting distribution patterns of gray whale sightings between early and mid- to late July 2013. During early July 2013, when consolidated sea ice persisted in the northeastern Chukchi Sea, there were no observations of gray whales along the southern edge of Barrow Canyon between Pt. Franklin and Pt. Barrow (Fig. 2g). Over the course of a few days following the retreat of sea ice and the opening of a corridor northward to Pt. Barrow in mid-July 2013 (Fig. 2h), gray whales were observed in this habitat. Finally, a similar pattern emerged in late May (14–31 May) of 1980 and 1982, when gray whale observations were nearly absent in the eastern and central Chirikov Basin during periods when moderate con-

centrations of sea ice (30–80%) persisted in this area (Fig. 2a,c). This distribution pattern contrasts markedly with numerous gray whale observations recorded in the same area from 14–31 May 1981, when sea ice had largely retreated from this portion of the Chirikov Basin (Fig. 2b).

Among the numerous gray whale sightings between 1979 and 2019, visual observers recorded a small number of observations associated with *in situ* sea ice concentration values ranging from 40–95% (Fig. 3a,b). These sightings at high *in situ* sea ice concentration values were uncommon as a proportion of total observations (1.7%; Fig. 3a,b). Mapping these sightings in the context of broader sea ice spatial configuration patterns obtained from daily remotely sensed sea ice concentration layers (AMSR-E/AMSR-2) further revealed that these sightings almost exclusively occurred along the periphery of larger masses of sea ice or near stretches of open

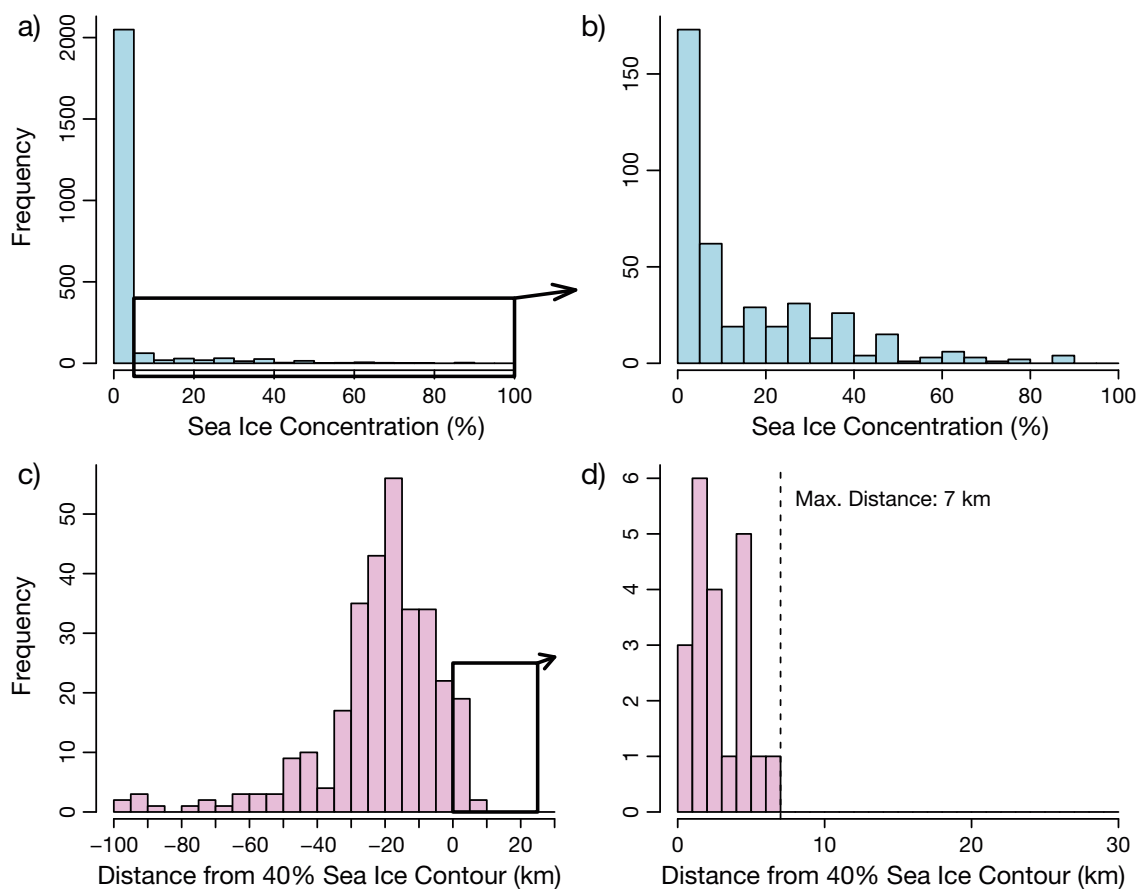


Fig. 3. (a,b) Distribution of *in situ* sea ice concentration values and (c,d) distances to the remotely sensed 40% sea ice concentration contour (Advanced Microwave Scanning Radiometer EOS/Advanced Microwave Scanning Radiometer-2; Spreen et al. 2008) associated with gray whale sightings in the Aerial Surveys of Arctic Marine Mammals aerial survey database from 2008–2019. Panels (b) and (d) show in greater detail the >0% or >0 km portions of the distributions shown in (a) and (c). Negative values in (c) indicate distance from the 40% sea ice concentration contour in the direction of open water (i.e. gray whales found in ≤40% sea ice concentration)

water penetrating into dense sea ice. In all of the ASAMM aerial survey effort covered by the AMSR-E/AMSR-2 sea ice data (2002–present), no gray whales were sighted more than 7 km deeper into sea ice than the remotely sensed 40% sea ice concentration contour (Fig. 3c,d).

3.2. Sea ice effects on encounter rates

Spatial–temporal GAMs allowed the quantitative estimation of the sea ice concentration effects on gray whale encounter rates. On the basis of Akaike weights (wAIC), GAMs containing *in situ* and remotely sensed sea ice smooth functions were heavily favored over a null model containing only the spatio-temporal tensor product spline and the residual spatial autocorrelation term (Table 1). Although smooth functions of both *in situ* and remotely sensed sea ice concentration (%) both represented significant terms (Table 1), models containing *in situ* sea ice information were also favored on the basis of wAIC over models containing remotely sensed sea ice information.

The effects of *in situ* and remotely sensed sea ice concentration terms were similar in their overall negative slopes (Fig. 4a,b). Both relationships were also non-linear, with a relatively mild negative slope up to values of 40–45% in the case of *in situ* sea ice cover and 50–55% in the case of remotely sensed AMSR sea ice concentration (Fig. 4a,b). Above these points

of curvature, the slope of both relationships became more negative at higher sea ice concentration values. Moreover, since the effects of the smooth functions shown in Fig. 4a,b relate to the natural logarithm of expected counts, the negative effects of high sea ice concentration values were even more pronounced when exponentiated to back-transform to the scale of the response variable (e.g. gray whale counts). Finally, comparing the functional form of the spatio-temporal tensor product spline term at different times within the period 2008–2019 also revealed a shift in gray whale spatial distribution patterns within the northeastern Chukchi Sea starting in approximately 2016 (Fig. 4c,d).

3.3. Sea ice and seasonal migratory timing

Examining the overall distribution of gray whale acoustic detections from 2013–2019 (Fig. 5) revealed that >99% of 10 min spectrogram segments containing positive gray whale vocal detections occurred during ice-free periods at both the NM1 and PH1 mooring locations.

Similar to the rare sightings of gray whales at high *in situ* sea ice concentration values in the aerial survey data set, there were also a small number of days at NM1 (n = 6) and PH1 (n = 4) with positive gray whale detections prior to the break-up dates when sea ice concentrations terminally dropped below 40% (Fig. 5b,d). More than 70% of these rare pre-

Table 1. Comparison of spatio-temporal generalized additive models (GAMs) with and without smooth functions representing the effects of *in situ* or remotely sensed sea ice concentration (%). Gray whale count data used in fitting these models were collected in June and July between 2008 and 2019. A residual autocorrelation (RAC) smooth term was included in each model to capture spatial dependence not accounted for by the spatio-temporal tensor product spline and to allow for unbiased inference regarding the effects of sea ice. Model comparisons were carried out on the basis of Akaike weights (wAIC) calculated from Akaike's information criterion (AIC) scores. Effective and reference df: degrees of freedom used in fitting smooth functions; AMSR: Advanced Microwave Scanning Radiometer

Formula	Smooth terms	Effective df	Reference df	χ^2	p	Deviance explained	Δ AIC	wAIC
GW_count ~ te(Easting, Northing, Time) + s(RAC)						0.68	218.4	0
	te(Easting, Northing, Time)	159.9	199	961.7	<0.001			
	s(RAC)	3	4	304.5	<0.001			
GW_count ~ te(Easting, Northing, Time) + s(AMSR Sea Ice) + s(RAC)						0.68	58.4	0
	te(Easting, Northing, Time)	138.5	173	921.3	<0.001			
	s(RAC)	3.4	4	319.7	<0.001			
	s(AMSR Sea Ice)	3.9	5	69.5	<0.001			
GW_count ~ te(Easting, Northing, Time) + s(<i>in situ</i> Sea Ice) + s(RAC)						0.68	0	1
	te(Easting, Northing, Time)	136.1	170	951.1	<0.001			
	s(RAC)	2.7	3	91.5	<0.001			
	s(<i>in situ</i> Sea Ice)	2.9	4	311.4	<0.001			

break-up detections occurred during the late April to mid-May transitional periods, when sea ice interspersed with open water was present in the vicinities of the NM1 and PH1 mooring sites (i.e. similar to the conditions associated with aerial survey detections of gray whales at high sea ice concentration values). However, there were also a small number of days in January ($n = 2$) and March ($n = 1$) when individual gray whale detections were recorded on the more southerly NM1 hydrophone during periods of extensive sea ice cover (Fig. 5d).

For the analysis of gray whale arrival timing relative to sea ice retreat, a linear mixed effects model based on 7 yr of acoustic onset dates at NM1 and 6 yr at PH1 indicated a highly significant positive fixed effect of ice break-up date (slope = 0.77, intercept =

44, $t_{10} = 7.1$, $p < 0.001$). The marginal coefficient of determination (R^2_m) indicated that the fixed effect component of this model explained upwards of 81% of the variance in onset dates. The random site effect estimate was essentially 0, indicating no intercept offset between the NM1 and PH1 mooring sites. Across the spectrum of sea ice break-up dates observed between 2013 and 2019, this model estimated a mean lag of 10–15 d between sea ice retreat below 40% concentration and the onset of vocal activity at both NM1 and PH1 mooring sites as indicated by the separation between the regression line and the line $y = x$ (Fig. 5c). Using a similar linear mixed effects model, we did not find a significant fixed effect of freeze-up date on the late-summer–autumn cessation of gray whale acoustic detections (t_{11}

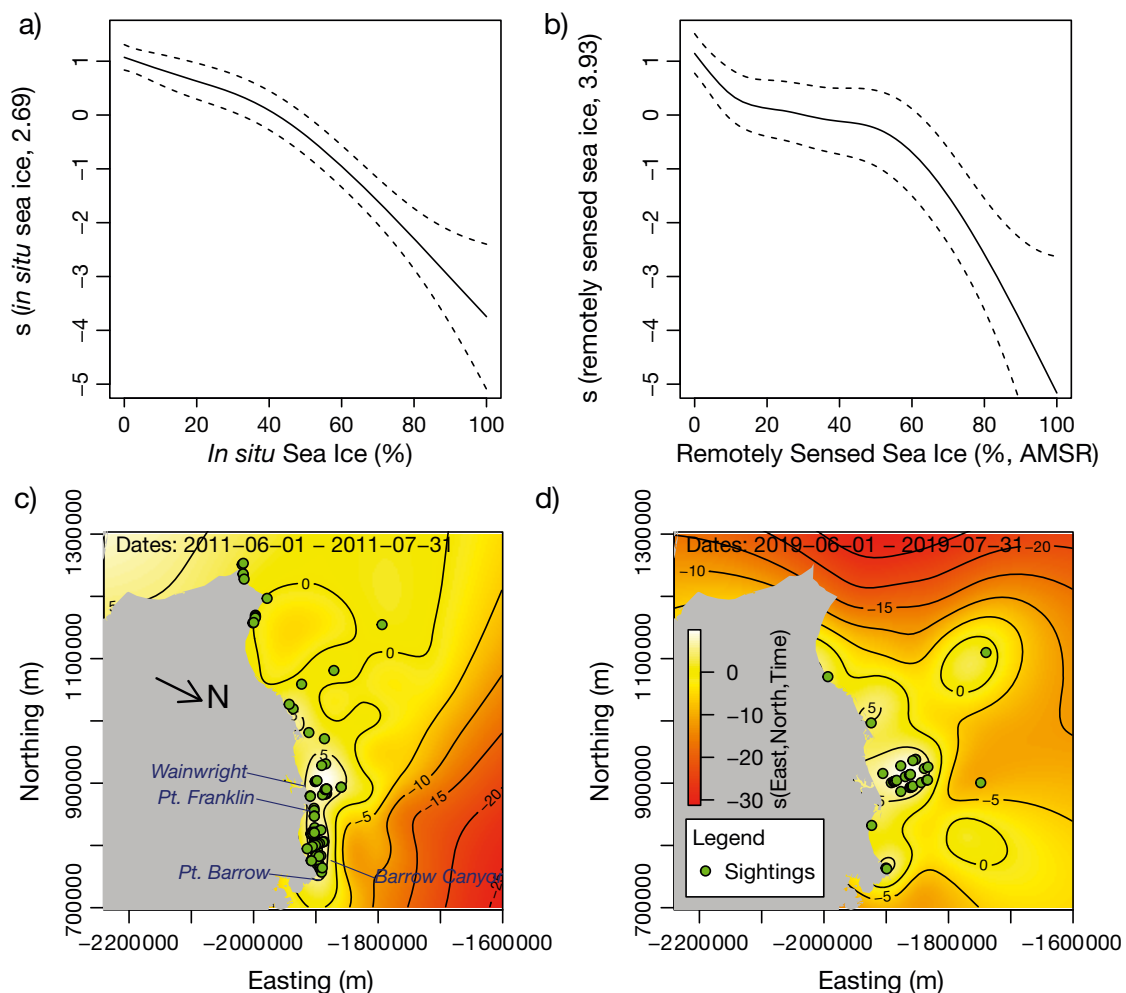


Fig. 4. Functional relationships of (a) *in situ* and (b) remotely sensed sea ice concentration smooth functions with the natural logarithm of gray whale counts from spatio-temporal generalized additive models fitted with a residual spatial autocorrelation term. Dashed lines: ± 1 SE relative to the main estimate. Panels (c) and (d) show instances of the spatio-temporal smooth function and corresponding observations from June–July (c) 2011 and (d) 2019. These maps are illustrative of a broader distribution shift away from the southern flank of Barrow Canyon with increased activity further from shore northwest of Wainwright that occurred around 2015. AMSR: Advanced Microwave Scanning Radiometer

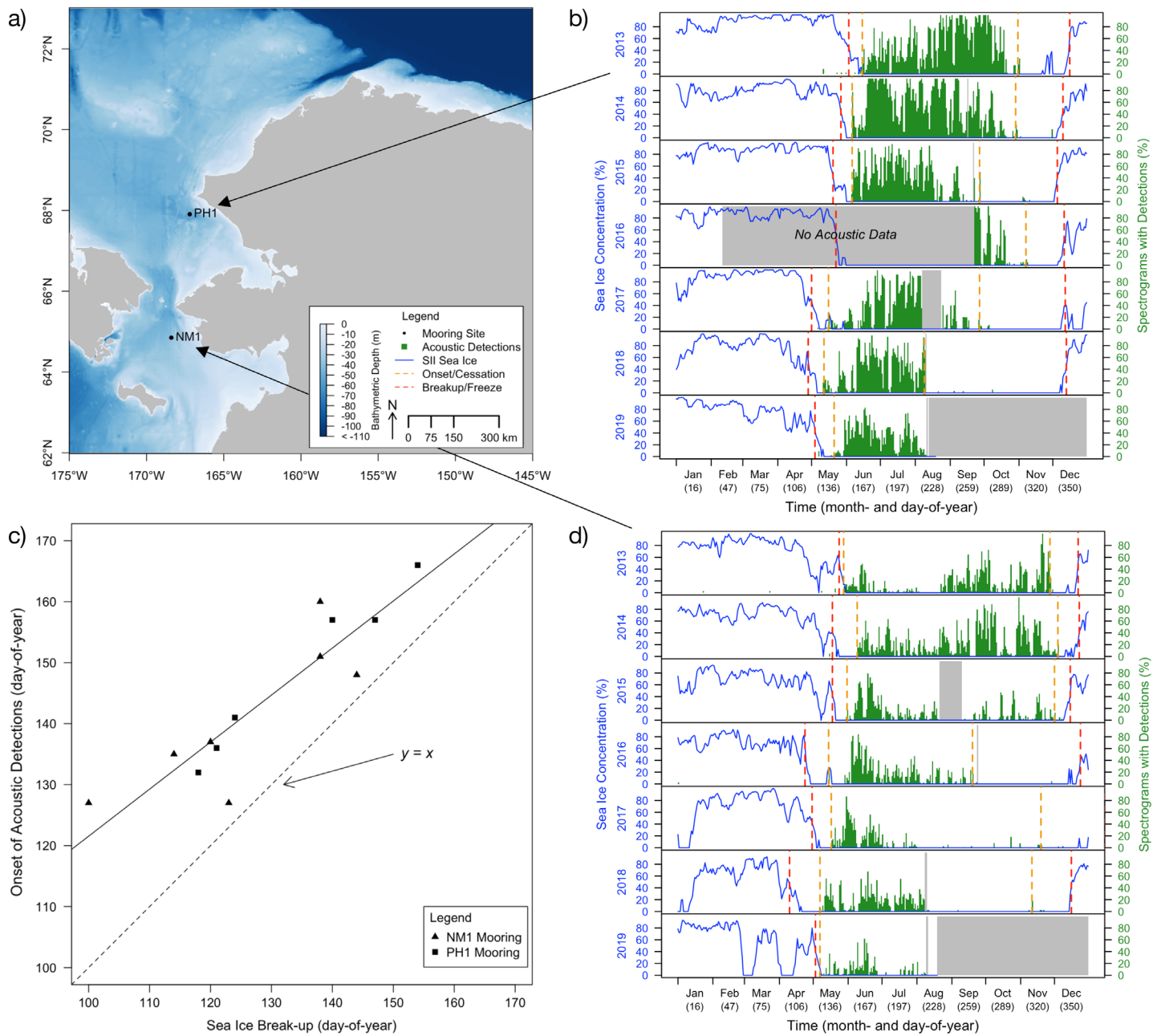


Fig. 5. Percentage of daily spectrograms with positive gray whale vocalizations. (a) Location of mooring sites NM1 and PH1; (b,d) distribution of gray whale vocal detections relative to the National Snow and Ice Data Center Sea Ice Index (SII) concentration estimates over the entire time series at PH1 and NM1. (c) Relationship between the onset date of gray whale detections and sea ice break-up in numeric day-of-year. Acoustic onset and sea ice break-up dates referenced in (c) are also shown in (b) and (d) as yellow and red dashed lines, respectively

$= -0.2$, $p = 0.830$), but we did find a significant fixed effect (slope = 0.61, intercept = 62, $t_{11} = 4.9$, $p = 0.001$) of sea ice break-up dates from the previous year on acoustic onset dates at NM1 and PH1. However, the variance explained by the 1 yr lagged sea ice break-up term ($R^2_m = 0.66$) was smaller than the variance explained by the within-year model ($R^2_m = 0.81$).

4. DISCUSSION

Qualitative examples and quantitative analyses of gray whale distribution patterns presented in this study together strongly suggest that sea ice plays an important role in gray whale habitat use during their late spring and early summer arrival on the Pacific

Arctic foraging grounds. Aerial and passive acoustic observations, indicating very limited gray whale observations and vocal detections during periods of dense sea ice cover, were likewise consistent with the 'sea ice exclusion' hypothesis proposed by Perryman et al. (2002, 2011, 2021) and Gailey et al. (2020). The strong relationship between break-up dates and the onset of gray whale acoustic detections similarly pointed to an important role of sea ice in gray whale migratory phenology. However, not all aspects of this relationship aligned with our expectations under the 'sea ice exclusion' hypothesis, and the relatively consistent lag between break-up and onset led us to consider potential alternate mechanisms by which sea ice may influence gray whale habitat use and migratory timing.

4.1. Spatial distribution patterns relative to sea ice

Within the limited early season aerial sampling that overlapped the tail end of sea ice retreat, gray whale distributions showed patterns of between- and within-year variability that qualitatively supported an important role of sea ice in gray whale habitat use. In particular, the notable absence of gray whale sightings along the southern edge of Barrow Canyon in late June 2008 and early July 2013 suggested that large contiguous patches of sea ice potentially played a limiting role in early season access to this foraging hotspot habitat. Similar patterns of inter-annual variability in the northern Bering Sea during the 1980s provided further qualitative support for an exclusionary role of sea ice, including at the time of year when gray whales first arrive on the Pacific foraging grounds.

4.2. Sea ice effects on encounter rates

Although there were limited examples like 2008 and 2013, when large contiguous masses of dense sea ice coincided with early season aerial survey effort, a larger data set consisting of all June and July surveys in the northeastern Chukchi Sea from 2008–2019 allowed spatio-temporal GAMs to more systematically address gray whale responses to different sea ice concentration levels and spatial configuration patterns. These models quantitatively affirmed the qualitative inference from the distribution maps and were likewise consistent with the hypothesized 'sea ice exclusion' mechanism. The statistical significance of the remotely sensed and *in situ* sea ice terms in these

spatio-temporal GAMs, and the fact that the models including sea ice terms were heavily favored on the basis of wAIC over the null model, together suggested that sea ice concentration represented an important contributor to early season gray whale habitat use patterns. We only had sufficient quantitative distribution data that temporally overlapped seasonal sea ice cover to model the effect of sea ice concentrations on gray whale habitat in the northeastern Chukchi Sea. However, we posit that the observed negative relationship and the increasingly negative slope at higher sea ice concentration values were likely indicative of more general gray whale responses to dense sea ice conditions across their Pacific Arctic range. Thus, the variability observed in the reproductive time series likely represents the aggregate effect of 'sea ice exclusion' effects not just in the northeastern Chukchi Sea, but also across more southerly hotspot habitats earlier in the foraging season.

The increase in negative slope of the *in situ* and remotely sensed sea ice concentration smooth functions around 45–50 and 50–55%, respectively, also corresponds closely with the 40% sea ice concentration level at which Gailey et al. (2020) found the highest sensitivity in WNP gray whale calf survival. Perryman et al. (2021) considered the correlation of ENP gray whale calf production with the amount of Pacific Arctic surface area covered by $\geq 15\%$ sea ice concentration in each month leading up to calving. The relatively shallow negative slope of the *in situ* and remotely sensed sea ice smooth relationships at 15% concentration along with numerous anecdotal observations of gray whales foraging at sea ice concentrations well in excess of 15% sea ice concentration (Fig. 3b) together suggest that the concentration threshold used in Perryman et al. (2021) was perhaps below the levels at which sea ice may exhibit a deterrent effect on gray whale habitat use. However, the amount of Pacific Arctic surface area covered by $\geq 15\%$ sea ice concentration was closely correlated with the area covered by $\geq 45\text{--}55\%$ sea ice concentration; therefore, it is likely that the correlation observed by Perryman et al. (2021) was potentially aliasing behavioral responses to higher sea ice concentration levels.

Despite the generally low gray whale encounter rates at high sea ice concentrations indicated by the spatio-temporal GAMs and the early season distribution maps, the extensive ASAMM database did include a selection of rare gray whale sightings at high *in situ* concentration values ranging from 40–95%. These potentially countervailing examples suggest that gray whales can tolerate dense sea ice

conditions, at least on a local scale. This finding is consistent with acoustic recordings of gray whale vocalizations off Pt. Barrow throughout the winter of 2003–2004 (Stafford et al. 2007) as well as scattered gray whale vocalizations detected on the NM1 mooring in Chirikov Basin during January and March 2013 and 2016. However, examining the individual ASAMM aerial sightings at high sea ice concentration values within a broader context of sea ice spatial configuration patterns revealed by satellite remote sensing indicated that these rare observations generally occurred along the periphery of larger masses of sea ice or along large open water leads penetrating into dense ice masses. Indeed, the observation that no gray whales were sighted >7 km inside the 40% sea ice concentration contour suggests that gray whales are capable of penetrating dense sea ice over relatively short distances; however, they may have faced challenges in progressing through larger patches of dense sea ice, such as those observed along the 100 km stretch between Pt. Franklin and Pt. Barrow in late June 2008 and early July 2013.

One additional caveat to consider in assessing the effect of sea ice on gray whale visual encounter rates is a potential confounding influence of sea ice on gray whale detectability during aerial surveys. Sea ice increases the visual complexity of the seascape that visual observers are scanning, and has been demonstrated to have a small negative effect on the detectability of bowhead whales (scale coefficient_{caticepct1} = -0.51 ± 0.135 SE; Table 3 in Ferguson et al. 2021). There were insufficient observations of gray whales in the presence of sea ice to simultaneously estimate the effect of sea ice on gray whale detectability in a distance sampling detection function while also estimating the effect of sea ice on the underlying gray whale habitat use patterns. However, there is reason to believe that the effect of sea ice on gray whale detectability may be even smaller than its already limited effect on bowhead whale detectability. This relates to the fact that one of the most common visual cues associated with gray whale aerial detections is the presence of mud plumes associated with benthic foraging. This cue is more persistent than the bodies or blows typically detected during bowhead whale sightings, and this visual cue is likely the reason that gray whale detectability shows a lower sensitivity to elevated Beaufort sea states (Clarke et al. 2020) which, like sea ice, also increase visual complexity. Moreover, it is unlikely that this small potential negative detectability effect could be responsible for the large negative effect of sea ice observed in our current spatio-temporal GAM analysis.

4.3. Sea ice and seasonal timing

Passive acoustic records of gray whale vocalizations were examined in this study to elucidate inter-annual differences in the timing of gray whale arrival and occupation of different foraging habitats in the Pacific Arctic relative to the seasonal retreat of sea ice. Because the passive acoustic hydrophones were recording nearly continuously during the periods of sea ice retreat from 2013 through 2019, they provided a more complete record of gray whale migratory phenology relative to the more sporadic and patchy early season aerial survey coverage in gray whale foraging habitats. This acoustic data set also provided information on gray whale phenology within the southernmost major Pacific Arctic foraging hotspot that gray whales encounter during their northbound migration (i.e. the Chirikov Basin; see Fig. 1). Coverage of this area may be particularly important, as it provides one of the first opportunities for gray whales to begin replenishing their energy stores following long-distance migration, apart from short-duration stopovers documented in various segments of the ENP migratory population at locations along the Pacific Coast of North America (Moore et al. 2007, Calambokidis 2018, Urbán Ramírez et al. 2021).

One of our major takeaways was the alignment of the passive acoustic records with the evidence from the aerial surveys in suggesting that gray whales showed limited penetration of habitats covered by dense sea ice cover. This information provided an additional line of evidence in support of the ‘sea ice exclusion’ hypothesis. Although it is possible that gray whales could have been present in the vicinity of the hydrophones without producing vocalizations, this is not supported by our best knowledge of their acoustic behavior. Gray whales have been observed to often be silent during feeding behavior (Ljungblad & Moore 1983, Vate Brattström et al. 2019), whereas during migration or periods of social interaction they typically show more consistent vocalization rates (Guazzo et al. 2017, Burnham et al. 2018). However, the gray whales detected will be migrating and likely vocalizing before stopping to feed, and therefore we find it most probable that the near-absence of acoustic activity prior to sea ice break-up represents the lack of gray whale presence in the vicinities of NM1 and PH1 or presence at minimal numbers.

The significant positive fixed effect of sea ice break-up dates on the onset dates of gray whale acoustic detections at NM1 and PH1 provides additional support for the importance of sea ice variability

in gray whale early season habitat use patterns. However, the relatively consistent 10–15 d lag observed between break-up dates and the onset date of gray whale acoustic detections diverged from some of our expectations under the ‘sea ice exclusion’ hypothesis, and raised some intriguing questions regarding the exact mechanism(s) underpinning the observed relationship.

Under the ‘sea ice exclusion’ hypothesis, sea ice is postulated to play a physical blocking role (Perryman et al. 2002, 2021). A reasonable prediction from this hypothesis is that if ice is the limiting factor in access to foraging habitats, then gray whales would likely be eager to take advantage of early foraging opportunities and might be expected to cue near the edge of retreating sea ice to access habitats as they become available. The spatial distribution of gray whale aerial sightings in the northeast Chukchi Sea during late June 2008 and early July 2013 aligns well with this prediction (Fig. 2). This hypothesis also potentially aligns with the close correspondence in time between sea ice retreat and the onset of acoustic activity at both NM1 and PH1 during 2013, which was the year with the latest break-up date during the acoustically monitored period (Fig. 5). However, during the remainder of acoustic time series from 2014–2019, sea ice had retreated not just below 40% but all the way to 0% concentration for a minimum of 3–5 d (and in some cases, 5–10 d) before gray whale acoustic activity ramped up (Fig. 5).

One possible explanation for this lag is that sea ice does indeed play a physical blocking role, but that the passive acoustic data set (with the possible exception of 2013) covers a historically unrepresentative set of years during which sea ice break-up dates ranged from average (e.g. 2014, 2015, 2019) to exceptionally early (e.g. 2016, 2017, 2018). Therefore, it is possible that we might not expect to see strong exclusionary effects in any year during the acoustically monitored period except 2013. It should also be noted that the acoustic time series covers a period (2013–2019) during which gray whale reproductive variability diverged strongly from the historically stable pattern of dependence on sea ice area (Perryman et al. 2021, Stewart & Weller 2021), and therefore there may have been other factors during this period that superseded the effects of sea ice variability. Another possible hypothesis is that the timing of gray whale arrival at the NM1 and PH1 mooring sites may potentially reflect a ‘long-term collective migratory memory’ of historical average sea ice conditions rather than a direct response to current conditions in any given year (e.g. Abrahms et al. 2019).

This explanation could potentially account for the observed lag between break-up and acoustic onset dates from 2014–2019 but does not provide a strong rationale for the ongoing correlation between break-up and onset dates observed over 2013–2019 (Fig. 5c). An additional possible hypothesis to explain this 10–15 d lag is that migratory timing may have reflected an inter-annually lagged response to cues gray whales encountered during the prior foraging season (e.g. Szesciorka et al. 2020). If gray whales were synchronizing the timing of their arrival on the foraging grounds with the timing of sea ice retreat during the prior foraging season, this behavior could potentially lead to mismatches and the observed 10–15 d lag during a set of years when sea ice retreated progressively earlier in each year except 2019. However, we found that break-up dates at a 1 yr lag explained a lower proportion of the variance in acoustic onset dates ($R^2_m = 0.66$) compared with break-up dates within the same year ($R^2_m = 0.81$); thus, the evidence from this study weighed in favor of a direct response to sea ice break-up dates within the same year.

4.4. Prey quality timing hypothesis

As a possible alternative to the ‘sea ice exclusion’ hypothesis that could potentially account for the observed 10–15 d lag, we put forward an alternate hypothesis: ‘prey quality timing’. This hypothesis still emphasizes an important role of sea ice variability in gray whale early season habitat use and, ultimately, calf production variability via the same energetic and reproductive biology mechanisms outlined in the introduction; however, this hypothesis posits a different mechanism of interaction with sea ice. Under this hypothesis, the arrival of migratory gray whales in different foraging hotspot habitats may spatially and temporally track a seasonal pulse of ice algae benthic deposition and/or the intense spring bloom that typically follows the retreat of sea ice in the Pacific Arctic (Lovvorn et al. 2005, Jin et al. 2007, Sigler et al. 2011). Benthic and pelagic macrofauna in the Pacific Arctic often face lean winter months during which only limited and highly refractory particulate organic carbon (POC) is available (Lovvorn et al. 2005), and thus benthic, epibenthic, and pelagic prey may not be as energetically rich food sources for gray whales prior to the retreat of sea ice. Under this scenario, the observed 10–15 d lag between sea ice break-up and acoustic onset dates may reflect gray whales intentionally following the retreat of sea ice at a lag to allow time for macrofaunal prey to uptake and incor-

porate the post-melt flux of labile POC into their lipid stores. This hypothesis is also consistent with the observed gray whale distribution shifts and the negative relationship between gray whale counts and sea ice cover in the aerial survey data set. Finally, the 'sea ice exclusion' and 'prey quality timing' hypotheses are not necessarily mutually exclusive, with sea ice potentially playing a dual role affecting both seasonal variation in prey quality and gray whale access to foraging habitats.

4.5. Unanswered questions

These results do leave unanswered questions regarding recent deviations from the historically strong relationship between ENP gray whale calf production and Pacific Arctic sea ice area (Perryman et al. 2021, Stewart & Weller 2021). The evidence from this study suggests that the strong relationship reported in Perryman et al. (2021) did not reflect a spurious correlation of reproductive output with sea ice variability over the earlier part of this time series (i.e. 1994–2012). Moreover, the spatial and temporal patterns of habitat use and migratory phenology presented in this study point to a role of sea ice itself, rather than the aliasing of some other latent covariate such as the Pacific Decadal Oscillation or variation in advective transport of nutrients and plankton-rich waters through the Bering Straits.

One potential explanation for the recent positive and negative deviations in the reproductive time series is that these excursions from the historical relationship represent separate events with distinct underlying drivers that may have superseded the effects of sea ice variability in recent years. Some examples of events that could potentially have played a role in recent reproductive volatility include bottom-up ecosystem changes, such as the marked increase in mean macrofaunal biomass observed within the southeastern Chukchi Sea starting in approximately 2012 (Grebmeier et al. 2018). This increase in macrofaunal biomass roughly coincides with the anomalously high calf production in 2013 and 2014 (Perryman et al. 2021) as well as an approximately 26% increase in primary production within the Chukchi Sea over the period 2012–2018 (Ardyna & Arrigo 2020).

During the more recent negative excursion of calf production estimates from the historical relationship with sea ice, the northern Bering Sea has experienced unprecedentedly early sea ice retreat, particularly during the winters of 2017–2018 and 2018–2019, that has resulted in ecological consequences at

multiple trophic levels (Duffy-Anderson et al. 2019, Nishizawa et al. 2020, Siddon et al. 2020). This period of rapid climatic and ecological change has also coincided with a shift in gray whale distribution patterns within the northeastern Chukchi Sea starting in approximately 2016 (Moore et al. 2022). The spatial-temporal tensor product spline component of the GAM models fitted in this study (Fig. 4c,d), which were based on the same aerial survey data used by Moore et al. (2022), also highlights this habitat shift, with a precipitous decline after 2016 in the expected counts of gray whales in the shallow shelf habitat along the southern edge of Barrow Canyon. Meanwhile, gray whale use of an offshore habitat northwest of Wainwright/Pt. Franklin, consisting of 3 submerged valleys flowing into the upper reaches of Barrow Canyon, increased markedly after 2016 (Fig. 4c). Moore et al. (2022) suggested that this habitat shift may have accompanied a dietary shift towards greater reliance on pelagic and/or epi-benthic zooplankton aggregations, particularly of krill *Thysanoessa* spp. However, a continued high prevalence of mud plumes associated with gray whale aerial detections in this more offshore habitat suggested at least a partial continued reliance on benthic macrofaunal prey.

If the 'prey quality timing' hypothesis is supported through further research, this may add additional insights into the recent deviations of reproductive output from sea ice conditions. In particular, under-ice blooms such as those documented by Arrigo et al. (2012) may have partially mitigated for the relatively late retreat of sea ice in 2012 and 2013, potentially resulting in the anomalously high calf production of 2013 and 2014. Meanwhile, lower phytoplankton bloom biomass may have occurred during the exceptionally early retreat of sea ice from the northern Bering Sea in March and April 2017–2018 and 2018–2019, as was found previously (Saitoh et al. 2002). This early sea ice retreat may also potentially have resulted in a mismatch between the timing of benthic biomass deposition (Coyle & Cooney 1988) and the timing of gray whale migratory arrival on the foraging grounds.

4.6. Conclusions and further research

Using complementary data sets from aerial surveys and moored hydrophones, which offered insights over large spatial areas and long temporal windows, respectively, this study was able to demonstrate that sea ice does appear to play an important role in shaping gray whale early season habitat use.

Together, these observations suggest that the 'sea ice exclusion' and/or 'prey quality timing' hypotheses represent biologically plausible mechanisms to explain a significant proportion of the observed ENP gray whale reproductive variability (Perryman et al. 2021, Stewart & Weller 2021). The simplicity and directness of the hypothesized 'sea ice exclusion' mechanism could potentially account for the historically strong relationships reported by Perryman et al. (2021) and Gailey et al. (2020), whereas the more indirect 'prey quality timing' mechanism, which is mediated through more complex physical, oceanographic, and ecological feedbacks, could potentially provide a better explanation for the totality of evidence from passive acoustics and aerial surveys presented in this study.

Further research is warranted to explore how recent changes in distribution since 2015 along with trends in primary productivity and macrofaunal biomass have potentially interacted with sea ice constraints on habitat access to influence recent reproductive anomalies (Perryman et al. 2021, Stewart & Weller 2021) and the ongoing gray whale UME from 2019 through 2022 (Raverty et al. 2020, Christiansen et al. 2021). In particular, future research should consider the possibility of non-linear or countervailing effects of sea ice in line with the findings of Christie et al. (2018) indicating that spectacled eider survival declined at both extremes of sea ice conditions. At one extreme, extensive sea ice may limit gray whale access to foraging habitats, but at the other extreme of low sea ice coverage, or in the future—potentially no sea ice coverage—there could be a range of potential downstream effects that could interfere with the ecological processes supporting the rich macrofaunal assemblages currently exploited by gray whales. This includes potential disruptions of benthic-pelagic coupling through reduced or altered timing of ice algae deposition and post-melt blooms (Coyle & Cooney 1988, Duffy-Anderson et al. 2019) as well as potential invasions of subarctic benthic and epibenthic predators previously excluded by cold bottom water temperatures (Sigler et al. 2011). In addition to bottom-up trends propelled by larger environmental drivers, it may also be important to consider the possibility of top-down effects of gray whale foraging on long-lived benthic prey communities (Moore et al. 2001, 2003, Coyle et al. 2007, Brower et al. 2017). Finally, telemetry studies tracking individual movements and dive behavior may provide greater detail on the effects of varying sea ice conditions relative to the phenology of migration and gray whale distribution patterns.

Acknowledgements. We first acknowledge the many survey leaders, aerial observers, and pilots who contributed their time and talents to the collection and maintenance of the aerial survey data sets contained in the ASAMM database. The Bureau of Ocean Energy Management funded and co-managed these surveys, while the Marine Mammal Laboratory at NOAA's Alaska Fisheries Science Center conducted and co-managed some of the surveys. We also thank the officers, crews, and research cruise participants who were instrumental in the deployment and recovery of the passive acoustic moorings. The Bureau of Ocean Energy Management likewise funded this passive acoustic study (Interagency Agreement Numbers. M12PG00021 and M13PG00026), along with the Office of Naval Research (Award Number N000141812792). Additionally, we acknowledge the contributions of the many acoustic analysts who contributed to the processing of the passive acoustic recordings. We also extensively utilized sea ice remote sensing products made freely available by Gunnar Spreen, Christian Melsheimer, and Georg Heygster at the University of Bremen and the National Snow and Ice Data Center. Finally, Sue Moore and Jacqueline Grebmeier provided helpful feedback on early versions of the aerial survey analyses, as well as insights into benthic data and ecosystem processes.

LITERATURE CITED

- ✦ Abrahms B, Hazen EL, Aikens EO, Savoca MS and others (2019) Memory and resource tracking drive blue whale migrations. *Proc Natl Acad Sci USA* 116:5582–5587
- ✦ Anonymous (1989) NOAA aids rescue of gray, beluga whales. *Mar Fish Rev* 51:51
- ✦ Ardyna M, Arrigo KR (2020) Phytoplankton dynamics in a changing Arctic Ocean. *Nat Clim Chang* 10:892–903
- ✦ Arrigo KR, Perovich DK, Pickart RS, Brown ZW and others (2012) Massive phytoplankton blooms under Arctic sea ice. *Sci* 1215065
- ✦ 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 II* 54:2919–2933
- ✦ Bromaghin JF, McDonald TL, Stirling I, Derocher AE and others (2015) Polar bear population dynamics in the southern Beaufort Sea during a period of sea ice decline. *Ecol Appl* 25:634–651
- ✦ Brower AA, Ferguson MC, Schonberg SV, Jewett SC, Clarke JT (2017) Gray whale distribution relative to benthic invertebrate biomass and abundance: northeastern Chukchi Sea 2009–2012. *Deep Sea Res II* 144:156–174
- ✦ Burnham R, Duffus D, Mouy X (2018) Gray whale (*Eschrichtius robustus*) call types recorded during migration off the west coast of Vancouver Island. *Front Mar Sci* 5:329
- ✦ Calambokidis J, Flynn K, Dobson E, Huggins JL, Perez A (2018) Return of the giants of the Salish Sea: increased occurrence of humpback and gray whales in inland waters. *Salish Sea Ecosystem Conference*, 4 June 2018, Seattle, WA. <https://cedar.wvu.edu/ssec/2018ssec/allsessions/593/> (accessed 13 February 2023)
- ✦ Christiansen F, Rodríguez-González F, Martínez-Aguilar S, Urbán J and others (2021) Poor body condition associated with an unusual mortality event in gray whales. *Mar Ecol Prog Ser* 658:237–252
- ✦ Christie KS, Hollmen TE, Flint P, Douglas D (2018) Non-linear effect of sea ice: spectacled eider survival declines

- at both extremes of the ice spectrum. *Ecol Evol* 8: 11808–11818
- Clarke J, Stafford K, Moore SE, Rone B, Aerts L, Crance J (2013) Subarctic cetaceans in the southern Chukchi Sea: evidence of recovery or response to a changing ecosystem. *Oceanography* 26:136–149
- Clarke JT, Brower AA, Ferguson M, Willoughby AL, Rotrock AD (2020) Distribution and relative abundance of marine mammals in the eastern Chukchi Sea, eastern and western Beaufort Sea, and Amundsen Gulf: 2019 annual report. OCS BOEM 2020-027. Bureau of Ocean Energy Management, Anchorage, AK
- Cohen J, Screen JA, Furtado JC, Barlow M and others (2014) Recent Arctic amplification and extreme mid-latitude weather. *Nat Geosci* 7:627–637
- Coyle KO, Cooney RT (1988) Estimating carbon flux to pelagic grazers in the ice-edge zone of the eastern Bering Sea. *Mar Biol* 98:299–306
- Coyle KO, Bluhm B, Konar B, Blanchard A, Highsmith RC (2007) Amphipod prey of gray whales in the northern Bering Sea: comparison of biomass and distribution between the 1980s and 2002–2003. *Deep Sea Res II* 54: 2906–2918
- Crance JL, Berchok CL, Wright DL, Brewer AM, Woodrich DF (2019) Song production by the North Pacific right whale, *Eubalaena japonica*. *J Acoust Soc Am* 145:3467–3479
- Crase B, Liedloff AC, Wintle BA (2012) A new method for dealing with residual spatial autocorrelation in species distribution models. *Ecography* 35:879–888
- Dai A, Luo D, Song M, Liu J (2019) Arctic amplification is caused by sea-ice loss under increasing CO₂. *Nat Commun* 10:121
- Duffy-Anderson JT, Stabeno P, Andrews AG III, Cieciel K and others (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
- Ferguson MC, Clarke JT, Willoughby AL, Brower AA, Rotrock AD (2021) Geographically stratified abundance estimate for Bering–Chukchi–Beaufort seas bowhead whales (*Balaena mysticetus*) from an August 2019 aerial line-transect survey in the Beaufort Sea and Amundsen Gulf. NOAA Tech Memo NMFS-AFSC-428. https://repository.library.noaa.gov/view/noaa/33451/noaa_33451_DS1.pdf (accessed 13 February 2023)
- Gailey G, Sychenko O, Tyurneva O, Yakovlev Y and others (2020) Effects of sea ice on growth rates of an endangered population of gray whales. *Sci Rep* 10:1553
- Grebmeier JM, Bluhm BA, Cooper LW, Danielson SL and others (2015) Ecosystem characteristics and processes facilitating persistent macrobenthic biomass hotspots and associated benthivory in the Pacific Arctic. *Prog Oceanogr* 136:92–114
- Grebmeier JM, Frey KE, Cooper LW, Kędra M (2018) Trends in benthic macrofaunal populations, seasonal sea ice persistence, and bottom water temperatures in the Bering Strait region. *Oceanography* 31:136–151
- Guazzo RA, Helble TA, D’Spain GL, Weller DW, Wiggins SM, Hildebrand JA (2017) Migratory behavior of eastern North Pacific gray whales tracked using a hydrophone array. *PLOS ONE* 12:e0185585
- Hartig F (2020) DHARMA: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.3.3.0. <https://CRAN.R-project.org/package=DHARMA> (accessed 23 June 2021)
- Hijmans RJ (2019) geosphere: spherical trigonometry. R package version 1.5-10. <https://CRAN.R-project.org/package=geosphere> (accessed 23 June 2021)
- Hijmans RJ (2020) raster: geographic data analysis and modeling. R package version 3.3-13. <https://CRAN.R-project.org/package=raster> (accessed 23 June 2021)
- Huntington HP, Danielson SL, Wiese FK, Baker M and others (2020) Evidence suggests potential transformation of the Pacific Arctic ecosystem is underway. *Nat Clim Chang* 10:342–348
- Jay CV, Fischbach AS, Kochnev AA (2012) Walrus areas of use in the Chukchi Sea during sparse sea ice cover. *Mar Ecol Prog Ser* 468:1–13
- Jin M, Deal C, Wang J, Alexander V and others (2007) Ice-associated phytoplankton blooms in the southeastern Bering Sea. *Geophys Res Lett* 34:L06612
- Kochnev AA (1998) Death of whales (Cetacea) in the Chukchi Sea and the Long Strait: species composition, distribution and causes of death. *Zool Zh* 77:601–605
- Kovacs KM, Lydersen C (2008) Climate change impacts on seals and whales in the North Atlantic Arctic and adjacent shelf seas. *Sci Prog* 91:117–150
- Laidre KL, Stern H, Kovacs KM, Lowry L and others (2015) Arctic marine mammal population status, sea ice habitat loss, and conservation recommendations for the 21st century. *Conserv Biol* 29:724–737
- Ljungblad DK, Moore SE (1983) Killer whales (*Orcinus orca*) chasing gray whales (*Eschrichtius robustus*) in the northern Bering Sea. *Arctic* 36:361–364
- Lovvorn JR, Cooper LW, Brooks ML, De Ruyck CC, Bump JK, Grebmeier JM (2005) Organic matter pathways to zooplankton and benthos under pack ice in late winter and open water in late summer in the north-central Bering Sea. *Mar Ecol Prog Ser* 291:135–150
- Moore SE, Huntington HP (2008) Arctic marine mammals and climate change: impacts and resilience. *Ecol Appl* 18:S157–S165
- Moore SE, Reeves RR (2018) Tracking Arctic marine mammal resilience in an era of rapid ecosystem alteration. *PLOS Biol* 16:e2006708
- Moore SE, Perryman WL, Gulland F, Wade PR, Rojas-Bracho L, Rowles T (2001) Are gray whales hitting ‘K’ hard? *Mar Mamm Sci* 17:954–958
- Moore SE, Grebmeier JM, Davies JR (2003) Gray whale distribution relative to forage habitat in the northern Bering Sea: current conditions and retrospective summary. *Can J Zool* 81:734–742
- Moore SE, Wynne KM, Kinney JC, Grebmeier JM (2007) Gray whale occurrence and forage southeast of Kodiak, Island, Alaska. *Mar Mamm Sci* 23:419–428
- Moore SE, Clarke JT, Okkonen SR, Grebmeier JM, Berchok CL, Stafford KM (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
- Nakagawa S, Johnson PC, Schielzeth H (2017) The coefficient of determination R² and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *J R Soc Interface* 14: 20170213
- Nishizawa B, Yamada N, Hayashi H, Wright C and others (2020) Timing of spring sea-ice retreat and summer seabird–prey associations in the northern Bering Sea. *Deep Sea Res II* 181–182:104898
- Paradis E, Schliep K (2019) ape 5.0: an environment for mod-

- ern phylogenetics and evolutionary analyses in R. *Bioinformatics* 35:526–528
- ✦ 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
- Perryman WL, Reilly SB, Rowlett RA (2011) Results of surveys of northbound gray whale calves 2001–2010 and examination of the full seventeen year series of estimates from the Piedras Blancas Light Station. International Whaling Commission Report SC/M11/AWMP3. <https://swfsc-publications.fisheries.noaa.gov/publications/CR/2011/2011Perryman.pdf> (accessed 13 February 2023)
- ✦ Perryman WL, Joyce T, Weller DW, Durban JW (2021) Environmental factors influencing eastern North Pacific gray whale calf production 1994–2016. *Mar Mamm Sci* 37:448–462
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2020) nlme: linear and nonlinear mixed effects models. R package version 3.1-148. <https://CRAN.R-project.org/package=nlme> (accessed 23 June 2021)
- R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Raverty S, Duignan P, Greig D, Huggins J and others (2020) Post mortem findings of a 2019 gray whale unusual mortality event in the Eastern North Pacific. International Whaling Commission Report SC/68B/IST/05
- ✦ Saitoh S, Iida T, Sasaoka K (2002) A description of temporal and spatial variability in the Bering Sea spring phytoplankton blooms (1997–1999) using satellite multi-sensor remote sensing. *Prog Oceanogr* 55:131–146
- ✦ Schonberg SV, Clarke JT, Dunton KH (2014) Distribution, abundance, biomass and diversity of benthic infauna in the northeast Chukchi Sea, Alaska: relation to environmental variables and marine mammals. *Deep Sea Res II* 102:144–163
- ✦ Screen JA, Simmonds I (2010) The central role of diminishing sea ice in recent Arctic temperature amplification. *Nature* 464:1334–1337
- ✦ Siddon EC, Zador SG, Hunt GL Jr (2020) Ecological responses to climate perturbations and minimal sea ice in the northern Bering Sea. *Deep Sea Res II* 181–182:104914
- ✦ Sigler MF, Renner M, Danielson SL, Eisner LB and others (2011) Fluxes, fins, and feathers: relationships among the Bering, Chukchi, and Beaufort seas in a time of climate change. *Oceanography* 24:250–265
- ✦ Spreen G, Kaleschke L, Heygster G (2008) Sea ice remote sensing using AMSR-E 89-GHz channels. *J Geophys Res C Oceans* 113:C02S03
- ✦ Stafford KM, Moore SE, Spillane M, Wiggins S (2007) Gray whale calls recorded near Barrow, Alaska, throughout the winter of 2003–04. *Arctic* 60:167–172
- Stewart JD, Weller DW (2021) Estimates of eastern North Pacific gray whale calf production 1994–2021. NOAA Tech Memo NMFS-SWFSC-653. <https://swfsc-publications.fisheries.noaa.gov/publications/CR/2021/2021Stewart4.pdf> (accessed 13 February 2023)
- ✦ Szesciorka AR, Ballance LT, Širović A, Rice A, Ohman MD, Hildebrand JA, Franks PJ (2020) Timing is everything: drivers of interannual variability in blue whale migration. *Sci Rep* 10:7710
- ✦ Urbán Ramírez J, Jiménez-López E, Guzmán HM, Viloria-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
- Vate Brattström L, Mocklin JA, Crance JL, Friday NA (eds) (2019) Arctic whale ecology study (ARCWEST): use of the Chukchi Sea by Endangered Baleen and other whales (westward extension of the BOWFEST). Final report of the Arctic whale ecology study (ARCWEST). BOEM 2018-022. Bureau of Ocean Energy Management, Seattle, WA, p 192–193. https://espis.boem.gov/final%20reports/BOEM_2018-022.pdf
- Wikle CK, Zammit-Mangion A, Cressie N (2019) Spatio-temporal statistics with R. CRC Press, New York, NY
- ✦ Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J R Stat Soc Series B Stat Methodol* 73:3–36
- ✦ Wright DL, Berchok CL, Crance JL, Clapham PJ (2019) Acoustic detection of the Critically Endangered North Pacific right whale in the northern Bering Sea. *Mar Mamm Sci* 35:311–362

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Woods Hole, Massachusetts, USA
Reviewed by: L. G. Torres and 2 anonymous referees*

*Submitted: November 14, 2022
Accepted: February 16, 2023
Proofs received from author(s): March 24, 2023*