Bowhead whale (*Balaena mysticetus*) and killer whale (*Orcinus orca*) co-occurrence in the U.S. Pacific Arctic, 2009–2018: evidence from bowhead whale carcasses

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ABSTRACT

Imagery and sighting data on bowhead whale (*Balaena mysticetus*) carcasses documented from 2009 to 2018 during aerial surveys in the eastern Chukchi and western Beaufort seas have provided evidence for killer whale (*Orcinus orca*) predation on bowhead whales of the Bering-Chukchi-Beaufort Seas stock. The Aerial Surveys of Arctic Marine Mammals (ASAMM) project provides information on distribution, behavior, and relative density of marine mammals. ASAMM surveys large areas of bowhead whale and killer whale summer and autumn habitat and offers consistent information on bowhead whale carcasses. Thirty-three bowhead whale carcasses were documented in July–October, from 2009 to 2018. Carcasses were distributed across the eastern Chukchi and western Beaufort seas from 141.6° W to 168.1° W and 68.9° N to 72.0° N. Carcass sighting rates (carcasses/1000 km) varied by month, year, and region. Statistical results suggest an alternating series of high and low annual carcass sighting rates. Eighteen bowhead whale carcasses having injuries consistent with probable killer whale predation were photo-documented: four each in 2016 and 2018, three each in 2013 and 2015, two in 2012, and one each in 2010 and 2017. Four carcasses, two in 2015 and one each in 2013 and 2018, were likely whales struck and lost during aboriginal subsistence hunting. Cause of death could not be determined for 11 carcasses. This study is the first systematic inquiry into non-harvest related mortality of bowhead whales in the U.S. Pacific Arctic and provides multi-year evidence for killer whale predation on bowhead whales in this portion of their range.

Keywords: Bowhead whale, Killer whale, Predation, Arctic, Survey-aerial, Line-transect

INTRODUCTION

Tracking mortality, including number of deaths, causes of mortality, and understanding threats that may lead to mortality, is an essential component for assessing the status of the Bering-Chukchi-Beaufort (BCB) Seas stock of bowhead whales (*Balaena mysticetus*). In the eastern Chukchi and western Beaufort seas, the large expanse of coastline relative to the few coastal village communities makes monitoring the shoreline for beach-cast bowhead whale carcasses difficult. Only a small number of carcasses can be investigated annually and few forensic necropsies are performed.

From 2009 to 2018, the Aerial Surveys of Arctic Marine Mammals (ASAMM) project conducted annual line-transect aerial surveys that were designed to coincide spatially and temporally with bowhead whales in the eastern

Chukchi and western Beaufort seas during summer (July–August) and early autumn (September–October). These surveys, provide information on distribution, behavior, and relative abundance of marine mammals, including BCB bowhead whales and their only natural predator, killer whales (*Orcinus orca*). ASAMM effectively surveys large areas of bowhead whale and killer whale habitat, and thus offers a long time series of consistent information on bowhead whales, floating and beach-cast bowhead whale carcasses, and killer whales (Willoughby et al. 2018).

The BCB bowhead whale stock is listed as endangered under the U.S. Endangered Species Act (NOAA 2020). Bowhead whales inhabit seasonally ice-covered waters of the Bering, Chukchi, and Beaufort seas (Braham 1984; Moore and Reeves 1993). In spring (April–May), most BCB bowhead whales migrate along the Alaska coast from wintering (December–March) habitat in the Bering Sea into the Chukchi Sea, past Point Barrow, and continue eastward into the Beaufort Sea, where they spend much of the summer and autumn (June–October) (Moore and Reeves 1993; Quakenbush et al. 2013). Bowhead whales are important nutritional, economical, spiritual, and cultural resources for 11 Alaska Native whaling communities who hunt them for subsistence (Braund et al. 2018).

Killer whale attacks, ship strikes, and entanglement in commercial fishing gear have been identified as potential non-harvest related causes of morbidity and mortality of bowhead whales (Hay et al. 2000; Ferguson et al. 2012; George et al. 2017; Shpak and Stimmelmayr 2017; North Slope Borough [NSB] Department of Wildlife Management [DWM] unpubl. data). These determinations were based on scarring and injury evidence from landed whales, stranding and necropsy data on beach-cast bowhead whales in Alaska, examination of images of bowhead whale carcasses, and traditional ecological knowledge (TEK) from Alaskan and Canadian aboriginal whaling communities. In an examination of 514 bowhead whales harvested in Alaska from 1990 to 2012, George et al. (2017) determined that 59 whales carried scar patterns consistent with definite line entanglement injuries, 10 whales had scarring from propeller injuries, and 29 whales had scarring consistent with killer whale injuries. However, these findings provide insight on whales who survived these incidents. Due to the remoteness and extensive geographical range of BCB bowhead whales, it is likely that many bowhead whales killed by entanglement, ship strike, and killer whale predation go undetected (George et al. 2017).

Killer whales are widely distributed throughout the Pacific Ocean and Bering Sea (Forney and Wade 2006). Transient (mammal eating) killer whales overlap spatially and temporally with BCB bowhead whales and are year-round inhabitants of the Bering Sea (Dahlheim 1997; Dahlheim and White 2010; Higdon et al. 2013). During the summer and autumn sea ice-free season in the U.S. Pacific Arctic, killer whales inhabit the northeastern Chukchi Sea. Killer whales are sighted annually adjacent to Utqiaġvik, Alaska, and are seen by Inupiaq hunters who hunt along the shoreline and on the water (George et al. 1994; NSB DWM Wildlife observation database unpubl.data). Confirmed sightings of killer whales in the western Beaufort Sea are scant, but Higdon et al. (2013) provides evidence for killer whale observations in the eastern Beaufort Sea and Amundsen Gulf. In the eastern Chukchi Sea, killer whale predation on gray whales (*Eschrichtius robustus*) has been observed firsthand and documented during necropsies (Lowry et al. 1987; George et al. 1994; George and Suydam 1998; NSB DWM stranding program unpubl.data; Willoughby et al. 2020). Interactions between killer whales and bowhead whales in the eastern Chukchi and western Beaufort seas has not been directly witnessed or reported; however, killer whales have been documented predating bowhead whales in most other areas of their geographical range, including near the Chukotka Peninsula (Melnikov and Zagrebin 2005), Sea of Okhotsk (Shpak and Paramonov 2018), Bering Sea (George et al. 1994), and eastern Canadian Arctic (Finley 1990; Jefferson et al. 1991; Ferguson et al. 2012; Higdon et al. 2012). From these reports we can draw insight to apply to observations of bowhead whale carcasses and killer whale observations made during line-transect aerial surveys in the eastern Chukchi and western Beaufort seas.

On the basis of bowhead whale carcass sighting and imagery data from 2009 to 2018, we provide new evidence for killer whale predation on BCB bowhead whales in the U.S. Pacific Arctic and discuss the ecological implications of our findings.

METHODS

The ASAMM study area encompasses the eastern Chukchi and western Beaufort seas. From 2009 to 2013 the study area comprised the area between 68°–72° N and 140°–169° W, and in 2014 was expanded south to 67° N, covering 242,000 km^2 (Fig. 1). Surveys were flown in De Havilland Twin Otters in 2009 and 2010 and Turbo Commanders from 2009 to 2018. All aircraft were equipped with left- and right-side bubble windows for a complete view of the survey trackline. Surveys were conducted daily, weather permitting, from approximately 2 July through 30 October. Survey flights were flown at a targeted speed of approximately 213 km/h, altitudes of 365–457 m, and Beaufort wind force ≤ 5. The marine mammal observer team consisted of one primary observer stationed at each bubble window and one dedicated data recorder. All marine mammal sightings, including carcasses, were recorded. A laptop computer with specialized data entry software that streamed location data from a global positioning system was used to collect, display, store, and summarize all survey data. Data collected at regular intervals during surveys included date, time, location, and environmental conditions. Additional data recorded during sighting events included species, initial and final group size, calf number, behavior, habitat, reaction, and swim direction. Changes in weather were updated as they occurred.

Beginning in 2009, ASAMM implemented standard methods to collect imagery of bowhead whale carcasses. When survey parameters and flight safety allowed, sightings of large whale carcasses were investigated by diverting to circle the carcass to verify species, determine level of decomposition, and, when possible, obtain photographs. Photos were collected using either a Canon EOS 7D or 1DX DSLR camera with a Canon 100–400 mm lens or similar from 2009 to 2018. Immediately following a flight, bowhead whale carcasses located on or within 18 km of shore were reported to NSB DWM. Within approximately 24 h, NOAA Marine Mammal Stranding Report - Level A Data forms were compiled for every new bowhead whale carcass sighted and disseminated with photos (when available) to the appropriate authorities, including the National Marine Fisheries Service Alaska Stranding Network Coordinators, NSB DWM, and Alaska Sea Grant.

Carcasses were identified as bowhead whale when sufficient visual data were available to make a positive species determination during in-field observations or from photos. Characteristics used to classify a carcass as bowhead whale included an overall rotund physique accompanied by a combination of other key identifiers, such as a large head relative to the body, upward arching lip line, bowed rostrum; white chin patch; long dark baleen; paddle-shaped pectoral fins; smooth black or non-mottled skin; and no dorsal fin, hump, or knuckles (Jefferson et al. 2019).

When ASAMM biologists could not determine a positive species identification, experts with the NSB DWM were consulted to evaluate species ID based on imagery. Unidentified cetacean or unidentified marine mammal was assigned when positive species ID was not possible.

All bowhead carcass images were systematically evaluated by biologists (ASAMM; NSB DWM) and a wildlife veterinarian (NSB DWM) for level of carcass decomposition (Geraci and Lounsbury 2005), body size, and signs of human interaction (ship strike; entanglement) (Moore et al. 2013; George et al. 2017), struck and lost (aboriginal subsistence hunting), and wounds associated with killer whale bites (Jefferson et al. 1991; George and Suydam 1998; Melnikov and Zagrebin 2005). Through image evaluation, individual bowhead whale carcasses were then categorized accordingly. Results from investigating cause of death were categorized in three ways:

1. *Probable killer whale predation* when imagery contained visual evidence of serious injuries consistent with killer whale predation to support that mortality was caused by killer whales or post-mortem scavenging; for example, killer whale dentition.
2. *Aboriginal subsistence hunting* based on timing of hunting activity, proximity to a whale reported as struck with hunting equipment (e.g., harpoon or floats) but not retained (a "struck and lost" whale), image review, or physical examination of the carcass.
3. *Could not be determined* when a minor injury was typical of that from killer whales, but there was insufficient evidence to classify as probable killer whale predation, or when the carcass was too decomposed, lacked visible or significant external injuries, or the image quality was too poor to determine cause of death.

Bowhead whale carcass sighting rates (number of bowhead whale carcasses per 1000 km of effort) were computed to evaluate the variability in carcass sightings between the eastern Chukchi Sea (EC: 67°–72° N and 157°–169° W) and western Beaufort Sea (WB: south of 71.2° N, 140°–146° W; south of 71.3° N, 146°–150° W; and south of 72° N, 150°–157° W) study areas, and across months and years. To maximize the sample size and to provide an index of relative occurrence, bowhead whale carcass sighting rates were calculated using sightings during all survey modes except deadhead, when no sighting or environmental data are recorded.

To quantify the multivariate effects of *month*, *year*, and *region* on bowhead whale carcass sighting rates, a generalized additive model (GAM; Wood 2006) was constructed. The analytical sample unit corresponded to a particular combination of *month*, *year*, and *region*, resulting in 80 total sample units in the model. Sighting rate was modeled as

$$ln(E(W_{i,j,k})) = ln(\mu_{i,j,k}) = \beta_0 + \boldsymbol{\beta}_{mo} month_i + \beta_{reg} region_j + s(year_k) + offset(ln(L_{i,j,k})) \qquad (1)$$

where

$W_{i,j,k}$: random variable for the number of bowhead whale carcasses in *month i*, *region j*, and *year k*. $W_{i,j,k}$ refers to the associated observations and $E(W_{i,j,k}) = \mu_{i,j,k}$ is the expected value (mean) of $W_{i,j,k}$;

β_0: intercept;

$\boldsymbol{\beta}_{mo}$: vector of parameters for the effect of *month*;

$month_i$: survey *month*, a factor variable;

β_{reg}: parameter for the *region* effect;

$region_j$: survey *region*, a factor variable;

$s(year_k)$: thin plate regression spline (Wood 2003), a smooth function, for the *year* effect;

$L_{i,j,k}$: length (km) of non-deadhead survey effort in *month i*, *region j*, and *year k*, which was incorporated into the model as a constant (an offset) to account for spatiotemporal heterogeneity in survey effort.

During preliminary analyses, Poisson, quasi-Poisson, Tweedie, and negative binomial GAMs were evaluated. Plots of mean squared response residuals against $\mu_{i,j,k}$ suggested that the quasi-Poisson model provided the best fit to the data due to overdispersion and the linear relationship between the variance and the mean (Ver Hoef and Boveng 2007), so this model structure was used going forward. All submodels of Eq. (1), in addition to a model with an interaction between *month* and *region*, were evaluated as candidate models. Model selection was based on minimizing the Generalized Cross Validation (GCV) score (Wood 2006). The analysis was conducted in R version 3.5.2 (R Core Team 2018) using package mgcv (Wood 2006).

RESULTS

A total of 33 bowhead whale carcasses were documented in the ASAMM database from 2009 to 2018 (Table 1, Fig. 1). Temporal and spatial variability were evident in bowhead whale carcass data. Twenty-five carcasses were found floating and eight were beach-cast. Carcasses were distributed across the EC and WB study areas from 141.6° W to 168.1° W and 68.9° N to 72.0° N (Fig. 1). Twenty-five carcasses occurred in the EC study area; eight were seen in the WB study area (Table 1, Fig. 1). Despite the WB having similar and, in some years (2015, 2016, 2017, and 2018), more, annual effort than the EC study area, the WB area accounted for only 24% of carcass sightings (Table 1, Fig. 2).

In the ASAMM study area as a whole, and in the EC portion of the study area, bowhead whale carcasses were seen in all years except 2011 and 2014 (Table 1). In contrast, in the WB portion of the study area, bowhead whale carcasses were seen only in four of ten years: 2013, 2015, 2016, and 2018 (Table 1). The most carcass sightings (*n*) in a single year was observed in 2015 (n = 10), followed by 2013 and 2018 (n = 6 each year), and 2016 (n = 5) (Table 1). In both study areas, more carcass sightings occurred in September than in other survey months: 14 of 25 in the EC and 4 of 8 in the WB (Table 1). When survey areas and years are combined, September had the most survey effort and highest carcass sighting rate. The maximum monthly sighting rate in any given year and region occurred in October 2015 in both the EC and WB.

The GAM was a valuable and successful distillation of information from the 33 carcass sightings, and model results were consistent with results from the univariate analysis described above. Out of the 80 possible analytical sample units (i.e., combinations of *region*, *month*, and *year*) included in the analysis, 22 sample units had at least one bowhead whale carcass sighting. The best GAM, based on GCV, included all covariates, *month*, *region*, and *year*, but did not include an interaction between *month* and *region.* The model incorporated 13.3 effective degrees of freedom, including 8.29 effective degrees of freedom associated with the smooth function for *year*. The model explained 70.6% of the deviance. The effect of *year* on total carcass sighting rate (regardless of cause of death) when *month* and *region* were included in the model is shown in Fig. 3, suggesting an alternating series of high and low annual sighting rates. The point estimates and 95% confidence intervals for each of the parametric terms (the β's) in the linear predictor (right side of Eq. 1) are shown in Fig. 4. The intercept represents the carcass sighting rate in the EC in August. Sighting rates were lowest in August (the intercept), increased through July and September, and were highest in October (Fig. 4). In this multivariate analysis, carcass sighting rates in October were found to be higher than September because there was only a single year (2013) in which sighting rates were high in September, and that influence was incorporated into the smooth function for *year*. Simply put, the GAM attributed the spike in carcass sighting rates in September 2013 to a *year* effect, whereas our univariate analyses attributed it to a *month* effect. Sighting rates in the WB were less than the EC.

ASAMM collected imagery for 32 of the 33 bowhead whale carcass sightings. The unphotographed sighting was recorded during an ASAMM survey conducted on 30 July 2018, and its location conflicted with Wiley Post-Will Rogers Memorial (Utqiaġvik, Alaska) airport airspace. The carcass was subsequently investigated by the NSB DWM marine mammal stranding program during a boat-based survey on 3 August 2018, allowing us to include it in our analysis. ASAMM imagery review provided insight into the probable cause of death for 22 of the 33 carcasses recorded since 2009.

Over the 10-season study period, 18 bowhead whale carcasses were categorized as probable killer whale predation (four carcasses per year in 2016 and 2018, three carcasses per year in 2013 and 2015, two carcasses in 2012, and one carcass per year in 2010 and 2017) (Table 1). Carcasses exhibited bodily injuries consistent with killer whale predation, including evidence of bites (i.e., single or in combination large semi-circular tissue defects to the head, body, and appendages); evisceration of abdomen; skin and blubber peeled away from body (flensed); tongue and throat region missing or torn; and tissue fraying around mouth opening, on pectoral flippers, and flukes.

Eight of the bowhead whale carcasses categorized as probable killer whale predation were small whales considered to be calves or yearlings, one each in 2013, 2016, 2017, two in 2018, and three in 2015. Each of the calf/yearling carcasses was photographed and showed signs of probable killer whale predation, including flesh missing from head and ventral "chin", suggesting death was likely due to predation. Two had healed rake marks on their right pectoral flippers (Fig. 5). Ten of the predated carcasses appear larger than calves/yearlings.

Four whales were likely struck and subsequently died as the result of aboriginal subsistence hunting (one each in 2013 and 2018 and two in 2015). A whale carcass sighted on 16 September 2013 was near Cross Island, Alaska, and likely struck and lost by subsistence whalers from the village of Nuiqsut, who base from Cross Island. A struck and lost whale carcass, sighted on 4 October 2015 northeast of Utqiaġvik, Alaska, was retrieved and brought ashore by Utqiaġvik hunters, and images of the whale's ventral chin patch confirmed it was the same whale sighted by ASAMM (R. Suydam, NSB DWM, pers. comm. on 5 October 2015). The second struck and lost whale in 2015 was sighted on 27 October, after fall whaling had concluded. This carcass was >250 km west of Utqiaġvik, so close examination was not possible. Photos of the carcass showed that the gear attached (orange buoy and attached line) was consistent with commonly used aboriginal subsistence hunting equipment but not commercial fishing gear (C. George, NSB DWM, pers. comm. to J. Clarke, Joint Institute for the Study of the Atmosphere and Ocean, on 28 October 2015). The struck and lost whale carcass sighted on 30 July 2018 near Utqiaġvik was likely from spring subsistence whale hunting based on the level of decomposition and time lapse from most recent subsistence hunting. This carcass was physically examined by the NSB DWM veterinarian and an Inupiaq hunter who identified characteristic harpoon and explosive projectile wounds, confirming the whale's cause of death was by aboriginal subsistence hunting.

Cause of death could not be determined for the remaining 11 bowhead whale carcasses in this study. Seven carcasses, one of which was skeletal remains, had no discernable injuries that would have resulted in death. Three carcasses exhibited minor injuries that may have been caused by killer whales. Lastly, one carcass appeared to have a long linear cut associated with removed blubber and possible biological defects (semi-circular in shape); however, the advanced state of decomposition of the carcass makes it impossible to determine if the linear cut and blubber removal were flensing from killer whale predation or if this was a landed whale that had been partially butchered and either broke through the shorefast sea ice (sea ice attached to the coast) butchering site or could not be pulled onto the ice for complete butchering.

The EC and WB study areas have been the subject of aerial surveys conducted as far back as the 1980s (Clarke et al. 2013); however, the first sighting of killer whales did not occur until 2012. Since then, killer whale sightings in the ASAMM study area have been highly variable (Fig. 1). Killer whales were seen in August 2012 (one sighting of thirteen whales) and 2018 (one sighting of four whales), and in September 2012 (one sighting of five whales), 2016 (five sightings of thirty whales), 2017 (one sighting of two whales), and 2018 (one sighting of twelve whales). Most (70%) killer whale sightings occurred in September. Of ASAMM's 10 killer whale sightings, all were in the Chukchi Sea ecosystem, although the sighting in August 2012 was approximately 10 km southwest of Point Barrow and technically within this study's WB study area.

DISCUSSION

The value of ASAMM's imagery for determining probable cause of death for bowhead whale carcasses was unforeseen when standardized methods for collecting imagery were implemented in 2009. Review of imagery and sighting data on BCB bowhead whale carcasses and killer whale sighting data from 10 seasons (2009–2018) of aerial surveys in the eastern Chukchi and western Beaufort seas have provided new and robust evidence that killer whales are preying on bowhead whales in the eastern Chukchi and western Beaufort seas.

Given what is known about the behavior and ecology of killer whales, the potential dual origins of injuries seen on bowhead whale carcasses, either ante-mortem (i.e., killer whale predation) or post-mortem (i.e., scavenging on carcasses that died from other causes) need to be considered. From whaling records, Whitehead and Reeves (2005) provide evidence of scavenging behavior by killer whales during the commercial whaling era of the mid-twentieth century, when killer whales used loud acoustic signals from commercial whaling ships to locate clusters of floating balaenopterid whale carcasses, in queue to be processed, adjacent to the ships. Thus, natural mortality of bowhead whales, albeit thought to be very low (e.g., estimated survival rate of 0.976–0.996, Givens et al. 2017), combined with struck and lost whales from aboriginal hunts, could potentially provide carcasses that could be eaten by scavenging killer whales. That said, scavenging by killer whales of struck and lost bowhead whales originating from aboriginal hunts has never been documented by TEK or other scientists. Prolonged feeding, where killer whales return to previous kills to continue feeding, has been observed for bowhead whale carcasses in the Sea of Okhotsk (Olga Shpak pers comm., 2020) and described for gray whales carcasses in Alaska (Barrett-Lennard et al. 2011).

Firsthand accounts of killer whale attacks on bowhead whales are historically rare (Mitchell and Reeves 1982, 1988; Finley 1990; Jefferson et al. 1991; Reeves et al. 2006). However, increasing evidence of killer whale predation on bowhead whales is emerging in published research. Inuit and Yupik traditional ecological knowledge studies provide strong evidence that killer whales successfully hunt bowhead whales (George et al. 1994; Hay et al. 2000; Melnikov and Zagrebin 2005; Higdon and Ferguson 2009; Ferguson et al. 2012; Huntington and Quakenbush 2013; Matthews et al. 2011; Reinhart et al. 2013; Young et al. 2019). Evidence for the potential significance of killer whale predation on bowhead whales comes from firsthand accounts of killer whale predation on bowhead whales in the Sea of Okhotsk (Shpak and Paramonov 2018). Post-mortem examinations, albeit limited in number, of stranded bowhead whales with fatal injuries from killer whales provides further evidence of killer whale predation in Alaska and eastern Canada (NSB DWM 13BFD skull cliff; DeMarban 2015; Suydam et al. 2016; Young et al. 2019). Lastly, studies of scar patterns on live and subsistence hunted bowhead whales provide evidence for killer whale predation pressure in at least three of the four recognized bowhead whale stocks (Sea of Okhotsk, Shpak and Stimmelmayr 2017; BCB, George et al. 1994, 2017; Eastern Canada-West Greenland, Reinhart et al. 2013). Given all available historic and recent data on predatory killer whale and bowhead whale interactions, we conclude, while acknowledging the limitations of our study where carcass examination was based only on image evaluation, that the 18 BCB bowhead whale carcasses documented over the 10-season study period represent likely fatal outcomes from killer whale predation events, rather than scavenging events.

Our findings also complement Stafford's (2018) results from passive acoustic data collected in the southern Chukchi Sea, which show that the number of days transient killer whales were acoustically detected increased from September to November over a seven-year series from 2009 to 2015, and increased from June through November from 2013 to 2015. Our results also corroborate the work of George et al. (2017), who found an increasing prevalence of injuries or scars from killer whale predation attempts in landed bowhead whales, with a higher probability of killer whale rake mark scars on bowheads from 2002 to 2012 compared to the prior two decades (1990–2011). Increased killer whale predation on bowhead whales in the eastern Chukchi and western Beaufort seas may be associated with the dramatic sea ice reduction during summer and autumn that may allow killer whales to hunt in areas that were previously ice covered, similar to conditions occurring in the eastern Canadian Arctic (Higdon and Ferguson 2009; Reinhart et al. 2013) and Sea of Okhotsk (Shpak 2016).

The higher number of bowhead whale carcass sightings in the eastern Chukchi Sea compared to the western Beaufort Sea cannot be accounted for by differences in survey effort between the two areas. It seems likely that more carcasses occur in the eastern Chukchi Sea study area because killer whales frequent this area more often than the western Beaufort Sea study area. Utqiaġvik residents have reported seeing a few killer whales annually in the vicinity of Point Barrow in July and August (George at al. 1994). Also, two pods of nine killer whales were seen in the northeastern Chukchi Sea during vessel surveys in 2008 (Aerts et al. 2013). Hannay et al. (2013) acoustically detected killer whales in the northeastern Chukchi Sea periodically during the sea ice-free season (July–October) in 2009 and 2010, with the most detection days occurring in September. Likewise, September is also the month when most killer whale and bowhead whale carcasses were sighted by ASAMM. There is one report of killer whales in the Alaska Beaufort Sea (George and Suydam 1998) and sightings of killer whales in the eastern Beaufort Sea and Amundsen Gulf (Higdon et al. 2013). Killer whales seen in the eastern Beaufort Sea are likely extralimital animals from the Bering Sea transient stock (Higdon et al. 2013). The identity of most of the killer whales encountered by ASAMM remains a mystery. However, analysis of killer whale imagery did match one killer whale ASAMM sighted in August 2012, approximately 10 km northwest of Utqiaġvik, to a transient male known from several encounters near False Pass and Unimak Island in the Aleutian Islands (Clarke et al. 2013).

Killer whales in the U.S. Pacific Arctic do not appear to be targeting small (calf or yearling) bowhead whales exclusively. Of the 18 bowhead whale carcasses classified as probable killer whale predation, only eight were small whales considered to be calves or yearlings. Classifying bowhead whales as calf or yearling was based primarily on field observations and analysis of oblique aerial imagery, and defining age class further was not possible within the limits of these methods. George et al. (1994, 2017) found that scarring from killer whale predation attempts were more commonly documented on mature bowhead whales than immature. Similarly, Weller et al. (2018) found that more non-calf western gray whales acquired killer whale rake marks than calves during their study. The whales comprising these studies did not sustain lethal injuries and the ages of the whales when the killer whale attacks occurred are unknown. However, calves may be more likely to sustain lethal injuries while older whales have more time to be exposed to killer whale attacks and accumulate scarring over a long lifetime, providing additional evidence to support that killer whales attack bowhead whales larger than calves/yearlings. Killer whales hunt in coordinated groups and use several techniques to immobilize and kill large prey, including bowhead whales. Attacking killer whales have been reported as biting and holding onto pectoral fins and tail flukes to slow prey down, drowning whales by holding them underwater and/or covering their blowholes, and ramming the whale's ribs and underside, likely causing internal hemorrhaging and rib fractures (Hay et al. 2000; Melnikov and Zagrebin 2005; Ferguson et al. 2012; Weller et al. 2018). Although observed killer whale attacks on large baleen whales are fairly uncommon, such attacks are well documented (Jefferson et al. 1991; Ferguson et al. 2012).

In spring, bowhead whales of the BCB stock migrate annually from nutrient rich waters of the Bering Sea to the Beaufort Sea, perhaps because of the higher likelihood of killer whale predation in the Bering Sea (George et al.

1994; Ford and Reeves 2008). Sea ice extent during summer and autumn in the Chukchi and Beaufort seas has declined dramatically since the beginning of the sea ice satellite record in 1979 (Vihma 2014). In this region there has also been earlier seasonal sea ice melting, later seasonal sea ice freeze up, and thinner sea ice, and these downward trends are expected to continue (Wang et al. 2018). For bowhead whales who use dense sea ice cover to escape attacking killer whales, or who shift from ice-free water to ice-covered water when killer whales are present (Finley 2001; Ford and Reeves 2008; Matthews et al. 2020), the reduction in summer and autumn sea ice cover due to climate change may negate these avoidance strategies. What effects would increased predation by killer whales in the U.S. Pacific Arctic have on BCB bowhead whales from a behavioral and population perspective?

To avoid killer whales, bowhead whales could potentially change their migration habits, though the effects of this strategy are unpredictable. Bowhead whales are typically in dense sea ice during their spring migration from the Bering Sea to the Chukchi and Beaufort seas; however, during their autumn migration from the Beaufort Sea back to the Bering Sea, the Chukchi Sea is ice-free, and bowhead whales usually fan out across the broad Chukchi Sea shelf until they reach Chukotka, then migrate south along the Chukotka coastline (Quakenbush et al. 2013). To avoid killer whales, bowhead whales could possibly travel farther north into the late summer-autumn sea ice edge where Pacific killer whales are not known to range. Alternatively, bowhead whales could stay closer to the Alaskan Chukchi coastline in shallower water. Bowhead whales moving into shallow water or undertaking long deep dives are observed predator avoidance strategies in areas other than the U.S. Pacific Arctic (Finley 2001; Ferguson et al. 2012; Shpak and Paramonov 2018; Matthews et al. 2020). Other whale species (e.g., gray whales along western North America), stay close to the shoreline in shallow water along their migration route, likely to avoid killer whale predation. From a population perspective, it is difficult to predict if killer whale predation will become relevant for the BCB bowhead whales. Alternative killer whale prey species, including gray whales (Ford and Reeves 2008) and, more recently, fin whales (*Balaenoptera physalus*) and humpback whales (*Megaptera novaeangliae*), are increasingly present in the eastern Chukchi Sea during summer and autumn months (Brower et al. 2018; Clarke et al. 2019).

This study includes bowhead whales that were struck and lost during aboriginal subsistence hunting. Efficiency of the harvest (number of whales landed and number of whales struck) is greatly influenced by environmental effects (e.g., weather, sea ice, etc.) and whale behavior. The BCB bowhead whale hunt in Alaska had an efficiency of 77% from 2008 to 2017 (Suydam and George 2018). Strong shorefast sea ice is needed to pull landed bowhead whales onto a stable platform for butchering in spring. According to aboriginal hunters, sea ice breakage during spring whaling, at least in Utqiaġvik, is becoming more frequent (Stimmelmayr et al. 2020). Minimal butchering due to weak shorefast sea ice is the most likely explanation for the bowhead whale with a long linear cut and removed blubber discussed above as a carcass classified as "could not be determined." Lack of additional supporting information prohibited it from being classified as "aboriginal subsistence hunting."

No active entanglement in fishing gear was observed on any of the carcasses, and sharp trauma from vessel collisions (e.g., propeller cuts, severed tail stock, or fins) (Costidis et al. 2013) was not apparent, although only half of each whale's body is visible in the images. As the U.S. Pacific Arctic warms and becomes more accessible to killer whales, marine traffic, and commercial fisheries, these carcass data and cause of death classification can provide context for interpreting future information on bowhead whale mortality occurrence and causes of death.

Nearly all of the bowhead whale carcasses ASAMM detected would have gone undocumented in the absence of these aerial surveys. Monitoring and documenting bowhead whale carcasses and killer whale occurrence in areas not visible from land is important for assessing ecological impacts of a changing Arctic—in this case, the apparent increased occurrence of an apex predator. This study brings to light, based on several lines of evidence, that bowhead whales are being predated on by killer whales in the U.S. Pacific Arctic. Determining causes of mortality and morbidity is a necessary tool for assessing stock health (Muto et al. 2019) and assists in implementing effective management and conservation of an endangered species.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest: The authors declare that they have no conflicts of interest.

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Table 1

All bowhead whale (*Balaena mysticetus*) carcasses (2009–2018) detected during line-transect aerial surveys in the eastern Chukchi Sea study area (EC; see Fig.1), western Beaufort Sea study area (WB; see Fig. 1), and both study areas combined (A; see Fig. 1), tallied by month and year. The number of bowhead whales whose cause of death was categorized as probable killer whale (*Orcinus orca*) predation are provided inside brackets. Years when killer whales were sighted are indicated in bold

	JUL			AUG			SEP			OCT			
	EC	WB	A	EC	WB	A	EC	WB	A	EC	WB	A	Total
2009	0	0	0	1	0	1	0	0	0	0	0	0	1
2010	1[1]	0	1[1]	0	0	0	1	0	1	0	0	0	2[1]
2011	0	0	0	0	0	0	0	0	0	0	0	0	0
2012	0	0	0	0	0	0	1[1]	0	1[1]	1[1]	0	1[1]	2[2]
2013	0	0	0	0	0	0	5[3]	1	6[3]	0	0	0	6[3]
2014	0	0	0	0	0	0	0	0	0	0	0	0	0
2015	0	0	0	1	0	1	2[1]	1	3[1]	4[1]	2[1]	6[2]	10[3]
2016	1[1]	0	1[1]	0	1	1	2[2]	1[1]	3[3]	0	0	0	5[4]
2017	0	0	0	0	0	0	1[1]	0	1[1]	0	0	0	1[1]
2018	1[1]	1	2[1]	1	0	1	2[2]	1[1]	3[3]	0	0	0	6[4]
Total	3[3]	1	4[3]	3	1	4	14[10]	4[2]	18[12]	5[2]	2[1]	7[3]	33[18]

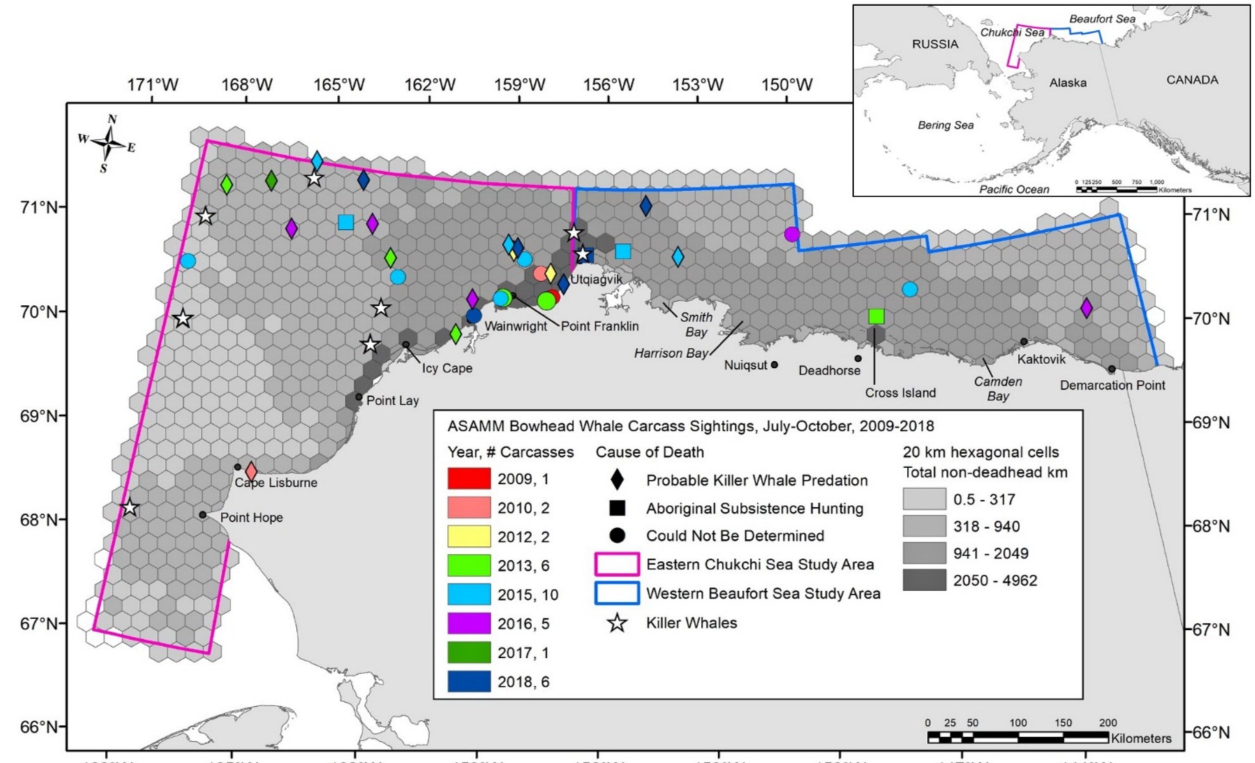

Fig. 1

ASAMM study area, including the eastern Chukchi Sea study area (EC; 2009–2013: 68°–72° N, 157°–169° W; 2014–2018: 67°–72° N, 157°–169° W) and western Beaufort Sea study area (WB; 2009–2018: south of 71.2° N, 140–146° W; south of 71.3° N, 146–150° W; and south of 72° N, 150–157° W). The light to dark grey 20-km hexagonal cells depict the amount of combined non-deadhead survey effort from 2009 to 2018, where lighter cells had the least survey coverage and darker cells had the most. Bowhead whale (*Balaena mysticetus*) carcasses and killer whale (*Orcinus orca*) sightings overlay the hexagonal survey effort cells. Bowhead whale carcasses are color-coded by year and symbol shapes indicate the cause of death category. Killer whale sightings are indicated with white stars

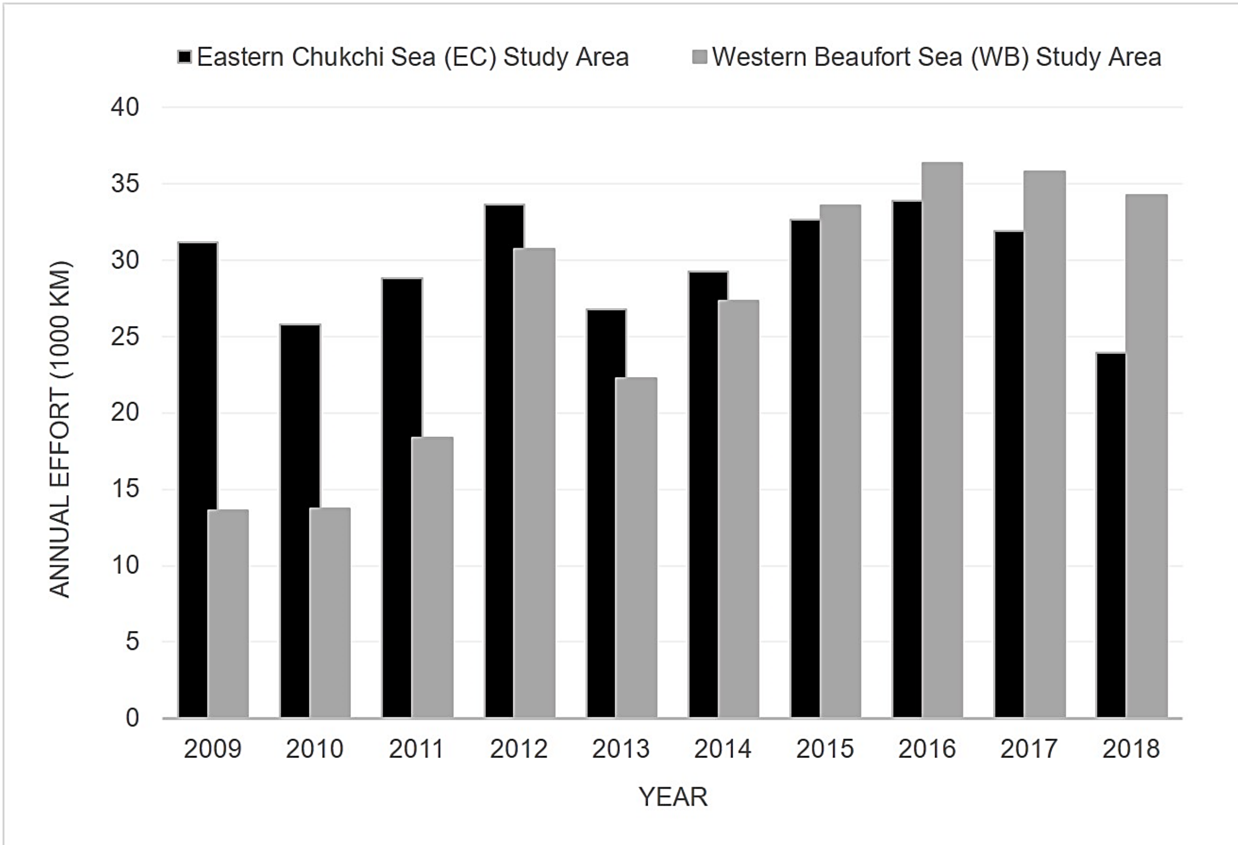

Fig. 2

ASAMM annual non-deadhead survey effort, by study area, 2009–2018. Note that consistent Beaufort Sea surveys in 2009–2011 did not begin until September

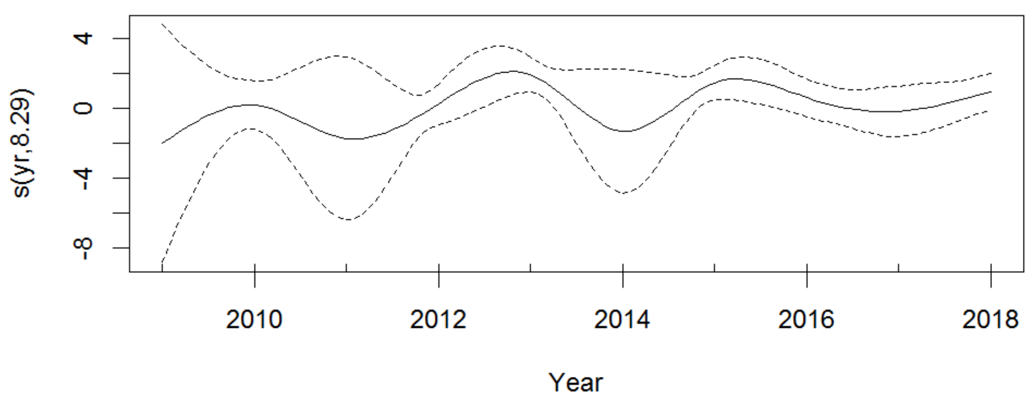

Fig 3

Interannual variability in bowhead whale (*Balaena mysticetus*) carcass sighting rate, described by the smooth function (thin plate regression spline) in the generalized additive model with *month* and *region* also included. The dashed curves represent the 2-standard error bounds (n = 80). The effective degrees of freedom are shown in the parentheses on the y-axis label. Simply stated, the effect of *year* on carcass sighting rate when *month* and *region* were included suggests an alternating series of high and low carcass sighting rates

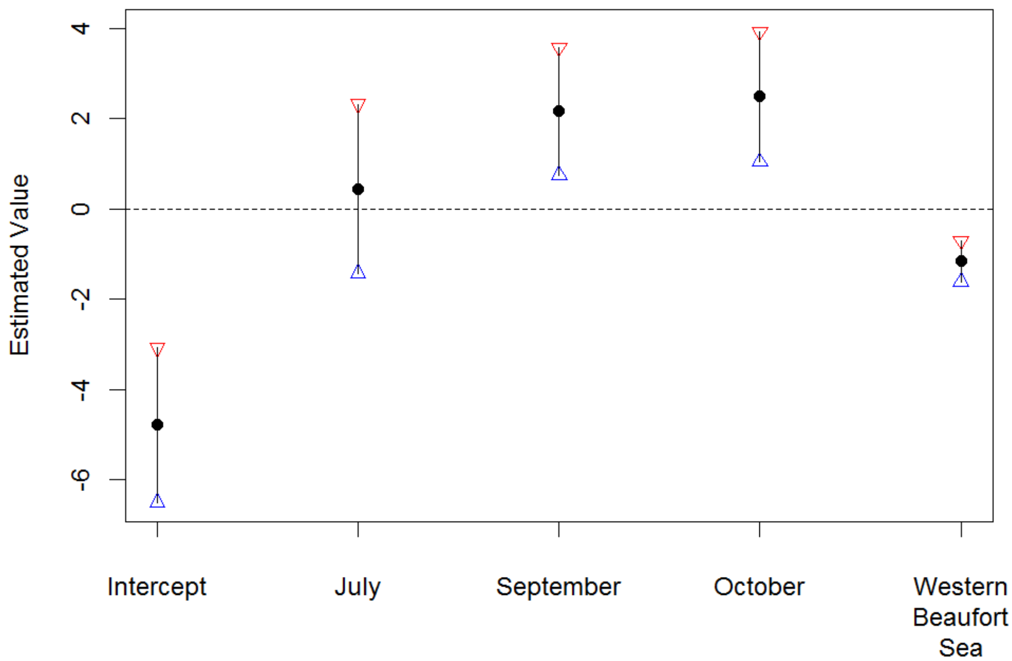

Fig 4

Point estimates and 95% confidence intervals for the parametric terms in the generalized additive model of bowhead whale (*Balaena mysticetus*) carcass sighting rate (n = 80). The intercept (β_0) represents the base case: carcass sighting rates in August in the eastern Chukchi Sea were lowest. The parameters in the vector β_{mo} quantify the difference between the base case and each of the remaining three months, July, September, and October. The parameter β_{reg} quantifies the difference between sighting rates in the western Beaufort Sea relative to the eastern Chukchi Sea; this effect is labelled "Western Beaufort Sea" in the figure above. Sighting rates in the western Beaufort Sea were less than the eastern Chukchi Sea. Parameters located above the dashed line (located at zero) identify factors that increase carcass sighting rate relative to the base case, and vice versa. In other words, the value of the linear predictor (right side of Eq. 1) is increased by parameters located above the dash line and it is decreased by parameters located below the dash line

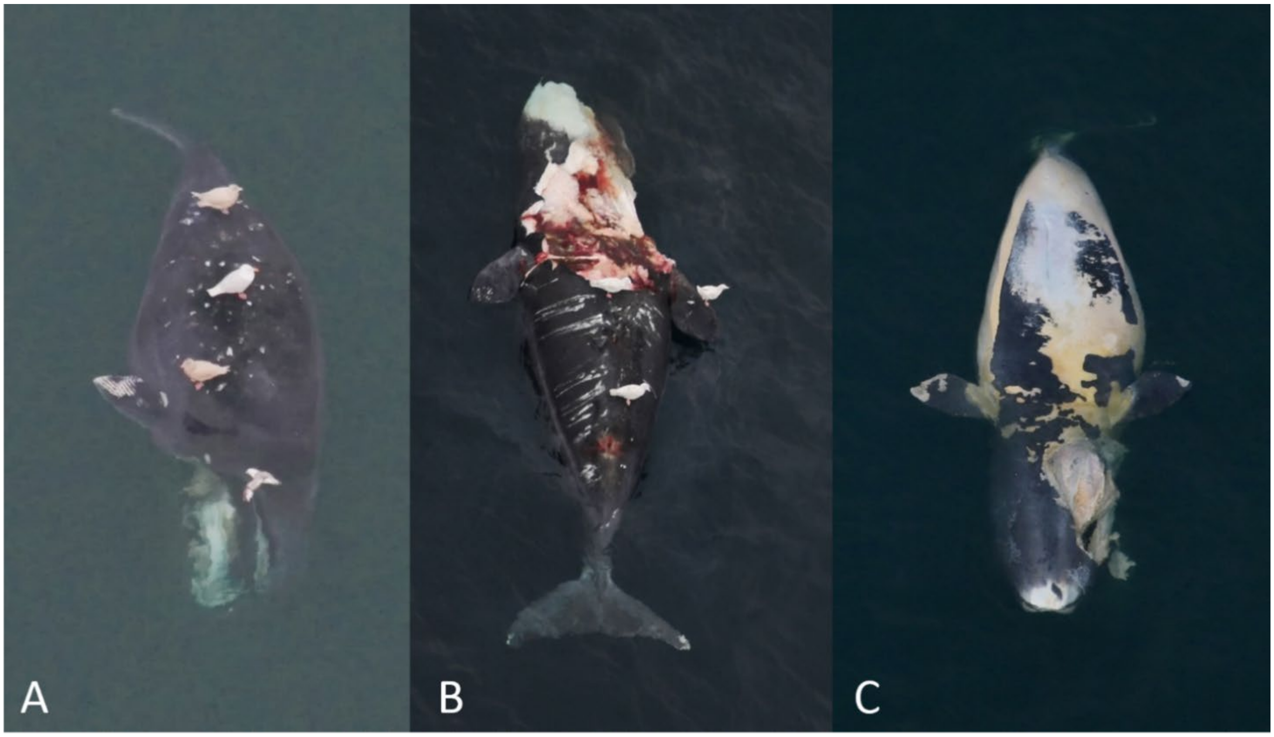

Fig. 5

Examples of severe injuries consistent with probable killer whale (*Orcinus orca*) predation on a bowhead whale (*Balaena mysticetus*) calf /yearling. Images A (calf), B (calf or yearling), and C (calf or yearling) show flesh missing from heads and ventral “chins.” Image A and B also show rake mark scarring on the whale’s right pectoral flippers