Bowhead whale mortality event in Nunavut, Canada – Autumn, 2020

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ABSTRACT

Cetacean mortality events in the Arctic often go underreported compared with events in more highly populated regions. Here, we report a mortality event involving the death of 11 bowhead whales around the Gulf of Boothia, Canada. The whales were discovered between October 2020–April 2021. Reports of 11 dead bowhead whales within six months in one area raised concerns among local hunters and community members. Due to the remoteness of these strandings and challenges with access, complete necropsies were not performed, but local Inuit collected tissue samples from eight of the whales. Possible reasons for these deaths include unusual weather events, nutritional stress/starvation, metabolic abnormalities, infectious disease, anthropogenic impacts (such as vessel collisions) and killer whale predation. To determine the most likely cause of these strandings, demographic, temporal, environmental, epidemiological, pathologic and contaminant analyses were performed. Results were compared with published accounts and historical data where appropriate. Killer whale sightings by local Inuit both before and during the stranding events confirmed the presence of these predators in close proximity to the carcass locations, with predation marks observed in several carcasses. We conclude that this was the most probable direct contributing factor to the mortality event. Indirect contributing factors might also include reduced ice coverage as a result of climate change and nutritional stress. Further monitoring of this population is required to assess health from both a scientific and an Indigenous perspective.

KEYWORDS: CLIMATE CHANGE; CUMULATIVE STRESSORS; HEALTH; KILLER WHALE PREDATION; POPULATION MONITORING

INTRODUCTION

In the Canadian Arctic, bowhead whales (*Balaena mysticetus*) are divided into two spatially distinct populations: the Bering-Chukchi-Beaufort (BCB) population and the Eastern Canada-West Greenland (ECWG) population. The ECWG population is currently estimated to comprise 5,173 individuals (95% CI: 3,436–7,788) (Biddlecombe *et al.*, 2023). Sustainable harvest of the BCB population is undertaken by the Inuvialuit and Inupiat, while the ECWG population is harvested by Inuit in the eastern Canadian Arctic and Greenlanders in West Greenland (Heide-Jørgensen *et al.*, 2012; Ferguson *et al.*, 2021). The distribution of the ECWG population extends from the Canadian Arctic Archipelago to the west Greenland coast (Chambault *et al.*, 2018). The ECWG bowhead whale

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population is currently recovering from historical commercial overharvesting. However, the late onset of sexual maturity and extended inter-birthing interval in bowhead whales result in naturally slow population increases (George *et al.*, 2004; Higdon, 2010). Current threats to bowhead whales include anthropogenic causes of mortality such as vessel collisions, fishing gear entanglement, pollution, harmful algal blooms and climate change (Lefebvre *et al.*, 2016; George *et al.*, 2017; Stimmelmayr *et al.*, 2021; Martin *et al.*, 2023). Indirect threats to bowhead whales include shifts in prey distribution and abundance, adverse weather conditions and increased species overlap as a result of climate change, which can increase the risk of killer whale predation (*Orcinus orca*) and disease due to novel pathogen exposure (Ferguson *et al.*, 2010a; Stimmelmayr *et al.*, 2021; Barratclough *et al.*, 2023; Domínguez-Sánchez *et al.*, 2023). For the ECWG population, predation by killer whales, strandings, ice entrapments and net entanglement due to the expansion of commercial fisheries are also potential causes of morbidity and mortality (Hay *et al.*, 2000; Ferguson *et al.*, 2021; Reeves *et al.*, 2022).

A cetacean mass mortality event is a stranding event where multiple cetaceans are found dead in a specific area within a short period of time. Despite multidisciplinary efforts to understand factors contributing to individual and mass mortality events in cetaceans, it is not always possible to determine an underlying cause (Bogomolni et al., 2010). As a result, these events are less likely to be reported in literature than mortality events where a diagnosis was obtained, even in cases involving significant levels of mortality (Gulland, 2006). In mysticetes, mortality events are usually distributed over a prolonged period rather than presenting as a unique mass stranding (Christiansen et al., 2021). In addition, they can be difficult to document due to the lack of carcass availability, with more pelagic species or malnourished individuals more likely to sink than wash up onshore (Moore et al., 2020). Frequently, mortality events are determined to be multifactorial, requiring scientists to consider both intrinsic and extrinsic factors in addition to environmental and biological conditions, known as a multiple stressors approach (Oldach et al., 2022; Pirotta et al., 2022). Intrinsic factors can include individual health status, nutritional state, behaviour and reproductive state (Bradford et al., 2012). Extrinsic factors can be environmental, such as weather, sea ice and temperature, harmful algal blooms, as well as anthropogenic influences previously mentioned (Häussermann et al., 2017; Rockwood et al., 2021). Biological considerations can be both inter and intraspecific, and include social status, predator-prey interactions and food availability (Puig-Lozano et al., 2020). With the dynamic and complex interplay of these multiple potential influences, it is rare that a cetacean mortality event can be attributed to a single factor (Gulland & Hall, 2007).

Beginning in October 2020, 11 bowhead whale carcasses were found in the vicinity of the Gulf of Boothia, Canada, over a six-month period. Given that the carcass locations (onshore) were not accessible to whales after freeze-up, the mortality event likely occurred in Autumn 2020. Two carcasses were discovered in January and April 2021, covered in snow. Based on Inuit Qaujimanituqangit (Inuit traditional knowledge, Hay et al., 2000; Arnakak, 2002) and historic stranding reports, this event represented a high mortality rate and warranted investigation. Due to the travel restrictions and related public health concerns in place at the time due to the COVID-19 pandemic, and the remoteness of some of these stranding locations, the response to the stranding reports was limited and full necropsy examinations were not feasible. The high number of carcasses within a localised area within a short period of time raised concerns among Inuit in the nearby communities of Kugaaruk and Taloyoak, Nunavut, and prompted a multidisciplinary collaborative investigation of the mortality event between DFO and Inuit hunters from the communities Kugaaruk, Taloyoak and Naujaat. Several potential causes of the unprecedented mass mortality event were evaluated, including increased predation by killer whales (Kay et al., 2000; Ferguson et al., 2010a; Ferguson et al., 2012; George et al., 2017; Young et al., 2020; Willoughby et al., 2022); starvation potentially due to lack of prey availability or change in the nutritive quality of available prey; vessel collision or entanglement in fishing gear (Reeves et al., 2012; George et al., 2017); and/or ice entrapments (Savelle et al., 2000; Ferguson et al., 2010b). Although not previously detected in BCB bowhead whale health surveys, cetacean diseases of concern, such as morbillivirus, influenza A and Brucella spp., have been detected in mass mortality events of other cetaceans, including other mysticetes (Duignan, 1999; Nielsen et al., 2001; Ohishi et al., 2016; Stimmelmayr et al., 2021; Gass et al., 2022; Barratclough et al., 2023). Subsequently, we deemed it necessary to determine the potential involvement of these pathogens as contributing factors to mass mortality. Finally, the potential influence of high contaminant levels contributing to the mortality event was also explored.

Our investigation of the bowhead whale mortality event at Gulf of Boothia involved documentation of the spatial distribution of mortalities, examination of photographs and tissue samples provided by Inuit hunters for gross abnormalities or microscopic lesions, screening for potential persistent organic pollutants (PCBs) and pathogens, and identification of contributing environmental factors, such as sea ice freeze-up and coverage. Where possible, results from stranded carcasses were compared with healthy bowhead whales from aboriginal Inuit hunts to provide a baseline comparison. We describe the results of these investigations to determine the cause of this mortality event and how a diagnosis via exclusion was obtained.

MATERIALS & METHODS

Study area

Between October 2020 and April 2021, 11 beach-cast bowhead whale carcasses were reported in the vicinity of the Gulf of Boothia, near the communities of Kugaaruk and Taloyoak, Nunavut (Fig. 1). All carcasses were within a 200 km radius of Kugaaruk, in Nunavut, Canada. Initial reports of four dead whales were reported in the local news (Nunatsiaq News, 13 October 2020⁷) and via social media platforms. Members of the local Hunters and Trappers Associations (HTA) from Kugaaruk, Taloyoak and Naujaat assisted in the collection of data, photographs and tissue samples from the carcasses for Fisheries and Oceans Canada (DFO). As a result of local community cooperation and collaboration, additional data, including morphometrics (total body length, axillary girth; George, 2009) and tissue samples (muscle, skin, blubber, baleen plates) were obtained from eight of 11 whales. Biological tissue samples were included in various diagnostic analyses.



Figure 1. Locations of 11 stranded ECWG bowhead whale carcasses (red circles; ID Table 1) in the Gulf of Boothia area, discovered between Oct 2020 to Jan 2021, with outline of satellite images searched for additional carcasses (black rectangular boxes).

⁷ https://nunatsiaq.com/stories/article/dead-mutilated-bowhead-whales-beached-near-kugaaruk-nunavut-point-to-killer-whale-attacks/

Environmental samples

Wind speed (km/hr), temperature (°C) and sea ice concentration and coverage over the stranding period were assessed and compared with available historic data from the same station (downloaded from Climate Data for a Resilient Canada.⁸

Sea ice concentration data were extracted from the Canadian Ice Service (CIS) database in both tabular and spatial (GIS) formats. Tabular data were extracted from the CIS Ice Graph 2.0 web application data tool and consisted of Autumn 2020 weekly sea-ice concentration data plus long-term mean and median normal data for a retrospective 30-year period from 1991–2020 for three of the standard Ice Graph regions that capture the Gulf of Boothia (Prince Regent – Boothia, Foxe Basin and Eastern Parry Sound). The CIS 'regular ice season' runs from the week of 14 March to the week of 15 October, with data outside this season regarded as less reliable. Spatial sea-ice concentration data were downloaded as weekly CIS Regional Ice Charts for three regions: Western Arctic, Eastern Arctic and Hudson Bay. Data (.e00 files) were imported into a GIS (ArcView 3.3 and QGIS Desktop 3.10.1) for geoprocessing.

Killer whale predation

Killer whales enter the Gulf of Boothia on a seasonal basis (Pomerleau *et al.*, 2011; Matthews *et al.*, 2020). Field observations on the presence of killer whales, as well as examination of the stranded bowhead whales for evidence of attempted killer whale predation were compiled from sightings, photographs and interviews with Inuit hunters.

Carcass review and image analysis

Inclement weather conditions limited exploration of the stranding area. We therefore compiled and reviewed satellite images to search for additional carcasses which may not have been visible or accessible to local hunters following established methodology (Fretwell *et al.*, 2019). Satellite images were obtained from six areas covering approximately 670 km² (3–5% of the southern Gulf of Boothia region; Fig. 1). Two of the six areas had prior bowhead whale strandings documented by local community members and four additional sites were randomly chosen to broaden the search. Images were obtained from the DigitalGlobe WorldView-3 satellite at 30 cm panchromatic resolution and 1.24 m multispectral resolution. Images were reviewed by three co-authors (BGY, JWH, SHF) to confirm the presence/absence of bowhead whale carcasses.

Age and sex determination

Eight whales had skin samples submitted to University of California, Los Angeles (UCLA) Health Sciences for age estimation via DNA methylation analysis and epigenetics (Parsons *et al.*, 2023). Skin samples enabled sex determinations of the whales through epigenetic analysis and both LGL331 and LGL335 amplification of zinc finger gene introns (Shaw *et al.*, 2003).

Contaminant analysis

Blubber samples from six whales were assessed for levels of polychlorinated biphenyls (PCB, 209 congeners) by SGS AXYS (Sidney, BC, Canada), submitted to Environment and Climate Change Canada (ECCC). The contaminant class to be analysed was selected based on the presence of a former military base in the region. Extracts were analysed by high resolution gas chromatography – high-resolution mass spectrometry according to the US Environmental Protection Agency's (EPA) 1668 method (Grant *et al.*, 2011; Megson *et al.*, 2022).

Adipocyte and fatty acid analysis

Blubber samples from seven whales were examined for adipocyte number, size, lipid proportion and fatty acid (FA) analysis. The full blubber depth was subsampled into inner, middle and outer layers. Lipids were quantitatively extracted using a modified Folch method (Folch *et al.*, 1957; Iverson *et al.*, 2001). Lipid extractions were

⁸ https://climatedata.ca/

performed at the DFO Freshwater Institute, Winnipeg, MB, Canada. Results were expressed as the lipid content on a wet weight basis. Adipocyte analysis was conducted on additional inner, middle and outer layer blubber subsamples (approx. $1.5 \times 2 \times 0.4$ cm) fixed in 10% neutral buffered formalin. Fixed samples were embedded in paraffin, sectioned, stained (hematoxylin and eosin) and mounted on slides at the Centre for Phenogenomics (Toronto, ON). Slides were scanned and analysed using HALO image analysis software (v3.1.1076.301; Indica Labs, Albuquerque, NM). Each image was overlaid with a fixed analysis area ($1.8 \times 106 \mu m^2$) that included at least 100 adipocytes and minimised the inclusion of non-adipocyte components (e.g., muscle fibers, blood vessels). Ruptured cells and other artefacts were manually excluded. The vacuole detection software 2.2 algorithm was used to identify and measure the diameter, perimeter and two-dimensional area of adipocytes. Seven blubber samples were analysed for 17 fatty acids which have previously been confirmed as representative of marine mammal diets (Thiemann *et al.*, 2007, 2008). Fatty acid analysis was performed according to established methodology (Iverson *et al.*, 2004; Thiemann *et al.*, 2004).

For comparison with presumed 'healthy' animals, blubber samples were analysed from ECWG bowhead whales harvested by Inuit before the mortality event from 2008–20 around Kugaaruk, Nunavut (n = 6). These samples were analysed for lipid content, adipocyte size, fatty acid composition and concentrations of 209 PCB congeners using the EPA-1668 method (Grant *et al.*, 2011; Megson *et al.*, 2022).

Histopathology and pathogen screening

Blubber and skin were histopathologically examined at the Animal Health Center (Abbotsford, BC) according to standard cetacean histology techniques (Parlee *et al.*, 2014; Castrillon *et al.*, 2017). Muscle tissue from three whales was screened for *Toxoplasma gondii* via polymerase chain reaction and histopathology (Owen & Trees, 1998). Pathogen screening was also performed on frozen skin and blubber samples for *Brucella* spp. and morbillivirus (Hall, 1995; Ohishi *et al.*, 2016). Though influenza A infection was considered an important pathogen which affects cetaceans (e.g., Murawski *et al.*, 2024), we did not screen for Influenza A infection as available tissue including skin, blubber and skeletal muscle do not generally contain influenza A viruses.

Stable isotope analysis

Stable isotope analysis was performed on skin (n = 9) collected from five whale carcasses (with multiple samples collected from two whales) for measures of carbon and nitrogen according to established methodologies and compared with levels from the harvested whales (n = 18) via ANOVA (Matthews & Ferguson, 2015).

Statistical analysis

Linear mixed effects models were used to test sample origin (harvest, stranded), blubber depth (inner, middle, outer) and age (years) as fixed factors. Whale ID was treated as a random effect. For all linear models, the *performance* package (Lüdecke *et al.*, 2021) was used to generate R2 values, confirm normality of residuals, homogeneity of variance, linearity and normality of random effects. Parameter p-values were generated using likelihood ratio tests. All analyses were performed in R (version 4.0.4; R Core Team, 2020). A permutation MANOVA was performed to compare differences in fatty acids between stranded and harvested bowhead whales and between age classes of juveniles and adults. Samples were limited to the middle blubber layer which has been reported to best reflect changes in diet and body condition (Kershaw *et al.*, 2019), with both statistical analysis performed with data log-transformed using 18:0 as a reference and PERMANOVA based on Euclidian distance dissimilarity matrix and 1,000 permutations (Budge *et al.*, 2020).

RESULTS

Study area

Precise locations were provided by local hunters who found the stranded whales, with seven of these locations matching the exact coordinates determined on satellite imagery (Fig. 1). The eighth carcass was within 2 km of the recorded field coordinates when confirmed on satellite imagery. No carcasses were observed in the four randomly selected satellite image of coastal areas.

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Figure 2. Maximum daily wind speed (km/hr) at the Kugaaruk Climate Weather Station for Aug to Dec 2020 (solid line) and maximum daily wind speed recorded in any year between 2004 and 2019 at the same station.



Figure 3. Weekly sea ice concentration for three Canadian Arctic Regions, as defined in the Canadian Ice Service IceGraph 2.0 web application. Bars show mean weekly 2020 ice concentration, while the dashed line shows 30-year normal (median) for 1991–2020.

Environmental samples

Daily maximum wind speed during the mortality event ranged from 12–27 km/hr in September 2020 and 8– 53 km/hr in October 2020 (Fig. 2). These values were within the range of the wind speeds recorded between 2004 and 2019, with values below previously recorded maximum levels.

Sea ice concentration was 50% below normal values for the time of year and region where the strandings occurred. Normal ice cover of > 90% was not achieved until November 2020 with some variation between the three locations (Fig. 3). The Gulf of Boothia was largely open water until late October with heavy ice reaching normal levels in November 2020.

Killer whale predation

Killer whales were observed in the Gulf of Boothia region by Kugaaruk hunters (approx. location 69.1778; –89.4099) when sea ice started to form during the first week of October 2020 (Raymond Kayasark, Chair of the Kurtairojuark HTA, Kugaaruk, pers. comm.). Observers on a DFO Conservation and Protection surveillance flight from Iqaluit in a De Havilland DHC-8-311 (Dash 8) on 4 October 2020 also observed three to five killer whales (69.8729; –83.2536) in the Gulf of Boothia region (Fig. 1).

Carcass review and image analysis

Four carcasses were reported at the suspected time for the mortality event on 1 October 2020, 70 km north of Kugaaruk. Four additional carcasses were discovered on 10 November in Committee Bay. A single carcass was documented on 25 November near Taloyoak. A single whale was found on 26 January 2021 at Keith Bay. The

for the wh	ales was estimated from	m satellite images.		5	1	2	5		2	3	0			0	
Date	Location	Field ID	No. of skin and blubber samples	Blubber sample	No. of muscle samples	Sex	Age class	Epigenetic age (yrs)	Length (cm)	Axilla girth (cm)	PCR Brucella	PCR Morbilli	PCR T. gondii	Fat atrophy	Total PCB conc. (ng/g lipid weight)
01/10/20	70km N Kugaaruk	BM-2020-13	1	2	1	ш	Adult	32	2,134	305	Neg	Neg	I	+ + +	29.38
01/10/20	70km N Kugaaruk	BM-2020-14	1	Ч	I	Σ	Juvenile	18	1,030	356	Neg	Neg	I	Normal	93.05
01/10/20	70km N Kugaaruk	BM-2020-15	4	I	1	Σ	Juvenile	12	780	496	Neg	Neg	Neg	Normal	141.98
01/10/20	70km N Kugaaruk	BM-2020-16	I	I	I	ш	Adult	I	1,580	I	I	I	I	I	
10/11/20	Committee Bay	BM-2020-01	1	I	1	Σ	Juvenile	80	890*	I	Neg	Neg	Neg	Normal	33.27
10/11/20	Committee Bay	BM- 020-03	2	I	I	Σ	Juvenile	12	*062	I	Neg	Neg	I	+	
10/11/20	Committee Bay	BM-2020-06	2	I	1	ш	Juvenile	18	$1,000^{*}$	I	Neg	Neg	Neg	+	41.41
10/11/20	Committee Bay	BM-2020-17	I	I	I	I	Juvenile	I	750*	I	I	I	I	I	
25/11/20	Near Taloyoak	BM-2020-12	2	I	I	щ	Adult	43	I	I	Neg	Neg	I	‡	22.83
26/01/21	Keith Bay	BM-2020-18	I	I	I	Σ	Juvenile	16	I	I	I	I	I	I	
14/04/21	Near Taloyoak	Taloyoak 2021-02	I	I	I	I	I	I	I	I	I	I	I	I	

Metadata for the bowhead whales included in the mortality event in the Gulf of Boothia, Canada, 2020/21, with demographic and tissue sampling information where available, results from morphologic diagnosis

Table 1

final whale was reported on 14 April 2021 near Taloyoak (Table 1). It is suspected that this was a single mortality event with protracted carcass discovery times across this isolated area.

Hunters reported killer whale rake marks on the body of one of the whales, with hemorrhaging on the tongue and damage to the throat also observed (Fig. 4). On a second whale, tooth punctures were present on the right pectoral flipper (Fig. 5). Post-mortem feeding on the carcasses by polar bears (*Ursus maritimus*) was also observed (Fig. 6).

Age and sex determination

Epigenetic age estimations ranged from eight to 43 years (Table 1). Nine whales had sex determined with four females and five males confirmed. Length estimates ranged from 750 to 2,134cm. Age and length estimates indicate three of the females were likely sexually mature and all five males likely juvenile (George *et al.*, 2021).

Contaminant analysis

Concentrations of PCBs in the whales (n = 8) sampled during the mortality event ranged between 22.83 and 141.98 ng/g wet weight (see lipid weight values in Table 1) with a mean value of 60.32 ng/g lipid weight. The total PCB concentrations detected were similar to those in individuals harvested before the mortality event (n = 6) (Fig. 7) (mean = 58.96 ng/g; range 20.72–129.72 ng/g).

Adipocyte and fatty acid analysis

Linear mixed models found that both the circumstances associated with mortality (stranding vs harvest, likelihood ratio test: p = 0.015), depth of the blubber sample (p < 0.001), and age (p = 0.007) were all significant predictors of adipocyte size (linear mixed model R² = 0.761). Adipocytes were larger in older animals, but the mean age did not differ between harvested and stranded whales (t-test: t15 = 0.441, p = 0.666). Importantly, adipocytes were larger in harvested whales than in stranded whales (Fig. 8) and smaller in the outer blubber layer than in middle or inner layers (p < 0.001).

Fatty acid profiles did not differ (permutation MANOVA) between stranded and harvested whales (p = 0.20). However, fatty acids differed between juveniles and adult animals (p = 0.001).

Histopathology and pathogen screening

Histopathology of blubber sample (BM-2020-13) demonstrated marked diffuse atrophy of all three blubber layers in two of three anatomic sample sites, with no abnormalities in the third site. In three additional animals, within the deeper regions of the blubber, there was mild (BM-2020-03 and BM-2020-06) to moderate (BM-2020-12) fat atrophy. In these animals, there was variation in the amount of intervening collagen fibres in the affected blubber with artefactual shearing (n = 5) of fat lobules and multifocal proteinaceous deposits. Intravascular proteinaceous deposits were also observed in the superficial areas of blubber which were most likely associated with post-mortem haemolysis rather than thromboemboli. Due to the level of inflammation and lack of discernible pathogens, a specific etiology could not be identified. A low grade, persistent bacteraemia or possible localised trauma could be considered as the underlying cause. These lesions are likely incidental and unrelated to the stranding event.

Microscopic evaluation of available muscle samples was hampered by post-mortem change and freeze artefacts. However, variable interstitial accumulation of oedema fluid, myofiber size and dimension, and occasional degeneration were observed. These changes could be associated with autolysis, possible metabolic derangements (adrenergic surge, acidosis), exertional myopathy, hypoxia (ischemia with live stranding, compartmental type syndrome), nutritional state and other factors. The muscle lesions appeared to be limited and likely would not have resulted in significantly systemic antemortem morbidity. In the blubber (BM-2020-01, BM-2020-03) and skeletal muscle, there were small, refractile, peripherally-radiating yellow crystalline arrays within fat cells, myocytes and the interstitium, which most likely represent post-mortem change rather than a distinct pathological entity.



Figure 4. Photo panel of first whale discovered at stranding location 70 km north of Kugaaruk. Adult female bowhead whale (ID BM-2020-13, length 2,134 cm). Credit: Gordon Kukkuvak. A: Damage to bowhead whale mouth, tongue was observed to be missing with possible congestion and haemorrhage visible. B: Damage to baleen likely inflicted by a predator. C: Additional cutaneous lesions along the mandible, possibly consistent with killer whale predation. Molecular studies were negative for morbillivirus and *Brucella* spp. in the epidermis and blubber in all cases. In four animals (BM-2020-01, BM-2020-06, BM-2020-12, BM-2020-15), skeletal muscle screened for *T. gondii* were negative. No protozoa were observed microscopically in the skeletal muscle sections (Table 1). This is consistent with findings in healthy bowhead whales.

Skin microbiome data were previously reported (Dominguez-Sanchez *et al.*, 2023) with stranded bowhead whales demonstrating reduced microbiome diversity in comparison with healthy whales. Findings included six bacterial classes in the stranded bowhead whales (*Bacilli, Clostridia, Fusobacteriia, Actinobacteria, Gammaproteobacteria* and *Bacteroidia*). Pathogens of the genera *Clostridium, Streptococcus, Aeromonas* and *Vibrio* were identified. In addition, bacteria that have been reported as beneficial for skin health (*Tenacibaculum* spp. and *Psychrobacter* spp.) were identified in low abundance.

Stable isotope analysis

Results for stable isotope analysis of the skin for stranded animals (n = 9 from five whales) showed no significant differences in δ^{13} C (p = 0.78) when compared with hunted animals. However, δ^{15} N in stranded whales (ANOVA, p = 0.002) were significantly higher (Fig. 9).

DISCUSSION

Our investigation into this mortality event yielded no definitive cause of death. Based on our findings we conclude that a combination of nutritional stress and killer whale predation, likely facilitated by the reduced ice coverage, were the primary causes of this multifactorial mortality event.

Killer whale predation

There are a number of factors which suggest killer whale predation was a contributing cause: cutaneous rake marks, hemorrhage or complete absence of the tongue, damage to the baleen, acute muscle fiber degeneration (possible exertional myopathy), all supported by reports of killer whales in the vicinity before or coinciding with the strandings (Fig. 5). Gordon Kukkuvak, who discovered the stranded whales, provided a report as follows: 'Not sure what happen but my guess is they may run away from killer whales there was bunch of killer whales in Baffin area this summer and one of the bowhead seem to have a killer whale teeth mark on the right forearm flipper'. Bowhead whales and killer whales are sympatric in the Gulf of Boothia during the open-water season, with pronounced non-consumptive predator impacts on bowhead whale behaviour confirmed via telemetry data from tagging studies conducted on both species (Matthews et al., 2020). Environmental assessment confirmed late ice formation, i.e., there was greater temporal access to the area for killer whales and less sea-ice refuge for bowhead whales, likely resulting in more predator-prey interactions. Though speculative, increased predation pressure and intensity could result in decreased bowhead feeding activity and a nearshore distribution due to predator avoidance behaviour (Shpak & Pomonova, 2019; Lefort et al., 2020). Nearshore proximity of bowhead whales could also result in greater probability of beach-cast carcass detection (Lefort et al., 2020). Comparison of body condition between the stranded whales and previously hunter-harvested whales demonstrated that some of the stranded animals were in suboptimal nutritional condition. Suboptimal nutritional status was also supported by the increased δ^{15} N in the stranded whales compared with the hunterharvested counterparts (Matthews & Ferguson, 2015). Increased energetic cost of predator avoidance could have contributed to this nutritional stress, as killer whales were present in the area from August to October (Matthews et al., 2020). Summer foraging is important for recovering body reserves for all Arctic whales (Christiansen et al., 2023).

Carcass and image review

The two carcasses reported in 2021 likely died in the same event as the other whales in 2020. These carcasses were found completely iced over during the winter season. Killer whales would have been excluded from this area after October / November due to ice coverage, indicating the mortality occurred much earlier. These carcasses were not immediately detected or thoroughly sampled due to their inaccessibility. Ice conditions



Figure 5. A: Tooth marks observed on the right pectoral flipper of the second bowhead whale – a juvenile male (ID B,-2020-14, length 1,030 cm) – suspected to be killer whale marks. Credit: Gordon Kukkuvak. B: Fourth whale from stranding event 70 km north of Kugaaruk. Adult (sex unknown) bowhead whale (ID BM-2020-16, length 1,580 cm) in lateral recumbency with head and thorax visible. Credit: Norm Qavvik.

prevented carcass decomposition, but minimal information could be gathered (Fig. 6C). Morphometrics were available on several but not all carcasses. Those animals that were discovered buried in snow could not be appropriately measured.

Biological samples

Although PCB concentrations were higher than levels reported in bowheads in the Canadian Arctic between 1994 and 2003 (concentrations range between 6.2 and 20.8 ng/g ww for 104 PCB congeners) (Stern *et al.*, 2009), they were lower than found in bowhead whales harvested in Barrow, Alaska (Lowry, 1993; O'Hara *et al.*, 1999). While these results warrant additional monitoring, PCB concentrations from the stranded whales (n = 8,



Figure 6. A: Stranded carcass of a bowhead whale in Taloyoak, Nov 2020, discovered by local Inuit. Adult female whale (ID BM-2020-12, length unavailable). B: Evidence of scavenging on a bowhead whale carcass at Taloyoak, likely by polar bears. Photos demonstrate frozen condition of the carcass. C: Juvenile male (ID BM-2020-18, length unavailable) discovered in Keith Bay in Jan 2021 with just the baleen visible, demonstrating the challenges of finding and accessing the carcasses and the likelihood that this whale stranded many months prior to discovery.

mean 60.32ng/g) were similar to levels previously reported from harvested whales (n = 6, mean 58.96ng/g) from 2008–16 (Bolton *et al.*, 2020; Desforges *et al.*, 2023). The harvested whales included both males and females and were similar ages (Fig. 7). It is possible that contaminant levels are altered in stranded whales due to effects of decomposition process, such as lipid leaching or with lipid mobilisation prior to death and concentration of contaminants (Hayes *et al.*, 2022).



Figure 7. Concentrations of Σ PCBs in the blubber of bowhead whales collected before (green dots) and during the 2020/21 bowhead whale mortality event (black dots) in the Gulf of Boothia, Canada.

Nutritional stress was likely a contributing factor to the mortality event. This conclusion is based on body condition assessments, and analysis of stable isotopes, fatty acids, adipocytes and lipids. The reduced body condition of the stranded whales in October in comparison with hunter-harvested whales was anticipated due to the timing of the bowhead harvest which typically occurs earlier in the year, when whales are in more robust body condition (Department of Fisheries, 2015). Reduced dietary intake has been observed over winter periods which could be supported by the stable isotope results, given that higher δ^{15} N values measured in the stranded whale skin have been associated with nutritional stress in other species (Borrell et al., 2012; Ryan et al., 2012). A larger sample size and complete baleen sections would enable assessment of shifts in nutritional status immediately prior to stranding relative to longer term foraging patterns (Florin et al., 2011; Matthews & Ferguson, 2015). The mortality event occurred in the autumn after the summer feeding season, when a larger adipocyte size and greater fat content in the blubber would be expected. While considering age, epigenetic analysis revealed seven juvenile bowheads, which could indicate a growing population with lower body condition. However, fat atrophy was most prominent in the two adult whales (Table 1). Juvenile and adult age classes demonstrated differences in fatty acid composition, but similar profiles in stranded and hunter-harvested whales indicate similar diets between the two groups (Pomerleau et al., 2014). Age-specific differences in fatty acid profiles have previously been documented in bowhead whales, suggesting ontogenetic differences in diet (Budge et al., 2008). Loss of body condition can also reflect reproductive status, particularly for females. Four carcasses were female, but without fecal steroid levels or necropsy exams, the reproductive status of these whales could not be determined.

Adipocyte analysis and lipid content

The smaller adipocyte size and lower lipid content in the stranded whales were consistent with nutritional stress (Castrillon & Bengtson Nash, 2020). The relationship between lipid content and body condition in baleen whales is complex and dynamic, with variations expected between inner, middle and outer layers (Kershaw *et al.*, 2019). Adipose lipid content can be challenging to measure due to lipid loss during the extraction process and high sensitivity to sample storage, handling and decomposition (McKinney *et al.*, 2014; Yurkowski *et al.*, 2015; Sciullo *et al.*, 2016). Bowhead whale blubber is specifically adapted for extreme thermoregulation in the Arctic, with the outermost layer developed for thermoregulation and both the middle and inner layers more metabolically active to enable dynamic response to energy storage or mobilisation (George *et al.*, 2021). Adipocyte size has been documented to vary between inner, middle and outer layers, with the largest adipocytes present in the middle layer of bowhead whales (Ball *et al.*, 2015). In addition, adipocyte size varies seasonally, with smaller cell sizes most prominent during the spring fasting period (Ball *et al.*, 2015). Comparison of adipocytes size between hunter-harvested whales and stranded whales demonstrated that the largest adipocytes were present in the middle layer of harvested whales, consistent with energy storage, whereas the smallest adipocytes in stranded whales were in the outer layer of blubber and could therefore have affected their ability to thermoregulate



Figure 8. Scatterplots of adipocyte size (lipid droplet area) and blubber lipid content determined by histological analysis. A, B: chemical extraction. C, D: by both histological analysis and chemical extraction. E, F: 44 samples from stranded and harvest bowhead whales, split by sample type and blubber depth.

effectively (Fig. 8). This supports the theory that the whales were nutritionally compromised, perhaps resulting from the presence of killer whales disrupting foraging, which, in turn, might have made the whales more vulnerable to killer whale predation or stranding (Matthews *et al.*, 2020; Domínguez-Sánchez *et al.*, 2023).

Histopathology and pathogen screening

Though reduced body condition may also occur with chronic inflammation or infection, neoplasia and other disease processes, few diseases and parasites have been documented in bowhead whales (Stimmelmayr, 2015; Stimmelmayr *et al.*, 2021). With limited tissue sampling and possible loss of more fastidious pathogens



Figure 9. Stable isotope analysis of skin from stranded bowhead whales from the Gulf of Boothia, 2021+0/2021 compared with healthy harvested whales. Significantly different levels of Nitrogen were observed p = 0.02. Carbon was not different between the two groups p = 0.78 via ANOVA.

with prolonged freezing, infectious disease could not be entirely ruled out. However, PCR tests for *Brucella* spp. and morbillivirus were negative. *T. gondii* was also negative by PCR and no tissue protozoa were observed microscopically.

Recommendations for future mortality events include more complete post-mortem examinations, with additional tissue collections to document the reproductive status and feeding activity and improve infectious disease screening (Barratclough *et al.*, 2023). Table 2 provides recommendations for tissue sampling and pathogen screening. While skin and muscle tissue were sampled, it would be preferable to screen lung and brain tissue (Barratclough *et al.*, 2023). Therefore, we cannot completely rule out the presence of these pathogens.

Reduced skin microbiome diversity has been linked to both increased skin pathology and a reduction in overall health status (Zha *et al.*, 2018; Pereira *et al.*, 2022; Domínguez-Sánchez *et al.*, 2023). In this study, the identification of pathogens, through skin microbiome analysis, such as *Aeromonas* spp., which were not present in apparently healthy bowhead whales, and an overall reduction in skin microbiome diversity in the stranded whales compared with apparently healthy ones, could indicate a reduction in health status. In addition, a low abundance of bacteria, such as *Tenacibaculum* spp. and *Psychrobacter* spp., that have been reported to be beneficial for skin health in other marine species (Hooper *et al.*, 2019; Smies *et al.*, 2022), was also detected in the stranded bowhead whales. The identification of both harmful and beneficial bacteria underscores the importance of understanding the complex interactions between these microbes and their hosts and highlights the need for further research in this area. Therefore, continued monitoring of pathogen transmission between these two species could support evidence of predator-prey interactions. Overall, skin microbiome analysis provides valuable insights into the microbial communities associated with stranded bowhead whales.

Pathogen	Recommended tissue sampling	Diagnostic test	Reference
Morbillivirus	Lung	cELISA	Kennedy (1998)
	Brain	Virus neutralisation test Real-time PCR	
	lymphoid tissue CSF	Virus isolation and sequencing	
	Post-mortem heart blood		
Influenza A	Lung	cELISA	Nielsen <i>et al.</i> (2001)
(HPAI)(H5N1)	Brain	Agar gel immunodiffusion	
		Virus isolation	
		PCR with sequencing	
Brucella spp.	Lung	Serology	Foster <i>et al.</i> (2002)
	Brain	PCR	Nymo et al. (2013)
	Lymphoid tissue	Prolonged culture on Farrell's medium	, , ,
	Reproductive organs	Immunohistochemistry	
	CSF		
	Post-mortem heart blood		
Toxoplasma gondii	Blood serum	Modified agglutination test	Owen (1998)
	Fresh/frozen tissue	Serology	
	-	PCR	

Table 2 Recommended tissue sampling and diagnostic screening for priority pathogens in bowhead whale mortality

Environmental samples

No unusual weather events were reported prior to or during the mortality event. However, reduced sea ice coverage can have secondary effects, such as less moderation of high wind speeds and storm surges which could impact whale strandings (Barnhart *et al.*, 2014). Reduced levels of ice coverage in October 2020 relative to normal coverage for other years could have influenced the preferred environment and movement patterns of bowhead whales (Ferguson *et al.*, 2010).

Direct anthropogenic causes of cetacean mortality, including vessel collisions, sonar or seismic surveys, were excluded due to lack of known vessels in the area at the time, in addition to no reported sonar activity and no evidence of vessel collisions, blunt force trauma or propeller injury on gross visual exam (Balcomb & Claridge, 2001; Halliday *et al.*, 2020). While vessel strikes cannot be completely ruled out in the absence of complete necropsy, the number of carcasses and disparate stranding locations tends to make multiple vessel collisions unlikely. Harmful algal bloom was also excluded due to lack of environmental evidence. However, with increasing ocean temperatures and decreased ice coverage throughout the Arctic, future consideration of HABs events is warranted (Häussermann *et al.*, 2017).

In future stranding events, full necropsy examinations are recommended to document baseline natural history and facilitate tissue collection for identification of the cause of death. However, in harsh, remote environments, it is likely that unreported or inaccessible carcasses may preclude precise determination of a cause. Nevertheless, as demonstrated in this study, detailed investigations can be performed with skin, blubber and muscle samples. Collection of complete baleen plates and faecal samples could enable additional hormone analysis. Studies of bowhead whales (Hunt *et al.*, 2014) and the closely related North Atlantic right whale (Lysiak *et al.*, 2018) have linked baleen corticosterone concentrations to intrinsic and extrinsic stressors (e.g., entanglement). The use of drones to collect additional samples such as morphometrics using LIDAR application could also be implemented in the future.

In conclusion, while no definitive cause of death could be determined in these 11 bowhead whale mortalities, the most likely explanation was a combination of reduced sea ice coverage, poor nutritional status and killer whale presence/predation. Other underlying causes to be considered for the reduced nutritional status of the carcasses include climate change shifting prey availability and nutritional value, and whether the current ECWG population may be approaching carrying capacity (Biddlecombe *et al.*, in press). Nunavut Inuit communities played a pivotal role in the discovery, documentation and sample collection related to this event. Their significant effort facilitated an improved understanding of the factors impacting this bowhead whale mortality event. In future, we propose further collaboration with systematic, community-led monitoring programmes to assess marine mammal health. Inter-disciplinary partnerships are required to integrate scientific methods with Inuit

knowledge systems, enabling a comprehensive approach to evaluating the resilience of this bowhead whale population to environmental changes and increased killer whale interactions.

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REFERENCES

- Arnakak, J. (2002). Incorporation of Inuit Qaujimanituqangit, or Inuit traditional knowledge, into the Government of Nunavut. J. Aborig. Econ. Dev. 3(1): 33–39. [Available at: https://doi.org/10.29173/jaed187]
- Balcomb, K.C., & Claridge, D.E. (2001). A mass stranding of cetaceans caused by naval sonar in the Bahamas. Bahamas J. Sci. 8: 2–12.
- Ball, H.C., Stavarz, M., Oldaker, J., Usip, S., Londraville, R.L., George, K.C., Thewissen, J.G.M., & Duff, R.J. (2015). Seasonal and ontogenetic variation in subcutaneous adipose of the bowhead whale (*Balaena mysticetus*). Anat. Rec. 298: 1416–1423. [Available at: https://doi.org/10.1002/ar.23125]
- Barratclough, A., Ferguson, S.H., Lydersen, C., Thomas, P.O., & Kovacs, K.M. (2023). A Review of Circumpolar Arctic Marine Mammal Health: A Call to Action in a Time of Rapid Environmental Change. *Pathogens* 12: 937. [Available at: https://doi.org.10.3390/ pathogens12070937]
- Barnhart, K.R., Overeem, I., & Anderson, R.S. (2014). The effect of changing sea ice on the physical vulnerability of Arctic coasts. *Cryosphere* 8(5): 1777–1799. [Available at: https://doi.org/10.5194/tc-8-1777-2014]
- Biddlecombe, B.A., Ferguson, S.H., Heide-Jørgensen, M.P., Gillis, D.M., & Watt, C.A. (2023). Estimating abundance of Eastern Canada-West Greenland bowhead whales using genetic mark-recapture analyses. *Glob. Ecol. Conserv.* 45: e02524. [Available at: https://doi.org/10.1016/j.gecco.2023.e02524]
- Biddlecombe, B., Watt, C., Gillis, D., Heide-Jørgensen, M.P., & Ferguson, S.H. (in press). Combining multiple data sources to model population dynamics of Eastern Canada-West Greenland bowhead shales. Social Science Research Network [Pre-print available: https://doi.org/10.1016/j.marpolbul.2019.110857]
- Bogomolni, A.L., Pugliares, K.R., Sharp, S.M., Patchett, K., Harry, C.T., Larocque, J.M., Touhey, K.M., & Moore, M. (2010). Mortality trends of stranded marine mammals on Cape Cod and southeastern Massachusetts, USA, 2000 to 2006. *Dis. Aquat. Organ.* 88:143–155.
- Bolton, J.L., Ylitalo, G.M., Chittaro, P., George, J.C., Suydam, R., Person, B.T., Gates, J.B., Baugh, K.A., Sformo, T., & Stimmelmayr, R. (2020). Multi-year assessment (2006–2015) of persistent organic pollutant concentrations in blubber and muscle from Western Arctic bowhead whales (*Balaena mysticetus*), North Slope, Alaska. *Mar. Poll. Bull.* 151: 110857. [Available at: https://doi.org/10.1016/ j.marpolbul.2019.110857]
- Borrell, A., Abad-Oliva, N., Gómez-Campos, E., Giménez, J., & Aguilar, A. (2012). Discrimination of stable isotopes in fin whale tissues and application to diet assessment in cetaceans. *Rapid Commun. Mass Spectrom.* 26: 1596–1602. [Available at: *https://doi.org/10.1002/rcm.6267*]
- Bradford, A.L., Weller, D.W., Punt, A.E., Ivashchenko, Y.V., Burdin, A.M., Vanblaricom, G.R., & Brownell, R.L. (2012). Leaner leviathans: Body condition variation in a critically endangered whale population. J. Mammal. 93: 251–266. [Available at: https://doi.org/10.1644/ 11-MAMM-A-091.1]
- Budge, S.M., Springer, A.M., Iverson, S.J., Sheffield, G., & Rosa, C. (2008). Blubber fatty acid composition of bowhead whales, Balaena mysticetus: Implications for diet assessment and ecosystem monitoring. J. Exp. Mar. Biol. Ecol. 359: 40–46. [Available at: https://doi.org/10.1016/j.jembe.2008.02.014]
- Budge, S.M., Townsend, K., Lall, S.P., & and Bromaghin, J.F. (2020). Dietary fat concentrations influence fatty acid assimilation patterns in Atlantic pollock (*Pollachius virens*). *Philos. Trans. R. Soc. B.* 375: 20190649. [Available at: *https://doi.org/10.1098/rstb.2019.0649*]
- Castrillon, J., Huston, W., & Bengtson Nash, S. (2017). The blubber adipocyte index: A nondestructive biomarker of adiposity in humpback whales (*Megaptera novaeangliae*). Ecol. Evol. 7:5131–5139. [Available at: https://doi.org/10.1002/ece3.2913]
- Castrillon, J., & Bengtson Nash, S. (2020). Evaluating cetacean body condition; a review of traditional approaches and new developments. *Ecol. Evol.* 10: 6144–6162. [Available at: https://doi.org/10.1002/ece3.6301]
- Chambault, P., Albertsen, C.M., Patterson, T.A., Hansen, R.G., Tervo, O., Laidre, K.L., & Heide-Jørgensen, M.P. (2018). Sea surface temperature predicts the movements of an Arctic cetacean: The bowhead whale. Sci. Rep. 8: 9658. [Available at: https://doi.org/ 10.1038/s41598-018-27966-1]
- Christiansen, F., Rodríguez-González, F., Martínez-Aguilar, S., Urbán, J., Swartz, S., Warick, H., Vivier, F., & Bejder, L. (2021). Poor body condition associated with an unusual mortality event in gray whales. *Mar. Ecology Prog.* 658: 237–252. [Available at: *https://doi.org/* 10.3354/meps13585]

- Christiansen, F., Tervo, O.M., Heide-Jørgensen, M.P., & Teilmann, J. (2023). Prey consumption of bowhead whales in West Greenland estimated from drone measurements of body size and condition. *Polar Biol.* 47: 17–39. [Available at: *https://doi.org/10.1007/s00300-023-03207-8*]
- Department of Fisheries and Oceans, Canada (2015). Updated abundance estimate and harvest advice for the Eastern Canada-West Greenland bowhead whale population. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 52.
- Desforges, J.-P., Ferguson, S.H., Remili, A., Mckinney, M.A., Watt, C.A., & Matthews, C.J.D. (2023). Assessment of persistent organic pollutants in killer whales (*Orcinus orca*) of the Canadian Arctic: Implications for subsistence consumption and conservation strategies. *Environ. Res.* 244: 117992. [Available at: https://doi.org/10.1016/j.envres.2023.117992]
- Domínguez-Sánchez, C.A., Ferguson, S.H., Edkins, T., Young, B.G., & Kringorn, J. (2023). Pilot study: Decoding the skin microbiome of bowhead (*Balaena mysticetus*) and killer whales (*Orcinus orca*) in Nunavut, Canada. *Arct. Sci.* 10. [Available at: *https://doi.org/10.1139/ as-2023-0028*]
- Duignan, P.J. (1999). Morbillivirus infections of Marine Mammals. Saunders, University of California.
- Ferguson, S.H., Higdon, J.W., & Chmelnitsky, E.G. (2010a). The rise of killer whales as a major Arctic predator. In: A Little Less Arctic (pp.117– 136). Springer.
- Ferguson, S.H., Dueck, L., Loseto, L.L., & Luque, S.P. (2010b). Bowhead whale *Balaena mysticetus* seasonal selection of sea ice. *Mar. Ecol. Prog. Ser.* 411: 285–297. [Available at: https://doi.org/10.3354/esr00373]
- Ferguson, S.H., Higdon, J.W., & Westdal, K.H. (2012). Prey items and predation behavior of killer whales (Orcinus orca) in Nunavut, Canada based on Inuit hunter interviews. Aquat. Biosyst. 8(3): 1–16. [Available at: https://doi.org/10.1186/2046-9063-8-3]
- Ferguson, S.H., Higdon, J.W., Hall, P.A., Hansen, R.G., & Doniol-Valcroze, T. (2021). Developing a Precautionary Management Approach for the Eastern Canada-West Greenland Population of Bowhead Whales (*Balaena mysticetus*). Front. Mar. Sci. 8: 709989. [Available at: https://doi.org/10.3389/fmars.2021.709989]
- Florin, S.T., Felicetti, L.A., & Robbins, C.T. (2011). The biological basis for understanding and predicting dietary-induced variation in nitrogen and sulphur isotope ratio discrimination. *Funct. Ecol.* 25: 519–526. [Available at: https://doi.org/10.1111/j.1365-2435.2010.01799.x]
- Folch, J., Lees, M., & Sloane Stanley, G.H. (1957). A simple method for the isolation and purification of total lipids from animal tissues. *J. Biol. Chem.* 226: 497–509.
- Foster, G., Macmillan, A.P., Godfroid, J., Howie, F., Ross, H.M., Cloeckaert, A., Reid, R.J., Brew, S., & Patterson, I.A.P. (2002). A review of Brucella sp. infection of sea mammals with particular emphasis on isolates from Scotland. Vet. Microbiol. 90: 563–580. [Available at: https://doi.org/10.1016/s0378-1135(02)00236-5]
- Fretwell, P.T., Jackson, J.A., Ulloa Encina, M.J., Häussermann, V., Perez Alvarez, M.J., Olavarría, C., & Gutstein, C.S. (2019). Using remote sensing to detect whale strandings in remote areas: The case of sei whales mass mortality in Chilean Patagonia. *PLoS One* 14: e0222498. [Available at: https://doi.org/10.1371/journal.pone.0222498]
- Gass, J.D. Jr., Kellogg, H.K., Hill, N.J., Puryear, W.B., Nutter, F.B., & Runstadler, J.A. (2022). Epidemiology and Ecology of Influenza A Viruses among Wildlife in the Arctic. Viruses 14: 1531. [Available at: https://doi.org/10.3390/v14071531]
- George, J.C. (2009). Growth, morphology and energetics of bowhead whales (Balaena mysticetus). University of Alaska, Fairbanks.
- George, J.C., Follmann, E., Zeh, J., Sousa, M., Tarpley, R., & Suydam, R. (2004). Inferences from bowhead whale ovarian and pregnancy data: Age estimates, length at sexual maturity and ovulation rates. SC/56/BRG/08 presented to the IWC Scientific Committee, Sorrento, 2004. [Available from the IWC Publications Team]
- George, J.C., Sheffield, G., Reed, D.J., Tudor, B., Stimmelmayr, R., Person, B.T., Sformo, T., & Suydam, R. (2017). Frequency of injuries from line entanglements, killer whales, and ship strikes on Bering-Chukchi-Beaufort Seas bowhead whales. Arctic 70: 37–46. [Available at: https://doi.org/10.14430/arctic4631]
- George, J.C., Horstmann, L., Fortune, S., Sformo, T.L., Elsner, R., & Follmann, E. (2021). Thermoregulation and energetics. In: *The Bowhead Whale* (pp.237–260). Elsevier.
- Grant, P.B.C., Johannessen, S.C., Macdonald, R.W., Yunker, M.B., Sanborn, M., Dangerfield, N., Wright, C., & Ross, P.S. (2011). Environmental fractionation of PCBs and PBDEs during particle transport as recorded by sediments in coastal waters. *Environ. Toxicol. Chem.* 30: 1522–1532. [Available at: https://doi.org/10.1002/etc.542]
- Gulland, F.M.D. (2006). Review of the marine mammal unusual mortality event response program of the National Marine Fisheries Service. NOAA Technical Memorandum, NMFS-OPR 33.
- Gulland, F.M.D., & Hall, A.J. (2007). Is marine mammal health deteriorating? Trends in the global reporting of marine mammal disease. *EcoHealth* 4: 135–150. [Available at: https://doi.org/10.1007/s10393-007-0097-1]
- Hall, A.J. (1995). Morbilliviruses in marine mammals. Trends. Microbiol. 3: 4–9. [Available at: https://doi.org/10.1016/ s0966-842x(00)88861-7]
- Halliday, W.D., Pine, M.K., & Insley, S.J. (2020). Underwater noise and Arctic marine mammals: Review and policy recommendations. *Environ. Rev.* 28: 438–448. [Available at: https://doi.org/10.1139/er-2019-0033]
- Hay, K., Aglukark, D., Igutsaq, D., Ikkidluak, J., & Mike, M. (2000). Final Report of the Inuit Bowhead Knowledge Study, Nunavut, Canada. Nunavut Wildlife Management Board.
- Hayes, K.R., Ylitalo, G.M., Anderson, T.A., Urbán R, J., Jacobsen, J.K., Scordino, J.J., Lang, A.R., Baugh, K.A., Bolton, J.L., Brüniche-Olsen, A., & Calambokidis, J. (2022). Influence of life-history parameters on persistent organic pollutant concentrations in blubber of Eastern North Pacific Gray Whales (*Eschrichtius robustus*). *Environ. Sci. Technol.* 56(23): 17119–17130. [Available at: https://doi.org/10.1021/acs.est.2c05998]
- Häussermann, V., Gutstein, C.S., Bedington, M., Cassis, D., Olavarria, C., Dale, A.C., Valenzuela-Toro, A.M., Perez-Alvarez, M.J., Sepúlveda, H.H., & Mcconnell, K.M. (2017). Largest baleen whale mass mortality during strong El Niño event is likely related to harmful toxic algal bloom. *PeerJ* 5: e3123. [Available at: https://doi.org/10.7717/peerj.3123]

Heide-Jørgensen, M.P., Garde, E., Nielsen, N.H., Andersen, O.N., & Hansen, S.H. (2012). A note on biological data from the hunt of bowhead whales in West Greenland 2009–2011. J. Cetacean. Res. Manage. 12(3): 329–333. [Available at: https://doi.org/10.47536/jcrm.v12i3.563]
Higdon, J.W. (2010). Commercial and subsistence harvests of bowhead whales (Balaena mysticetus) in eastern Canada and West Greenland. J. Cetacean Res. Manage. 11(2): 185–216. [Available at: https://doi.org/10.47536/jcrm.v11i2.623]

- Hooper, R., Brealey, J.C., Van Der Valk, T., Alberdi, A., Durban, J.W., Fearnbach, H., Robertson, K.M., Baird, R.W., Bradley Hanson, M., & Wade, P. (2019). Host-derived population genomics data provides insights into bacterial and diatom composition of the killer whale skin. *Mol. Ecol.* 28: 484–502. [Available at: https://doi.org/10.1111/mec.14860]
- Hunt, K.E., Stimmelmayr, R., George, C., Hanns, C., Suydam, R., Brower, H., & Rolland, R.M. (2014). Baleen hormones: A novel tool for retrospective assessment of stress and reproduction in bowhead whales (*Balaena mysticetus*). Conserv. Physiol. 2. [Available at: https://doi.org/10.1093/conphys/cou030]
- Iverson, S.J., Lang, S.L.C., & Cooper, M.H. (2001). Comparison of the Bligh and Dyer and Folch methods for total lipid determination in a broad range of marine tissue. *Lipids* 36: 1283–1287. [Available at: https://doi.org/10.1007/s11745-001-0843-0]
- Iverson, S.J., Field, C., Don Bowen, W., & Blanchard, W. (2004). Quantitative fatty acid signature analysis: A new method of estimating predator diets. *Ecol. Monogr.* 74: 211–235. [Available at: https://doi.org/10.1890/02-4105]
- Kennedy, S. (1998). Morbillivirus infections in aquatic mammals. J. Comparative Pathol. 119: 201–225. [Available at: https://doi.org/ 10.1016/s0021-9975(98)80045-5]
- Kershaw, J.L., Brownlow, A., Ramp, C.A., Miller, P.J.O., & Hall, A.J. (2019). Assessing cetacean body condition: Is total lipid content in blubber biopsies a useful monitoring tool? *Aquat. Conserv.* 29: 271–282. [Available at: https://doi.org/10.1002/aqc.3105]
- Lefort, K.J., Garroway, C.J., & Ferguson, S.H. (2020). Killer whale abundance and predicted narwhal consumption in the Canadian Arctic. *Glob. Change Biol.* 26 :4276–4283. [Available at: https://doi.org/10.1111/gcb.15152]
- Lowry, L.F. (1993). Foods and feeding ecology. In: The Bowhead Whale. Society for Marine Mammalogy.
- Lüdecke, D., Ben-Shachar, M.S., Patil, I., Waggoner, P., & Makowski, D. (2021). performance: An R package for assessment, comparison and testing of statistical models. *J. Open Source Softw.* 6(60): 3139. [Available at: https://doi.org/10.21105/joss.03139]
- Lysiak, N.S.J., Trumble, S.J., Knowlton, A.R., & Moore, M.J. (2018). Characterizing the duration and severity of fishing gear entanglement on a North Atlantic right whale (*Eubalaena glacialis*) using stable isotopes, steroid and thyroid hormones in baleen. *Front. Mar. Sci.* 5: 168. [Available at: https://doi.org/10.3389/fmars.2018.00168]
- Martin, M.J., Halliday, W.D., Citta, J.J., Quakenbush, L., Harwood, L., Lea, E.V., Juanes, F., Dawson, J., Nicoll, A., & Insley, S.J. (2023). Exposure and behavioural responses of tagged bowhead whales (*Balaena mysticetus*) to vessels in the Pacific Arctic. Arct. Sci. 9(3). [Available at: https://doi.org/10.1139/AS-2022-0052]
- Matthews, C.J.D., & Ferguson, S.H. (2015). Seasonal foraging behaviour of Eastern Canada-West Greenland bowhead whales: An assessment of isotopic cycles along baleen. *Mar. Ecol. Prog. Ser.* 522: 269–286. [Available at: *https://doi.org/10.3354/meps11145*]
- Matthews, C.J.D., Breed, G.A., Leblanc, B., & Ferguson, S.H. (2020). Killer whale presence drives bowhead whale selection for sea ice in Arctic seascapes of fear. *Proc. Natl. Acad. Sci.* 117: 6590–6598. [Available at: https://doi.org/10.1073/pnas.1911761117]
- Mckinney, M.A., Atwood, T., Dietz, R., Sonne, C., Iverson, S.J., & Peacock, E. (2014). Validation of adipose lipid content as a body condition index for polar bears. *Ecol. Evol.* 4: 516–527. [Available at: https://doi.org/10.1002/ece3.956]
- Megson, D., Brown, T., Jones, G.R., Robson, M., Johnson, G.W., Tiktak, G.R., Sandau, C.D., & Reiner, E.J. (2022). Polychlorinated biphenyl (PCB) concentrations and profiles in marine mammals from the North Atlantic Ocean. *Chemosphere* 288: 132639. [Available at: https://doi.org/10.1016/j.chemosphere.2021.132639]
- Moore, M.J., Mitchell, G.H., Rowles, T.K., & Early, G. (2020). Dead cetacean? Beach, bloat, float, sink. Front. Mar. Sci. 7: 333. [Available at: https://doi.org/10.3389/fmars.2020.00333]
- Murawski, A., Fabrizio, T., Ossiboff, R., Kackos, C., Jeevan, T., Jones, J.C., Kandeil, A., Walker, D., Turner, J.C., Patton, C., & Govorkova, E.A. (2024). Highly pathogenic avian influenza A (H5N1) virus in a common bottlenose dolphin (*Tursiops truncatus*) in Florida. *Commun. Biol.* 7(1): 476. [Available at: https://doi.org/10.1038/s42003-024-06173-x]
- Nielsen, O., Clavijo, A., & Boughen, J.A. (2001). Serologic evidence of influenza A infection in marine mammals of Arctic Canada. J. Wildl. Dis. 37: 820–825. [Available at: https://doi.org/10.7589/0090-3558-37.4.820]
- Nymo, I.H., Godfroid, J., Åsbakk, K., Larsen, A.K., Das Neves, C.G., Rødven, R., & Tryland, M. (2013). A protein A/G indirect enzyme-linked immunosorbent assay for the detection of anti-Brucella antibodies in Arctic wildlife. *J. Vet. Diag. Invest.* 25: 369–375. [Available at: https://doi.org/10.1177/1040638713485073]
- O'hara, T.M., Krahn, M.M., Boyd, D., Becker, P.R., & Philo, L.M. (1999). Organochlorine contaminant levels in Eskimo harvested bowhead whales of arctic Alaska. J. Wildl. Dis. 35: 741–752. [Available at: https://doi.org/10.7589/0090-3558-35.4.741]
- Ohishi, K., Bando, T., Abe, E., Kawai, Y., Fujise, Y., & Maruyama, T. (2016). Long-term and large-scale epidemiology of Brucella infection in baleen whales and sperm whales in the western North Pacific and Antarctic Oceans. J. Vet. Med. Sci. 78(9): 1457–1464. [Available at: https://doi.org/10.1292/jvms.16-0076]
- Oldach, E., Killeen, H., Shukla, P., Brauer, E., Carter, N., Fields, J., Thomsen, A., Cooper, C., Mellinger, L., & Wang, K. (2022). Managed and unmanaged whale mortality in the California Current Ecosystem. *Mar. Pol.* 140: 105039. [Available at: https://doi.org/10.1016/ j.marpol.2022.105039]
- Owen, M.R., & Trees, A.J. (1998). Vertical transmission of *Toxoplasma gondii* from chronically infected house (*Mus musculus*) and field (*Apodemus sylvaticus*) mice determined by polymerase chain reaction. *Parasitology* 116: 299–304. [Available at: https://doi.org/ 10.1017/s003118209700231x]
- Parlee, S.D., Lentz, S.I., Mori, H., & Macdougald, O.A. (2014). Quantifying size and number of adipocytes in adipose tissue. *Methods Enzymol.* 537: 93–122. [Available at: https://doi.org/10.1016/b978-0-12-411619-1.00006-9]
- Parsons, K.M., Haghani, A., Zoller, J.A., Lu, A.T., Fei, Z., Ferguson, S.H., Garde, E., Hanson, M.B., Emmons, C.K., & Matkin, C.O. (2023). DNA methylation based biomarkers for aging long-lived cetaceans. *Mol. Ecol. Res.* 23(6): 1241–1256. [Available at: *https://doi.org/10.1111/* 1755-0998.13791]

- Pereira, M.S., Redanz, S., & Kriegel, M.A. (2022). Skin deep: The role of the microbiota in cutaneous autoimmunity. J. Invest. Dermatol. 142: 834–840. [Available at: https://doi.org/10.1016/j.jid.2021.12.005]
- Pirotta, E., Thomas, L., Costa, D.P., Hall, A.J., Harris, C.M., Harwood, J., Kraus, S.D., Miller, P.J., Moore, M., & Photopoulou, T. (2022). Understanding the combined effects of multiple stressors: A new perspective on a longstanding challenge. *Sci. Total. Environ.* 821: 153322. [Available at: *https://doi.org/10.1016/j.scitotenv.2022.153322*]
- Pomerleau, C., Patterson, T.A., Luque, S., Lesage, V., Heide-Jørgensen, M.P., Dueck, L.L., & Ferguson, S.H. (2011). Bowhead whale Balaena mysticetus diving and movement patterns in the eastern Canadian Arctic: Implications for foraging ecology. Endanger. Species Res. 15: 167–177. [Available at: https://doi.org/10.3354/esr00373]
- Pomerleau, C., Lesage, V., Winkler, G., Rosenberg, B., & Ferguson, S.H. (2014). Contemporary diet of bowhead whales (*Balaena mysticetus*) from the Eastern Canadian Arctic inferred from fatty acid biomarkers. *Arctic* 67(1): 84–92. [Available at: *https://doi.org/10.14430/ arctic4366*]
- Puig-Lozano, R., Fernández, A., Saavedra, P., Tejedor, M., Sierra, E., De La Fuente, J., Xuriach, A., Díaz-Delgado, J., Rivero, M.A., & Andrada, M. (2020). Retrospective study of traumatic intra-interspecific interactions in stranded cetaceans, Canary Islands. *Front. Vet. Sci.* 7: 107. [Available at: https://doi.org/10.3389/fvets.2020.567258]
- Reeves, R., Rosa, C., George, J.C., Sheffield, G., & Moore, M. (2012). Implications of Arctic industrial growth and strategies to mitigate future vessel and fishing gear impacts on bowhead whales. *Mar. Pol.* 36: 454–462. [Available at: https://doi.org/10.1016/ j.marpol.2011.08.005]
- Reeves, R., & Lee D.S. (2022). Bowhead whales and whaling in the central and eastern Canadian Arctic, 1970–2021. J. Cetacean Res. Manage. 23: 1–25. [Available at: https://doi.org/10.47536/jcrm.v23i1.359]
- Rockwood, R.C., Adams, J.D., Hastings, S., Morten, J., & Jahncke, J. (2021). Modeling whale deaths from vessel strikes to reduce the risk of fatality to endangered whales. *Front. Mar. Sci.* 8: 649890. [Available at: https://doi.org/10.3389/fmars.2021.649890]
- Ryan, C., Mchugh, B., Trueman, C.N., Harrod, C., Berrow, S.D., & O'Connor, I. (2012). Accounting for the effects of lipids in stable isotope (δ13C and δ15N values) analysis of skin and blubber of balaenopterid whales. *Rapid Commun. Mass. Spectom*. 26: 2745–2754. [Available at: http://dx.doi.org/10.1002/rcm.6394]
- Savelle, J.M., Dyke, A.S., & Mccartney, A.P. (2000). Holocene Bowhead Whale (Balaena mysticetus) Mortality Patterns in the Canadian Arctic Archipelago. *Arctic* 53: 414–421. [Available at: *https://doi.org/10.14430/arctic871*]
- Sciullo, L., Thiemann, G.W., & Lunn, N.J. (2016). Comparative assessment of metrics for monitoring the body condition of polar bears in western Hudson Bay. J. Zool. 300: 45–58. [Available at: https://doi.org/10.1111/jzo.12354]
- Shaw, C.N., Wilson, P.J., & White, B.N. (2003). A reliable molecular method of gender determination for mammals. J. Mammal. 84: 123–128. [Available at: https://doi.org/10.1644/1545-1542(2003)084%3C0123:ARMMOG%3E2.0.CO;2]
- Smies, A., Wales, J., Hennenfent, M., Lyons, L., Dunn, C., Robbins, J., Lee, B.P., Zerbini, A., & Rajachar, R.M. (2022). Non-antibiotic antimicrobial polydopamine surface coating to prevent stable biofilm formation on satellite telemetry tags used in cetacean conservation applications. *Front. Mar. Sci.* 9: 989025. [Available at: https://doi.org/10.3389/fmars.2022.989025]
- Stern, G.A. (2009). Contaminants in Canadian Arctic bowhead whales. DFO. Can. Sci. Advis. Sec. Res. Doc. 2009/028.
- Stimmelmayr, R. (2015). Health assessment of subsistence harvested Bering-Chukchi-Beaufort Seas bowhead whales (*Balaena mysticetus*): an Overview. SC/66A/E/08 presented to the IWC Scientific Committee, San Diego, CA., 2015. [Available from the IWC Publications Team]
- Stimmelmayr, R., George, J.C., Clarke, J., Ferguson, M., Willoughby, A., Brower, A., Sheffield, G., Stafford, K., Givens, G., Von Duyke, A., Sformo, T., Person, B., De Sousa, L., & Suydam, R. (2020). 2018–2019 Health Report for the Bering-Chukchi-Beaufort Seas Bowhead Whales-Preliminary Findings. SC/68B/ASW/03 presented to the IWC Scientific Committee, Virtual, 2020. [Available from the IWC Publications Team]
- Stimmelmayr, R., Rotstein, D., Sheffield, G., Brower, H.K., & George, J.C. (2021). Diseases and parasites. In: *The Bowhead Whale* (pp.471–498). Academic Press, San Diego, CA.
- Thiemann, G.W., Budge, S.M., & Iverson, S.J. (2004). Determining blubber fatty acid composition: a comparison of in situ direct and traditional methods. *Mar. Mammal Sci.* 20(2): 284–295.
- Thiemann, G.W., Iverson, S.J., & Stirling, I. (2007). Variability in the blubber fatty acid composition of ringed seals (*Phoca hispida*) across the Canadian Arctic. *Mar. Mammal Sci.* 23(2): 241–261.
- Thiemann, G.W., Iverson, S.J., & Stirling, I. (2008). Variation in blubber fatty acid composition among marine mammals in the Canadian Arctic. *Mar. Mammal Sci.* 24(1): 91–111.
- Willoughby, A.L., Ferguson, M.C., Stimmelmayr, R., & Brower, A.A. (2022). Bowhead whale (Balaena mysticetus) carcasses documented during the 2019 aerial surveys in the eastern Chukchi and western Beaufort seas: A follow-up to evidence of bowhead whale and killer whale (Orcinus orca) co-occurrence during 2009–2018. Pol. Biol. 45(12): 1723–1728. [Available at: https://doi.org/10.1007/ s00300-022-03097-2]
- Young, B.G., Fortune, S.M., Koski, W.R., Raverty, S.A., Kilabuk, R., & Ferguson, S.H. (2019). Evidence of killer whale predation on a yearling bowhead whale in Cumberland Sound, Nunavut. Arct. Sci. 6(1): 53–61. [Available at: https://doi.org/10.1139/as-2019-0014]
- Yurkowski, D.J., Hussey, N.E., Semeniuk, C., Ferguson, S.H., & Fisk, A.T. (2015). Effects of lipid extraction and the utility of lipid normalization models on δ 13 C and δ 15 N values in Arctic marine mammal tissues. *Pol. Biol.* 38: 131–143. [Available at: *https://doi.org/10.1007/ s00300-014-1571-1*]
- Zha, Y., Eiler, A., Johansson, F., & Svanbäck, R. (2018). Effects of predation stress and food ration on perch gut microbiota. *Microbiome* 6. [Available at: *https://doi.org/10.1186/s40168-018-0400-0*]

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