

Seasonal diving and foraging behaviour of Eastern Canada–West Greenland bowhead whales

Sarah M. E. Fortune^{1,5,*}, Steven H. Ferguson², Andrew W. Trites¹, Bernard LeBlanc³,
Valerie LeMay⁴, Justine M. Hudson², Mark F. Baumgartner⁵

¹Department of Zoology and Marine Mammal Research Unit, Institute for the Oceans and Fisheries,
University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada

²Fisheries and Oceans Canada, Freshwater Institute, Winnipeg, Manitoba R3T 2N2, Canada

³Fisheries and Oceans Canada, Quebec, Quebec G1K 7Y7, Canada

⁴Department of Forest Resources Management, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada

⁵Biology Department, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543-1050, USA

ABSTRACT: Climate change may affect the foraging success of bowhead whales *Balaena mysticetus* by altering the diversity and abundance of zooplankton species available as food. However, assessing climate-induced impacts first requires documenting feeding conditions under current environmental conditions. We collected seasonal movement and dive-behaviour data from 25 Eastern Canada–West Greenland bowheads instrumented with time-depth telemetry tags and used state-space models to examine whale movements and dive behaviours. Zooplankton samples were also collected in Cumberland Sound (CS) to determine species composition and biomass. We found that CS was used seasonally by 14 of the 25 tagged whales. Area-restricted movement was the dominant behaviour in CS, suggesting that the tagged whales allocated considerable time to feeding. Prey sampling data suggested that bowheads were exploiting energy-rich Arctic copepods such as *Calanus glacialis* and *C. hyperboreus* during summer. Dive behaviour changed seasonally in CS. Most notably, probable feeding dives were substantially shallower during spring and summer compared to fall and winter. These seasonal changes in dive depths likely reflect changes in the vertical distribution of calanoid copepods, which are known to suspend development and overwinter at depth during fall and winter when availability of their phytoplankton prey is presumed to be lower. Overall, CS appears to be an important year-round foraging habitat for bowheads, but is particularly important during the late summer and fall. Whether CS will remain a reliable feeding area for bowhead whales under climate change is not yet known.

KEY WORDS: *Balaena mysticetus* · Feeding ecology · Zooplankton · State-space modeling · Dive analysis · Satellite telemetry

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1. INTRODUCTION

The Arctic is warming at a rate more than double the global average (Screen et al. 2012) and is experiencing unprecedented decreases in the extent and thickness of sea ice (Stroeve et al. 2007, Kwok et al. 2009). Such environmental changes are likely affecting the community structure, distribution and abun-

dance of Arctic zooplankton, which are sensitive to changes in water temperature (Hays et al. 2005, Chust et al. 2014). Continued warming of Arctic waters may result in the large, lipid-rich Arctic species being replaced with smaller temperate/subarctic species that thrive in warmer conditions and are comparatively lower in energy content (Beaugrand et al. 2002, Beaugrand 2009). Such ecosystem changes will likely alter

*Corresponding author: s.fortune@oceans.ubc.ca

the stability of current food web structures (McMeans et al. 2013) and impact the foraging success of zooplanktivorous marine predators, such as bowhead whales *Balaena mysticetus* (Meyer-Gutbrod & Greene 2018).

Bowhead whales are considered to be moderately vulnerable to future environmental changes that will likely alter their current prey resource (Moore & Huntington 2008). The replacement of large-bodied zooplankton with comparatively smaller species has already been documented during short-term warming events in the Arctic (Lalande et al. 2013). Long-term trends in decreasing zooplankton body size have also been observed in the North Sea (Beaugrand 2009), and the abundance, distribution, and diversity of zooplankton species available to bowhead whales are also likely to change in the future. Such potential changes to the feeding regime of bowheads in the Eastern Canadian Arctic makes understanding how they forage under current environmental conditions essential to evaluating the sensitivity of the species to future changes in prey quality and quantity.

Much of what is known about the foraging strategy of the Eastern Canada–West Greenland (ECWG) bowhead whale population is the result of archival tagging (Laidre et al. 2007, Heide-Jørgensen et al. 2010, 2013, Laidre & Heide-Jørgensen 2012) and prey sampling (Madsen et al. 2001, Laidre et al. 2007, Swalethorp et al. 2011) studies in Disko Bay on the western coast of Greenland, in late winter and early spring. Relatively little is known about the diet and feeding behaviour of this population in Canadian waters. Furthermore, the sex ratio in these studies was heavily skewed towards non-lactating adult females (85:15 female:male), and is thus not representative of the entire population (Laidre et al. 2007, Heide-Jørgensen et al. 2010). During the spring (February–May), adult females in Disko Bay consumed predominately temperate/subarctic calanoid copepods such as *Calanus finmarchicus*. These female bowhead whales made deep, long dives during late winter and comparatively shallower dives during spring (Heide-Jørgensen et al. 2013). Such temporal differences in diving behaviour were likely due to seasonal vertical movements of their prey. The tagged whales were presumed to seasonally adjust their foraging strategy to maximize prey consumption by feeding on dormant (i.e. diapausing) copepods at depth during winter, and on active copepods nearer the surface during spring (Heide-Jørgensen et al. 2013). It is not known whether this is a general strategy across different habitats, seasons and demographic groups.

Little is known about the foraging ecology of bowhead whales in other regions of the ECWG population range. For example, despite the long history of bowhead whale occupancy and commercial exploitation that occurred in Cumberland Sound (Reeves et al. 1983), few foraging studies have been conducted to date. The sex ratio of whales in Cumberland Sound between 2011 and 2013 was 80:125 (female:male), closer to parity than in Disko Bay, but somewhat biased towards males (Frasier et al. 2020). Both males and females are found along the east coast of Baffin Island (Nielsen et al. 2015, Chambault et al. 2018), which suggests that these males and those in Cumberland Sound may be the counterparts to the adult females found in Disko Bay (Heide-Jørgensen et al. 2010). Given the apparent use of Cumberland Sound by all demographic groups (including juveniles and mother–calf pairs), assessing diets, foraging behaviour and habitat use in this region fills an important gap in knowledge about the foraging ecology of the ECWG bowhead population.

Regional differences in zooplankton species composition and abundance have been attributed to the strong influence of the Baffin Island Current, which is of Arctic origin in Cumberland Sound (Dunbar 1951, Aitken & Gilbert 1989, McMeans et al. 2012), along with the West Greenland Current, which is of Atlantic Origin in Disko Bay (Heide-Jørgensen et al. 2013). However, both locations are likely to contain some Arctic and Atlantic fauna because the Baffin Island Current and West Greenland Current are known to mix in both regions (McMeans et al. 2012, Heide-Jørgensen et al. 2013). This may be particularly true along the Davis Strait sill, which may sometimes facilitate the movement of the West Greenland Current to Cumberland Sound (Bedard et al. 2015). Consequently, the quality and quantity of bowhead prey and thus their feeding ecology likely differs seasonally and between habitats due to physical oceanographic processes.

Zooplankton communities are expected to differ between Disko Bay and Cumberland Sound, which in turn should influence the feeding behaviour and relative quality of prey consumed by bowhead whales. For example, bowheads in Disko Bay feed predominately on the smaller temperate/subarctic calanoid copepod *Calanus finmarchicus*, rather than on the less abundant, but larger-bodied Arctic copepods *C. hyperboreus* and *C. glacialis* (Laidre et al. 2007). Laidre et al. (2007) collected zooplankton at 25 stations in Disko Bay and found that the mean \pm SD biomass concentration (mg C m^{-3}) of *C. finmarchicus* was 49 ± 39 compared with 12.3 ± 14.9 for *C. hyperboreus* and 2.8 ± 2.3

for *C. glacialis*. Conversely, zooplankton species in Cumberland Sound are likely to be dominated by Arctic copepods, but it is not known whether they are preferred by the bowhead whales that feed there. Furthermore, differences in the life histories of the Arctic and temperate/subarctic copepods likely require different feeding strategies to capture them.

To examine the seasonal foraging behaviour of different demographic groups of ECWG bowhead whales in Cumberland Sound, we used time–depth telemetry tags that recorded horizontal and vertical movements. We examined spatiotemporal trends in movement to determine how bowhead whales used Cumberland Sound (Fig. 1) throughout the day, month and year. We characterized how feeding behaviour (dive depth, shape and duration) changed over seasonal and diel time scales. We then analysed bowhead whale dive shape, depth and duration and combined information on the species composition and biomass of zooplankton obtained through net collections to determine the importance of Cumberland Sound as a foraging ground. This research improves our understanding of the diet and seasonal foraging characteristics of an understudied segment of the ECWG bowhead whale population.

2. MATERIALS AND METHODS

2.1. Telemetry

Bowhead whales ($n = 25$) were equipped with long-term platform transmitter terminal (PTT) satellite telemetry tags containing time–depth recorders and Argos radio transmitters (Wildlife Computers SPLASH MK10) to record horizontal and vertical movements. The SPLASH tag provided information on date, time, location and summary dive behaviour (e.g. depth, duration and shape). To increase longevity of the tag, the PTTs were programmed to transmit up to 400 times a day every second hour during summer, and less frequently during winter (i.e. 100 times every second day). For our study, summer included June to August, fall was between September and November, winter ranged from December to February, and spring occurred between March and May.

The whales were tagged in Foxe Basin and Cumberland Sound during summer (2012 and 2013; Table 1). Juvenile and non-lactating adult animals were selected for tagging, which meant excluding animals <9 m long that were likely calves and those in mother–calf pairs. Each tag was attached with a

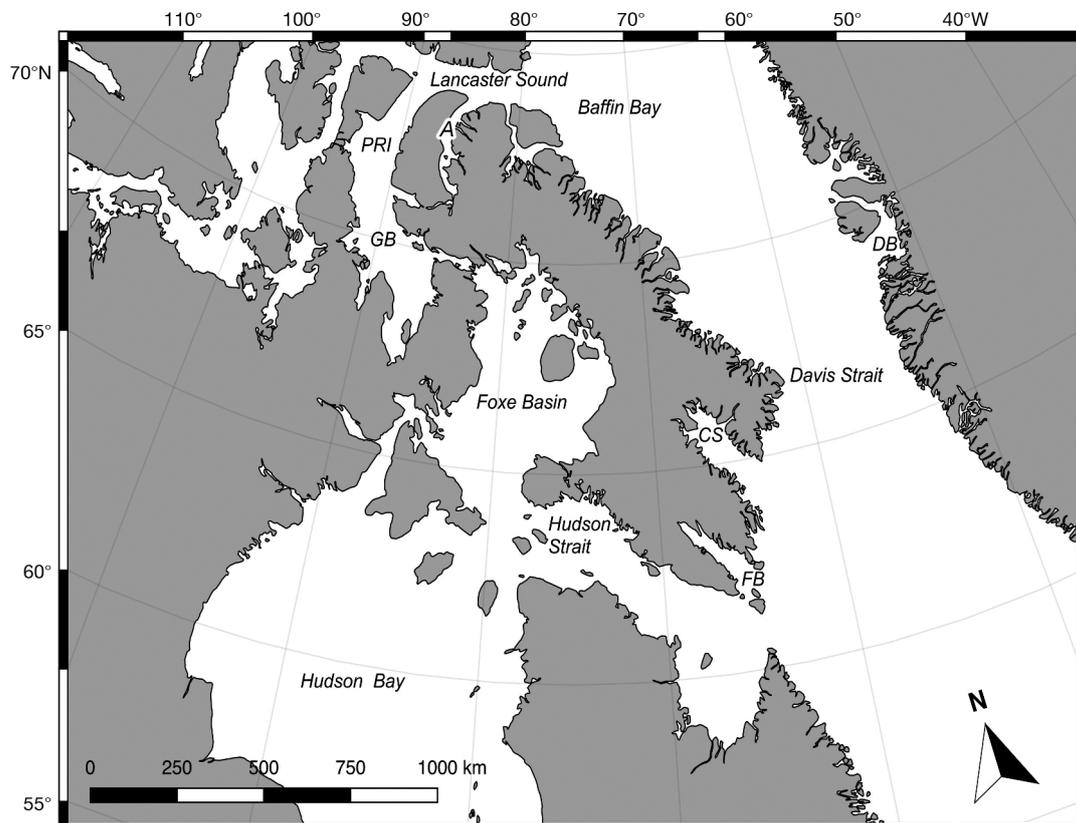


Fig. 1. Known range of Eastern Canada–West Greenland bowhead whales with key areas identified: FB: Frobisher Bay, CS: Cumberland Sound, DB: Disko Bay, A: Admiralty Inlet, PRI: Prince Regent Inlet and GB: Gulf of Boothia

Table 1. Summary information for all 25 bowhead whales tagged in Cumberland Sound (CS) and Foxe Basin (FB) with SPLASH Tags (Wildlife Computers, MK10) between 2012 and 2013. PTT: platform transmitter terminal used to identify unique individuals (animals that visited CS are in **bold**); HSSSM: total number of days for which hierarchical switching-state-space model (HSSSM) locations were predicted after running the 'vmask' function; Gap: number of days for which HSSSM locations were predicted after removing locations resulting from gaps >4 consecutive days in raw satellite telemetry data; CS: total number of days a given animal was in CS as predicted by the HSSSM with gaps removed; Location: habitat where the animal was tagged; Length: body length estimated from the tagging vessel. -: instances where data were not available

PTT	HSSSM (d)	Gap (d)	CS (d)	Location	Length (m)	Sex
114494	265	26	–	FB	12	F
114495	723	678	6	FB	11–12	F
114496	529	306	1	FB	11	F
114497	309	226	–	FB	12	M
114498	187	134	1	FB	11	M
114499	338	338	2	FB	13–14	F
114500	593	479	–	FB	12–13	M
114501	184	173	–	FB	–	–
114502	338	243	177	CS	10	M
114503	519	338	25	CS	10	F
114504	345	290	250	CS	10–11	F
114505	319	319	118	CS	11–12	M
114506	19	19	19	CS	13–14	F
114507	400	92	72	CS	10	M
114508	738	249	95	CS	9–10	M
114509	289	227	111	CS	9–10	M
128145	504	498	–	FB	11–12	F
128146	694	557	–	FB	13–14	F
128148	335	287	–	FB	13	F
128149	13	13	–	FB	12–13	–
128150	728	677	–	FB	10	F
128151	721	700	–	FB	9–10	M
128152	684	677	157	FB	9–10	M
128153	384	348	–	FB	12–13	M
128154	320	320	9	FB	11–12	M

~20 cm stainless steel anchor, and a skin and blubber sample was simultaneously collected from a 4 cm biopsy tip attached to the tag deployment device. The anchor and biopsy tip were both sterilized with 1:10 bleach:water solution prior to use. The tags were deployed from a wooden canoe freighter using an 8 m fiberglass hand-held tagging pole. The tags were attached dorsally and behind the blow holes to improve data transmission by maximizing the time the transmitter was out of water during a surfacing event. Biopsy samples were collected to genetically determine sex by amplification of a zinc finger gene intron using LGL331 and LGL335 primers (Shaw et al. 2003). The PCR product was subsequently stained

with GelRed (Biotium) and then visualized on a 1.5% agarose gel. To infer sex, we then used the banding pattern of X (~975 bp) and Y (~1040 bp) fragments.

2.2. Horizontal movement analysis

To increase the number of useful positions and improve the accuracy of low quality Argos locations (e.g. 0, A and B) that are common for large whale tagging studies (Silva et al. 2014, Lowther et al. 2015), the data are often filtered. In our study, we re-processed the data with the square root unscented Kalman filter (SRUKF) by Service Argos. The SRUKF algorithm uses a correlated random walk model that predicts the future position of an animal and its estimated error based on the individual's previous location and estimated error (Silva et al. 2014) as a result of the diving behaviour of the whales (e.g. short surface intervals).

The SRUKF-filtered data were subsequently run through a speed filter using the 'vmask' function in the 'argosfilter' package in R version 3.2.1 (R Development Core Team 2019). This function filters Argos satellite tracking data and is especially useful for marine animal telemetry data because of the prevalence of poor-quality data and the need to filter unlikely locations. We used a speed threshold of 2 m s^{-1} , as this speed approaches the maximum swimming speed of bowhead whales (2.5 m s^{-1}) and encompasses both foraging and migratory behavioural states for balaenids (Mayo & Marx 1990, Baumgartner & Mate 2003, Werth 2004, Simon et al. 2009, Nielsen et al. 2015). Argos locations that resulted from swimming speeds above this threshold were subsequently removed.

We fit a hierarchical switching-state-space model (HSSSM) (Jonsen et al. 2005, 2013) to our filtered telemetry data to: (1) estimate the horizontal movement (e.g. swimming speed, tortuosity) of individual animals; and (2) determine individuals' behavioural states (area-restricted movement and travelling). The 'bsam' package in R (R Development Core Team 2019) provided in the supplement of Jonsen et al. (2013) was used to fit a correlated random walk (CRW) model that switched between 2 CRWs that reflected probable area-restricted movement (ARM) and travelling behavioural states (Jonsen et al. 2005). The 2 CRWs and the associated behavioural states differ in mean turn angle and movement persistence (autocorrelation in speed and direction). ARM reflected instances of low swimming speeds and high turning angles (consistent with foraging behaviour),

whereas travelling consisted of faster, more linear movements. The model (HSSSM) was fit to each data set ($n = 25$) containing individual specific location data with 40 000 Markov chain Monte Carlo (MCMC) iterations, dropping the first 30 000 (i.e. burn-in) and retaining every 10th sample from the remaining 10 000 iterations, resulting in a total of 1000 samples per chain ($n = 2$ chains). The HSSSM predicts 2 locations per day (i.e. 12 h timestep), per individual.

The HSSSM was chosen because it yields regularly spaced location estimates and categorizes movement behaviour by simultaneously fitting a single model to all individual bowhead whale tracks, which is necessary for evaluating the seasonal foraging behaviour of bowhead whales. Behavioural states (b) were classified based on mean estimates from the MCMC samples, which assumed that $b = 1$ was traveling and $b = 2$ was ARM. The cut-off points we used were the same as in previous studies and locations, where mean estimates of $b > 1.75$ were assumed to indicate ARM; $b < 1.25$ reflected transient behaviour; and values of b between 1.25 and 1.75 were unclassified. We applied the same HSSSM formulated by Silva et al. (2013), using the transition equation established by Jonsen et al. (2007), such that each individual whale (or PTT) is indexed by k , whereby:

$$d_{t,k} \sim N_2[\gamma_{bt,k}T(\theta_{bt,k})d_{t-1,k},\Sigma] \quad (1)$$

where $d_{t-1,k}$ represents the displacement of an individual whale (k) between 2 unobserved locations (x_{t-1} and x_{t-2}) and $d_{t,k}$ is the displacement of the same whale between 2 unobserved locations (x_t and x_{t-1}) that occurred earlier in time, $T(\theta)$ is the transition matrix providing the mean turning angle (θ , i.e. tortuosity or change in heading) required to transition from d_{t-1} to d_t . Furthermore, the move persistence coefficient (γ) combines autocorrelation in both direction and speed, and the randomness in whale movement (N_2) is represented by a bivariate Gaussian distribution with a covariance matrix Σ . Most importantly, the mean turning angle (θ) and move persistence coefficient (γ) are indexed by behavioural state (bt) such that each individual whale (k) at each displacement (t) corresponds to an estimated behavioural state (b) that yields the best model fit. A set of previously established priors were placed on the movement parameters (θ and γ) as determined by Breed et al. (2009) such that during travel, swim direction will be more linear (e.g. turn angle close to 0°) while ARM behaviour occurs when speed and turning angle are highly autocorrelated.

Many empirical studies describe the movement of predators relative to the distribution and abundance

of their prey. Feeding, or expected feeding based on prior experiences of the animal, has been inferred from ARM (or area-restricted search) over different spatial scales in fish (Hill et al. 2000), birds (Paiva et al. 2010) and terrestrial (Byrne & Chamberlain 2012) and aquatic mammals (Thums et al. 2011). Predators exhibiting ARM alter their movement pattern to increase the time spent in productive areas by increasing their turning rate after detecting prey (or anticipating the detection of food) and reducing their speed if prey abundance is high (e.g. Kareiva & Odell 1987, Haskell 1997, Fauchald & Tveraa 2003). Consequently, feeding animals are thought to spend more time in a given area if they are consuming or searching for food. However, it is also possible that animals conducting other non-feeding behaviours such as mating (Würsig et al. 1993, Richardson et al. 1995) and rock-rubbing (Fortune et al. 2017) can produce similar movement patterns (e.g. low swimming speed and high tortuosity). Therefore, it is important to consider vertical movements when inferring feeding behaviour from horizontal movement patterns.

2.3. Vertical movement analysis

We analyzed the vertical movement of SPLASH-tagged animals to determine how foraging effort changed seasonally in Cumberland Sound using the time-depth-recorder dive data. Dive duration, shape and minimum and maximum dive depth were recorded with the time-depth recorder (TDR). Dives were classified as vertical excursions to depths ≥ 8 m, because this was the minimum depth threshold used by Wildlife Computers for dive classification and thus dives shallower than this threshold were not recorded. This dive threshold is also biologically relevant, as it approaches the minimum estimated body length of the tagged whales. However, it prevented us from quantifying surface foraging behaviour such as skim-feeding, which is expected to occur during spring. The dive shape was classified according to 3 broad categories defined by Wildlife Computers: V-shaped dives represented those where $\leq 20\%$ of dive duration was spent at maximum depth, U-shaped dives occurred when > 20 and $\leq 50\%$ of the dive duration was spent at maximum depth, and square dives included those where $> 50\%$ of the dive duration was spent at maximum depth. Previous studies that examined dive profiles of balaenid whales (North Atlantic right whales *Eubalaena glacialis* and bowhead whales) in

relation to prey availability found that V-shaped dives reflected search behaviour (i.e. non-feeding dives), whereas square and U-shaped dives where whales maximized their bottom time were most likely representative of foraging dives (Baumgartner & Mate 2003, Laidre et al. 2007, Heide-Jørgensen et al. 2013). For example, during springtime in Disko Bay, bowhead whales conducted deep U-shaped dives near the sea bottom where high abundances of pre-ascension *Calanus finmarchicus* occurred. Following fine-scale foraging studies on North Atlantic right whales (e.g. Baumgartner & Mate 2003, Baumgartner et al. 2003, 2017) that showed animals feeding at the maximum depth of their square or U-shaped dive where zooplankton abundance was greatest, bowheads were shown to undergo temporal changes in dive depth, suggesting that individuals adjust their foraging behaviour according to the vertical distribution of their prey (Heide-Jørgensen et al. 2013). Consequently, foraging behaviour may be inferred by examining bowhead whale dive characteristics.

We filtered the predicted locations from the HSSSM to include those that occurred within Cumberland Sound only (i.e. latitude ranged from 64° 00' to 67° 00' N and longitude ranged from 67° 00' to 63° 30' W) and removed gaps exceeding 4 consecutive days based on the SRUKF data as a way to exclude uncertain location estimates. We then filtered the bowhead whale dive behaviour data based on the HSSSM-predicted location data by matching dates when tagged animals were inside Cumberland Sound. We assumed that animals did not make short (<24 h) excursions outside of Cumberland Sound and that if there was an Argos location within Cumberland Sound on a particular day, all dives occurring during that same day were conducted inside Cumberland Sound.

We investigated whether there were diel and seasonal impacts on bowhead diving behaviour (e.g. dive depth and duration) using linear-mixed effects models with the 'lme' statistical function in R 3.6.1 (R Development Core Team 2019). We separated dives that occurred during the day from those that occurred at night during early and late August 2012 and used day/night as a fixed effect and maximum depth (m) and dive duration (min) for square dives as the response variables. Similarly, we examined whether there were seasonal and dive shape effects (fixed effects) on maximum depth (m) and dive duration (min) (response variables). We fitted several nested linear mixed-effects models and used likelihood ratio tests to examine how season and

time of day affect bowhead whale dive depth and duration, along with Akaike's information criterion (AIC) to indicate model support. Since there were multiple dive records per animal (i.e. repeated measures), we included a hierarchical error structure of individual, year, month and day, along with a continuous autoregressive process within day since measures were irregularly spaced in time (i.e. 'CAR(1)' process; Pinheiro & Bates 2000). We found support for the random effects structure (i.e. lower AIC and supported by likelihood ratio tests) relative to other simpler random effect error structures for all models. We also used graphs of standardized residuals to further confirm this error structure along with normality.

2.4. Zooplankton sampling and species identification and enumeration

We collected prey samples to understand why bowhead whales may be using Cumberland Sound as a summertime feeding habitat and how the species composition of zooplankton may differ from Disko Bay (69° 15' N, 53° 33' W; straight line distance from mouth of Disko Bay to Cumberland Sound is ~675 km). Zooplankton samples were collected in the fluke print of diving bowhead whales using vertical hauling methods where we sampled from 10 m above the sea bottom to the sea surface with a sampling depth (mean \pm SD) of 207.6 \pm 30.52 m using a 333 μ m conical mesh net with a 60 cm diameter mouth opening. The net was outfitted with a General Oceanics helical flow meter and a Sensus Ultra time–depth recorder to determine the sampling distance used to calculate the volume of sampled water. All samples were obtained between 23 and 26 August 2013 from Kingnait Fiord (65° 55' N, 65° 25' W), where bowhead whales are regularly observed conducting deep and long dives. Once the vertical tow was completed, the net was sprayed down immediately with seawater and all collected organisms were concentrated into the cod-end bucket at the end of the net. The concentrated organisms were first transferred to a 333 μ m mesh sieve and then to a 250 ml sample jar and fixed with 5% buffered formalin for preservation.

Zooplankton species composition and abundance was determined using taxonomic identification and enumeration methods in the laboratory. Each sample was filtered through a 333 μ m mesh sieve, and subsequently rinsed with freshwater and transferred to a beaker and diluted with water. The

sample volume was recorded and a Hensen-Stempel pipette was used to obtain a homogeneous aliquot (i.e. sub-sample of known volume). A Folsom plankton splitter was used to sub-sample dense samples, and the total number of times each sample was split depended on the total number of sample organisms. Each aliquot contained a minimum of 200 calanoid copepods, and each organism was identified to the lowest possible taxon (e.g. species and genus for calanoid copepods) and life stage for *Calanus* spp. and *Pseudocalanus* spp. using a dissecting microscope. We discriminated between morphologically similar *Calanus* species (e.g. *C. hyperboreus*, *C. glacialis* and *C. finmarchicus*; Grainger 1961, Jaschnov 1970) by measuring prosome lengths (e.g. Unstad & Tande 1991, Hirche et al. 1994) for all *Calanus* spp. with undamaged exoskeletons using a dissecting microscope, stage micrometer and ocular micrometer. To minimize measurement variability, we measured all organisms from the same orientation (right lateral side down). We used species-specific prosome size ranges reported by Madsen et al. (2001) to differentiate species. However, *Calanus* spp. are known to overlap in prosome length, which is particularly likely to introduce error into the identification of early life-stages of *C. glacialis*, resulting in an over-estimation of *C. finmarchicus* (Parent et al. 2011).

Zooplankton biomass was estimated for all *Calanus* organisms with prosome measurements (PL) using known relationships between prosome length (mm) and body weight (mg C) using:

$$C_{\text{mg}} = a \times \text{PL}_{\text{mm}}^b \quad (2)$$

where $a = 0.0048$ and $b = 3.5687$ for *C. finmarchicus* and *C. glacialis* (Madsen et al. 2001), and $a = 0.0014$ and $b = 3.3899$ for *C. hyperboreus* (Hirche & Mumm 1992, Thor et al. 2005). We estimated the individual carbon content of early (CI–CIV) and late (CV–adult) *Pseudocalanus* spp. by assuming that early-stage organisms had mean PL of 0.597 mm and late-stage organisms measured 1.009 mm (Liu & Hopcroft 2008).

Previously collected vertical zooplankton data (Madsen et al. 2001) were also used to further elucidate whether square dives were feeding dives and whether temporal shifts in dive depth reflected changes in the vertical distribution of prey. We compared the maximum depth of square dives with the depth of maximum zooplankton biomass (samples collected over a 14 mo period between 1996 and 1997 using vertical hauling methods) in Disko Bay (Madsen et al. 2001).

3. RESULTS

3.1. Telemetry

The sex ratio of the tagged whales occupying Cumberland Sound was somewhat biased towards males (57:43%) with 8 males and 6 females, and estimated body lengths ranged from 9.5 to 13.5 m (Table 1). Age class was broadly inferred based on previous studies (George et al. 1999, 2011, Higdon & Ferguson 2010, Koski et al. 2010) using boat-based estimates of body lengths that approximated the distance between the tip of the whale's snout to the fluke notch. These estimates revealed that 33% ($n = 2$) of the 6 females were probable adults (>13 m, >25 yr), and 66% ($n = 4$) were sub-adults (≥ 10 and ≤ 12.5 m and <25 yr). No estimated female body lengths were within the range of calves (<7.5 m and 0–1 yr) or young juveniles (≥ 7.5 and <10 m and 1–4 yr). However, we found that 62.5% ($n = 5$) of the 8 males were sub-adults, and 37.5% ($n = 3$) were young juveniles. Consequently, our body length estimates suggested that young juveniles, sub-adults and adult animals use Cumberland Sound. However, our tagged whale data were dominated by reproductively immature animals for both sexes—particularly males, as no adults appear to have been tagged. The average body length (mean \pm SD) of tagged animals was relatively small (10.9 ± 1.3 m) in part because of our somewhat biased sampling design (e.g. not tagging mothers and calves).

Animals tagged in 2012 transmitted for 397 d on average (range: 19–737 d), while those tagged in 2013 transmitted for 485 d (13–729 d; Table 1). The HSSSM predicted 2 daily locations for each animal, resulting in 16 406 locations throughout the Eastern Canadian Arctic. We chose this 12 h time-step for the HSSSM because the majority of tagged animals had at least 2 Argos locations per day. A portion of these locations occurred within Cumberland Sound (12.5%). However, of the 14 animals that visited Cumberland Sound (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m643p197_supp.pdf), almost one-quarter (24%; $n = 2044$) of their 8446 locations were inside the sound. Furthermore, 1 animal (PTT 114506) stayed nearly an entire year (from 9 August 2012 to 18 July 2013) inside Cumberland Sound and just outside the mouth of the sound. When excluding gaps (>4 consecutive days), we found that the mean number of days that individuals spent in Cumberland Sound was highly variable, mean \pm SD 75 ± 79.6 d. We found 21% ($n = 3$) of the tagged whales spent only 1–2 d in Cumberland Sound, while

29% ($n = 4$) spent 6 to 25 d, 43% ($n = 6$) spent 72 to 177 d, and 7% ($n = 1$) resided in Cumberland Sound for 250 d.

We found that 10 of the animals that occurred in Cumberland Sound had gaps in the SRUKF data that exceeded 4 consecutive days when including all data (i.e. locations outside of Cumberland Sound). Overall, there were 11 482 HSSSM-predicted locations for all 14 animals that visited Cumberland Sound, of which 13% ($n = 1530$) were generated during gaps >4 d. Furthermore, we found that HSSSM-predicted locations generated by identified gaps were most common during fall (31%; $n = 480$), followed by winter (27%; $n = 420$), spring (22%; $n = 340$) and summer (19%; $n = 290$).

Seasonal patterns in Cumberland Sound occupancy were found for SPLASH-tagged whales. When data for all years were combined, bowhead whales ($n = 14$) had the greatest number of locations (2 per day) in Cumberland Sound during the fall ($n = 882$, 43%), followed by summer ($n = 537$, 26%), spring ($n = 405$, 20%) and winter ($n = 220$, 11%) (Fig. S2). When data were separated by year, tagged animals had the highest occupancy in Cumberland Sound during the

fall of 2012 ($n = 841$ locations), summer of 2012 ($n = 295$) and spring 2013 ($n = 243$) (Fig. S2). Tagged bowhead whales spent the least amount of time in Cumberland Sound during the winter (range 21–116 d between 2012 and 2015). The low occupancy during winter may be partially an artifact of the tag settings, as fewer transmissions were scheduled during winter months to increase tag longevity. However, the greatest proportion of gaps in HSSSM-predicted locations occurred during the fall, which provides support for these seasonal patterns in occupancy.

3.2. Behaviour

The bowhead whales in Cumberland Sound displayed pronounced differences in the proportions of behavioural states (b) as determined by the HSSSM. The majority of all estimated locations in Cumberland Sound ($n = 2044$) were associated with ARM (presumably foraging behaviour) based on the weighted average (mean \pm SD: $91.4 \pm 10.82\%$; Fig. 2), whereby the percentage of HSSSM locations with ARM for an individual whale was weighted by the total number

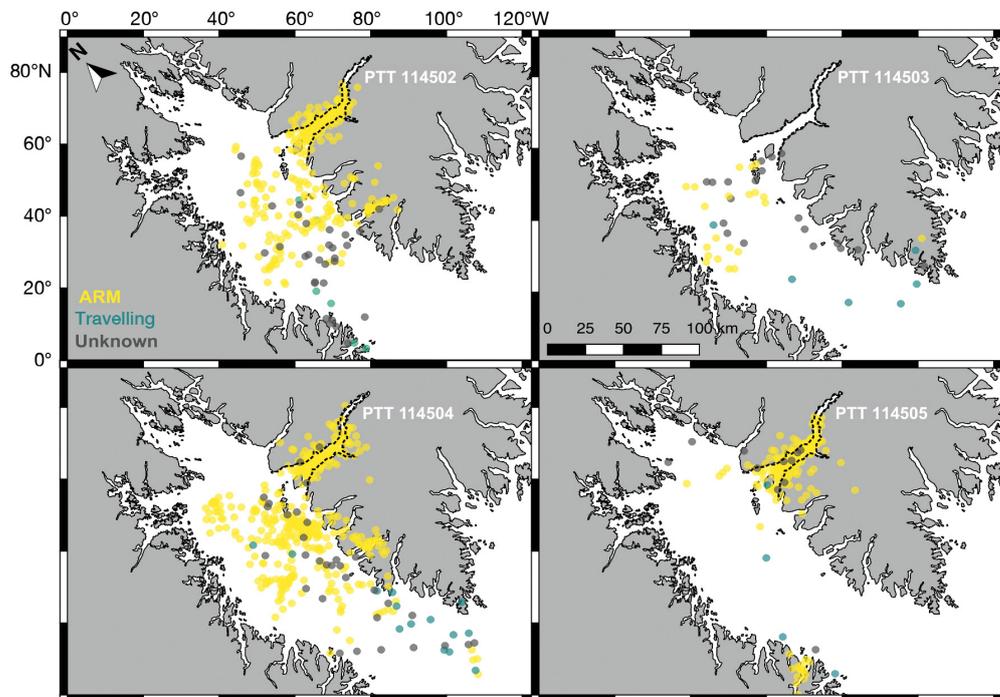


Fig. 2. Argos satellite locations for 4 SPLASH-tagged bowhead whales (PTT 114502, 114503, 114504, 114505) derived from hierarchical switching state-space models (HSSSM) in Cumberland Sound with 2 locations per day for illustrative purposes. HSSSM-predicted locations resulting from gaps in Kalman-filtered Argos data exceeding 4 consecutive days were considered less reliable than predictions made from locations closer in time, and were removed from analysis. Three behavioural states derived from the HSSSM are indicated, with yellow, green and grey circles reflecting area-restricted movement (ARM, i.e. probable feeding), travelling behaviour and an unknown behavioural state, respectively. HSSSM-predicted locations that occurred between 64.00 and 67.00 latitude and 67.00 and 63.50 longitude (decimal degrees) were considered to occur within Cumberland Sound. Kingnait Fiord is outlined (----) for identification purposes

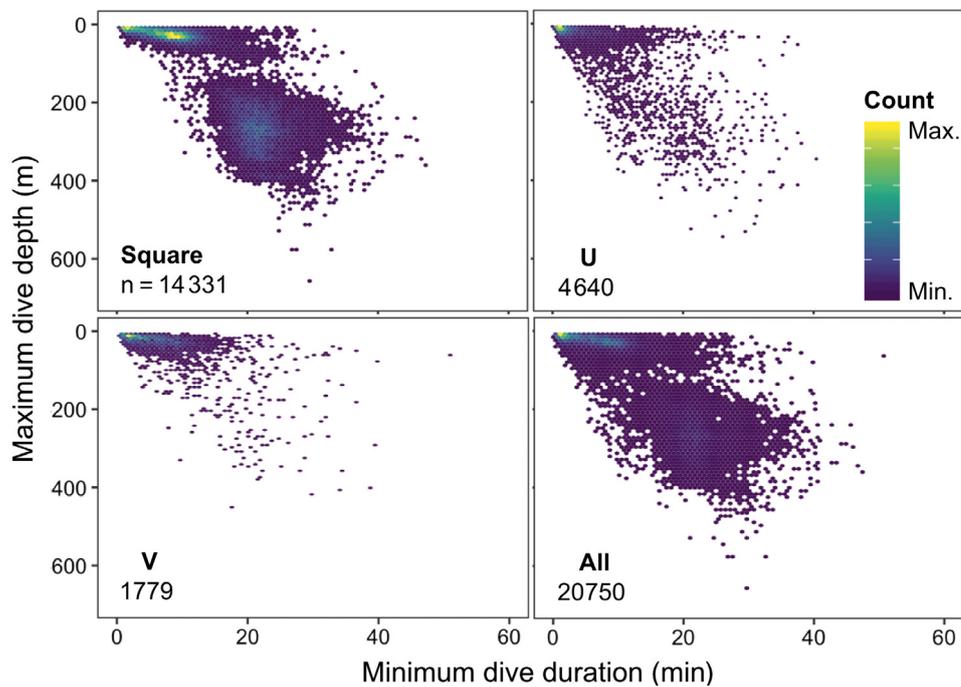


Fig. 3. Maximum depth (m) and minimum dive duration (min) for square, U- and V-shaped dives for 13 bowhead whales equipped with SPLASH tags while in Cumberland Sound between 2012 and 2015. Data were pooled across months and seasons, and were plotted using a hexagonal heatmap, which divides the area of the graph into hexagons and counts the number of data points contained within each hexagon. The minimum number of counts per hexagon is 1 for all dive shapes, and the maximum value is 150 for square dives, 240 for U-shaped, 60 for V-shaped and 450 when all data are combined. Square dives were considerably deeper and longer in duration compared to V-shaped dives, and are likely indicative of feeding behaviour

of HSSSM locations for that whale when calculating the weighted average. Traveling behaviour rarely occurred and represented only $2.20 \pm 3.71\%$ of all locations. The remaining $6.41 \pm 7.93\%$ of locations were of an unknown behavioural state. Furthermore, we found seasonal differences in the proportion of locations assumed to be associated with ARM behaviour. Most notably, ARM was greatest during the fall ($95.2 \pm 8.03\%$ of all locations based on weighted mean), followed by the spring ($91.1 \pm 19.77\%$), summer ($89.2 \pm 12.68\%$) and winter ($81.8 \pm 26.4\%$). The high percentages of ARM behaviour suggest that bowhead whales consistently allocated time to foraging activities while occupying Cumberland Sound.

3.3. Diving

Of the 14 tagged whales that visited Cumberland Sound, 1 individual (PTT 114498) had only a single location within the sound and no associated dives. The remaining 13 whales dove a total of 20 976 times over 450 d in Cumberland Sound (Fig. 3, Table S1). The whales conducted predominately square (68.3%, $n = 14\,331$) and U-shaped dives (22.1%, $n = 4\,640$),

whereas V-shaped (8.5%, $n = 1\,781$) and unclassified dives (1.1%, $n = 226$) represented a small portion of the total (Fig. 3, Table 2). We inspected the summary dive statistics (e.g. range, mean \pm SD) for unusually high values that would exceed the physiological diving limits of the species. We found 2 V-shaped dives that were extraordinarily deep and long in duration (maximum depth: 976 m, minimum dive duration: 114 h). We subsequently removed these biologically

Table 2. Summary dive statistics for square, V- and U-shaped dives in Cumberland Sound between 2012 and 2015 for 13 bowhead whales. Data were pooled across months and years. Two V-shaped dives (>700 m depth and >75 min in duration) were considered erroneous and were removed from the analysis

Dive shape	Range (min.–max.)	Mean \pm SD	Skew	Kurtosis
Maximum dive depth (m)				
Square	8–655.5	165.45 \pm 128.90	0.099	1.52
U	8–543.5	62.11 \pm 88.57	3.352	15.70
V	8–451.5	45.70 \pm 58.51	2.206	7.16
Minimum dive duration (min)				
Square	0.42–47.4	16.47 \pm 8.31	–0.081	2.15
U	0.12–40.3	6.69 \pm 6.71	1.632	6.92
V	0.58–50.8	8.06 \pm 6.34	1.597	5.44

Table 3. Linear mixed-effects models for the impacts of bowhead whale dive type (square, U-, and V-shaped, and unknown) and season (summer, fall, winter and spring) on dive duration and maximum depth. The null model includes no fixed effects. The random effects are consistent across models and included the platform transmitter terminal (PTT) used to identify unique individuals, year, month and day in a hierarchical order. The change in AIC (Δ AIC) and likelihood ratio tests (LRT) are relative to the model earlier in the list for dive duration and for maximum depth following stepwise selection. These indicate that there are interactions between dive shape and season for both dive duration and maximum depth. Instances where there are no fixed-effects, LRT or Δ AIC values are noted (-)

Model	Fixed	df	AIC	LRT (p)	Δ AIC
Dive duration (min)					
Null	-	19979	306397.9	-	-
1	Shape	19976	302483.3	3920.647 (<0.0001)	3914.6
2	Shape+Season	19976, 31	302457.8	31.43108 (<0.0001)	25.5
3	Shape \times Season	19967, 31	301258.6	1217.196 (<0.0001)	1199.2
Maximum dive depth (m)					
Null	-	19979	241789.2	-	-
4	Shape	19976	240354.7	1440.476 (<0.0001)	1434.5
5	Shape+Season	19976, 31	240342.1	18.5641 (0.0003)	12.6
6	Shape \times Season	19967, 31	239081.1	1278.991 (<0.0001)	1261

improbable outliers from our analysis. Furthermore, only 2 tagged animals occupied Cumberland Sound during February ($n = 354$ square dives) and March ($n = 410$ square dives), which is fewer than other times of year.

When evaluating whether bowheads allocated more or less time to probable feeding dives during different seasons, we found an interaction between season and dive shape for dive duration (Table 3; log-likelihood ratio test [LRT] = 1217.2, $p < 0.0001$). In particular, square dives had the longest duration, particularly during winter (Fig. 4). To permit inferences about the seasonal vertical movement of zooplankton based on the assumed connection between the zooplankton depth and bowhead whale probable feeding depth, we examined impacts of dive shape and season on dive depth. As with dive duration, we found an interaction between dive shape and

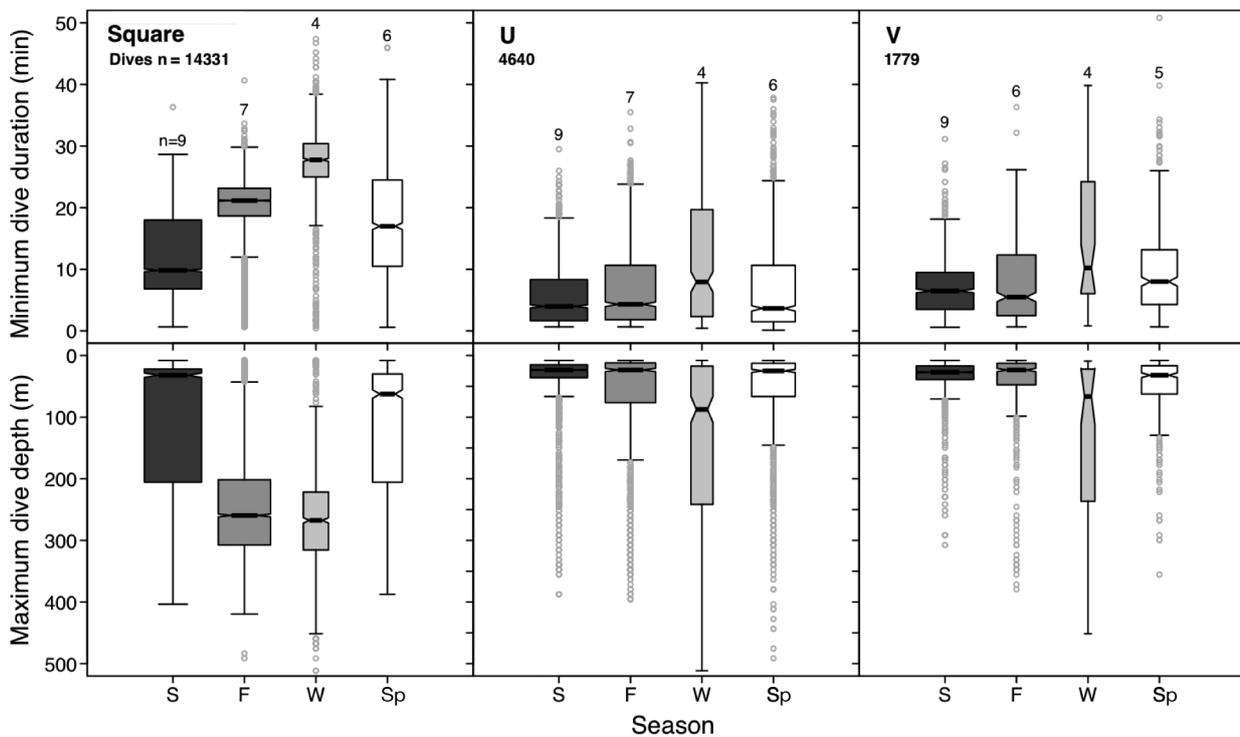


Fig. 4. Minimum dive duration (min) and maximum dive depth (m) by season (S: summer, F: fall, W: winter and Sp: spring) and type of dive (square, U- and V-shaped) for 13 bowhead whales that occupied Cumberland Sound. The number of tagged whales is indicated above the boxplot whiskers. The width of the boxes is proportional to the square-root of the number of dives per month (i.e. the wider the box, the greater the sample size). Instances where the notches of 2 boxes do not overlap provide evidence that the medians differ. The black bar represents the median, the box represents the interquartile range, the whiskers reflect the non-extreme maximum and minimum values, and the grey dots indicate extreme values

season (Table 3; LRT = 1278.9, $p < .0001$). For example, square dive depth was shallow (≤ 50 m) during spring and early to mid-summer and comparatively deeper (≥ 150 m) during fall and winter (Fig. 4). We also found that the maximum depth of square dives agreed well with the seasonal depths of maximum zooplankton biomass in Disko Bay (Madsen et al. 2001) (Fig. 5), providing further evidence that the depth where bowhead whale feeding occurs changes seasonally in Cumberland Sound.

Through initial examination of bowhead whale dive depths during the day and night (Figs. 6 & 7), we found evidence of diel diving behaviour for 8 animals during early and late August 2012. During early August (1–15 August), we found that the maximum depth (Table 4; LRT = 20.2, $p < 0.0001$) and minimum dive duration (Table 4; LRT = 29.7, $p < 0.0001$) of square dives differed for periods of daylight (day) versus darkness (night). However, these results concerning diel effects should be interpreted with caution, since the changes in AIC compared to the null model were relatively small. During early August, the maximum depths (mean \pm SD) of square dives were 122 ± 80 m during the day and 59 ± 46 m during the night based on the average depth of each individ-

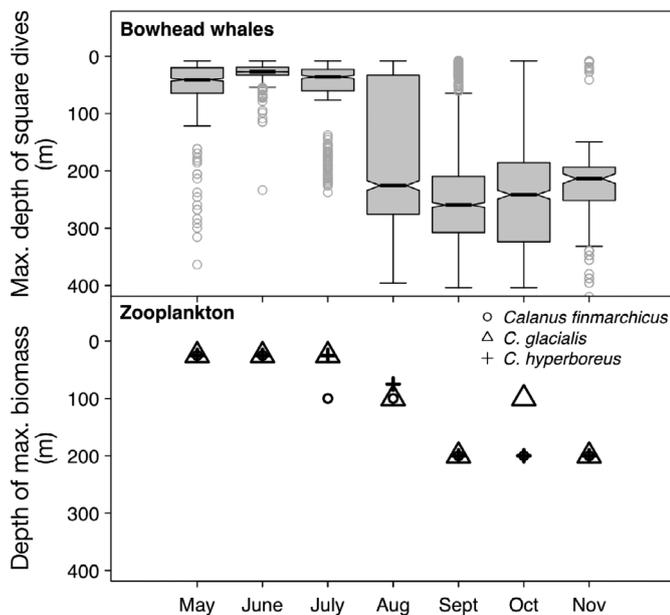


Fig. 5. Comparison of the maximum depth (m) of square dives for bowhead whales during the daytime in Cumberland Sound ($n = 13$ animals) and the depth of maximum zooplankton biomass (m) of 3 dominant calanoid copepod species (*Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus*) collected in Disko Bay, a habitat along western Greenland at a similar latitude to Cumberland Sound. The plotted zooplankton data were collected and reported by Madsen et al. (2001). Boxplot definitions are the same as in Fig. 4

ual's mean square dive depth. Similarly, we found that the depth (Table 4; LRT = 36.4, $p < 0.0001$) and duration (Table 4; LRT = 69.9, $p < 0.0001$) of square dives differed substantially in late August (16–31 August) during the day and night. Although less pronounced than during early August, the depths of square dives were considerably deeper during the day (250 ± 32 m) compared with the night (159 ± 59 m) during late August. Bowhead whales similarly conducted longer dives during the daytime (18.85 ± 1.936 min) than the nighttime (14.61 ± 2.664 min) during late August.

Overall, we found that bowhead whales conducted deeper and longer square dives during daylight hours in August (Figs. 5 & 6). However, there was considerable variability in dive depth that is likely due to individual variation in foraging strategies and variability in the vertical distribution of prey (Fig. 7). It is important to consider that these diel diving models were constructed for specific time periods based on initial examination of the dive data and our prediction that zooplankton would undergo diel vertical migration during summer when surface phytoplankton concentrations are expected to occur.

We found that bowhead whales spent a portion of their day (21–22%) conducting square and U-shaped dives in Cumberland Sound during summer. Overall, the whales appeared to allocate the most time to probable feeding dives during summer (5.0 ± 1.52 h) and the least during spring (2.5 ± 0.76 h; Table 5). However, the time bowheads allocated to probable foraging dives on a daily basis was quite variable during summer. For example, the maximum time individual animals spent conducting square dives

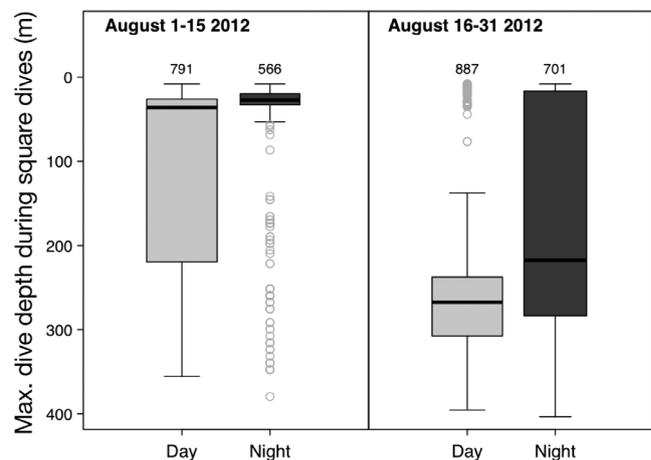


Fig. 6. Maximum dive depth (m) during square dives for 8 bowhead whales in Cumberland Sound during early (1–15 August) and late (16–31 August) August 2012. Boxplot definitions are the same as in Fig. 4

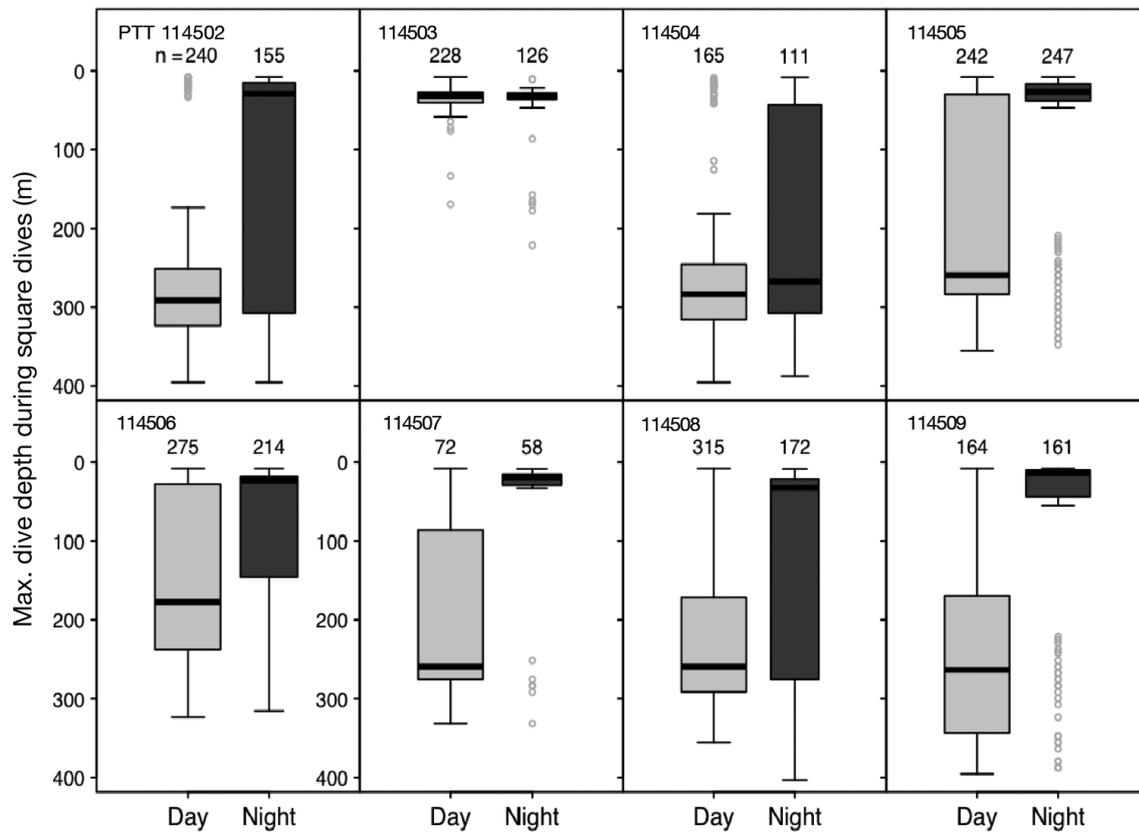


Fig. 7. Maximum dive depth (m) of square dives during the day and night for 8 bowhead whales in Cumberland Sound during August 2012. Boxplot definitions are the same as in Fig. 4

Table 4. Linear mixed-effects models for the impacts of time of day (i.e. categorical variable 'day.night' where each bowhead whale dive is classified as occurring during the day or night based on the time of sunset and sunrise during early and late August 2012) on square dive duration (August) and maximum depth (August). The random effects are consistent across models and included the platform transmitter terminal (PTT) used to identify unique individuals, year, month and day in a hierarchical order. The null model includes no fixed effects. The change in AIC (Δ AIC) and likelihood ratio tests (LRT) are relative to the model earlier in the list for dive duration and for maximum depth and indicate that there are diel effects on both dive duration and maximum depth. Instances where there are no fixed effects, LRT or Δ AIC values are noted (-)

Model	Fixed	df	AIC	LRT (p)	Δ AIC
Early August maximum square dive depth (m)					
Null	-	1313	14324.1	-	-
7	day.night	1312	14306.1	20.043 (<0.0001)	18.05
Early August minimum square dive duration (min)					
Null	-	1313	18642.0	-	-
8	day.night	1312	18614.0	30.057 (<0.0001)	28.05
Late August maximum dive depth (m)					
Null	-	1490	18682.0	-	-
9	day.night	1489	18644.6	39.474 (<0.0001)	37.5
Late August minimum dive duration (min)					
Null	-	1490	22651.6	-	-
10	day.night	1489	22579.1	74.439 (<0.0001)	72.4

ranged from 9.7 to 14.2 h in 2012 and between 5.8 and 11.7 h in 2013. These results suggest that individuals occasionally allocated considerable time to feeding activities, but tended to use a relatively small portion of the day to feed on average (i.e. 20.8% or 5 h).

3.4. Zooplankton

We collected 7 zooplankton samples near diving bowhead whales in King-nait Fiord during August 2013. Species identification revealed that the full water-column tows consisted almost exclusively of calanoid copepods (mean \pm SD: $94 \pm 0.03\%$). Of the copepods, *Pseudocalanus* spp. were the most common ($55 \pm 0.05\%$) followed by *Calanus* spp. ($36 \pm 0.57\%$; Fig. 8). Due to the prevalence of *Pseudocalanus* spp. and *Calanus* spp., we only calculated abundance (ind. m^{-3}) for these organisms.

Table 5. Average time (mean \pm SD) spent by bowhead whales making square dives per day in Cumberland Sound. Dive durations were pooled across years for each animal that spent a minimum of 5 d in Cumberland Sound per season. Dive durations were first averaged to provide a mean daily dive time per individual, and then averaged across individuals

Season	Square dives (h)	Years	Animals (n)
Summer	5.0 \pm 1.52	2012, 2013	9
Fall	4.6 \pm 1.56	2012, 2013	6
Winter	4.7 \pm 2.44	2012–2015	3
Spring	2.9 \pm 0.72	2013, 2015	5

We found that *Pseudocalanus* spp. represented the greatest proportion of total abundance (61 \pm 5.9%) on average, followed by *C. glacialis* (27% \pm 5.8), *C. finmarchicus* (8.4 \pm 2.0%) and *C. hyperboreus* (4.2 \pm 1.5%; Fig. 9). We measured prosome lengths for 91% (n = 623) of all staged *Calanus* spp. (n = 682). Prosome measurements were variable within and between taxa due to species-specific and ontogenetic variation in size. On average, an individual copepod was estimated to contain 0.015 \pm 0.036 mg C ind.⁻¹ for *C. finmarchicus* as compared with 0.107 \pm 0.159 mg C ind.⁻¹ for *C. glacialis* and 0.124 \pm 0.122 mg C ind.⁻¹ for *C. hyperboreus*. We used mean estimates of dry weight (mg C ind.⁻¹) for early (CI–CIV) and late (CV–adult) individuals per species and their associated abundance per tow to calculate mean dry weight per cubic meter (mg C m⁻³). We found that estimated dry weight was dominated by *C. glacialis* (72 \pm 7.9%; 0.87 \pm 0.41 mg m⁻³), followed by *Pseudocalanus* spp.

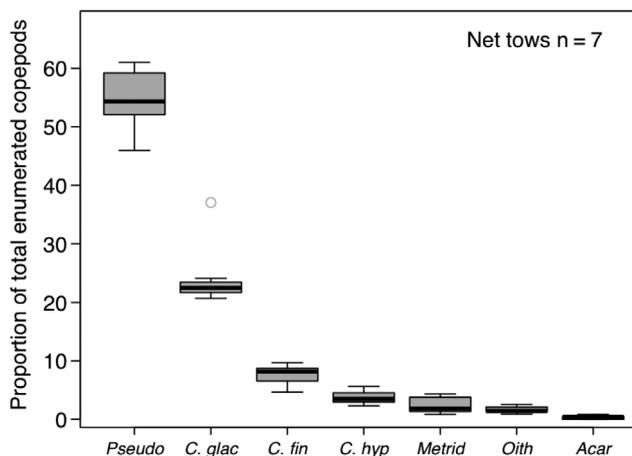


Fig. 8. Proportion of enumerated calanoid copepods per sample from Cumberland Sound for *Pseudocalanus* spp., *Calanus glacialis*, *C. finmarchicus*, *C. hyperboreus*, *Metridia* spp., *Oithona* spp. and *Acartia longiremis* with all life-stages grouped together. Boxplot definitions are the same as in Fig. 4

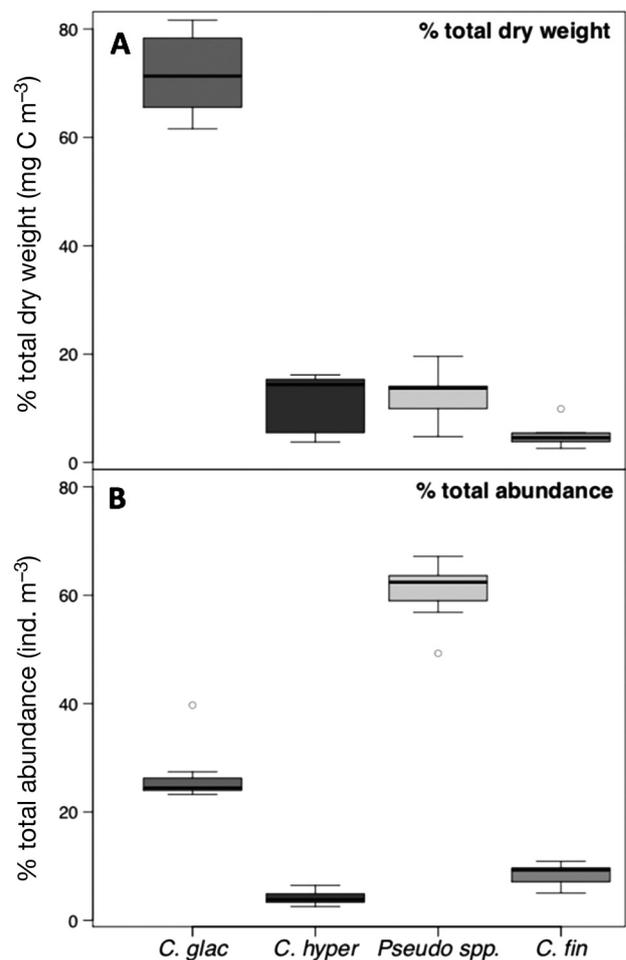


Fig. 9. Percent contribution by species to (A) total biomass (mg C m⁻³) and (B) total abundance (ind. m⁻³) based on 7 net tows in Kingnait Fiord during August 2013. Abundance and biomass calculations were made for the most common species identified, i.e. *Calanus glacialis*, *C. hyperboreus*, *C. finmarchicus* and *Pseudocalanus* spp. The boxplot shading is relative to the total lipid content per individual species, with the darkest shading representing the species with the highest energy content (*C. hyperboreus*) and the lightest representing the lowest-energy prey (*Pseudocalanus* spp.) (DeLorenzo Costa et al. 2006, Falk-Petersen et al. 2009); other boxplot definitions are the same as in Fig. 4

(12 \pm 4.7%; 0.13 \pm 0.04 mg m⁻³), *C. hyperboreus* (11 \pm 5.6%; 0.13 \pm 0.11 mg m⁻³), and *C. finmarchicus* (5 \pm 2.4%; 0.06 \pm 0.02 mg m⁻³; Fig. 9).

4. DISCUSSION

Our analysis of long-term (including attachments \geq 365 d) bowhead whale horizontal and vertical movements provides new insights into habitat-use patterns and feeding behaviour that previous studies have not captured using smaller datasets and with biologgers

that provided less detailed dive information. Most notably, we found that whales resided in Cumberland Sound during all 4 seasons, with 1 animal remaining all year. Some animals tended to be infrequent visitors to Cumberland Sound, spending only a day to several weeks, while others had considerably longer residency times, spending several consecutive months in the area that occasionally includes overwintering ($n = 1$). However, peak occupancy occurred during summer (26%) and fall (43%). Furthermore, almost all of the satellite telemetry locations (91%) were associated with ARM, suggesting that Cumberland Sound is a year-round feeding area. These findings provide a new understanding of the feeding behaviour of bowhead whales, and the biological significance of Cumberland Sound to the ECWG population.

4.1. Evidence of feeding behaviour

The feeding behaviours of bowhead whales and the closely related North Atlantic right whale have been inferred from horizontal movement data collected from satellite telemetry tags and from vertical dive data recorded using time–depth recorders. Previous studies that examined dive profiles of right whales (Baumgartner & Mate 2003, Baumgartner et al. 2017) and bowhead whales (Laidre et al. 2007, Heide-Jørgensen et al. 2013) in relation to prey availability found that square and U-shaped dives where whales maximized their bottom time were representative of foraging dives. In one study, bowhead whales conducted deep U-shaped dives near the sea bottom in Disko Bay where high abundances of pre-ascension *Calanus finmarchicus* occurred (Laidre et al. 2007). Other studies of bowhead whales in the Eastern Canadian Arctic found that changes in swimming speed, turning radius and diving frequency could be used to evaluate bowhead whale feeding activity (Pomerleau et al. 2011, Nielsen et al. 2015). Together, these studies demonstrate that at-surface locations (satellite telemetry) and summarized dive data (time–depth recorder) can provide useful information regarding the sub-surface foraging behaviour of large whales. Furthermore, because of the longevity of our biologgers, we were able to make seasonal inferences about individual foraging behaviour, which high-resolution biologgers used to study the kinematics of foraging-related behaviour using accelerometry and fine-scale time–depth recorders are unable to capture because of their limited deployment durations (e.g. Simon et al. 2009, Wright et al. 2017, Tennessen et al. 2019).

We observed the tagged whales occupying Cumberland Sound during all months. However, peak foraging likely occurs during late summer and early fall based on high occupancy during that time inferred from HSSSMs that were parameterized with satellite telemetry data (Figs. 3 & 4). The greatest number of HSSSM locations occurred during August (2012 = 14.3%; 2013 = 3%), followed by September (2012 = 14.9%; 2013 = 1.9%), October (2012 = 15.1%; 2013 = 0%) and November (2012 = 11.1%; 2013 = 0.09%) for 14 animals. The residency period was long (25 d; 6–31 August 2012) for the 8 animals tagged in Cumberland Sound during August 2012, suggesting that this is an important area for a portion of the population. Furthermore, results from the state-space models demonstrated that just over 90% of all HSSSM locations were associated with behaviours typically thought to reflect feeding activities (e.g. slow swimming speed and high turning angles).

Bowhead whales in Cumberland Sound allocated a small proportion of their daily activities to feeding based on the vertical dive data (≥ 8 m). They made mostly square (68%) and U-shaped (22%) dives that were consistent with foraging dives recorded for North Atlantic right whales (Baumgartner & Mate 2003) in the western Atlantic. However, unlike North Atlantic right whales that are believed to spend the majority (50–90%; Goodyear 1996) of their day foraging while occupying their summer feeding grounds such as the Bay of Fundy, bowhead whales spent only a small fraction (21–22%) of their day conducting square and U-shaped dives during the summer in Cumberland Sound. This finding provides support that Cumberland Sound is a multi-use habitat that serves functions beyond feeding, such as rock-rubbing for exfoliation (Fortune et al. 2017).

Overall, the dive durations for right whales (8–15 min, Goodyear 1996; and 12.2 ± 2.22 min, Baumgartner & Mate 2003) and bowhead whales (12.0 ± 3.3 min) were remarkably similar during the summer. Both species dove to comparable depths on average (mean dive data averaged across individuals): right whales dove to 121.2 ± 24.2 m in the Bay of Fundy and Roseway Basin (Baumgartner & Mate 2003) and 134 m on average in the Bay of Fundy (Goodyear 1996), and bowheads similarly dove to 117.4 ± 52.4 m. This suggests that the increased time that right whales allocated to foraging is unlikely related to differences in the vertical distribution of their prey. Interspecific differences in daily feeding activities may instead reflect disparities in: (1) the quality and quantity of available prey; (2) the spatial heterogeneity of prey patches; (3) energetic requirements; and (4) environmental conditions.

4.2. Seasonal feeding patterns

Some large whales have highly seasonal feeding periods marked by intense feeding during summer in productive high latitude habitats, and fasting over winter in lower latitude areas (e.g. Corkeron & Connor 1999, Kenney et al. 2001, Christiansen et al. 2013). However, unlike a proportion of right whales that presumably fast for a significant portion of the year while occupying southern calving grounds between December and March (Keller et al. 2012), bowheads appear to feed year-round in Cumberland Sound based on >50% of their dives each season being probable foraging dives. We found that bowheads allocated the most time to foraging dives during the summer in Cumberland Sound on average (5.0 ± 1.52 h) and the least amount during spring (2.5 ± 0.76 h; Table 5). However, there was a lot of variability in the time allocated to probable foraging dives, suggesting that bowheads alternated between days when they spent over half the day feeding (e.g. 60%) and others when they spent only a small fraction of the day engaged in feeding activities. Variability in daily feeding times may reflect differences in energy requirements based on age, sex, reproductive and nutritive condition (Lockyer 1981, George 2009, Fortune et al. 2013).

The apparent reduced feeding time during spring may reflect the presence of zooplankton near the surface during the phytoplankton bloom, making it more accessible with less effort by the whales. It is also possible that feeding time was underestimated during spring if whales were exploiting prey patches located between 0 and 7 m in the water column (as North Atlantic right whales do during spring; Baumgartner et al. 2017). Another possible explanation for why bowhead whales may allocate less time than right whales to feeding activities during the summer is that they may have comparatively lower daily food requirements, in part because they appear to feed continuously throughout the year. Bowheads also have comparatively thicker blubber stores (Haldiman & Tarpley 1993, Rosa 2006, George et al. 2007) compared with North Atlantic right whales (Moore et al. 2004, Miller et al. 2011) and may opt to catabolize this energy store during lean years, providing a greater capacity to fast. It is also possible that bowhead whales have lower basal metabolic rates (i.e. hypometabolic condition; George 2009), and hence lower daily energy requirements, compared to North Atlantic right whales.

Our conclusion that bowheads feed year-round in Cumberland Sound is consistent with prior telemetry and diet studies. Previous satellite-tagging studies

similarly found that bowhead whales occupied Cumberland Sound during winter months. One study reported that predominately adult females, originating from Disko Bay, occupied Cumberland Sound between late July and mid-December (Nielsen et al. 2015). Another study recorded one whale in Cumberland Sound during late July that then travelled to the high Arctic and subsequently returned to Cumberland Sound in early January and remained within the area until the start of May (Pomerleau et al. 2011). Our conclusion that bowhead whales are feeding year-round is further supported by dietary stable isotope analysis of ECWG bowhead whales that also reported year-round foraging (Matthews & Ferguson 2015). However, Cumberland Sound may be one of the only areas where ECWG bowhead whales feed during all seasons. Year-round feeding may be a consequence of (1) a population below carrying capacity and (2) favourable physical and biological oceanographic conditions that support calanoid copepod production throughout their range. Consequently, due to their apparently flexible feeding strategy, bowhead whales may be able to reduce their summertime foraging effort compared to right whales.

The plasticity of the bowhead whale feeding strategy is also reflected by seasonal adjustments in dive behaviour. The depth of probable foraging dives (i.e. square dives) varied seasonally, suggesting that the vertical distribution of zooplankton fluctuates seasonally in Cumberland Sound. This was seen in the maximum depth of square dives becoming increasingly deeper during summer (122.7 ± 59.3 m), fall (218.9 ± 22.5 m) and winter (253.1 ± 111.5 m), and becoming shallower during spring (73.5 ± 50.4 SD; all years combined for all individuals that spent a minimum of 5 d inside Cumberland Sound per season; Fig. 4).

Inferences may be made about the vertical distribution of bowhead prey in Cumberland Sound based on the life-history characteristics of calanoid copepods and zooplankton sampling research conducted in an adjacent habitat: Disko Bay, Greenland. The composition of zooplankton in Disko Bay is similarly dominated by herbivorous calanoid copepods, such as *Calanus finmarchicus*, *C. hyperboreus* and *C. glacialis*, which occur in maximum numbers at depths that change seasonally (Madsen et al. 2001). However, we found that summertime biomass in Cumberland Sound was dominated by larger-bodied Arctic species on average (*C. glacialis* 72%, *C. hyperboreus* 11% and *C. finmarchicus* 5%), which differs from Disko Bay, where *Calanus* spp. biomass was dominated by *C. finmarchicus* (76%), a temperate/subarctic species, followed by *C. hyperboreus* (20%) and *C. glacialis* (4%). Interestingly,

depths of maximum zooplankton biomass from Disko Bay were similar across taxa and compared well with seasonal differences in the depths of bowhead whale foraging dives in Cumberland Sound (Fig. 5). This agreement between summertime zooplankton depth distribution and bowhead diving behaviour suggests that *Calanus* spp. have similar seasonal vertical movements at comparable latitudes on either side of Davis Strait, and that bowhead whales likely adjust their foraging behaviour during summer (e.g. deep vs. shallow square dives) in response to changes in the vertical distribution of their prey. However, the seasonal timing of changes in copepod vertical distribution may be somewhat different in Cumberland Sound than in Disko Bay because of oceanographic differences. Consequently, for a rigorous analysis, these data should be collected concurrently.

Calanoid copepods of the families Calanidae and Eucalanidae have life cycles that correspond with seasonal changes in physical and biological oceanographic conditions and feature pronounced vertical movements. In response to reductions in food availability following the spring phytoplankton bloom and increasing predator abundance, lipid-rich life stages of *Calanus* spp. descend to deeper waters (below the winter convective mixed layer for organisms in fiords and shelf seas; Irigoien 2004). Once organisms have vertically migrated, they commence diapause (a form of dormancy). At this time, the cooler water temperatures and reduced activity suppress metabolic rates to decrease catabolism of lipid reserves (Madsen et al. 2001, Heide-Jørgensen et al. 2007, Laidre et al. 2007). Some species (e.g. *C. finmarchicus* and *C. glacialis*) may ascend prior to or at the start of the spring phytoplankton bloom to either refuel their lipid reserves to permit spawning or replenish their energy reserves after egg production (Tande 1982, Niehoff et al. 2002, Madsen et al. 2008). Larger-bodied and longer-lived species such as *C. hyperboreus*, however, employ a different reproductive strategy and spawn during the winter while at depth using stored energy (Hirche & Niehoff 1996). The lipid-rich and positively buoyant eggs develop to feeding stage nauplii as they ascend to the surface waters, ready to begin grazing at the start of the phytoplankton bloom (Jung-Madsen et al. 2013).

Zooplankton biomass should be high in the surface waters during the spring phytoplankton bloom and decrease over the late summer months as phytoplankton is grazed down and copepods begin to migrate to depth and enter diapause. The timing and duration of diapause, however, is highly variable and depends on the life history and reproductive strategy

of different species (Falk-Petersen et al. 2009) and on seasonally induced changes in environmental conditions such as ice retreat and solar irradiance (Baumgartner & Tarrant 2017).

Bowhead whale diving behaviour is likely to reflect seasonal movements in the vertical distribution of their prey. Previous studies found that phytoplankton production was highest in Cumberland Sound during late June 2007 and August 2008 (McMeans et al. 2012). Consequently, we would anticipate surface aggregations of zooplankton to begin forming during early to mid-summer following the retreat of sea ice and persisting until late summer, with diapause commencing during early fall. These seasonal patterns in vertical zooplankton distribution should be reflected in the depth of probable foraging dives of bowhead whales (e.g. Figs. 6 & 7). We found that tagged bowheads made shallow square dives during May–August and began making deep dives during the latter half of August—presumably when a pronounced reduction in phytoplankton occurred and zooplankton initiated diapause. Consequently, it appears as though August and September are a transitional period in Cumberland Sound at which time zooplankton begin their vertical migration to depth.

4.3. Diel patterns in feeding activity

Zooplankton undergo short-term daily vertical movements in addition to longer-term seasonal shifts in their distribution. For example, *Calanus* spp. make daily excursions below the euphotic zone at dawn to avoid presumed visual predators such as zooplanktivorous fish (Bollens & Frost 1989). Zooplankton will ascend towards the surface after dusk to graze on phytoplankton that is concentrated at the mixed layer (e.g. Bollens & Frost 1989, Durbin et al. 1995, Baumgartner et al. 2011, Sainmont et al. 2013, Vestheim et al. 2013). Such diel vertical migration (DVM) appears to be a strategy employed to minimize predation risk. However, predator avoidance means foregoing feeding opportunities for part of the day and incurring energetic costs to move through the water column.

Not all copepods undergo DVM. One possible reason is that some size classes may be too small to be at risk of being eaten by visual predators and therefore can remain feeding (i.e. smaller copepods are less likely to be visually detected and thus less likely to undergo vertical migration; Hays 1995). However, some copepods are also known to undertake reverse DVM, whereby organisms occupy surface waters during the day and descend to depth at night in response

to standard DVM by their invertebrate predators (Ohman et al. 1983). Finally, individuals with full or nearly full oil sacs may conduct DVM to avoid predators, whereas organisms with less full oil sacs may remain in the surface waters to feed during the day and night because the benefit of accumulating more lipid outweighs the potential risk of predation (Huntley & Brooks 1982, Baumgartner et al. 2011). In all likelihood, the avoidance of predators and accumulation of lipid during most years of high primary productivity likely drives strong diel rhythms in copepod vertical distribution in Cumberland Sound during summer.

We observed changes in bowhead whale diving behaviour that were consistent with DVM of their prey. Interestingly, the depth of square dives was consistently deeper during the day compared with the night during August, when there are pronounced periods of daylight and darkness (12 h separation). Between the end of June and the beginning of July there are over 20 h of daylight, leaving little darkness to warrant DVM. We found that square dive depth was consistently deeper during the day compared with the night for 8 whales occupying Cumberland Sound during August 2012. During the first 2 wk of August, the depth of square dives was significantly deeper during the day (122 ± 80 m; mean dive depth averaged for each unique individual) and shallower at night (59 ± 46 m; Fig. 8). Similarly, in late August, bowhead whale dives were significantly deeper during the day (250 ± 32 m) and shallower during the night (159 ± 60 m). However, these late August dives were consistently deeper than dives made earlier that month regardless of time of day. Changes in photoperiod and light intensity may be a circadian cue that initiates diel vertical migration, thus affecting the vertical distribution of bowhead whale prey (Forward 1988). Furthermore, we hypothesize that the lack of a diel pattern in bowhead diving behaviour during September and October (when daylight lengths were 12 h 58 min and 9 h 48 min, respectively) reflects of the initiation of diapause.

In contrast to our observation of diel patterns in bowhead diving behaviour in Cumberland Sound, a prior study in the Eastern Canadian Arctic (Pomerleau et al. 2011) found no such behaviour. One possible explanation for this difference is that bowhead whales in the Eastern Arctic study were at higher latitudes (e.g. Gulf of Boothia), where day length is comparatively longer. Longer daylight (e.g. midnight sun) may diminish or eliminate the mass diel movement of zooplankton (Blachowiak-Samolyk et al. 2006). Further south in Disko Bay, which is at a similar latitude to Cumberland Sound, bowhead whale

prey (e.g. *C. glacialis* and *C. hyperboreus*) have been reported to undergo DVM during late April and early May (Swalethorp et al. 2011).

In the absence of data on the vertical distribution of zooplankton in Cumberland Sound, we can only speculate about what influenced bowhead whale foraging behaviour. It seems unlikely that the shift in dive depths during early and late August was due to temporal differences in day length, because there was only about one additional hour of darkness during late August (~16 h day length) compared with early August (~17 h day length). Of the bowhead Argos locations in Cumberland Sound during early August, only 57.9% of the locations were in Kingnait Fiord. Conversely, during late August, the spatial distribution of tagged whales changed, as they were almost exclusively found in Kingnait Fiord. It is possible that physical oceanographic processes differed in Kingnait Fiord, thus altering the vertical structure of prey in the water column or that the prey bowhead whales were targeting in Cumberland Sound during early August (Rogachev et al. 2008) were following classic DVM due to the co-occurrence of other known zooplanktivorous predators, such as Arctic char *Salvelinus alpinus* and capelin *Mallotus villosus* (Marcoux et al. 2012), that were otherwise absent in Kingnait Fiord. However, during late August, some copepods (e.g. lipid-rich *C. glacialis* and *C. hyperboreus*) may have begun their vertical descent to depth to commence diapause.

It is possible that copepods with less accumulated lipid may remain in the surface waters to continue foraging, and only enter diapause once they have accumulated sufficient lipids (e.g. Visser & Jónasdóttir 1999, Rey-Rassat et al. 2002, Campbell & Dower 2003, Irigoien 2004, Maps et al. 2010, 2012, Baumgartner & Tarrant 2017). Asynchronous diapause has been observed for *C. finmarchicus* in the North Atlantic Ocean (Tarrant et al. 2008). If diapause were similarly asynchronous in Cumberland Sound, bowheads may exploit deep-water aggregations of diapausing copepods during the day and night while also exploiting shallowly aggregated active prey after dusk. Future zooplankton sampling studies will be required to determine the spatio-temporal variability in diel vertical migration and the relationship between zooplankton depth distribution and bowhead whale dive behaviour (e.g. Baumgartner et al. 2011).

5. CONCLUSIONS

Our findings provide new insight into the flexible feeding strategy of an understudied segment of the

ECWG bowhead whale population and the importance of Cumberland Sound as a year-round foraging area. Through analysis of the time spent conducting horizontal (e.g. slow swimming speed and high tortuosity) and vertical (e.g. square dives) movements, we found that both sexes likely fed during all months in Cumberland Sound, although late summer and early fall appear to be particularly important feeding times. Unlike Disko Bay, where zooplankton biomass appears to be dominated by temperate/subarctic species (e.g. *C. finmarchicus*), it appears that bowheads in Cumberland Sound exploit mostly Arctic species (e.g. *C. glacialis*), which similarly comprise the greatest biomass and are comparatively larger in size and higher in lipid content than the temperate/sub-arctic species (Falk-Petersen et al. 2009). There were also distinct seasonal and diel patterns in bowhead whale dive behaviours that appear to correspond to temporal changes in the vertical distribution of their prey related to well-studied life-history characteristics. The apparent flexibility of bowhead whales to exploit seasonally available prey throughout the year in Cumberland Sound bodes well for their ability to adapt to climate-induced changes to their habitat. What is less certain, however, is how climate change will alter the species composition and abundance of their primary prey, and whether bowhead whales can adapt their foraging strategies to contend effectively with such changes to their prey base.

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Editorial responsibility: Elliott Hazen,
Pacific Grove, California, USA

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