Fisheries and Oceans Canada / Pêches et Océans Canada
Ecosystems and Oceans Science / Sciences des écosystèmes et des océans

Canadian Science Advisory Secretariat (CSAS)

Research Document 2015/046

Central and Arctic Region

Instantaneous availability bias correction for calculating aerial survey abundance estimates for bowhead whales (*Balaena mysticetus*) in the Canadian High Arctic

Cortney A. Watt[1, 2], Marianne Marcoux[2], Bernard Leblanc[2], and Steven H. Ferguson[2]

[1]Department of Biological Sciences,
University of Manitoba,
Winnipeg, MB, Canada, R3T 2N2

[2]Fisheries and Oceans Canada,
501 University Crescent,
Winnipeg, MB, Canada, R3T 2N6

July 2015

Canada

Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

Research documents are produced in the official language in which they are provided to the Secretariat.

Published by:

Fisheries and Oceans Canada
Canadian Science Advisory Secretariat
200 Kent Street
Ottawa ON K1A 0E6

http://www.dfo-mpo.gc.ca/csas-sccs/
csas-sccs@dfo-mpo.gc.ca

© Her Majesty the Queen in Right of Canada, 2015
ISSN 1919-5044

Correct citation for this publication:

Watt, C.A., Marcoux, M., Leblanc, B., and Ferguson, S.H. 2015. Instantaneous availability bias correction for calculating aerial survey abundance estimates for bowhead whales (*Balaena mysticetus*) in the Canadian High Arctic. DFO Can. Sci. Advis. Sec. Res. Doc. 2015/046. vi + 21.

TABLE OF CONTENTS

ABSTRACT

Twenty-five bowhead whales (*Balaena mysticetus)* were fitted with satellite tags near the communities of Igloolik and Pangnirtung, Nunavut in July-August 2012 and 2013 and twenty-two provided information on the time whales spent at 0-2, 0-3, 0-4, 0-6, 0-8 m depths in August. Bowhead whales diving to depths up to 8 m depths were considered possibly available to be viewed by observers during aerial surveys. To obtain an accurate estimate of bowhead abundance, for calculating total allowable catch and managing stocks, a correction for bowhead whales that are present but not visible to aerial observers is necessary. An instantaneous availability correction factor used to correct aerial surveys can be estimated from the proportion of time diving animals spend near the surface where they can be detected and identified. To provide a bias correction for the 2013 aerial survey, the proportion of time bowhead whales spent at different depths (0-2, 0-3, 0-4, 0-6, 0-8 m) was analyzed in a mixed effect model with individual whale as a random variable and period of August (early (August 1-15), mid (August 16-23), and late (August 24-31)), time of day (day or night), sex, and summering area (Prince Regent Inlet/Gulf of Boothia/Foxe Basin (PRI/GoB/FB), or Cumberland Sound) as fixed factors. To investigate other environmental factors related to bowhead diving behaviour, we also tested models with slope and depth as fixed factors.

Models that included time of day and period of August performed the best in the 0-2 m and 0-3 m bins, while models that included time of day, period of August, and area of tagging performed best in the 0-4, 0-6, and 0-8 m bins. Since aerial surveys were primarily conducted in early and mid-August, always during the day, an availability bias which excluded night, and combined both sexes for each area was calculated. Without experimentation, previous studies have relied on a correction for bowhead whales based on the 0-4 m bin. Since we are unsure of the deepest depth to which bowhead whales can be seen, we wanted to increase the variance around our estimate and calculated uncertainty in the availability bias correction based on a combination of the 0-2, 0-4, and 0-6 m depth bins since there is no evidence to suggest which depth is best. In early August, bowhead whales spent 21.6 ± 3.12 % of their time in the 0-2, 0-4, and 0-6 m combined depth bins in Cumberland Sound and 24.7 ± 5.11 % in the PRI/GoB/FB region, and thus we recommended an instantaneous availability bias correction of 4.63 (± 0.669) for Cumberland Sound and 4.05 (± 0.838) for the PRI/GoB/FB region for strata surveyed in early August 2013. In mid-August, bowhead whales spent 17.6 ± 1.65 % of their time in the 0-2, 0-4, and 0-6 m combined depth bins in Cumberland Sound and 29.1 ± 7.09 % in PRI/GoB/FB; thus, we recommend an instantaneous availability bias correction of 5.68 (± 0.533) for Cumberland Sound and 3.44 (± 0.838) for the PRI/GoB/FB region for strata surveyed in mid-August 2013. For areas surveyed outside of Cumberland Sound or the PRI/GoB/FB region in 2013 we recommend using a combined estimate for the areas based on the 0-2, 0-4, and 0-6 m combined depth bins. In early and mid-August, bowhead whales from both areas spent 24.3 ± 4.52 % and 25.1 ± 5.30 % of their time respectively in the 0-2, 0-4, and 0-6 m combined depth bins, resulting in an instantaneous availability bias correction of 4.12 (± 0.766) for early and 3.98 (± 0.840) for mid-August. Future research is necessary to determine the depth at which aerial observers can detect bowhead whales.

Correction instantanée du biais de disponibilité pour le calcul des estimations de l'abondance des baleines boréales (*Balaena mysticetus*) tirées de relevés aériens dans l'Extrême-Arctique canadien

RÉSUMÉ

Vingt-cinq baleines boréales (*Balaena mysticetus)* ont été équipées d'émetteurs satellites près des collectivités d'Igloolik et de Pangnirtung, au Nunavut, en juillet-août 2012 et 2013, et 22 d'entre elles ont fourni des informations concernant le temps passé par les baleines à des profondeurs de 0-2, 0-3, 0-4, 0-6 et 0-8 m au mois d'août. On estimait que les observateurs pourraient voir les baleines boréales plongeant à des profondeurs maximales de 8 m lors des relevés aériens. Pour obtenir une estimation précise de l'abondance des baleines boréales ainsi que pour calculer le total autorisé des captures et gérer les stocks, nous avons besoin d'une correction du nombre de baleines boréales présentes, mais non visibles par les observateurs aériens. Un facteur de correction instantanée de la disponibilité utilisé pour corriger les relevés aériens peut être estimé à partir de la proportion de temps que les animaux en plongée passent près de la surface de l'eau, où ils peuvent être détectés et identifiés. Pour fournir une correction du biais du relevé aérien de 2013, le temps passé par les baleines boréales à différentes profondeurs (0-2, 0-3, 0-4, 0-6, 0-8 m) a été analysé dans un modèle à effets aléatoires où la baleine était la variable aléatoire et la période d'août (début du mois [1-15 août], milieu du mois [16-23 août] et fin du mois [24-31 août]), le moment de la journée (jour ou nuit), le sexe, l'aire d'estivage (inlet Prince-Régent/golfe de Boothia/bassin Foxe [PRI/GoB/FB] ou détroit de Cumberland) étaient les facteurs fixes. Pour étudier les autres facteurs environnementaux liés au comportement en plongée des baleines boréales, nous avons également testé des modèles avec des facteurs fixes de pente et de profondeur.

Les modèles incluant le moment de la journée et la période du mois d'août ont été les plus performants pour les profondeurs de 0-2 et 0-3 m, alors que les modèles incluant le moment de la journée, la période du mois d'août et la zone de marquage l'ont été pour les profondeurs de 0-4, 0-6 et 0-8 m. Comme les relevés aériens ont surtout été effectués au début et au milieu du mois d'août et toujours pendant la journée, un biais de disponibilité excluant la nuit et combinant les deux sexes dans chaque zone a été calculé. Sans expérimentation, les études précédentes reposaient sur une correction pour les baleines boréales établie à partir de la catégorie 0-4 m. Comme nous ne sommes pas sûrs de la profondeur maximale à laquelle les baleines boréales peuvent être observées, nous avons voulu augmenter l'écart autour de notre estimation et nous avons calculé le degré d'incertitude dans la correction du biais de disponibilité à partir d'une combinaison des catégories de profondeur 0-2, 0-4 et 0-6 m, puisque nous n'avions aucune indication de la meilleure catégorie. Au début du mois d'août, les baleines boréales ont passé 21,6 ± 3,12 % de leur temps à des profondeurs de 0-2, 0-4 ou 0-6 m dans le détroit de Cumberland et 24,7 ± 5,11 % dans la région PRI/GoB/FB, ce qui nous a amenés à recommander une correction instantanée du biais de disponibilité de 4,63 (± 0,669) pour le détroit de Cumberland et de 4,05 (± 0,838) pour la région PRI/GoB/FB pour les strates étudiées au début du mois d'août 2013. À la mi-août, les baleines boréales ont passé 17,6 ± 1,65 % de leur temps à des profondeurs de 0-2, 0-4 ou 0-6 m dans le détroit de Cumberland et 29,1 ± 7,09 % dans la région PRI/GoB/FB; nous recommandons donc une correction instantanée du biais de disponibilité de 5,68 (± 0,533) pour le détroit de Cumberland et de 3,44 (± 0,838) pour la région PRI/GoB/FB pour les strates étudiées à la mi-août 2013. Pour les zones étudiées en dehors du détroit de Cumberland et de la région PRI/GoB/FB en 2013, nous recommandons d'utiliser une estimation combinée basée sur les catégories de profondeurs combinées de 0-2, 0-4 et 0-6 m. Au début du mois d'août et à la mi-août, les baleines boréales des deux zones ont passé respectivement 24,3 ± 4,52 % et 25,1 ± 5,30 % de leur temps à des

profondeurs de 0-2, 0-4, et 0-6 m, ce qui donne une correction instantanée du biais de disponibilité de 4,12 (± 0,766) pour le début du mois et de 3,98 (± 0,840) pour le milieu du mois. De plus amples recherches sont nécessaires pour déterminer la profondeur à laquelle les observateurs aériens peuvent détecter les baleines boréales.

INTRODUCTION

Bowhead whales (*Balaena mysticetus*) have a circumpolar distribution and there are currently four defined bowhead whale populations in the world (COSEWIC 2009). Currently there is one population in the eastern Canadian Arctic that is shared among communities in Canada and West Greenland and is known as the Eastern Canada-West Greenland (EC-WG) population (DFO 2007). EC-WG bowhead whales are part of the annual subsistence hunt in Canada and Greenland, and the hunt is an important part of Inuit culture. This population summers in northern Hudson Bay, Foxe Basin, Lancaster Sound, and western Baffin Bay, and spends winter in the Davis and Hudson Straits (COSEWIC 2009). In order to manage the population and make recommendations for a total allowable harvest an accurate estimate of bowhead abundance in the EC-WG population is needed. In March 1981, aerial surveys of bowhead whales in the Hudson Strait estimated there were 1,349 whales (Koski et al. 2006). The most recent aerial survey was conducted in 2002 and estimated a much larger population than had been previously reported, and provided a partial population estimate of 14,400 (95% CI 4,811-43,105) animals (Dueck et al. 2007). This estimate has large uncertainty and areas that are potentially important for bowhead whales were surveyed in 2002-2004 but not all within one year. As a result, a call for another estimate of the abundance of this population during one season, with greater precision, was made (Dueck et al. 2007).

Aerial surveys were conducted in the Canadian Arctic in August 2013. Population estimates are often determined using aerial surveys, with cameras and multiple observers on each side of the aircraft. Although this method can cover a large area and capture a large proportion of the population, many whales may be diving deeper and unavailable to be seen from the air. As a result, many whales may be missed because the aircraft has flown over while they are submerged. Therefore, determining the proportion of time that bowheads are available to viewers and factoring this correction into the population estimate is required to estimate an accurate abundance. An instantaneous availability correction factor can be used to correct photographic aerial survey and is an important component of the availability correction factor used for visual aerial surveys, and can be estimated from the proportion of time diving animals spend near the surface where they can be detected and identified. Availability bias corrections for bowhead whale aerial surveys have been estimated previously, and found that bowhead whales spend approximately 26 % of their time in the 0-4 m depth bin (Dueck et al. 2005, Dueck et al. 2007); this was an updated estimate to the 25 % used by Cosens et al. (2006). However, Dueck et al. (2007) suggested that 4 m may actually be beyond the depth to which bowhead whales are visible from the air. Previous research on narwhals has suggested that they can be seen and identified to species at a depth of ~2 m at an altitude of 990 m in clear water (Richard et al. 1994). Heide-Jørgensen et al. (2007) determined an availability bias correction for bowhead whales using the 0-2 m depth bin (24 %, cv = 0.03) based on the experiments done with narwhals; however, bowheads are larger than narwhals and their white patch may be easier to detect, depending on the sea state. Since there is no agreed-upon depth to which bowhead whales can be detected, we analyzed data in all bins ≤ 8 m that were used in the tag configuration and calculated a correction and associated variance for the 0-2, 0-4 and 0-6 m bins combined. In this way, corrections can be adjusted depending upon the region the survey is being conducted and updated with new information. The previous availability bias was based on only three individual bowheads, a juvenile female and male, and an adult female with a calf (Dueck et al. 2005, Dueck et al. 2007). As a result, an updated estimate of bowhead availability bias with greater sample sizes, in the region where surveys were being conducted and at the same time of year was needed, since dive behaviour can change depending on location and season. We have two main objectives in this study. The first is to provide corrections for availability bias for the 2013 survey by evaluating traditional factors that have been incorporated in studies to assess availability bias estimates. Secondarily, we wanted to test the possible influence of environmental variables on dive behaviour of bowhead whales at the surface and thus provide information relevant to correcting past and future surveys

METHODS

INSTRUMENTING THE ANIMALS

Seventeen bowhead whales, eight females, seven males, and two unsexed individuals, were tagged near the community of Igloolik, Nunavut, Canada in Foxe Basin in 2012 and 2013 (Fig. 1; Table 1). Only fourteen of these whales transmitted data in the month of August and were included in this analysis (Table 1). In 2013, eight bowhead whales, five males and three females, were also tagged near Pangnirtung, Nunavut, Canada in Cumberland Sound (Fig. 1; Table 1) and all provided diving information for the month of August 2013. A minimum of two boats were used to tag bowhead whales in Foxe Basin and Cumberland Sound. Each boat is alternately used as the tagging boat or for providing safety support. Once a bowhead whale is located, boats approach the whale cautiously. During approaches, the person tagging the whale stands in the bow of the boat while the driver moves the boat close to the whale, typically approaching on the whale's right side. The second boat acts as a safety boat and to assist with keeping the whale in line with the tagging boat. All tags were attached to the whales by means of an anchor, which is firmly implanted in the blubber using a hand-held pole. The anchor is composed of stainless steel, and is held in the blubber through a single small hole in the skin.

DATA ANALYSIS

Wildlife Computer SPLASH10 tags were used and programmed to transmit location and dive information. Location data was obtained from the ARGOS system (CLS America). Data was transmitted every two hours, but was summarized into four 6-hour histograms every day throughout the month of August with a single location (longitude and latitude) reported for each 6-hour time block, which is the most accurate location estimate collected in the previous 24-hours. All tags were programmed with the same depth bins to calculate the proportion of time bowhead whales spent in the 0-2, 0-3, 0-4, 0-6 and 0-8 m depth categories with a resolution of 0.5 m (Wildlife Computers). Diving behaviour 24-hours post tagging was ignored for analysis because the whale's behaviour may have been altered as a result of the tagging process (Geertsen et al. 2004, Norman et al. 2004, Elwen et al. 2006).

Models with the variables period of August, time of day, sex, and area as fixed effects, and whale as a random effect, were fitted to predict the logged proportion of time bowhead whales spent at different depths. The dependent variable of the models was the proportion of time spent in each different depth bin. For the variable period of August, the first 15 days of August were identified as "early August", days 16-23 as "mid-August", and the final seven days were identified as "late August", as this may be a period of ice formation and therefore may change the time bowhead whales spend at the surface. For the variable time of day, 6-hour time blocks from the periods starting at 7:00, 9:00, 13:00 and 15:00 were identified as day behaviours, while those from the periods starting at 19:00, 21:00, 1:00, and 3:00 were identified as night behaviours (some tags were programmed to summarize the data at 7:00, 13:00, 19:00, and

1:00, and others at 9:00, 15:00, 21:00, 3:00). Bowhead whales were originally tagged in Foxe Basin; however, all but one (which remained in Foxe Basin) travelled into the Prince Regent Inlet/Gulf of Boothia complex and were found there in August. These whales were grouped into one category known as the Prince Regent Inlet/Gulf of Boothia/Foxe Basin (PRI/GoB/FB) region to compare to bowhead whales that were in Cumberland Sound in August. Individual percentage of time in different depth bins was estimated as an average of all the 6-hour bins collected for that whale (Table 2; n is reported in Table 1).

We modeled the percentage of time bowhead whales spent in each depth bin with a linear mixed-effect model of log-transformed data (logged percentage of time; Fig. 2, Table 3). This approach has been suggested for log-normal data (Zuur et al. 2010, Borcard et al 2011, Sokal and Rohlf 2012). We used a backwards-step-wise approach to evaluate the fixed-effect to include in the model for each of the depth bins. The selection started with the full model (with fixed effects period of August, time of day, sex, and area). The significance of each fixed effect was evaluated by comparing the fit of the models with and without the term of interest using maximum likelihood ratio tests ($\chi 2$ distribution, df = the difference in the degrees of freedom between the nested models). The least significant fixed effect was dropped and the process was repeated until no effect could be further removed ($p < 0.05$). Statistical analyses were performed using the package lme4 (Bates et al. 2014) in the statistical software R (R Development Core Team 2010).

To provide more general information on bowhead dive behavior that may be relevant to future investigations, we also considered environmental variables that likely impact the time bowhead spent at or near the surface. Variables of interest that may impact dive depths and time spent at the surface included depth (m), distance from shore (km), and bathymetric slope. Bathymetric 500 x 500 m tiff grid files were downloaded from the International Bathymetric Chart of the Arctic Ocean (IBCAO) and imported into ArcGIS in order to extract depth for each bowhead whale's position (a single location was provided for each 6-hour time block based on the best available location for the previous 24 hours) (Jakobsson et al. 2012). Slope and distance to land were extracted using the spatial analysis tools within ArcGIS. In some cases, particularly in narrow fiords and inlets, bowhead whale locations appeared on land as a result of the error associated with the location data points. In these instances, depth extractions were positive and inaccurate and the previous in-water depth measure was used. The previous in-water depth measure may have been up to two previous recordings or 12 hours earlier. Distance from shore and depth were significantly correlated ($r = 0.51$, $p < 0.0001$), and slope and distance from shore were also significantly correlated ($r = 0.27$, $p < 0.0001$); thus, only depth and slope were considered in further analysis. We evaluated the environmental factors affecting the time spent at depth using the same backwards-step-wise approach described above. The full model used at the start was the best model selected above with the addition of the fixed-effect slope and depth.

Lastly, we considered the significant factors from the previous statistical analysis to calculate weighted averages to determine the average time all whales spent in each depth bin. Weighted averages took the average for each whale, weighted it based on the number of 6-hour blocks collected, and calculated an overall average. Standard errors were calculated using a weighted standard deviation divided by the square-root of the number of bowhead whales used in each calculation. Weighted combined estimates were also calculated when warranted. We first estimated the proportion of time spent by bowhead whales in each depth bin. Each of these estimates has an error distribution around it, which we assumed to be normally distributed. These proportions and their CV were then used to calculate a correction factor to apply to surface abundance estimates. However, we do not know how deep visual observers can detect and identify bowhead whales, and therefore we do not know which depth bin should be used for the correction factor. Based on expert knowledge, plausible bins include 0-2, 0-4, and 0-6 m. With no information to select one over the others, we assume these three bins are equally likely and therefore that the proportion of time that bowhead whales can be detected by aerial survey observers is an equally-weighted mixture of the three corresponding distributions of means (Robertson and Fryer 1969).

A mixture of *k* normal distributions with means μ_j and standard deviation σ_j, with j=1,…,k, and weights w_j satisfying

$$\sum_{j=1}^{k} w_j = 1$$

has a mean µmix and a variance σ_{mix}^2 :

$$\mu_{mix} = \sum_{j=1}^{k} w_j \mu_j$$

$$\sigma_{mix}^2 = \sum_{j=1}^{k} w_j \left(\sigma_j^2 + \mu_j^2\right) - \mu_{mix}^2$$

Applying these formulas on bins 0-2, 0-4, and 0-6 m yields a mean proportion and confidence interval for each combined estimate (Fig. 3 for example).

RESULTS

The best linear mixed-effects models included time of day and period of August for the 0-2 and 0-3 m bins (Table 4). Time at 0-2 m depths was lower in late and early August compared to mid (Fig. 4, Table 5). Time spent at 0-2 and 0-3 m depths was higher at night than during the day (Fig. 5, Table 5). Individual bowhead whales spent anywhere from 14.0 % (± 0.32 %) to 27.3 % (± 1.39 %) of their time in the 0-2 m bin and 15.1 ± 0.3 % to 38.0 ± 1.95 % in the 0-3 m bin (Table 2).

Mixed effects models including time of day, period of August, and area best fitted the data for the 0-4, 0-6, and 0-8 m bins (Table 4, Fig. 2). Bowhead whales spent more time in the 0-4, 0-6, and 0-8 m depth bins in mid-August compared to early August (Fig. 4,Table 5), with whales in late August spending an intermediate amount of time in these zones. Whales also spent more time in the 0-4, 0-6, and 0-8 m bins during nighttime compared to day (Fig. 5, Table 5) and whales from PRI/GoB/FB spent more time at the surface than those from Cumberland Sound (Fig. 6, Table 5). A female bowhead whale from Cumberland Sound spent the least amount of time in these depth bins, while a male from PRI/GoB/FB spent the most (Table 2).

The effect of slope was not significant for any of the models while the effect of depth was significant for all the models (Table 4). Bowhead whales spent less time at the surface in deeper than in shallow water for all bins (Fig. 7).

Since surveys were primarily conducted in early and mid-August, and always during the day, it is most practical to obtain a correction estimate for early and mid-August during the day combining males and females from Cumberland Sound and then provide another estimate for the PRI/GoB/FB region. Given that it is unclear which depth bin bowhead whales can be seen from, we calculated estimates based on a combination of the 0-2, 0-4 and 0-6 m depth bins. Bowhead whales in Cumberland Sound spent 21.6 ± 3.12 % of their time in the 0-2, 0-4 and 0-6 m bins combined in early August and 17.6 ± 1.65 % of their time in mid-August (Table 6). In the PRI/GoB/FB region, bowhead whales spent 24.7 ± 5.11 % of their time in the 0-2, 0-4 and 0-6 m bins combined in early August and 29.1 ± 7.09 % of their time in mid-August (Table 6). However, not all survey strata occurred within Cumberland Sound or the PRI/GoB/FB region, and in these instances we recommend using a correction for early and mid-August that combines information from both areas. Bowhead whales from both regions together spent 24.3 ± 4.52 % of their time in the 0-2, 0-4 and 0-6 m bins combined in early August and 25.1 ± 5.30 % of their time in mid-August (Table 6).

DISCUSSION

2013 SURVEY

A number of factors can impact the time a marine mammal spends at or near the surface. For bowhead whales, differences in preferred prey and seasonal changes in prey availability can result in large changes in dive behaviour (Heide-Jørgensen et al. 2013). Time at the surface is typically higher for surface feeders (those targeting prey in the upper water column), and for mothers with calves (Dorsey et al. 1989). We found a single female bowhead whale tagged in Cumberland Sound spent the least amount of time in all the surface bins, and as a result, spent over 80 % of her time at depths > 8 m. Although it was originally thought that bowhead whales were surface feeders in Cumberland Sound, recent research suggests the upper water column is lacking prey in August and many of the copepod species, such as *Calanus hyperboreus* and *C. glacialis,* that bowhead whales feed on are deeper in the water column (Fortune et al. unpublished data). A male tagged in Foxe Basin that spent time in Prince Regent Inlet and Gulf of Boothia typically spent the most time in all of the depth bins analyzed. Pomerleau et al. (2011) identified Gulf of Boothia as an important summer foraging area for bowhead whales, and found that whales in this region spent most of their time close to the surface. Overall, prey appears to be distributed in August at different depths in the different regions, and it seems that some bowhead whales adjust their dive behaviours, and subsequently the time they spend at the surface, to monopolize on the prey. In the deeper depth bins (0-4, 0-6 and 0-8 m) we found PRI/GoB/FB whales spent more time in the upper water column than whales from Cumberland Sound, which would be expected if their prey were primarily in this zone.

We also found differences in time spent in the different depth bins during the day and night, which is typical for whales foraging on prey that make nycthemeral migrations. The typical nycthemeral migration is an evening ascent and a morning descent (Lampert 1989) and this has been found for Arctic copepods in August (Rabindranath et al. 2011). This would explain why bowhead whales spent significantly less time near the surface during the day compared to night, as night may be a more intensive foraging period near the surface. This pattern, however, may change depending on the time of year as it has also been found that Arctic zooplankton do not make nycthemeral migrations during the midnight sun in May (Blachowiak-Samolyk et al. 2006). For the purposes of estimating an availability bias for bowhead whales, nighttime dive behaviours should be ignored since these can be significantly different from day behaviours depending on the time of the year, and may misrepresent the time bowhead whales are available for viewing during daytime surveys.

Differences among the period in August were also evident for bowhead whales, and it appeared whales spent more time near the surface in mid-August. This may correspond with prey availability, or may be a result of activities related to socializing. In the western Arctic, social sexual activity of bowhead whales declined throughout the month of August, but there were also differences in this pattern among years (Würsig et al. 1985). Thus, it may be that in this region socializing activities peaked in mid-August. The aerial survey conducted in 2013 was flown from August 1-26. Cumberland Sound was surveyed in mid-August (August 20) and many bowhead whales were observed. Only two flights were actually flown after August 22. The last segment surveyed was on August 25 off of East Baffin Island and only one bowhead whale was observed. For the purposes of creating an availability bias for surveys conducted in August 2013, when strata were primarily sampled in the first three weeks of August, we recommend using different bias corrections for those surveyed in early (August 1-15) versus mid-August (August 16-23) since time at the surface, regardless of which bin is used, is greater in mid-August.

Although we did consider environmental variables, and depth was a significant factor in all of the models investigated, it is important to acknowledge that these depth extractions are only best estimates and for this reason we chose to use the model that excludes depth for the 2013 survey. The bottom bathymetry of this region has not been mapped in detail. We used IBCAO to assign a bottom bathymetry to each location. Bathymetries are largely based on ship tracking sounds with interpolation between soundings, and in the Arctic shipping traffic has been limited and thus many data points are interpolated (Jakobsson et al. 2012). For instance, a single depth is extracted within a 500 m^2 grid, which means at some points the nearest depth interpolated estimate can be up to 354 m away and the actual depth sounding measurements even further. Similarly, for the surveyors to use this information, they would also need to know the depth the sighted bowhead whales were at when surveyed, and would have a similar issue attempting to assign depths (i.e., large uncertainty). Because of the unknown bias this could incorporate into the abundance estimates, we suggest corrections for the 2013 survey estimates use the traditional model that does not incorporate depth. This is not ideal, but is currently the best bathymetric information for this region, and although it is important to consider these environmental variables when evaluating availability bias, it is also important to understand the limitations of the currently available data.

It is difficult to determine how deep a bowhead whale can be seen at altitudes upwards of 1,000 m without a controlled experiment using a life-sized bowhead model, much like what was done for narwhals and beluga whales (Richard et al. 1994). Previous bowhead availability biases have been calculated based on the 0-2 m bin for bowheads in west Greenland (Heide-Jørgensen et al. 2007) and on the 0-4 m bin for bowhead whales in the eastern Canadian Arctic (Dueck et al. 2005, Cosens et al. 2006, Dueck et al. 2007). We calculated the time spent in a number of different bins so that corrections may be adjusted depending on environmental conditions and study objectives, but we recommend using an estimate from combining multiple depth bins (0-2, 0-4, and 0-6 m bins) for the analysis of the 2013 survey results, since there is no scientific evidence to suggest which bin is the best to use. We used an equally-weighted mixture distribution to combine our results for three different depth bins. However, we stress that this ad-hoc approach is only useful to estimate a mean and a standard error that take into account our uncertainty about which bin to use. We do not suggest that the proportion of time that bowhead whales are visible for aerial survey observers follows this particular multimodal distribution.

The depth bins programmed for time spent at depth have an error associated with them of 0.5 m (Wildlife Computers). Essentially this means the depth at which a bowhead is at has an error of 0.5 m associated with it, and if a whale is at 1.4 m, the time that whale is at that depth would fall in the 1-2 m bin, but could fall into either 0-1 m or 1-2 m bins once the error is incorporated. We did not incorporate this error into the variance for the time spent at depth for corrections for the 2013 survey and it is important to recognize that we may be under-estimating the variance by not factoring in this error.

FUTURE SURVEYS

Significant differences among area, time of day, and period of August were generally found for all depth bins analyzed, and thus, regardless of which depth bin is chosen to make the correction, these are important variables that result in different availability biases and should be taken into consideration in future surveys. Although we did not find differences between males and females in the time spent at or near the surface, there may be a difference if many females with calves had been tagged. Pregnant or nursing females may spend a greater proportion of time at the surface (Dorsey et al. 1989).

Ice presence also has an impact on bowhead dive behaviour (Pomerleau et al. 2011) and should be evaluated in future studies. Future surveys may also want to consider depth as an important environmental covariate in availability corrections, since we did find that depth (even though it was only very roughly estimated in this study) has an impact on the time bowhead whales spend at the surface. More specifically, it appears that bowhead whales may spend more time at the surface when they are in shallow waters compared to deep regions and this may be useful information for correcting surveys in the future, when, we assume, the bathymetric profiles of these regions will be mapped in much better detail.

Future analyses may want to consider factoring in the error associated with the programmed tags (i.e., 0.5 m) as this may be important source of uncertainty in calculating abundance estimates. Although it would not change the average percent of time spent in the different depth bins, it would increase the error associated with the bins and the subsequently the error associated with the correction factors.

Finally, the presence of predators, such as killer whales (*Orcinus orca*) (Reinhart et al. 2013) in the area may impact the time bowheads spend at or near the surface and may need to be considered in future estimates. Future studies that evaluate bowhead whale abundance and estimate availability bias may also want to consider the activity state of the whales. Thomas et al. (2002) identified differences in detectability and availability depending on the whales behavioural state; whales in transit mode had the lowest probability of detection, followed by those that were engaging in foraging activities, and finally, those that were socializing had the highest probability of detection.

RECOMMENDATIONS FOR 2013 SURVEY

For bowhead whales surveyed in Cumberland Sound in early August when whales spend 21.6 ± 3.12 % of their time in the 0-2, 0-4, and 0-6 m combined depth bins we recommended an instantaneous correction factor of 4.63 (± 0.669). In mid-August bowhead whales in the Cumberland Sound region spent 17.6 ± 1.65 % of their time in the 0-2, 0-4, and 0-6 m depth bins and we recommend an instantaneous availability bias correction of 5.68 (± 0.533).

Bowhead whales surveyed in the PRI/GoB/FB region in early august spent 24.7 ± 5.11 % of their time in the 0-2, 0-4, and 0-6 m combined depth bins, and thus we recommend an instantaneous correction of 4.05 (± 0.838) for surveys occurring at this time. In mid-August bowhead whales in the PRI/GoB/FB region spent 29.1 ± 7.09 % of their time in the 0-2, 0-4, and 0-6 m combined depth bins and we recommend an instantaneous availability bias correction of 3.44 (± 0.838) for strata surveyed in this region in mid-August.

For areas that were surveyed outside of Cumberland Sound or the PRI/GoB/FB region we recommend using a combined estimate for the locations based on the 0-2, 0-4, and 0-6 m combined depth bins. In early and mid-August, bowhead whales from both locations spent 24.3 ± 4.52 % and 25.1 ± 5.30 % of their time respectively in the 0-2, 0-4, and 0-6 m combined depth bins, resulting in an instantaneous availability bias correction of 4.12 (± 0.766) for early and 3.98 (± 0.840) for mid-August.

RECOMMENDATIONS FOR FUTURE SURVEYS

We recommend future surveys and analyses on time spent by bowhead whales at the surface may benefit from

1) incorporating depth as an environmental covariate in their models,
2) evaluating factors such as time of day, area of tagging, and period of August since these factors seem to significantly impact the time bowhead whales spend in each of the depth bins, and;
3) considering other model types such as beta regressions because they are designed for data restricted between zero and one (Ferrari and Cribari-Neto 2004, Figueroa- Zúniga et al 2013), or generalized linear mixed-effect models with link functions.

ACKNOWLEDGEMENTS

All work was conducted under DFO License to Fish for Scientific Purposes, and prior approval was obtained from the Freshwater Institute Animal Care Committee (FWI-ACC-2012-034 and FWI-ACC-2013-018). We would like to thank the many dedicated people in the research field camps for their valuable assistance with the handling and instrumenting of the bowhead whales. We thank the Hunters and Trappers Organizations in Pangnirtung and Igloolik, Nunavut, Canada, for all of their support. We also would like to thank T. Doniol-Valcroze for his contribution and insight into calculating the combined bin variance for our estimates. We also thank Fisheries and Oceans Canada, the Nunavut Wildlife Management Board and Nunavut Implementation Fund for funding.

LITERATURE CITED

Bates, B., Maechler, M., Bolker, B., and Walker, S. 2014. lme4: Linear mixed-effects models using Eigen and S4. The Comprehensive R Archive Network (CRAN), Vienna, Austria.

Blachowiak-Samolyk, K., Kwasniewski, S., Richardson, K., Dmoch, K., Hansen, E., Hop, H. Falk-Petersen, S., and Mouritsen, L.T. 2006. Arctic zooplankton do not perform diel vertical migration (DVM) during periods of midnight sun. Mar. Ecol. Prog. Ser. 308: 101–116.

Borcard D., Gillet, F., and Legendre, P. 2011. Numerical Ecology with R. Springer, New York.

Cosens, S. E., Cleator, H., and Richard, P. 2006. Numbers of bowhead whales (*Balaena mysticetus*) in the Eastern Canadian Arctic, based on aerial surveys in August 2002, 2003 and 2004. DFO Can. Sci. Advis. Sec. Res. Doc.:2006/052.

COSEWIC. 2009. COSEWIC assessment and update status report on the bowhead whale *Balaena mysticetus,* Bering-Chukchi-Beaufort population and Eastern Canada-West Greenland population, in Canada. Committee on the Status of Endangered Wildlife in Canada. vii + 49 pp.

DFO. 2007. Assessment of eastern Arctic bowhead whales (*Balaena mysticetus*). DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2007/053.

Dorsey, E., Richardson, W.J., and Wursig, B. 1989. Factors affecting surfacing, respiration, and dive behaviour of bowhead whales, *Balaena mysticetus*, summering in the Beaufort Sea. Can. J. Zool. 67: 1801–1815.

Dueck, L., Heide-Jørgensen, M.P., Jensen, M.V., and Postma, L.D. 2005. Diving characteristics and sightability estimates of eastern Arctic bowhead whales, *Balaena mysticetus*, based on satellite-linked telemetry. DFO Can. Sci. Advis. Sec. Res. Doc. 2005/005.

Dueck, L., Richard, P., and Cosens, S. 2007. A review and re-analysis of Cosens et al. (2006) aerial survey assessment of bowhead whale abundance for the eastern Canadian Arctic. DFO Can. Sci. Advis. Sec. Res. Doc. 2007/080.

Elwen, S., Meyer, M.A., Best, P.B., Kotze, P.G.H., Thornton, M., and Swanson, S. 2006. Range and movements of female heaviside's dolphins (*Cephalorhynchus heavisidii*), as determined by satellite-linked telemetry. J. of Mammal. 87: 866–877.

Figueroa-Zúniga, J. I., Arellano-Valle, R.B., and Ferrari, S.L. 2013. Mixed beta regression: A Bayesian perspective. Computational Statistics & Data Analysis. 61: 137–147.

Ferrari, S., and Cribari-Neto, F. 2004. Beta regression for modelling rates and proportions. J. App. Stat. 31: 799–815.

Geertsen, B. M., Teilmann, J., Kastelein, R.A., Vlemmix, H.N.J., and Miller, L.A. 2004. Behaviour and physiological effects of transmitter attachments on a captive harbour porpoise (*Phocoena phocoena*). J. Cetacean Res. Manag. 6: 139–146.

Heide-Jørgensen, M. P., Laidre, K.L., Borchers, D., Samarra, F., and Stern, H. 2007. Increasing abundance of bowhead whales in West Greenland. Biology Letters 3: 577–580.

Heide-Jørgensen, M. P., Laidre, K.L., Nielsen, N.H., Hansen, R.G., and Røstad, A. 2013. Winter and spring diving behavior of bowhead whales relative to prey. Animal Biotelemetry 1: 15.

Jakobsson, M. et al. 2012. The International Bathymetric Chart of the Arctic Ocean (IBCAO) Version 3.0, Geophysical Research Letters. Geophysical Research Letters 39: DOI: 10.1029/2012GL052219.

Koski, W. R., Heide-Jørgensen, M.P., and Laidre, K.L. 2006. Winter abundance of bowhead whales, *Balaena mysticetus*, in the Hudson Strait, March 1981. J. Cetacean Res. Manag. 8: 139–144.

Lampert, W. 1989. The adaptive significance of diel vertical migration of zooplankton. Funct. Ecol. 3: 21–27.

Norman, S. A., Hobbs, R.C., Foster, J., Schroeder, J.P., and Townsend, F.I. 2004. A review of animal and human health concerns during capture-release, handling and tagging of odontocetes. J. Cetacean Res. Manag. 6: 53–62.

Pomerleau, C., Patterson, T.A., Luque, S., Lesage, V., Heide-Jørgensen, M.P., Dueck, L.L., and 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.

Rabindranath, A., Daase, M., Falk-Petersen, S., Wold, A., Wallace, M.I., Berge, J., and Brierly, A.S. 2011. Seasonal and diel vertical migration of zooplankton in the High Arctic during the autumn midnight sun. Mar. Biodivers. 41: 365–382.

R Development Core Team. 2010. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Reinhart, N. R., Ferguson, S.H., Koski, W.R., Higdon, J.W., LeBlanc, B., Tervo, O and Jepson, P.D. 2013. Occurrence of killer whale *Orcinus orca* rake marks on Eastern Canada - West Greenland bowhead whales *Balaena mysticetus*. Polar Biol. 36: 1133–1146.

Richard, P., Weaver, P., Dueck, L., and Barber, D.G. 1994. Distribution and numbers of Canadian High Arctic narwhals (*Monodon monoceros*) in August 1984. Meddelelser om Grønland, Bioscience 39: 41–50.

Robertson, C. A., and Fryer, J.G. 1969. Some descriptive properties of normal mixtures. Skand Aktuarietidskr 1969: 137–146.

Sokal R., and Rohlf, F.J. 2012. Biometry. Fourth Edition. MacMillan Publishing Company, New York.

Thomas, T. A., Koski, W.R., and Richardson, W.J. 2002. Correction factors to calculate bowhead whale numbers from aerial surveys of the Beaufort Sea *In* Bowhead whale feeding in the eastern Alaskan Beaufort Sea: Update of Scientific and Traditional Information. Edited by W. J. Richardson and D. H. Thomson. OCS Study MMS 2002–012. P 28.

Würsig, B., Dorsey, E.M., Fraker, M.A., Payne, R.S., and Richardson, W.J. 1985. Behavior of bowhead whales, Balaena mysticetus, summering in the Beaufort Sea: A description. Fishery Bulletin 83: 357–377.

Zuur, A. F., Leno, E.N., and Elphick, C.S. 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1: 3–14.

TABLES

Table 1. Deployment date, sex, approximate length, and number of 6-hour blocks collected for bowhead whales deployed with satellite-linked transmitters in Foxe Basin and Cumberland Sound. Whales tagged in Foxe Basin spent time in Prince Regent Inlet/Gulf of Boothia and Foxe Basin in August (PRI/GoB/FB).

Area in August	Deployment Date	Sex	Tag Number	Length (m)	# of 6-hour blocks
PRI/GoB/FB	2012-07-03	F	114494	12.0	Not included
PRI/GoB/FB	2012-07-03	F	114495	11.5	149
PRI/GoB/FB	2012-07-03	F	114496	11.0	34
PRI/GoB/FB	2012-07-06	M	114497	12.0	10
PRI/GoB/FB	2012-07-06	M	114498	11.0	61
PRI/GoB/FB	2012-07-06	F	114499	13.5	59
PRI/GoB/FB	2012-07-06	M	114500	12.5	114
PRI/GoB/FB	2012-07-06	-	114501	-	37
Cumberland Sound	2012-08-06	M	114502	10.0	22
Cumberland Sound	2012-08-06	F	114503	10.0	16
Cumberland Sound	2012-08-07	F	114504	10.5	20
Cumberland Sound	2012-08-08	M	114505	11.5	37
Cumberland Sound	2012-08-08	F	114506	13.5	18
Cumberland Sound	2012-08-12	M	114507	10.0	37
Cumberland Sound	2012-08-12	M	114508	9.5	25
Cumberland Sound	2012-08-12	M	114509	9.5	23
PRI/GoB/FB	2013-07-03	F	128145	11.5	29
PRI/GoB/FB	2013-07-03	F	128146	13.5	29
PRI/GoB/FB	2013-07-09	F	128148	13.0	41
PRI/GoB/FB	2013-07-09	-	128149	12.5	Not included
PRI/GoB/FB	2013-07-09	F	128150	10.0	78
PRI/GoB/FB	2013-07-09	M	128151	9.5	68
PRI/GoB/FB	2013-07-09	M	128152	9.5	77
PRI/GoB/FB	2013-07-03	M	128153	12.20	Not included
PRI/GoB/FB	2013-07-03	M	128154	11.5	16

Table 2. Average percent of time (±SE) each bowhead whale spent in each of the depth bins. Bold indicates the whales that spent the minimum and maximum amount of time in each depth bin.

Area	Whale ID	Sex	Average (%) ± SE for 0-2 m	Average (%) ± SE for 0-3 m	Average (%) ± SE for 0-4 m	Average (%) ± SE for 0-6 m	Average (%) ± SE for 0-8 m
PRI/GoB/FB	114495	F	18.2 ± 0.93	23.6 ± 1.36	30.2 ± 1.89	38.6 ± 2.28	44.4 ± 2.44
PRI/GoB/FB	114496	F	14.9 ± 0.50	16.1 ± 0.61	17.8 ± 0.99	21.6 ± .234	24.4 ± 2.80
PRI/GoB/FB	114497	M	15.6 ± 1.41	19.9 ± 3.92	22.2 ± 5.12	26.8 ± 6.92	34.0 ± 7.86
PRI/GoB/FB	114498	M	21.3 ± 2.15	23.9 ± 2.47	26.1 ± 2.69	29.0 ± 2.87	33.1 ± 3.06
PRI/GoB/FB	114499	F	16.2 ± 0.68	19.6 ± 1.14	22.3 ± 1.50	26.2 ± 1.86	29.8 ± 2.07
PRI/GoB/FB	114500	M	**27.3 ± 1.39**	**38.0 ± 1.95**	**45.7 ± 2.24**	**51.9 ± 2.28**	**56.9 ± 2.21**
PRI/GoB/FB	114501	-	23.0 ± 2.03	25.7 ± 2.21	28.4 ± 2.37	33.4 ± 2.57	38.3 ± 2.60
CS	114502	M	14.6 ± 0.46	15.5 ± 0.73	16.8 ± 1.36	19.5 ± 2.38	20.8 ± 2.70
CS	114503	F	20.6 ± 2.12	21.8 ± 2.06	22.7 ± 2.06	24.4 ± 2.12	26.6 ± 2.60
CS	114504	F	**14.0 ± 0.32**	**15.1 ± 0.33**	**15.7 ± 0.37**	**16.4 ± 0.44**	**17.0 ± 0.52**
CS	114505	M	21.0 ± 2.27	22.4 ± 2.34	23.4 ± 2.42	26.0 ± 2.67	28.4 ± 2.86
CS	114506	F	15.3 ± 0.38	16.1 ± 0.50	16.8 ± 0.65	18.2 ± 1.06	19.8 ± 1.73
CS	114507	M	17.2 ± 1.05	19.4 ± 1.59	20.6 ± 1.90	21.9 ± 2.06	23.3 ± 2.14
CS	114508	M	18.1 ± 1.64	19.9 ± 2.11	22.0 ± 2.92	23.9 ± 3.50	25.1 ± 3.69
CS	114509	M	14.9 ± 0.57	15.7 ± 0.72	16.6 ± 0.96	18.6 ± 1.63	20.3 ± 2.07
PRI/GoB/FB	128145	F	19.1 ± 2.91	20.3 ± 2.93	21.5 ± 2.99	23.8 ± 3.25	25.5 ± 3.40
PRI/GoB/FB	128146	F	19.5 ± 2.71	21.1 ± 2.69	22.3 ± 2.70	25.0 ± 2.78	28.5 ± 2.97
PRI/GoB/FB	128148	F	16.6 ± 1.13	19.2 ± 1.32	21.8 ± 1.73	25.1 ± 2.25	28.8 ± 2.59
PRI/GoB/FB	128150	F	19.2 ± 1.67	20.8 ± 1.82	22.5 ± 1.96	26.9 ± 2.30	31.1 ± 2.53
PRI/GoB/FB	128151	M	21.3 ± 2.40	23.6 ± 2.58	25.9 ± 2.77	31.3 ± 3.07	37.8 ± 3.28
PRI/GoB/FB	128152	M	18.3 ± 1.76	21.2 ± 1.96	24.4 ± 2.12	30.6 ± 2.43	35.8 ± 2.60
PRI/GoB/FB	128154	M	17.9 ± 4.87	20.0 ± 5.38	22.9 ± 5.84	28.8 ± 6.78	36.8 ± 7.63

Table 3. Summary statistics of residual errors for the best linear mixed-effect model of log-transformed data for different depth bins. The Filliben correlation coefficient is the coefficient of the correlation between the normal theoretical quantiles and the quantiles of the residual errors.

Summary statistics	0-2 m	0-3 m	0-4 m	0-6 m	0-8 m
Mean	0	0	0	0	0
Variance	0.206	0.25	0.29	0.318	0.316
Skewness	1.306	0.952	0.72	0.491	0.303
Kurtosis	5.126	3.843	3.152	2.613	2.397
Filliben Correlation	0.949	0.967	0.977	0.985	0.991

Table 4. Best linear mixed-effect models to predict the log-transformed proportion of time spent in depth bins. Models were selected using a backwards-step-wise approach. P-values were calculated using maximum likelihood ratio tests between the model with and without the effect investigated. All models include the random effect of whale.

	Fixed effect	Estimate	Standard Error	Likelihood Ratio Test (df)	P value
0-2 m	Intercept	-1.85	0.03697	-	-
	Time of day - night	0.0584	0.02913	4.01 (1)	0.045
	Period of August - Mid	0.0832	0.03629	6.24 (2)	0.044
	Period of August - Late	-0.00694	0.03741	-	-
0-2 m with environmental variable	Intercept	-1.79	0.04511	-	-
	Time of day - night	0.0624	0.02910	4.58 (1)	0.032
	Period of August - Mid	-0.0432	0.04041	5.61 (2)	0.061
	Period of August - Late	0.0570	0.03790	-	-
	Depth	-0.000422	0.0001807	5.44 (1)	0.020
0-3 m	Intercept	-1.78	0.04531	-	-
	Time of day - night	0.0809	0.03212	6.32 (1)	0.0119
	Period of August - Mid	0.123	0.04021	9.46 (2)	0.0088
	Period of August - Late	0.0265	0.04134	-	-
0-3 m with environmental variable	Intercept	-1.68	0.05389	-	-
	Time of day - night	0.0870	0.03200	7.21 (1)	0.007
	Period of August - Mid	0.0840	0.04176	6.52 (2)	0.038
	Period of August - Late	-0.0292	0.04452	-	-
	Depth	-0.000661	0.0002024	10.27	0.001
0-4 m	Intercept	-1.84	0.07718		
	Time of day - night	0.0851	0.03459	6.03	0.014
	Period of August - Mid	0.173	0.04358	15.69	<0.001
	Period of August - Late	0.0616	0.04453	-	-
	Area – PRI/GoB/FB	0.185	0.08810	4.04	0.044
0-4 m with environmental variable	Intercept	-1.74	0.07842	-	-
	Time of day - night	0.0930	0.03437	7.22 (1)	0.0072
	Period of August	0.122	0.04497	9.49 (2)	0.0087

	Fixed effect	Estimate	Standard Error	Likelihood Ratio Test (df)	P value
	– Mid				
	Period of August - Late	-0.0137	0.04780	-	-
	Area – PRI/GoB/FB	0.233	0.08576	5.97 (1)	0.0145
	Depth	-0.000900	0.0002181	16.46 (1)	<0.0001
0-6 m	Intercept	1.79	-0.08066		
	Time of day - night	0.0898	0.03625	6.11 (1)	0.0134
	Period of August - Mid	0.223	0.04567	23.55 (2)	<0.0001
	Period of August - Late	0.0815	0.04667	-	-
	Area – PRI/GoB/FB	0.283	0.09202	7.96 (1)	0.0048
0-6 m with environmental variable	Intercept	-1.74	0.07842	-	-
	Time of day - night	0.0930	0.03437	7.30 (1)	0.0069
	Period of August - Mid	0.122	0.04497	9.58 (2)	0.0083
	Period of August - Late	-0.0137	0.04780	-	-
	Area – PRI/GoB/FB	0.233	0.08576	6.44 (1)	0.0112
	Depth	-0.000900	0.0002181	16.84 (1)	<0.0001
0-8 m	Intercept	-1.74	0.08205		
	Time of day - night	0.0837	0.03610	5.36 (1)	0.0206
	Period of August - Mid	0.237	0.04549	26.90 (2)	<0.0001
	Period of August - Late	0.0968	0.04648	-	-
	Area – PRI/GoB/FB	0.377	0.09404	12.35	0.0004
0-8 m with environmental variable	Intercept	-1.63	0.08374	-	-
	Time of day - night	0.0925	0.03582	6.65 (1)	0.0099
	Period of August - Mid	0.180	0.04687	16.62 (2)	0.0002
	Period of August - Late	0.0132	0.04983	-	-
	Area – PRI/GoB/FB	0.430	0.09226	15.49	<0.0001
	Depth	-0.00100	0.0002281	19.04	<0.0001

Table 5. The weighted average percent of time (±SE) spent in each of the depth bins for different periods in August, day and night and different areas. Number of 6-hour blocks included in the analysis is also provided as well as the number of whales (used to calculate the standard error).

	Average (%) ± SE for 0-2 m	**Average (%) ± SE for 0-3 m**	**Average (%) ± SE for 0-4 m**	**Average (%) ± SE for 0-6 m**	**Average (%) ± SE for 0-8 m**
Period of August					
Early (n = 518 6-hour blocks, n = 22 whales)	19.2 ± 1.17	22.4 ± 1.74	25.0 ± 2.04	29.1 ± 2.14	33.0 ± 2.15
Mid (n = 257 6-hour blocks, n = 20 whales)	20.2 ± 0.87	23.9 ± 1.08	27.8 ± 1.51	33.6 ± 2.27	38.4 ± 2.86
Late (n = 225 6-hour blocks, n = 22 whales)	19.3 ± 1.35	23.5 ± 2.07	27.7 ± 2.88	32.3 ± 3.24	36.3 ± 3.39
Time					
Day (n = 472 6-hour blocks, n = 22 whales)	18.8 ± 0.79	21.8 ± 1.21	24.9 ± 1.62	29.3 ± 2.00	33.3 ± 2.30
Night (n = 528 6-hour blocks, n = 22 whales)	19.9 ± 0.85	23.8 ± 1.45	27.2 ± 1.89	32.0 ± 2.20	36.4 ± 2.45
Area					
Cumberland Sound (n = 198 6-hour blocks, n = 8 whales)	17.2 ± 0.91	18.6 ± 0.99	19.8 ± 1.03	21.6 ± 1.13	23.1 ± 1.29
PRI/GoB/FB (n = 802 6-hour blocks, n = 14 whales)	20.0 ± 0.94	24.1 ± 1.62	28.0 ± 2.13	33.3 ± 2.41	38.1 ± 2.57
Estimates based on significant factors					
Early August during daylight for PRI/GoB/FB (n = 207 6-hour blocks, n = 14 whales)	19.3 ± 1.92	22.6 ± 2.81	25.4 ± 3.31	29.4 ± 3.44	33.5 ± 3.54
Early August during daylight for Cumberland Sound (n = 33 6-hour blocks, n = 8 whales)	18.7 ± 1.52	20.5 ± 1.76	21.7 ± 2.00	24.5 ± 2.48	26.5 ± 2.86
Mid-August during daylight for PRI/GoB/FB (n = 80 6-hour blocks, n = 12 whales)	21.0 ± 2.06	24.7 ± 2.04	29.3 ± 2.55	37.1 ± 3.25	43.3 ± 3.90
Mid-August during daylight for Cumberland Sound (n = 43 6-hour blocks, n = 7 whales)	15.7 ± 0.34	16.9 ± 0.50	17.8 ± 0.64	19.4 ± 0.88	20.7 ± 1.05
Early & Mid-August during daylight for PRI/GoB/FB (n = 287 6-hour blocks, n = 14 whales)	19.8 ± 1.43	23.1 ± 2.21	26.4 ± 2.83	31.5 ± 3.13	36.3 ± 3.31
Early & Mid-August during daylight for Cumberland Sound (n = 75 6-hour blocks, n = 8 whales)	17.0 ± 0.93	18.3 ± 1.01	19.3 ± 1.07	21.2 ± 1.17	22.8 ± 1.42
Early August, during daylight for locations combined (n = 240 6-hour blocks, n = 22 whales)	19.2 ± 1.47	22.3 ± 2.12	24.9 ± 2.51	28.7 ± 2.64	32.6 ± 2.75
Mid-August, during daylight for locations combined (n = 123 6-hour blocks, n = 19 whales)	19.1 ± 1.45	22.0 ± 1.57	25.3 ± 2.07	30.9 ± 2.87	35.4 ± 3.54

Table 6. The weighted average percent of time (±SE) spent in each of the depth bins in early and mid-August for each area and for areas combined. The final column indicates averages (±SE) by combining the 0-2, 0-4 and 0-6 m bins. Number of 6-hour blocks included in the analysis is also provided as well as the number of whales (used to calculate the standard error).

	Average (%) ± SE for 0-2 m	**Average (%) ± SE for 0-4 m**	**Average (%) ± SE for 0-6 m**	**Average (%) ± SE 0-2, 4, and 6 m combined bins**
Estimates based on significant factors				
Early August during daylight for PRI/GoB/FB (n = 207 6-hour blocks, n = 14 whales)	19.3 ± 1.92	25.4 ± 3.31	29.4 ± 3.44	24.7 ± 5.11
Early August during daylight for Cumberland Sound (n = 33 6-hour blocks, n = 8 whales)	18.7 ± 1.52	21.7 ± 2.00	24.5 ± 2.48	21.6 ± 3.12
Mid-August during daylight for PRI/GoB/FB (n = 80 6-hour blocks, n = 12 whales)	21.0 ± 2.06	29.3 ± 2.55	37.1 ± 3.25	29.1 ± 7.09
Mid-August during daylight for Cumberland Sound (n = 43 6-hour blocks, n = 7 whales)	15.7 ± 0.34	17.8 ± 0.64	19.4 ± 0.88	17.6 ± 1.65
Early & Mid-August during daylight for PRI/GoB/FB (n = 287 6-hour blocks, n = 14 whales)	19.8 ± 1.43	26.4 ± 2.83	31.5 ± 3.13	25.9 ± 5.44
Early & Mid-August during daylight for Cumberland Sound (n = 75 6-hour blocks, n = 8 whales)	17.0 ± 0.93	19.3 ± 1.07	21.2 ± 1.17	19.2 ± 2.02
Early August, during daylight for areas combined (n = 240 6-hour blocks, n = 22 whales)	19.2 ± 1.47	24.9 ± 2.51	28.7 ± 2.64	24.3 ± 4.52
Mid-August, during daylight for areas combined (n = 123 6-hour blocks, n = 19 whales)	19.1 ± 1.45	25.3 ± 2.07	30.9 ± 2.87	25.1 ± 5.30

FIGURES

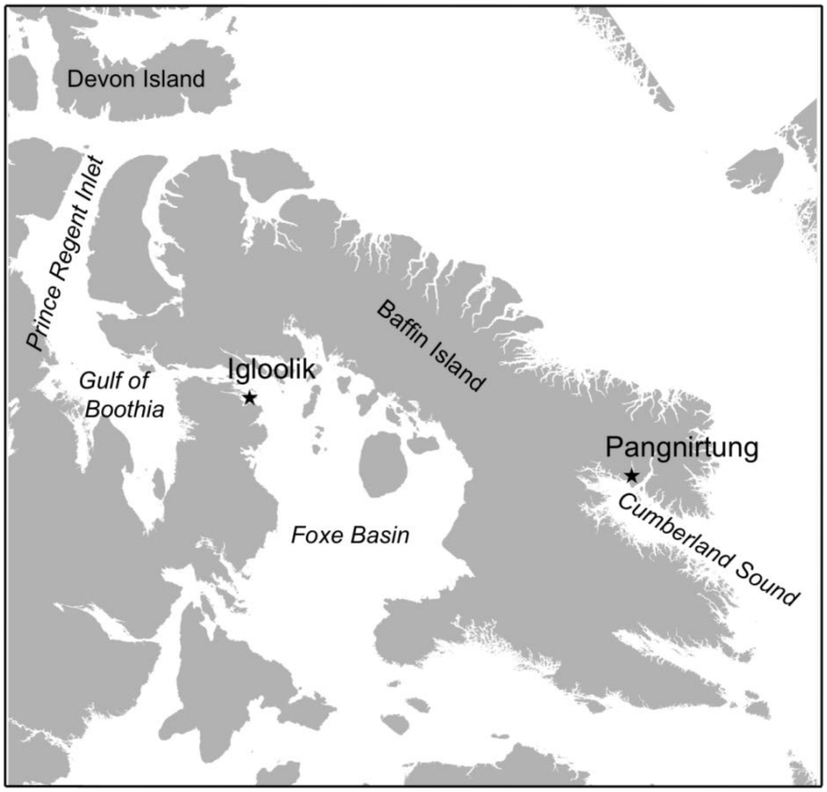

Figure 1. Map indicating the closest communities in Canada where bowhead whales were fitted with satellite telemetry tags.

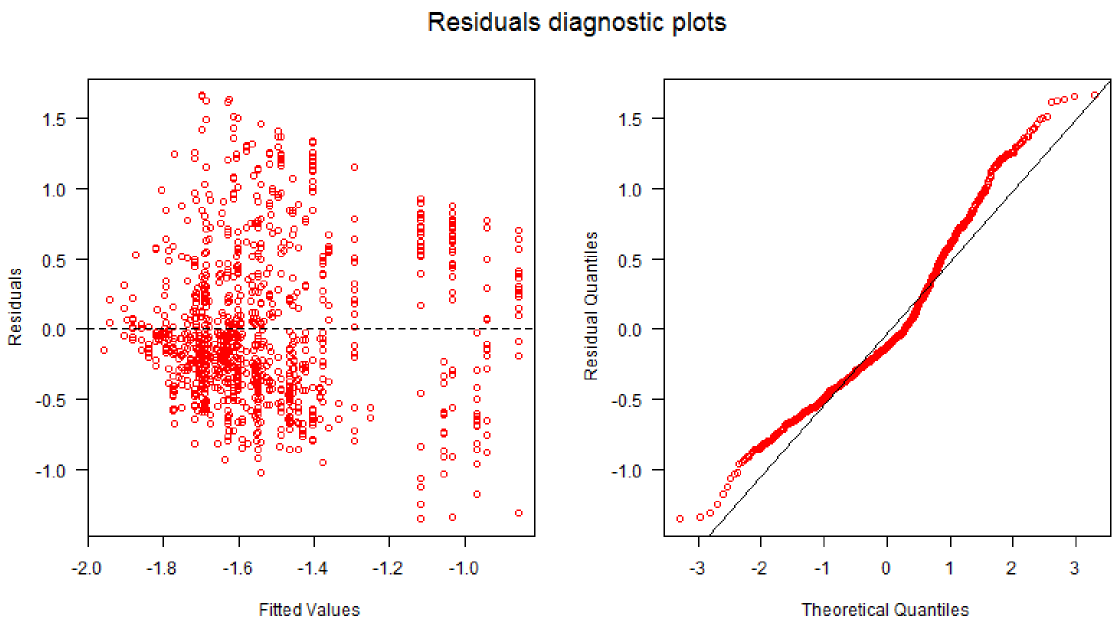

Figure 2. Example of residuals diagnostic plots for the best model to predict the logged proportion of time bowhead whales spent in the 0-4 m depth bin (model selected: log(time at 0-4m)~ Time of day + Period of August + Area + random (bowhead whale)).

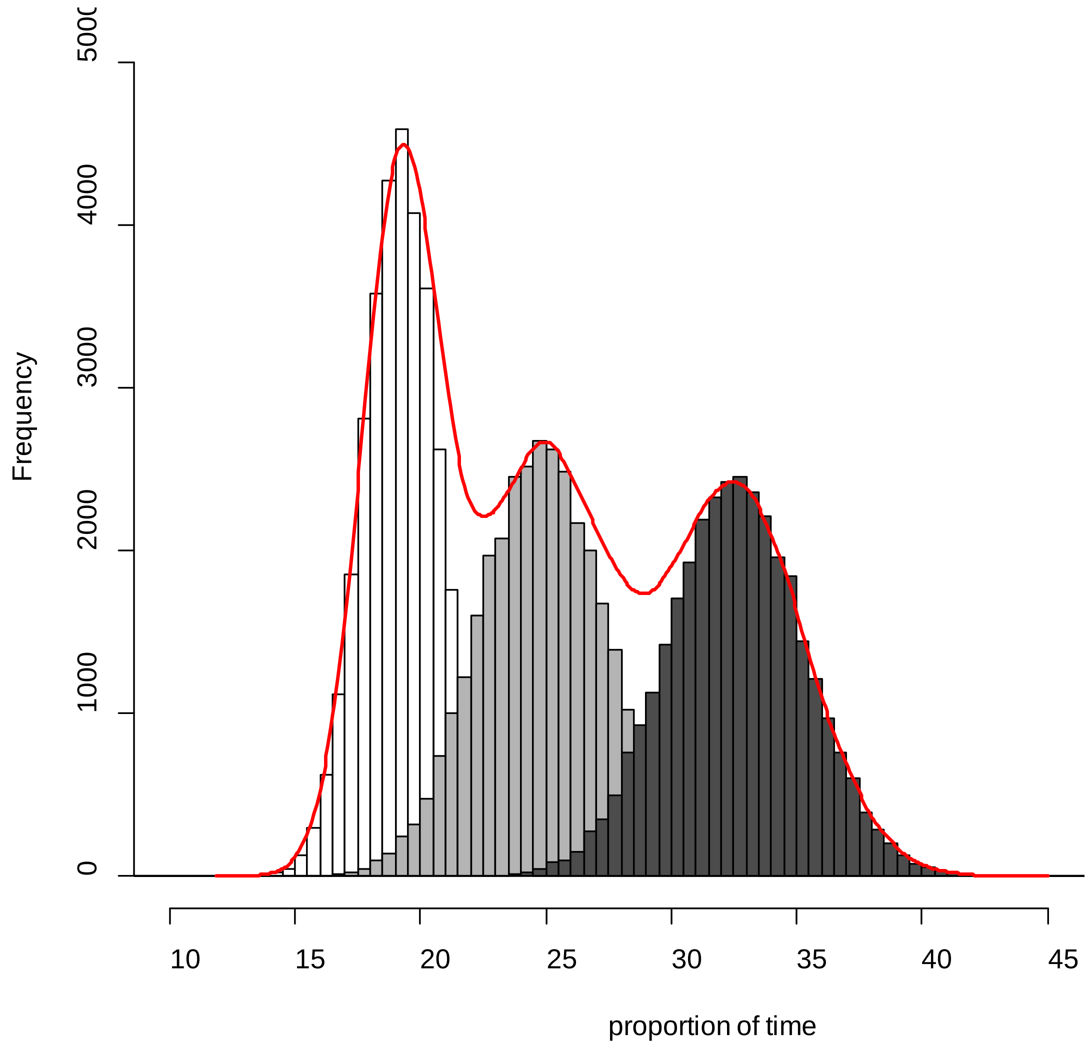

Figure 3. An example indicating the estimated proportion of time spent by bowhead whales in depth bins 0-2 m (white bars), 0-4 m (grey bars) and 0-6 m (dark bars). Red line: equally-weighted mixture distribution representing the proportion of time that bowhead whales are assumed to be visible by aerial survey observers.

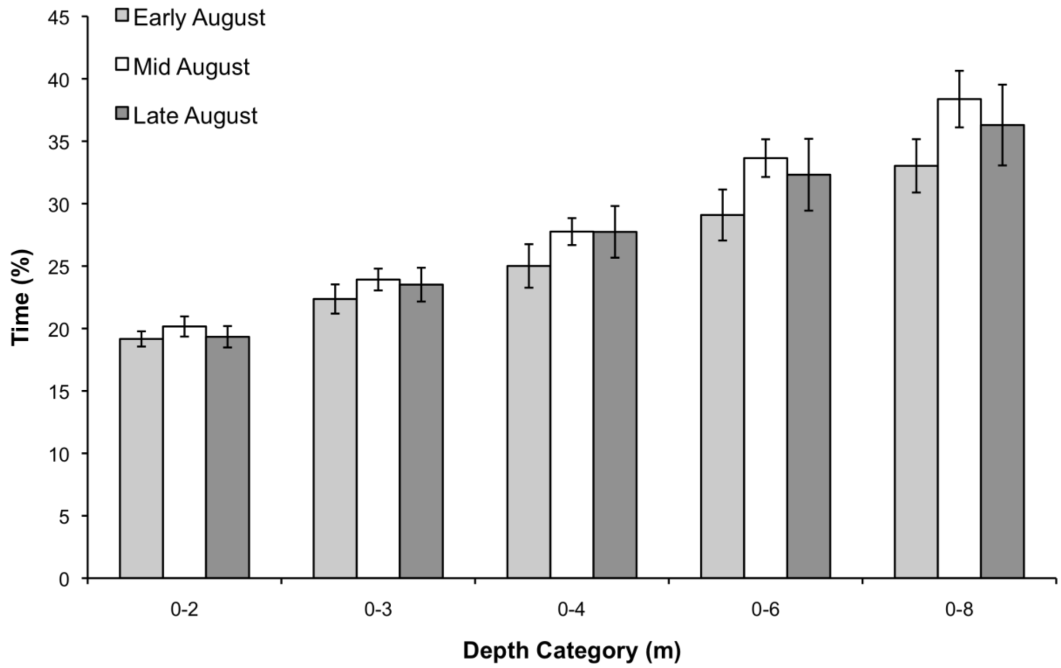

Figure 4. The weighted average percent of time (±SE) bowhead whales spent in each depth category in early, mid, and late August.

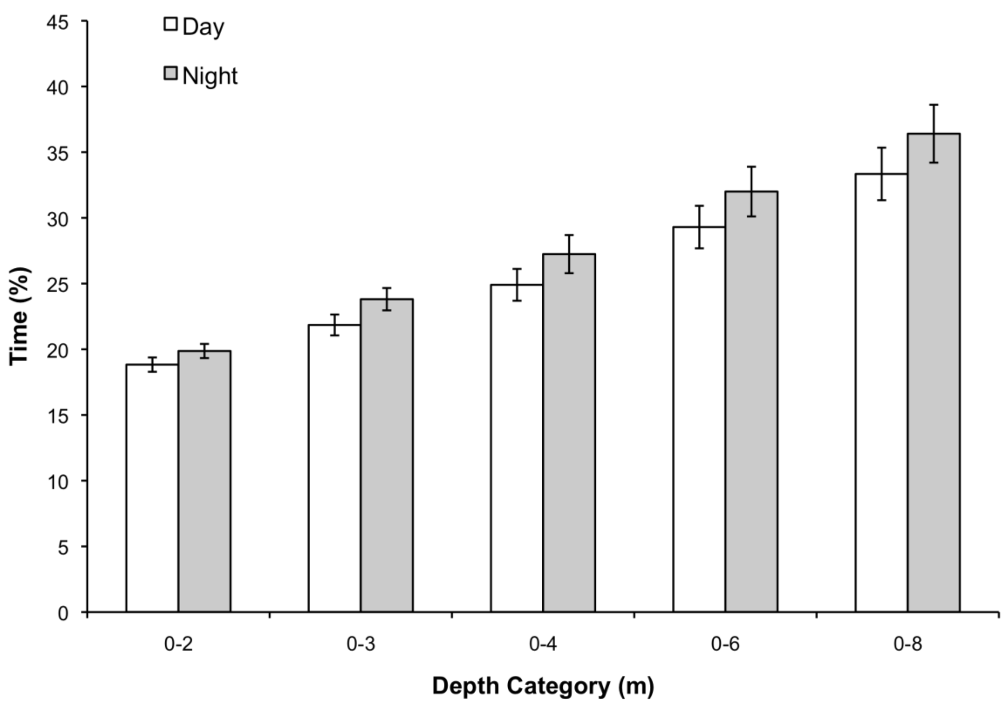

Figure 5. The weighted average percent of time (±SE) bowhead whales spent in each depth category during the day and night.

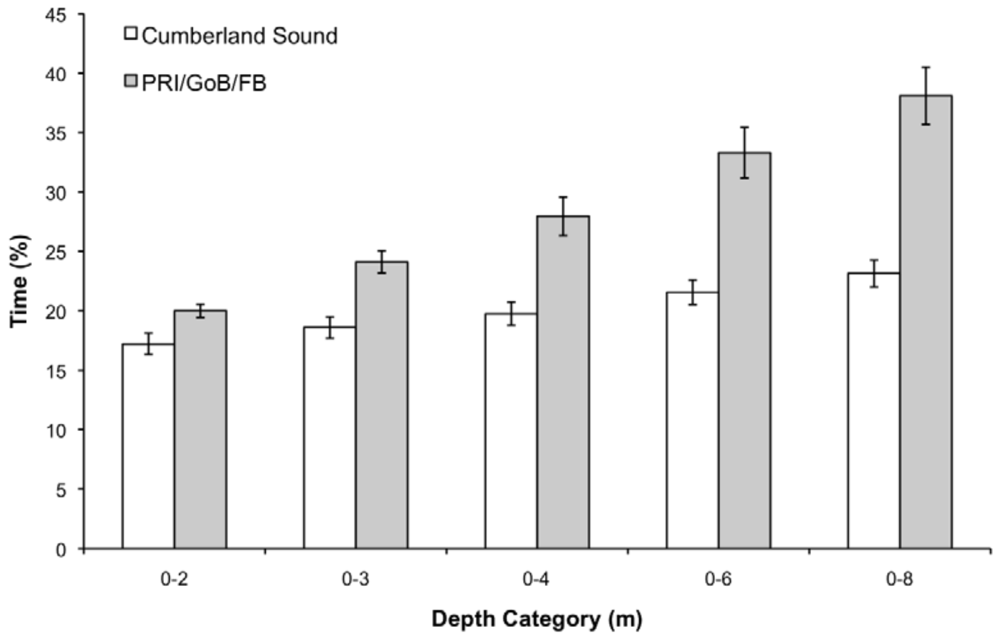

Figure 6. The weighted average percent of time (±SE) bowhead whales spent in each depth category in Cumberland Sound and PRI/GoB/FB.

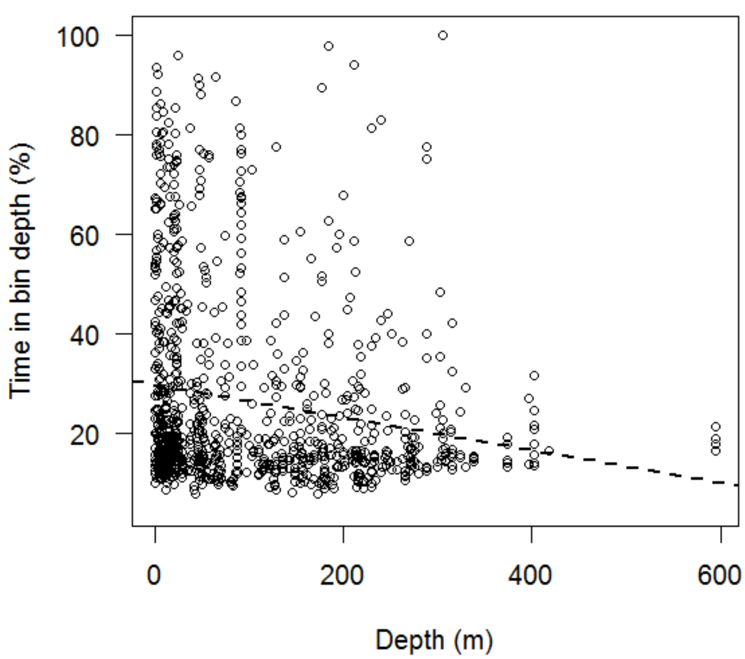

Figure 7. Relationship between water-column depth and percentage of time bowhead whales spent in the 0-4 m depth bin.