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Diving characteristics and sightability estimates of eastern Arctic bowhead whales, *Balaena mysticetus*, based on satellite-linked telemetry

Caractéristiques de plongée et estimations de la détectabilité des baleines boréales de l'est de l'Arctique, *Balaena mysticetus*, d'après la télémétrie satellite

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ABSTRACT

Satellite-linked dive-recording instruments were deployed on four eastern Arctic bowhead whales. Two of the tagged animals were sexually mature females accompanied by calves. The other two animals were inferred to be an adult male and a juvenile female. Dive measurement data was received between July 5 and August 11, 2003. Tags reported data for 17-34 days for a total of 96 tag-days. Approximately 17,500 dives ≥8 m in depth were recorded. Dive rate ranged from 2.8 dives/hr to 30.7 dives/hr, and both dive rate and variance increased with day-of-year. All four whales dove to depths ≥100 m. The maximum recorded dive depth was 400 m. Most dives (59%) were to depths ≤12 m; only 4.2% were to depths >50 m. Mean dive duration ranged from 2.6 min to 8.1 min (mean = 5.0 min., S.E. = 1.1 min, n = 4). Whales spent most of their dive time (63-78% of time-at-depth) at dive depths ≤12 m (mean = 71%, S.E. = 3%, n = 4). Overall surface time (≤ 4 m depth) for individuals ranged from 19% to 35% (mean = 28%, S.E. = 4%, n = 4). Differences between whales were evident for surface time and certain dive characteristics; females accompanied by calves had the lowest mean dive duration and spent more time at the surface than the other whales. No differences in surface time or dive characteristics were observed for time-of-day. Overall sightability estimates, based on pooled surface time (above 4 m depth) and partitioned by week, were 40% prior to breakup of landfast ice and ranged from 21% to 29% for subsequent weeks in which at least three tags were active. Adjustments to sightability estimates for application to aerial surveys of bowhead whales in the eastern Arctic are discussed.

RÉSUMÉ

Nous avons marqué quatre baleines boréales de l'est de l'Arctique avec des enregistreurs de plongée à liaison satellite, y compris deux femelles matures accompagnées de baleineaux. Les deux autres seraient un mâle adulte et une jeune femelle. Nous avons reçu des données de mesure sur les habitudes de plongée entre le 5 juillet et le 11 août 2003; les instruments ont enregistré des données pendant une période allant de 17 à 34 jours, sur un total de 96 enregistreurs/jours. Nous avons enregistré 17 500 plongées environ à une profondeur ≥ 8 m. Le taux de plongée a varié entre 2,8 plongées/h et 30,7 plongées/h, et tant le taux de plongée que la variabilité ont augmenté avec le jour de l'année. Les quatre baleines ont plongé à des profondeurs ≥ 100 m. La profondeur de plongée maximale enregistrée est de 400 m. La plupart des plongées (59 %) ont eu lieu à des profondeurs ≤ 12 m; seulement 4,2 % des plongées ont atteint des profondeurs > 50 m. La durée de plongée moyenne des individus a varié entre 2,6 minutes et 8,1 minutes (moyenne = 5,0 min., écart-type = 1,1 min., n = 4). Les baleines ont passé la plus grande partie de leur temps de plongée (63-78 % du temps en profondeur) à des profondeurs ≤ 12 m (moyenne = 71 %, écart-type = 3 %, n = 4). Le temps passé à la surface (≤ 4 m de profondeur) par les baleines a varié entre 19 % et 35 % (moyenne = 28 %, écart-type = 4 %, n = 4). On a constaté des différences évidentes entre les baleines pour ce qui est du temps passé en surface et de certaines caractéristiques de plongée; les femelles accompagnées des baleineaux ont affiché la plus faible durée de plongée moyenne et ont passé plus de temps à la surface que les autres baleines. On n'a observé aucune différence dans les caractéristiques de plongée ou le temps passé en surface selon la période du jour. Les estimations de la détectabilité selon le temps en surface combiné (au-dessus de 4 m), selon des segments d'une semaine, étaient de 40 % avant la dislocation de la banquise et variaient entre 21 % et 29 % pour les semaines suivantes au cours desquelles au moins trois enregistreurs de plongée ont été actifs. Les corrections à apporter aux estimations de la détectabilité pour l'application aux relevés aériens de baleines boréales de l'est de l'Arctique sont examinées.

INTRODUCTION

Efforts to re-assess the status of bowhead whales of the eastern Arctic have recently been made, through a combination of aerial surveys, movement studies, and genetic investigations. An important uncertainty in aerial survey abundance estimation is the lack of knowledge related to bowhead behaviour, particularly as it relates to diving and the sightability of whales. Since a significant proportion of time is spent by whales beneath the surface out of sight of passing observers, correction for unseen whales is an important component of estimating abundance.

Most studies of bowhead behaviour rely have relied on visual observations. These may be biased due to uncertainties in re-identifying diving whales that occur in groups or which dive for long periods. Recently, satellite-linked tag technology has allowed researchers to collect longer term location and behavioural data for animals that is not subject to the same biases as visual observations. This approach has begun to provide valuable insight into the seasonal movements and diving behaviour of bowhead whales (Krutzikowsky and Mate 2000; Heide-Jorgensen *et al.* 2003). As part of a larger research project conducted in Foxe Basin, Nunavut to study the distribution and movements of bowhead whales in the eastern Canadian Arctic, satellite-linked dive recording instruments were used to monitor the diving behaviour of a number of bowhead whales in 2003. This paper examines the diving characteristics of bowhead whales resulting from this work, in an effort to gain insight into bowhead behaviour and to address the sightability issues for application to aerial assessment surveys conducted in this region.

METHODS

Tag Description and Deployment

The tags used in this study were SDR-T16 Argos satellite-linked time-depth recorders, supplied by Wildlife Computers (Redland, Washington). The tag was housed in a torpedo-shaped float, 28 x 8 cm, attached by a metre long tether to the anchor that was implanted in the blubber layer of the whale's back (Heide-Jørgensen *et al.* 2006). The tags were powered by a lithium C-cell battery, were programmed to provide transmissions every day, and had an expected longevity of 100,000 transmissions.

All tags were attached to the whales by means of an anchor implanted in the blubber layer. The anchor, composed of stainless steel, consisted of a rod (25 or 33 cm long) with two to three flexible flat barbs alternately fixed along the shaft of the rod. The barbs were designed splay out with any outward pull of the tag so as to hold the tag in the blubber layer.

Tags were sterilized prior to deployment and deployed from the bow of a boat using an 8 m hand-held fibreglass pole. When the whale was within 4-5 metres of the boat, the tagger pushed the tag anchor into the blubber layer with the pole, as high on the back of the whale as possible. Skin biopsies for gender determination were obtained when the whale was tagged, using a small biopsy tip attached near the end of the pole. Biopsy samples were stored in DMSO until transported to the laboratory.

DNA was extracted from the skin samples using DNeasy tissue extraction kits (Qiagen). The sex of each of the animals sampled was then determined using a PCR (polymerase chain reaction) (Bérubé and Palsbøll 1996).

Between July 5th and July 18th 2003, four bowhead whales were tagged with satellite-linked dive-recording tags in northern Foxe Basin, Nunavut, within 50 km of Igloolik Island (Table 1). Two of the tags were placed on sexually mature females, as determined by their body length and close association with calves. The other two whales consisted of a female and a male. Based on gender and estimates of body length at sexual maturity, the 12 m female was likely a juvenile while the 13 m male was likely sexually mature (Koski *et al.* 1993; Cosens and Blouw 2003).

Data Recording and Analysis

Dive data was transmitted to Argos receivers on National Oceanic and Atmospheric Adminstration (NOAA) satellites when satellites were in range and whenever the tags appeared above the water surface. Tag positions are estimated by measuring the Doppler effect on the transmitted frequency whenever two or more signals are received during a single pass of the satellite (Harris *et al.* 1990, Priede and French 1991). Daily average positions were calculated to estimate daily movement and overall travel distances and to identify the region of activity.

The tags sampled depth every 10 seconds and were configured to define dives as submergence below 8 m depth. Data on dives >8 m was recorded in the form of histograms and status messages for four six-hour periods each day. The histograms provided data in the form of accumulated counts of dives in pre-defined ranges (or bins, as defined in more detail below) for three types of dive measures: depth, duration and time-at-depth. Dive rate was calculated for each period as the total number of dives per hour to depths >8 m.

Status messages contained information on the maximum depth recorded for the previous 24 hrs and the total surface-time for the previous period. The tags were capable of a maximum depth measurement of 490 m with a resolution of 2 m. Surface-time was measured for each bowhead whale as the total number of minutes spent above 4 metres depth in a six hour period. This measure was converted into the proportion-of-time spent at the surface (above 4 metres depth) for each period.

<u>Depth histograms</u>: Dives >8 m were classified into one of 14 depth bins according to the following depth categories (where the given value represents the maximum depth for that bin): 12 m, 16 m, 20 m, 24 m, 28 m, 32 m, 50 m, 100 m, 150 m, 200 m, 250 m, 300 m, 350 m, and >350 m. In addition to the depth histogram data, a mean depth for each

histogram was calculated as the sum of the weighted proportions of the counts of all bins:

$$d_i = \sum (d_j * (c_{ij} / \sum c_{ij}))$$

where

d_i = mean depth for the i^{th} histogram
d_i = mid-range value of the j^{th} depth bin
c_{ij} = count of dives in the j^{th} bin of the i^{th} histogram

Duration histograms: Dives > 8 m depth were classified into one of 10 duration bins according to the following duration categories (where the given value represents the maximum duration for that bin): 1 min, 3 min, 6 min, 9 min, 12 min, 15 min, 18 min, 21 min, 24 min, >24 min. In addition to the duration histogram data, a mean dive duration was calculated as the sum of the weighted proportions of the counts of all bins:

$$t_i = \sum (t_j * (c_{ij} / \sum c_{ij}))$$

where

t_i = mean duration for the i^{th} histogram
t_j = mid-range value for the j^{th} duration bin
c_{ij} = count of dives in the j^{th} bin of the i^{th} histogram

Time-at-depth histograms: Dives were classified into one of 14 depth bins, the same as those used for depth histograms. The count of each bin, taken as the fraction of the total counts over all bins, represented the portion of the six hour period that the animal spent in each depth range.

Statistical Analysis

Descriptive statistics and tests were conducted using SYSTAT (Version 11, Richmond, CA). Frequency distributions were examined using Chi-square. Tests for normality were conducted using the Shapiro-Wilk test. For parameters with normal distribution and equal variances, within and between group differences of measurement data were tested using ANOVA (multiple groups); for non-normal distributions and/or non-equal variances, Kruskal-Wallis non-parametric tests were used.

RESULTS

Tag Activity and Whale Movements

All four bowhead whales were tagged in northern Foxe Basin between July 5^{th} and July 18^{th}, 2003. Individual dive-recording tags were active for periods ranging from 17 to 34 days for a total of 96 tag-days, beginning July 5th and ending August 11th. Approximately 17,500 dives were recorded for the four bowhead whales (Table 2). Data records were well distributed across all four periods of day; i.e. there was no bias evident in the data received as a function of period-of-day, for pooled data (Chi-square, $p=0.955$), or for individual bowhead with sample size > 50 histograms (i.e. excluding data from tag #20160 due to low sample size; Chi-square, $p>0.9$).

Whale #20160 stayed in Foxe Basin for the entire active tag period. The other three whales moved out of Foxe Basin and spent a majority of time (53%-89% of recorded tag activity) outside of Foxe Basin, in the Gulf of Boothia and Prince Regent Inlet. Whale #20160 traveled a total of 240 km while whales that moved to other regions traveled for distances ranging from 592 km to 1174 km. Travel rate varied from less than one km/day to a maximum of 124 km/day (Table 1). Based on daily average positions, whale #20160 traveled ≤15 km/day while the other whales traveled as much as 76-124 km/day.

Tag uplink performance, as measured by the number of 6 hour periods for which data was collected, was variable. Three of the tags provided data for 78-97% of available periods. Tag #20160 had the poorest performance, providing data for only about 18% of available periods (Table 2).

Dive Rate

The maximum number of dives recorded in a single day was 510 dives, recorded by the 13 m male bowhead whale (#20167). The number of dives in a single six-hour period for any individual whale ranged from 17 to 184, translating to dive rates of 2.8 dives/hr to 30.7 dives/hr. There was no evidence of any effect on the frequency of dives occurring as a function of period (time-of-day)

The average dive rate for individual whales ranged from 7.0 dives/hr (SD = 3.3) to 11.4 dives/hr (SD = 4.0, Figure 1). Differences between whales in dive rate was evident when examined using all dives, shallow dives (8-12 m depth), and deep dives (>12 m depth). Whale #26712 had the lowest dive rate when examined for all dives and for shallow dives (Figure 1a, b), while the difference between individuals for deep dives could not be clearly attributed to specific individuals.

Both the dive rate and variance in dive rate for all pooled dives increased with day-of-year for three bowhead whales (Figure 2a). The same pattern was observed in two whales when the dive rate data was examined for shallow dives (8-12 m) (Figure 2b), while the dive rate for deeper dives (> 12 m) did not show any consistent trend across whales with day-of-year (Figures 2c).

For the three whales that moved out of Foxe Basin, average dive rates for all dive classes combined were significantly higher in Prince Regent Inlet relative to the other regions (KW, $p < 0.001$, d.f. = 2, for all three whales, Figure 3a). For two of these whales, average dive rates for the 8-12 m dive class were also significantly higher in Prince Regent Inlet (KW, $p < 0.001$, d.f. = 2 for whale #20167 and #21802, Figure 3b). For dive classes > 12 m, differences between regions was not consistent among whales; whale #26712 exhibited a higher dive rate in Prince Regent Inlet (KW, $p = 0.02$, d.f. = 2), while whale #21802 exhibited a lower dive rate in Prince Regent Inlet (KW, $p < 0.001$, d.f. = 2, Figure 3c).

Depth of Dives

The maximum dive depth recorded in this study was 400 m. Dives to all depth classes were observed, including the >350 m class. All four whales dove to depths >100 m; three whales dove to depths >200 m. The pattern of dive depth frequency was generally similar for all four whales (Figure 4). Shallow dives were most frequent and the frequency of dives decreased rapidly with increasing depth class. Over half of all dives occurred in the shallowest (12 m) dive depth class (59%); only 4.2% of dives were recorded to depths over 50 m. One individual (#26712) used the 8-12 m depth class less frequently relative to the other three whales, while accounting for five times the number of recorded dives beyond 150 m relative to the three other individuals (Pearson Chi-square = 1063, df = 27; depth categories > 150 m pooled, $p < 0.001$).

The mean dive depth for individuals ranged from 17.1 (SD = 4.5) to 22.4 m (SD = 13.8, Figure 5). The mean dive depth was lowest for whale #20160 ($p = 0.013$). Three of the whales (all except #20160) exhibited a negative correlation of mean dive depth with day-of-year ($p < 0.001$, Figure 6). When examined by location, the mean dive depth differed between locations for the three whales that moved out of Foxe Basin ($p < 0.001$ for all three comparisons). Mean dive depth was typically lowest in Prince Regent Inlet and generally higher in Foxe Basin and/or Gulf of Boothia (Figure 7). There was no difference in dive depth as a function of period-of-day for any of the four individuals (KW, $p > 0.30$).

Duration of Dives

Dive durations were recorded in all 10 duration categories, including the >24 min duration class. As with depth of dives, duration histograms were skewed to the left, with the greatest frequency of dives in the shortest duration category and a decreasing trend in frequency with increasing duration class (Figure 8). Only 2% of all recorded dives were greater then 15 min.

Mean dive duration for individual bowhead whales ranged from 2.6 (SD = 0.7) to 7.5 (SD = 3.6) minutes (average mean = 5.0 min/dive, S.E. = 1.1 min, n = 4). Mean dive duration was lowest for whale #20160 , highest for whale #26712, and of intermediate duration for the other two whales (KW = 39.9, $p < 0.001$; Figure 9). Two of the whales exhibited a negative correlation of mean dive duration with day-of-year, while a trend was not significant for the other two whales (Figure 10).

Differences in mean dive duration as a function of location were present for the three whales that moved out of Foxe Basin, but the differences were not consistent across individuals (Figure 11). There was no difference in dive duration as a function of period-of-day for any of the four individuals (KW, $p > 0.18$).

Time-at Depth

The distribution of time-at-depth results were the most highly skewed of all histograms (Figure 12). On average, 71% of dive time (S.E. = 3%, n = 4 whales) was spent during dives ≤12 m (the shallowest depth category), 92% (S.E. = 1%, n = 4) to depths ≤28 m, and 94% to depths ≤50 m.

Surface Time

The proportion of time at the surface (above 4 m depth) for individual whales in a six-hour period ranged from as little as 8% to as high as 80%. The average proportion of total time spent at the surface for individuals varied from 19% (SD = 8%) to 35% (SD = 15%), with an overall mean of 28% (S.E. = 4%, n = 4). Differences in surface time were evident between whales (Figure 13). The two females accompanied by calves spent the highest average proportion of time at the surface, both at 35%, while the other individuals averaged 19-22%.

Daily average pooled values for proportion of time-at-surface ranged from 11% to 40% (Figure 14). Excluding days for which data from less than 3 whales was recorded, the range for daily average values was 18% to 38%.

When the effect of location was examined, the lowest proportions of time at the surface appeared to occur in the Gulf of Boothia, although there was sufficient data to demonstrate a significant difference between locations for only two of the three whales that occurred in the three regions (Figure 15). When data for the four whales was pooled, there was a significant difference between locations, with the highest surface times occurring in Foxe Basin, followed by Prince Regent Inlet and lastly by Gulf of Boothia (Figure 16).

There was a significant correlation of surface time with day-of year for only one whale (Figure 17), which exhibited a positive relationship between these variables. There was no difference in proportion of time-at-surface as a function of period-of-day for any of the four individuals (KW, $p > 0.25$).

In order to calculate sightability of whales that would be applicable to aerial surveys conducted at specific times, the surface time data was pooled for all whales and partitioned on a weekly basis. Using only weekly periods with more than 25 sample periods and more than one active tag, the average proportion of time spent at the surface ranged from 21% to 40% with the maximum occurring during the first week, prior to breakup (Table 3). Examining data for the weeks after breakup, the mean proportion of time at the surface varied by less than 8%, ranging from 21-29%.

DISCUSSION

Dive Characteristics

Until recently, the diving capabilities of bowhead whales were known and described entirely on the basis of visual records. Early observations by whalers suggested that a harpooned bowhead whale could dive for periods of up to an hour or more (Scoresby 1820, Scammon 1874, NWMB 2000). More recent studies based on visual observations have estimated the maximum diving capability for undisturbed bowhead whales at about half that duration (Braham *et al.* 1979, Carroll and Smithhisler 1980, Würsig *et al.* 1984). The maximum dive duration recorded for bowhead whales using satellite-linked recorders is 61 min, although there is a possibility of upward bias in this record (Krutzikowsky and Mate 2000). In our study, only 42 of 17,800 recorded dives from four whales (0.2% of recorded dives) exceeded 24 min in duration (our maximum duration bin), suggesting that for undisturbed bowhead whales, dives >24 min are rare.

The general observation of a rapidly decreasing dive frequency with increasing dive duration class is similar to that found in other studies using either visual methods (Dorsey *et al.* 1989, Würsig *et al.* 1984) or data telemetry (Krutzikowsky and Mate 2000, Hiede Jørgensen *et al.* 2003). Overall dive durations recorded during visual studies typically range from means of about three to seven minutes (Davis *et al.* 1982, Würsig *et al.* 1984, Richardson *et al.* 1995). Overall mean dive durations recorded in our study were comparable (5 min), with some variability between individuals (ranging from means of 2.6 to 8.1 min, Figure 9). Differences in dive duration between individuals appeared to be related to activity or location. Dive durations recorded in visual studies are generally longer during activities classified as feeding, migration and local travel, and shorter during socializing (Carroll *et al.* 1987, Richardson *et al.* 1995). The whale with the lowest mean dive duration in our study (#20160, female with calf) also traveled the shortest overall distance and spent all of its active tag time in Foxe Basin, an area of relatively shallow depth and little ice cover. The other three whales traveled through Fury and Hecla Strait and Gulf of Boothia to Prince Regent Inlet, areas of greater depth, and requiring navigation through areas of heavy pack ice. Heide Jørgensen *et al.* (2003) noted an increase in mean dive depth while whales migrated across Baffin Bay through heavy ice, but did not report on changes in dive duration. Others have found positive relationship between water depth and dive duration (Würsig *et al.* 1984, Dorsey *et al.* 1989), but when we compared dive duration of individuals between areas of different depths this effect was evident for only one whale (Figure 11). The difference in mean dive duration between individuals was thus likely a function of migration through heavy ice as opposed to water depth.

The maximum dive depth recorded in our study (400 m) was comparable to that found by other satellite-linked dive recording studies of bowhead whales (Krutzikowsky and Mate 2000, Heide-Jorgensen *et al.* 2003). Although less than 5% of dives occurred to depths beyond 50 m, the average of the maximum depth of dives recorded per period for the four bowhead whales in this study ranged from 92 m to 164 m, indicating that at least some dives to considerable depth were regularly made during most periods sampled. Whales that traveled through Fury and Hecla Strait and Gulf of Boothia had larger mean dive depths than the whale that remained in Foxe Basin. When whales reached the summering area of Prince Regent Inlet, mean dive depth dropped back down to values comparable to that of the whale that stayed in Foxe Basin. It is likely that deep dives recorded in this study were used by whales to monitor their environment and to find their way through heavy ice during migration.

All three whales that traveled to the summering area in Prince Regent Inlet showed a difference in dive rate among locations (Figure 3a), reflected by the positive correlation of dive rate with day-of-year (Figure 2a). The lower dive rate in Foxe Basin and Gulf of Boothia is likely related to the effect of migration as described above, where whales use deeper dives of longer duration to find their way through ice. Once in Prince Regent Inlet, shallower more frequent dives result as whales are more likely to be engaged in feeding activities during the season of highest productivity.

Time-at-depth measurements best encapsulate the general dive characteristics of all four bowhead whales, and are supported by findings by others (Krutzikowsky and Mate 2000, Heide-Jorgensen *et al.* 2003). The majority of time by all whales was spent in dives less than 12 m. Some individual variation was noted, specifically for one whale (#26712), which spent a slightly greater proportion of time at slightly greater depth, but this did little to change the overall makeup of time-at depth. All whales spent over 94% of time above 50 m depth.

A lack of a diurnal effect on diving behaviour is supported by the findings of others (Würsig *et al.* 1984, Krutzikowsky and Mate 2000, Heide-Jorgensen *et al.* 2003).

Proportion of Time Visible at the Surface

Estimates of the proportion of time that bowhead are visible at the surface (sightability) appears to vary as a function of one or a combination of variables, including reproductive class, activity, environmental conditions and/or location. A lack of a diurnal effect on diving behaviour indicates that time-of-day is not a significant factor in the activity or sightability of bowhead whales. However, there was sufficient evidence to indicate that proportion-of-time at surface varies between individuals and with season. The two females accompanied by calves spent more time at the surface (35%) than the other tagged whales (19-22%, Figure 13), presumably due to the diving limitations of calves and requirements for nursing. This is the first study using satellite-linked dive recording tags to document this difference in dive behaviour between females with calves and other whales. Visual-based studies have reported differences between maternal females and other whales for some dive characteristics under particular conditions (Würsig *et al.* 1984, Koski *et al.* 2004), but these do not provide detailed information on proportion-of-time visible at the surface.

Results from visual studies indicate that proportion of time-at-surface is typically lowest during migration, followed by feeding and local travel, and finally socializing (Würsig *et al.* 1984, Carroll *et al.* 1987, Richardson *et al.* 1995). Variability in sightability with season in our study also appeared to be related to changes in activity, in combination with different environmental conditions, particularly between pre-breakup and breakup/open water seasons. Thomas (1999) reports that bowhead activity at or near the Foxe Basin ice-edge prior to breakup coincides with moderate amounts of time spent in open water feeding (42%), under-ice diving (21%), and socializing (29%), and small amounts of local travel and resting (7.7%). After breakup, this changed to activity dominated by under-ice diving (79%), moderate local travel (17%) and small amounts of socializing (4%). Breakup also coincides with the apparent migration of significant numbers of bowhead whales through the ice of Fury and Hecla Strait and Gulf of Boothia into Prince Regent Inlet as determined by complementary tracking studies (Dueck *et al.* unpublished). Given the expected difference in sightability between migration and socializing, these results correspond well to our findings. Proportion-of-time at surface was notably higher prior to breakup (Table 3), when fast ice was still present in northern Foxe Basin and Fury and Hecla Strait. The marked decrease in sightability upon breakup occurred at the same time as we observed bowhead whales advancing into the ice field using the ice leads, and reached a minimum during late July when migration through Fury and Hecla Strait and Gulf of Boothia peaked.

A pooled estimate of proportion of time-at-surface is the best estimate of overall sightability of bowhead whales in this study. Calculated on a weekly basis for the period after breakup when tags from at least three whales were active, the average pooled surface time fell between 21% and 29% (Table 3). Day-to-day variability by as much as 29 percentage points was recorded, as depicted by daily pooled sightability (range: 11% to 40%, Figure 14). However, the range in variation is reduced (18% to 38%) when we restricted the analysis to days in which data from at least three whales was available, indicating that small sample size is partially responsible for the extent of day-to-day variation observed. Undoubtably, the variability in the day-to-day measure of sightability would be reduced with greater sample size. The estimate for the last week of tag activity (week ending August 9, average = 25%, $LCL_{95\%}$= 16%, $UCL_{95\%}$= 34%) is likely the most reasonable, if not conservative estimate of sightability for the summering population of bowhead whales in Prince Regent Inlet, during the period when aerial surveys were conducted (Cosens *et al.* 2006).

Comparisons of sightability measures with other studies are complicated by the potential variability between regions and seasons, or low sample size. However, apart from estimates of sightability based strictly on single activities, such as socializing, most other estimates tend to be lower than those in our study (Richardson *et al.* 1995, Krutzikowsky and Mate 2000 Heide-Jørgensen and Aquarone 2002, Heide-Jørgensen *et al.* 2003). Estimates of sightability for western Arctic bowhead based on visual studies range from 7.0% to 35.7% (unweighted mean = 16.2%, S.D.=9.0%; see review in Krutzikowsky and Mate 2000). One estimate of sightability based on tag results for bowhead in the Western Arctic is 11.1% (S.D.=2.4%, n=8) although potential for under-estimation is reported (Krutzikowsky and Mate 2000).

Few estimates of sightability for eastern Arctic bowhead whales exist. Heide-Jorgensen *et al.* (2003) report the proportion of time at the surface for one (male adult) bowhead based on satellite-linked telemetry during movements between Greenland and Baffin Island waters ranging from 13% to 34%. Heide-Jørgensen (unpubl. data *in* Heide-Jørgensen and Aquarone 2002) report a percent surface time of 17-21% based on visual observations (41 to 90 minutes of observation) of two bowhead whales in west Greenland waters and one in Tremblay Sound, Baffin Island. Thus it appears that the sightability measures reported in this study are unlikely to be under-estimates.

Application of Sightability Measures to Aerial Survey Correction

A depth of 4 m was used to define “surface time”. This depth was chosen as a reasonable estimate of the maximum depth to which bowhead would be visible to observers during aerial surveys. Their general dark coloration of bowhead whales results in some difficulty in seeing them under water even in ideal conditions. Moreover, visibility to depth drops off rapidly with increases in sea state and with increasing distance from an aircraft due to increased reflection. Except when whales are near the transect line, survey observers are unlikely to detect many bowhead whales between the actual surface and 4 m depth. Thus, use of this depth threshold is likely a conservative one for estimating the instantaneous sightability of whales at or near the surface. Due to variation in colouration with age, calves are more difficult to detect than non-calves and thus there may be additional biases toward observations of older individuals (Würsig *et al.* 1984). Ideally these biases should be accounted for in aerial survey abundance estimates.

In terms of positive detection biases, observers in a survey aircraft have a window of time in which to detect whales rather than a single “snapshot” view of the survey area from the air. This effect increases the probability of detecting animals. Researchers have corrected for this “availability” bias in aerial survey abundance estimates by incorporating the length of this observer time window along with dive interval information to estimate the probability that an animal will be at, or appear at, the surface during the period of observation (Frost *et al.* 1985; Barlow *et al.* 1988; Laake *et al.* 1997, Hobbs *et al.* 2000). This approach, based on the McLaren’s (1961) formula for calculating *p,* the probability that an animal will be detected, is summarized by:

$$p = \frac{t}{s+u} + \frac{s}{s+u} ,$$

where t = observation time available, s = surface time, and u = dive time, and t is assumed to be less than u. Davis *et al.* (1982) estimated t at 18 seconds, based on the length of time to travel 1 km at 200 kph. However this is likely an over-estimate of the time window, given the documented behaviour of observers during other aerial surveys and is more likely considerably less than 10 seconds (Pierre Richard, pers. comm.).

Estimates of *s* and *t* are not available from this study to evaluate the effect of the approach. Davis *et al.* (1982) provide data which indicates an 18 second observer window would increase detection or sightability of whales by a factor 1.4-1.6x greater than that based on instantaneous sightability.

In order to apply correction factors to aerial survey estimates, sightability studies should ideally be based on a sufficient sample size and should be conducted in the same area and at the same time as the aerial surveys. Although only three whales contributed to estimates of sightability during the weeks following breakup, the number of dives that sightability estimates were based on was >3000 dives in any given week between breakup and August 9, reducing bias that would be expected if dive sampling was low. The individuals contributing to the results represent a mix of gender, age and reproductive class, which to a large extent controls for bias that would be expected if estimates were based on a single individual or class. The mix of whale classes in our sample is reasonably representative of the presumed composition of whales in Foxe Basin and Prince Regent Inlet (Finley 2001, Cosens and Blouw 2003).

Along with the previous discussion regarding the conservative nature of the sightability estimates, these arguments suggest that application of correction factors based on the results reported in this study to surveys conducted in the Gulf of Boothia and Prince Regent Inlet between mid-July and August 9, 2004 are unlikely to over-estimate population abundance. Application of the sightability estimates to other areas and times requires caution. Results from this study and others indicates that sightability varies with season, activity and location.

ACKNOWLEDGEMENTS

We wish to thank all those that participated in the field work. We would particularly like to acknowledge the work, advice and efforts of Solomon Qanatsiaq, Levi Qaunaq, and Natar Ungalaq, without whom this study would not have been successful. Other people who provided valuable support during our field work included Brad Parker, Tam Parker, and Kristin Laidre. We are grateful to the Nunavut Wildlife Management Board (NWMB) and the Hunters and Trappers organizations of Hall Beach and Igloolik for supporting this work. This study was funded by the Nunavut Wildlife Research Trust, Nunavut Implementation Funds, Greenland Institute of Natural Resources and by Fisheries and Oceans Canada.

LITERATURE CITED

Barlow, J., C. W. Oliver, T. D. Jackson, and B. L. Taylor. 1988. Harbor porpoise, *Phocoena phocoena*, abundance estimation for California, Oregon, and Washington: II. Aerial surveys. Fish. Bull. 86:433-444.

Bérubé, M. and P. Palsbøll. 1996. Identification of sex in cetaceans by multiplexing with three ZFX and ZFY specific primers. Molecular Ecology 5: 283-287.

Braham, H., B. Krogman, S. Leatherwood, W. Marquette, D. Rugh, M. Tillman, J. Johnson,and g. Carroll. 1979. Preliminary report of the 1978 spring bowhead whale research program results. Rep. Int. Whal. Comm. 29: 291-306.

Carroll, Geoffry M., John C. George, Lloyd F. Lowry and Kenneth O. Coyle. 1987. Bowhead whale (*Baleana mysticetus*) feeding near Point Barrow, Alaska, during the 1985 spring migration. Arctic 40(2): 105-110.

Carroll, G.M. and J.R. Smithhisler. 1980. Observations of bowhead whales during spring migration. Mar. Fish Rev. 42(9-10):80-85.

Cosens, S.E. and A. Blouw. 2003. Size- and age-class segregation of bowhead whales summering in northern Foxe Basin: A photogrammetric analysis. Marine Mammal Science 19: 284-296.

Cosens, Susan E., Holly Cleator and Pierre Richard. 2006. Results of Aerial Surveys of Bowhead Whales (*Balaena mysticetus*) in the Eastern Canadian Arctic in 2002, 2003 and 2004. DFO Can. Sci. Advis. Sec. Res. Doc. 2005/006.

Davis, Rolph A., William R. Koski, W. John Richardson, C. Robert Evans and W. George Alliston. 1982. Distribution, numbers and productivity of the western Arctic stock of bowhead whales in the eastern Beaufort Sea and Amundsen Gulf, summer 1981. Unpublished report by LGL Ltd.,Toronto, for Sohio Alaska Petroleum Co., Anchorage, Alaska, and Dome Petroleum Co. Anchorage, Alaska (co-managers). 134 pp.

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

Finley, K.J. 2001. Natural history and conservation of the Greenland Whale, or Bowhead, in the Northwest Atlantic. Arctic 54: 55-76.

Frost, K.J., L.F. Lowry, and R.R. Nelson. 1985. Radiotagging studies of belukha whales (*Delphinapterus leucas*) in Bristol Bay, Alaska. Marine Mammal Science 1(3): 191-202.

Harris, S., W.J. Cresswell, P.G. Forde, W.J. Trewhella, T. Woollard and S. Wray. 1990. Home-range analysis using radio-tracking data - a review of problems and techniques particularly as applied to the study of mammals. Mammal Review 20: 97-123.

Heide-Jørgensen, M.P., K.L. Laidre, Ø. Wiig, M.V. Jensen, L. Dueck, L.D. Maiers, H.C. Schmidt and R.C. Hobbs. 2003. From Greenland to Canada in ten days: tracks of Bowhead whales, *Balaena mysticetus*, across Baffin Bay. Arctic 56:21-31.

Heide-Jørgensen, M.P. and M. Acquarone. 2002 Size and trends of the bowhead whale, beluga and narwhal stocks wintering off West Greenland. NAMMCO Sci. Publ. 4:191-210.

Heide-Jørgensen, M.P., K.L. Laidre, M.V. Jensen, L. Dueck, L.D. Postma. 2006. Dissolving stock discreteness with satellite tracking: bowhead whales in Baffin Bay. Marine Mammal Science 22: 34-45.

Hobbs, Roderick C., Janice M. Waite and David J. Rugh. 2000. Beluga, *Delphinapterus leucas*, group sizes in Cook Inlet, Alaska, based on observer counts and aerial video. Marine Fisheries Review 62(3): 46-59.

Koski, W.R., R.A. Davis, G.W. Miller and D.E. Withrow. 1993. Reproduction. *In*: Burns,J.J., Montague, J.J., and Cowles, C.J. eds. The bowhead whale. Society for Marine Mammalogy, Special Publication No. 2. Lawrence, Kansas: Allen Press. pp. 239-274.

Koski, William R., Gary W. Miller, W, John Richardson and Bernd Würsig. 2004. Bowhead whale (*Balaena mysticetus*) mothers and calves during spring migration in the Alaskan Beaufort Sea: movements, behaviour, and life history data. IWC paper SC/56/BRG27.

Krutzikowsky, Gregory K. and Bruce R. Mate. 2000. Dive and surfacing characteristics of bowhead whales (*Balaena mysticetus*) in the Beaufort and Chukchi seas. Canadian Journal of Zoology. 78: 1182-1198.

Laake, J. L., J. Calambokidis, S. D. Osmek, and G. W. Garner. 1997. Probability of detecting harbor porpoise from aerial surveys: Estimating g(0). J. Wildl. Manage. 61:63-75.

McLaren, I. A. 1961. Methods of determining the numbers and availability of ringed seals in the eastern Canadian Arctic. Arctic 14(3):162-175.

NWMB (Nunavut Wildlife Management Board). 2000. Final Report of the Inuit Bowhead Knowledge Study. Nunavut Wildlife Management Board. Iqaluit, NU.

Priede, I.G. and J. French. 1991. Tracking of marine animals by satellite. International Journal of Remote Sensing 12: 667-680.

Richardson, W.J., K.J. Finley, G.W. Miller, R.A. Davis, and W.R. Koski. 1995. Feeding, social and migration behavior of bowhead whales, *Balaena mysticetus*, in Baffin Bay vs. the Beaufort Sea -- regions with different amounts of human activity. Marine Mammal Science 11: 1-45.

Scammon, C.M. 1874. The marine mammals of the north-western coast of North America, described and illustrated : together with an account of the American whale-fishery. John H. Carmany and Co, San Francisco.

Scoresby, W. 1820. An account of the Arctic regions with a history and description of the northern whale-fishery. Volume 2, The whale- fishery. David and Charles, Newton Abbot, England.

Thomas, Tannis A. 1999. Behaviour and habitat selection of bowhead whales (*Balaena mysticetus*) in Northern Foxe Basin, Nunavut. M.Sc. thesis. University of Manitoba.

Würsig, B. and C. Clark. 1993. Behavior. *In*: Burns,J.J., Montague, J.J., and Cowles, C.J. eds. The bowhead whale. Society for Marine Mammalogy, Special Publication No. 2. Lawrence, Kansas: Allen Press. pp. 157-199.

Würsig, B, E.M. Dorsey, M.A. Fraker, R.S. Payne, W.J. Richardson, R.S. Wells. 1984. Behavior of bowhead whales, *Balaena mysticetus*, summering in the Beaufort Sea: surfacing, respiration, and dive characteristics. Can. J. Zool. 62: 1910-1921.

Table 1. Description of bowhead whales tagged with satellite-linked dive-recording transmitters in Foxe Basin in 2003, summarizing tag longevity, travel distances and proportion of time spent in different geographic regions.

Whale ID #	Gender and estimated length of whale[1]	Date tagged	Tag days	Max daily travel distance (km)	Total distance travelled (km)	Proportion of time spent in given region:		
						Foxe Basin	Gulf of Boothia	Prince Regent Inlet
20160	15 m. adult female*	5-Jul-03	18	15	240	1.00	-	-
20167	13 m. adult male	7-Jul-03	34	76	592	0.14	0.11	0.75
21802	13 m. adult female*	11-Jul-03	27	124	1174	0.47	0.10	0.43
26712	12 m. juvenile female	18-Jul-03	17	88	476	0.11	0.11	0.78

[1] Whales identified with asterisks were accompanied by calves. Bowhead whale females are thought to reach sexual maturity at 13.0-13.5 and males at 12-13 m (Koski *et al.* 1993).

Table 2. Summary of data collected and tag performance for satellite-linked dive-recording tags deployed on bowhead whales in Foxe Basin in 2003, indicating the number of dives recorded, number of six-hour periods sampled, and proportion of periods sampled.

		Number of six-hour periods sampled for given dive measurement:				
Whale ID #	Number of dives recorded[1]	Depth[2]	Duration[2]	Time at depth[2]	Status message data[3]	Tag performance[4]
20160	957	14	14	11	12	18%
20167	7995	127	130	128	115	92%
21802	5972	105	108	108	97	97%
26712	2391	57	55	54	45	78%

[1] Number of dives determined from depth histogram data.
[2] Data for depth, duration and time-at-depth measurements obtained in histogram format.
[3] Status messages included data on surface time and maximum depth.
[4] Tag performance measured as the proportion of six-hour periods sampled to the total number available for sampling.

Table 3. Summary of the proportion of surface time for bowhead whales with dive recording tags as a function of week. Surface time is reported as the average of the proportion of time spent above 4 m depth per period. Only weekly periods with more than 25 sample periods and more than one active tag were used.

Week number	Date (week ending on)[1]	Number of tags active	Number of periods sampled	Estimated total number of dives occurring[2]	Mean of average proportion of time-at-surface	Lower 95% C.I.	Upper 95% C.I.
28	12-Jul-03	3	26	1354	0.40	0.13	0.66
29	19-Jul-03	3	48	3084	0.29	0.22	0.36
30	26-Jul-03	3	64	3740	0.21	0.15	0.27
31	02-Aug-03	3	76	4909	0.28	0.19	0.37
32	09-Aug-03	3	50	4152	0.25	0.16	0.34

[1] Breakup of fast ice in northern Foxe Basin occurred on July 13

[2] Number of dives determined from depth histogram data.

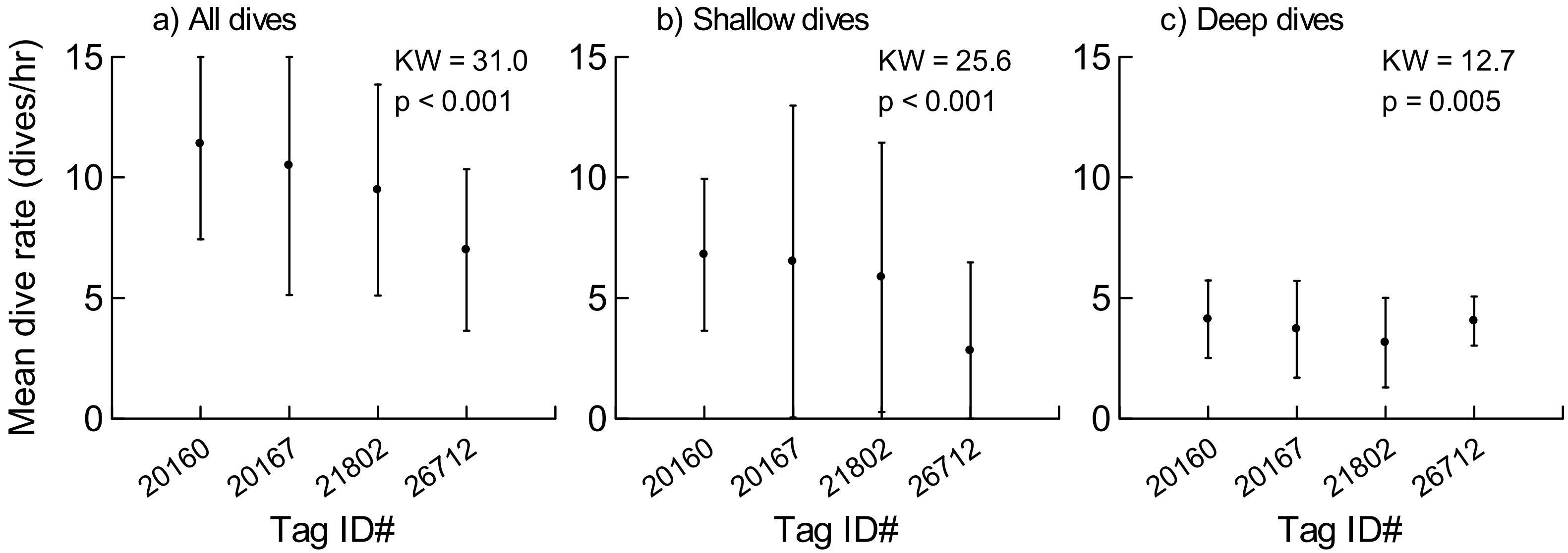

Figure 1. Plots of mean dive rate and SD for four bowhead whales for a) all dives, b) shallow dives (8-12 m), and c) deep dives (> 12 m)..

All dives

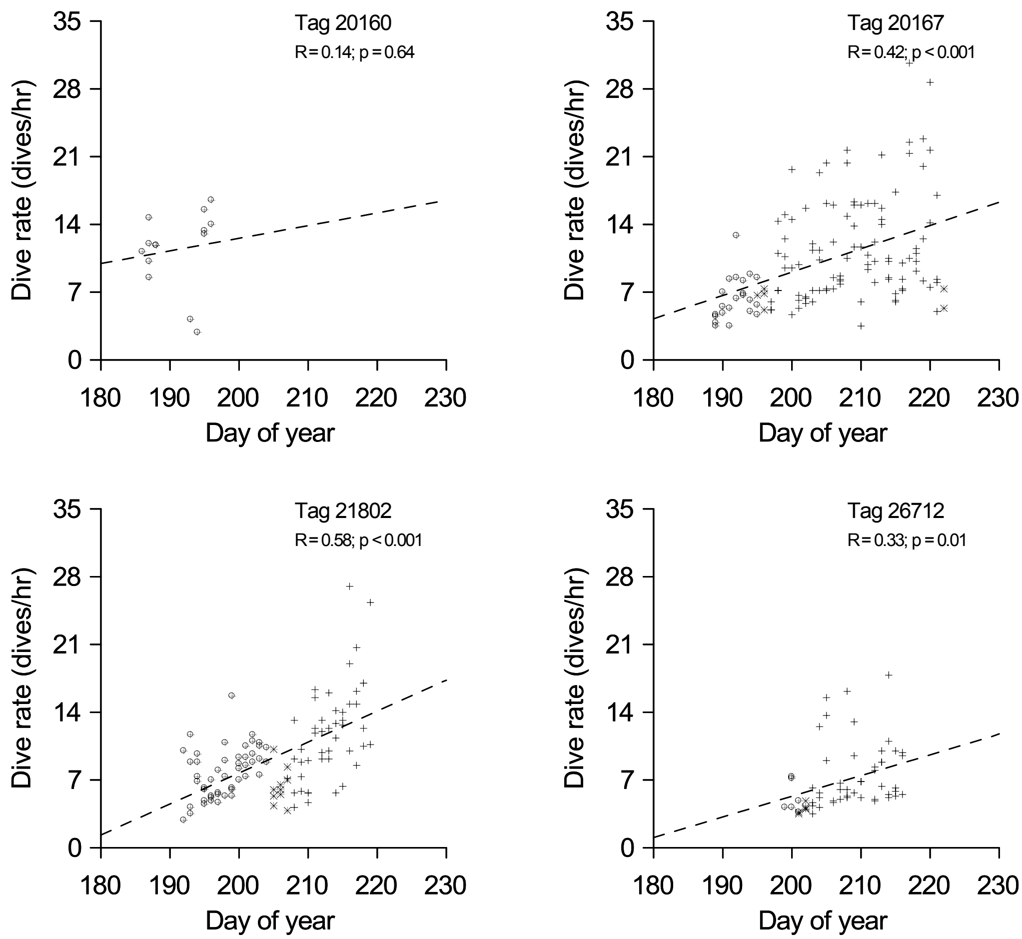

Figure 2a. Plots of dive rate for all dives as a function of day of year for four bowhead whales with satellite-linked dive-recording instruments in 2003. Symbols provide supplementary information on the geographic region that whales were located in: “o” = Foxe Basin, “x” = Gulf of Boothia and “+” = Prince Regent Inlet.

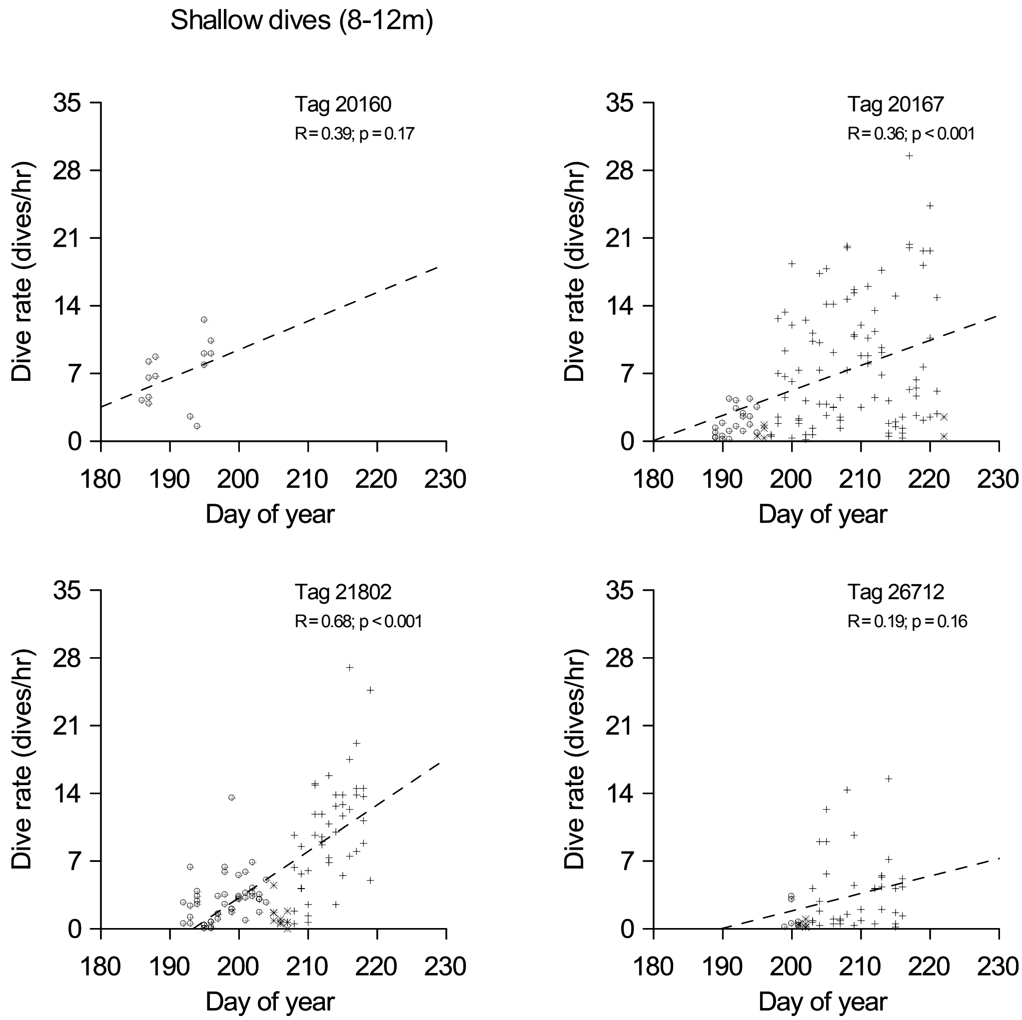

Figure 2b. Plots of dive rate for shallow dives (8 -12 m) as a function of day of year for four bowhead whales with satellite-linked dive-recording instruments in 2003. Symbols provide supplementary information on the geographic region that whales were located in: “o” = Foxe Basin, “x” = Gulf of Boothia and “+” = Prince Regent Inlet.

Deep dives (>12m)

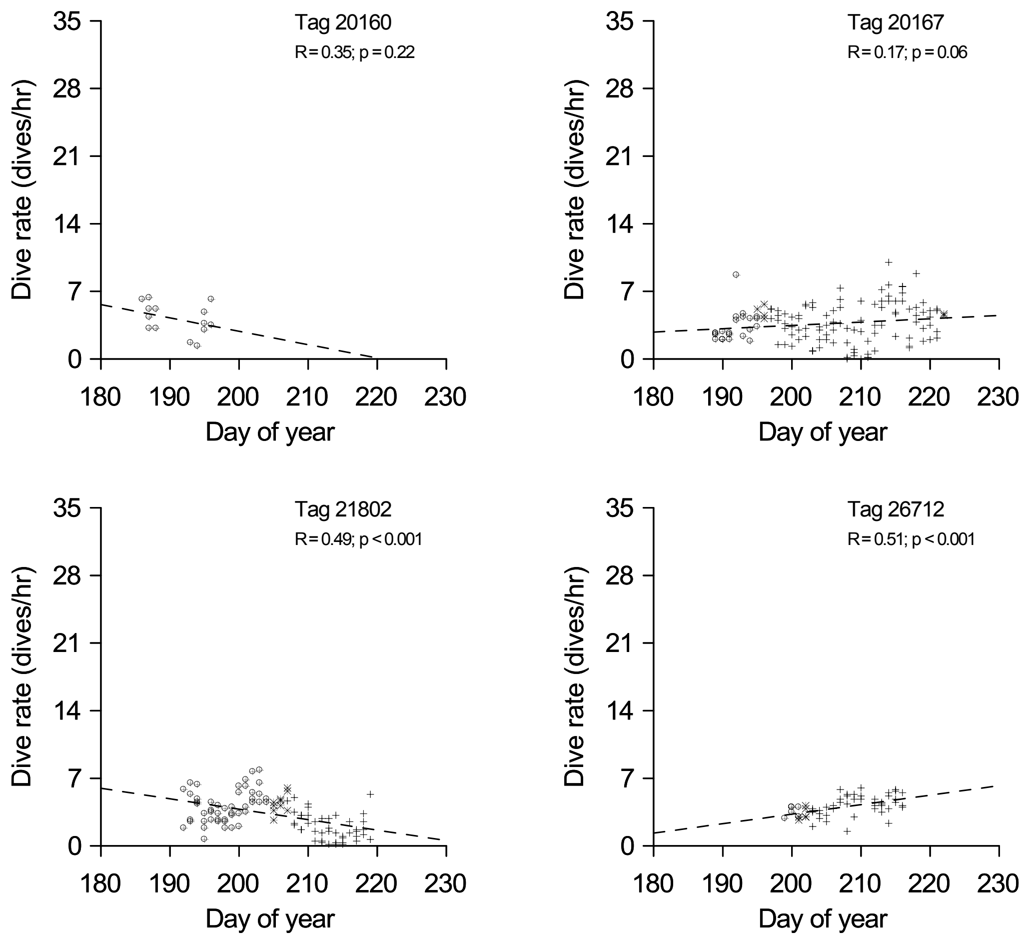

Figure 2c. Plots of dive rate for deep dives (> 12 m) as a function of day of year for four bowhead whales with satellite-linked dive-recording instruments in 2003. Symbols provide supplementary information on the geographic region that whales were located in: “o” = Foxe Basin, “x” = Gulf of Boothia and “+” = Prince Regent Inlet.

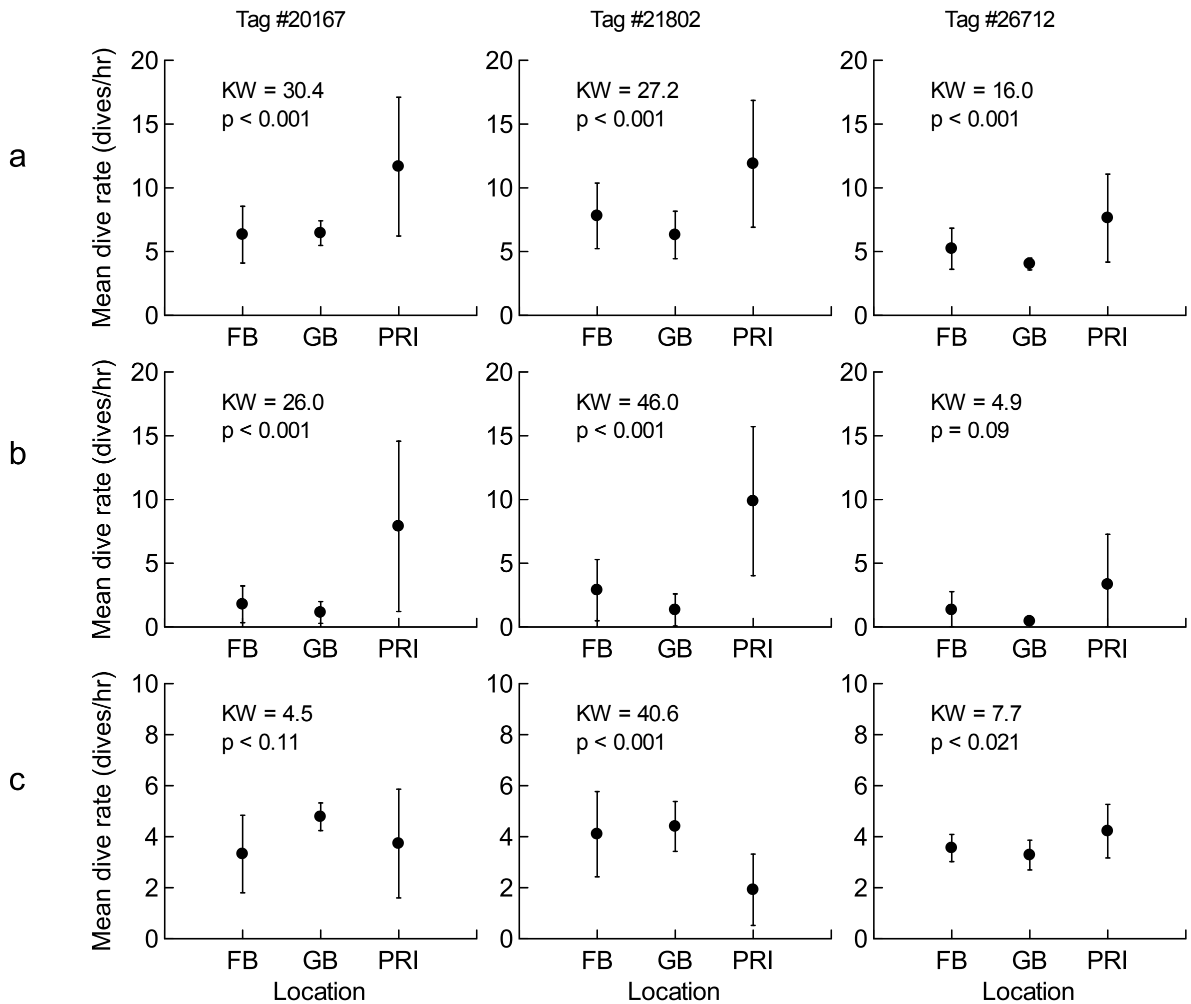

Figure 3. Plots of mean dive rate and SD for bowhead whales as a function of locality for a) all dives, b) shallow dives (8-12 m), and c) deep dives (> 12 m). Dive types arranged by row and whales arranged by column. Locations defined as FB = Foxe Basin, GB = Gulf of Boothia, and PRI = Prince Regent Inlet.

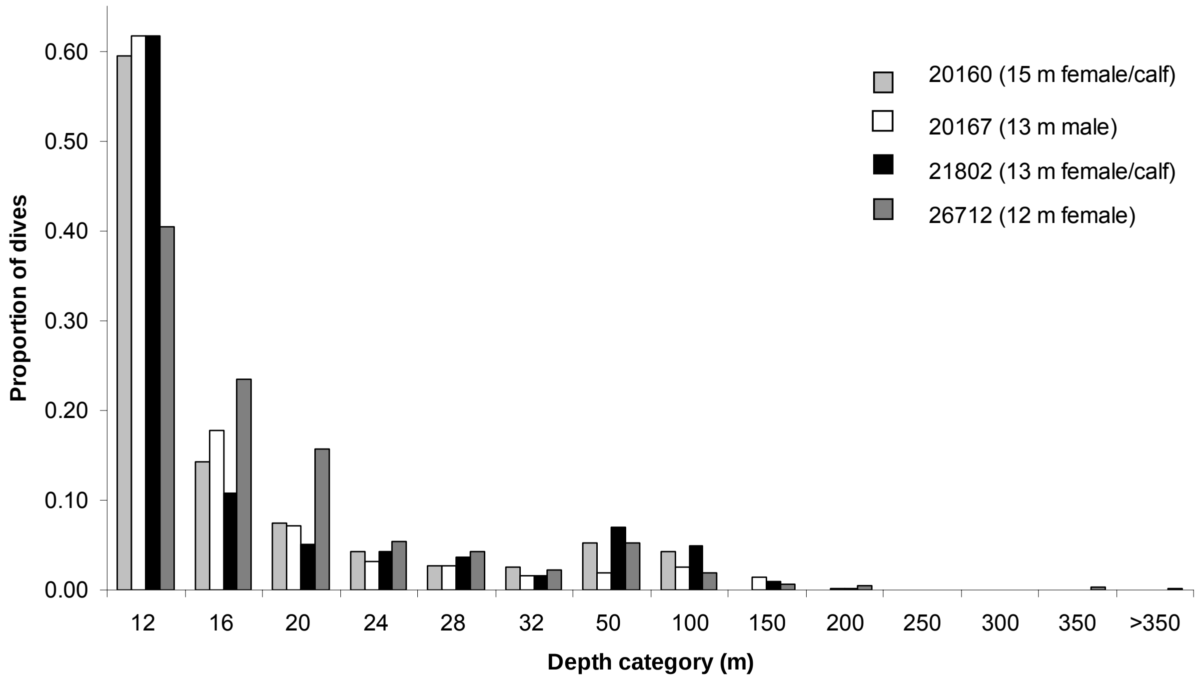

Figure 4. Plot of depth frequency histograms for four bowhead whales with satellite-linked dive-recording instruments in 2003, illustrating the frequency of dives as a function of depth class. Some occurrences of dives in depth classes of 200 m and above may be too rare (≤ 0.001) to be visible in the chart.

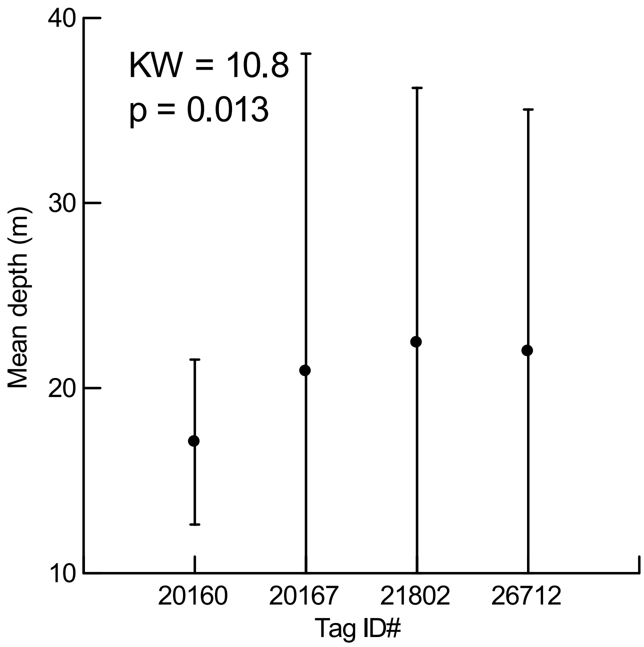

Figure 5. Plot depicting the mean dive depth and SD for four bowhead whales tagged with satellite-linked dive recording instruments in 2003.

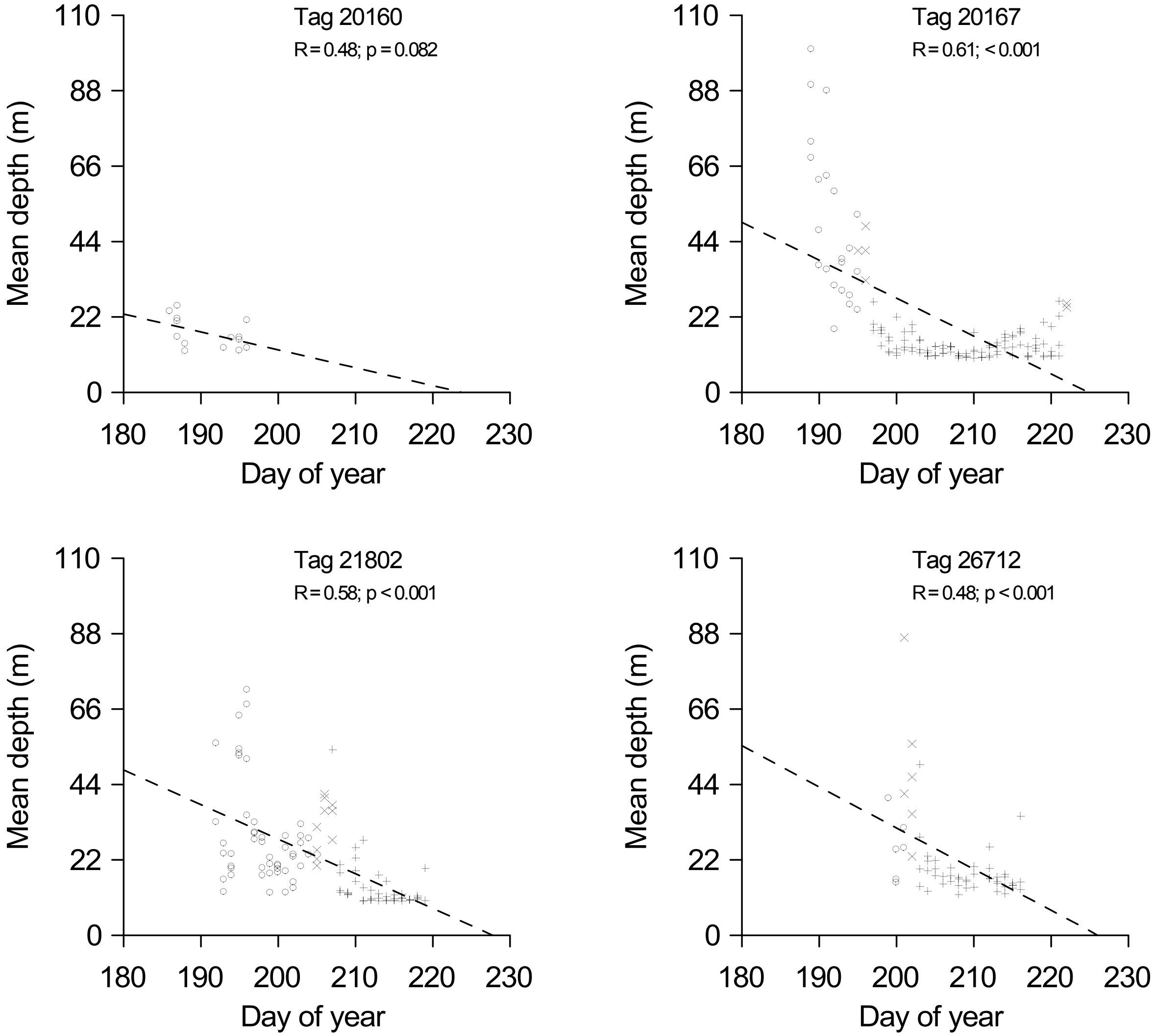

Figure 6. Plots of mean dive depth as a function of day of year for four bowhead whales tagged with satellite-linked dive-recording instruments in 2003. Symbols provide supplementary information on the geographic region that whales were located in: “o” = Foxe Basin, “x” = Gulf of Boothia and “+” = Prince Regent Inlet.

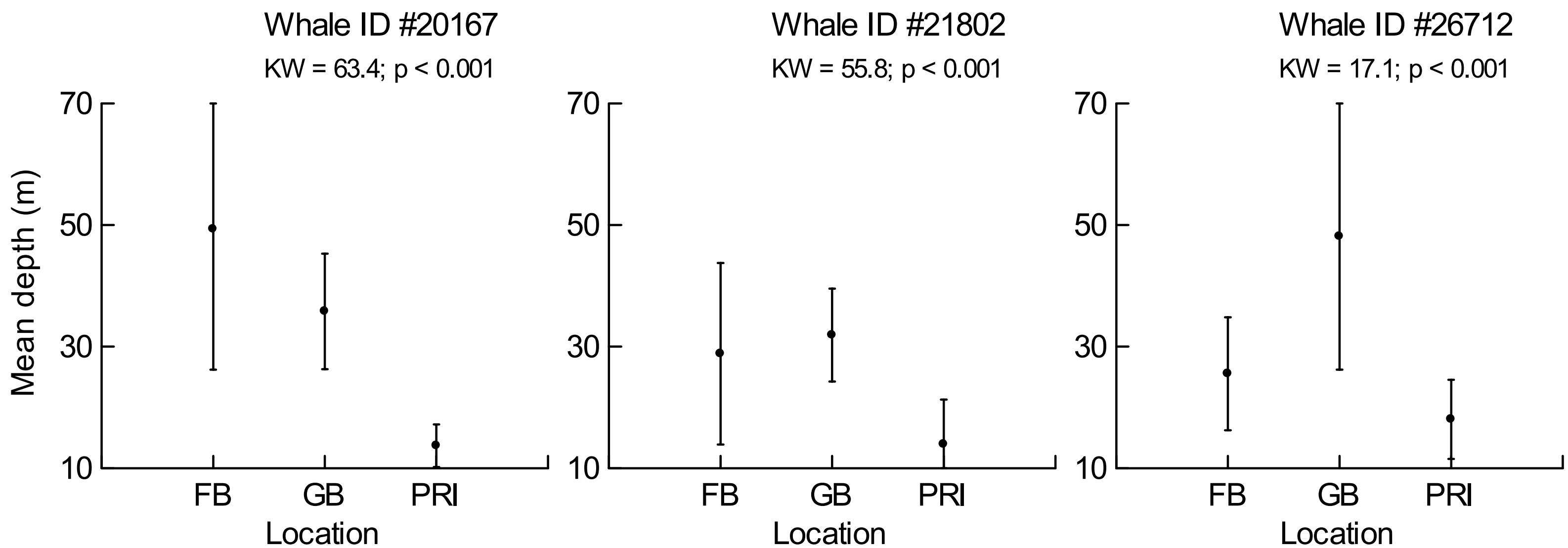

Figure 7. Plot of mean depth and SD as a function of location for four bowhead whales tagged with satellite-linked dive-recording instruments in 2003.

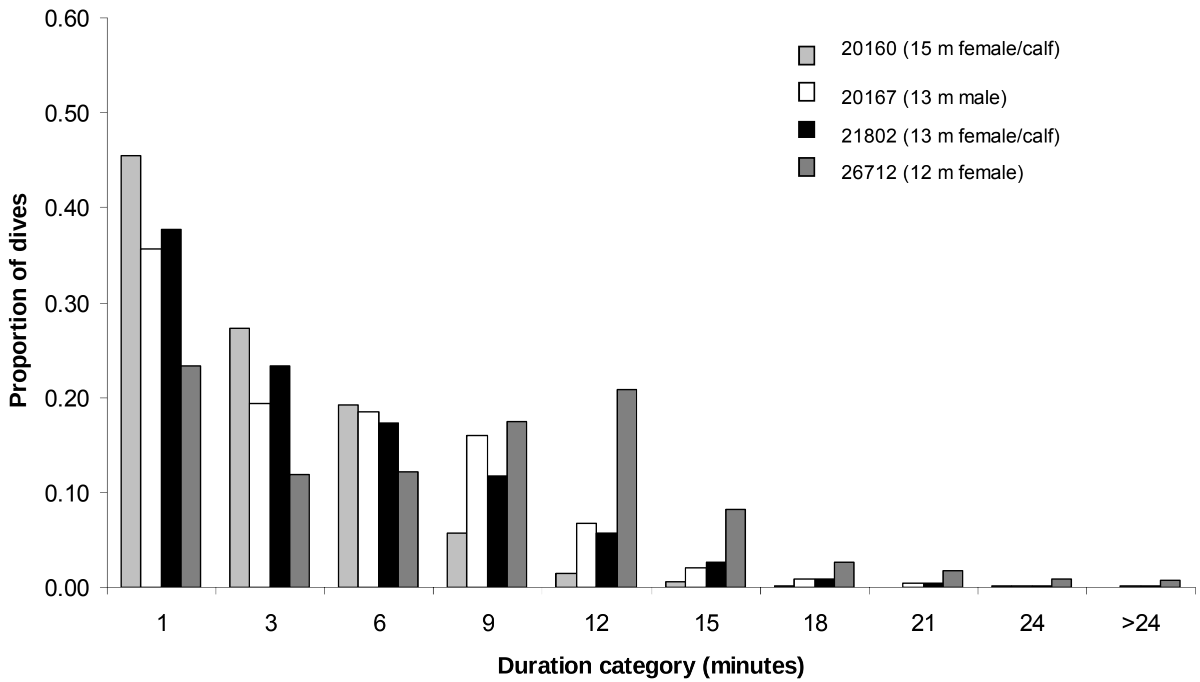

Figure 8. Plot depicting duration histograms for four bowhead whales tagged with satellite-linked dive-recording instruments in 2003, illustrating the frequency of dives as a function of dive duration class.

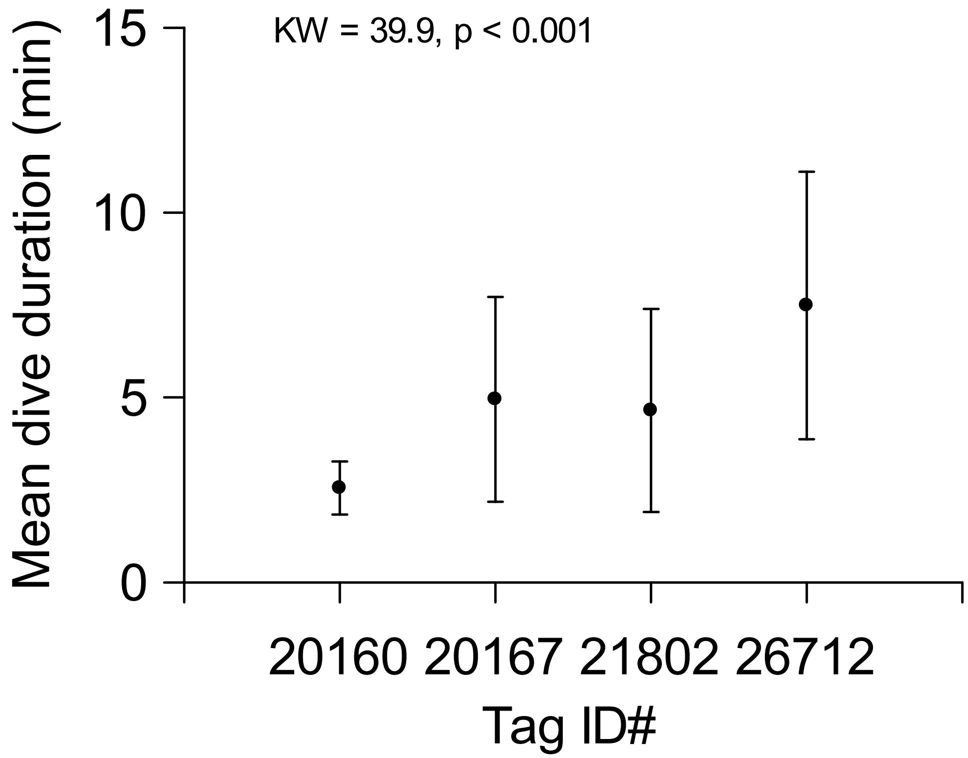

Figure 9. Plot of mean dive duration and SD for four bowhead whales tagged with satellite-linked dive-recording instruments in 2003.

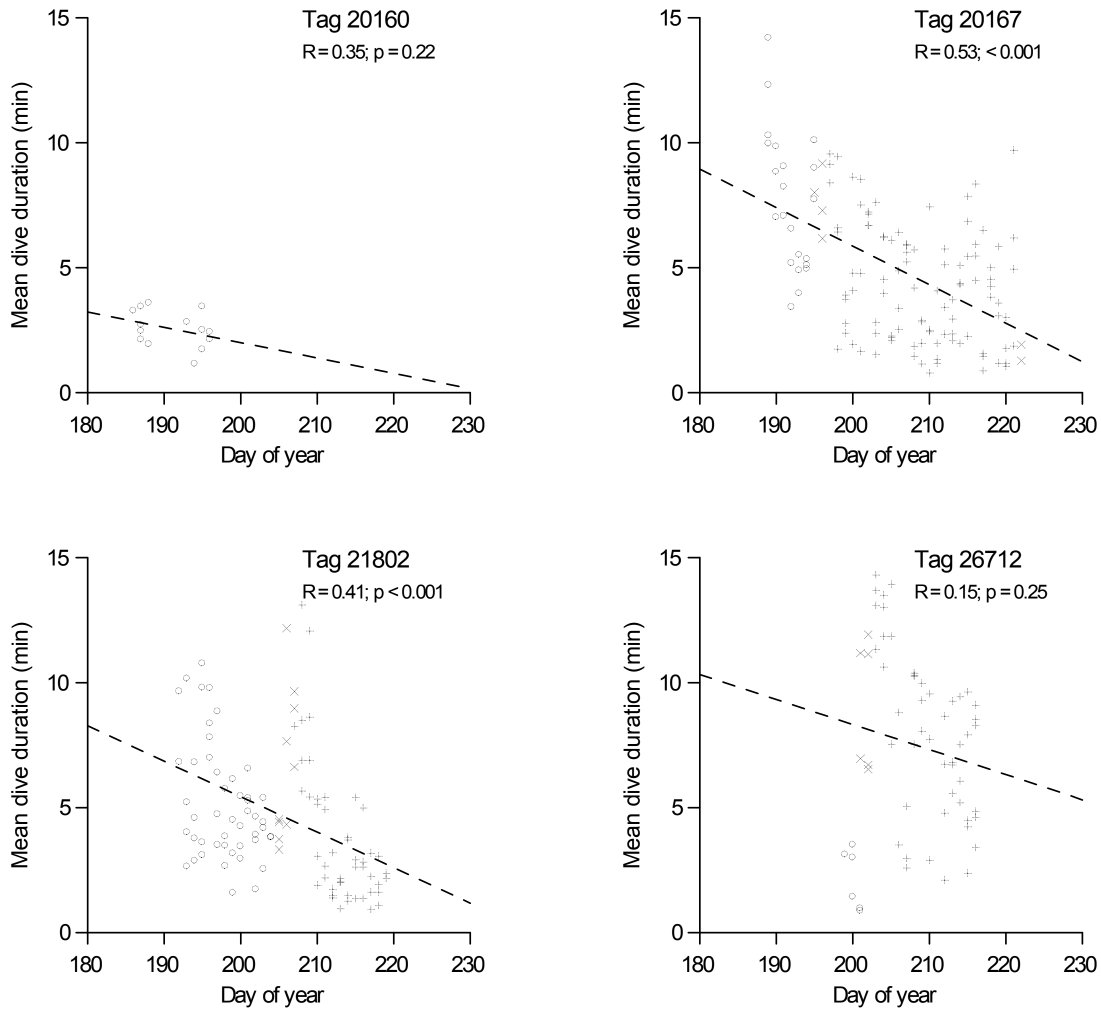

Figure 10. Plot of mean dive duration and 95% confidence intervals as a function of day of year for four bowhead whales tagged with satellite-linked dive-recording instruments in 2003. Symbols provide supplementary information on the geographic region that whales were located in: “o” = Foxe Basin, “x” = Gulf of Boothia and “+” = Prince Regent Inlet.

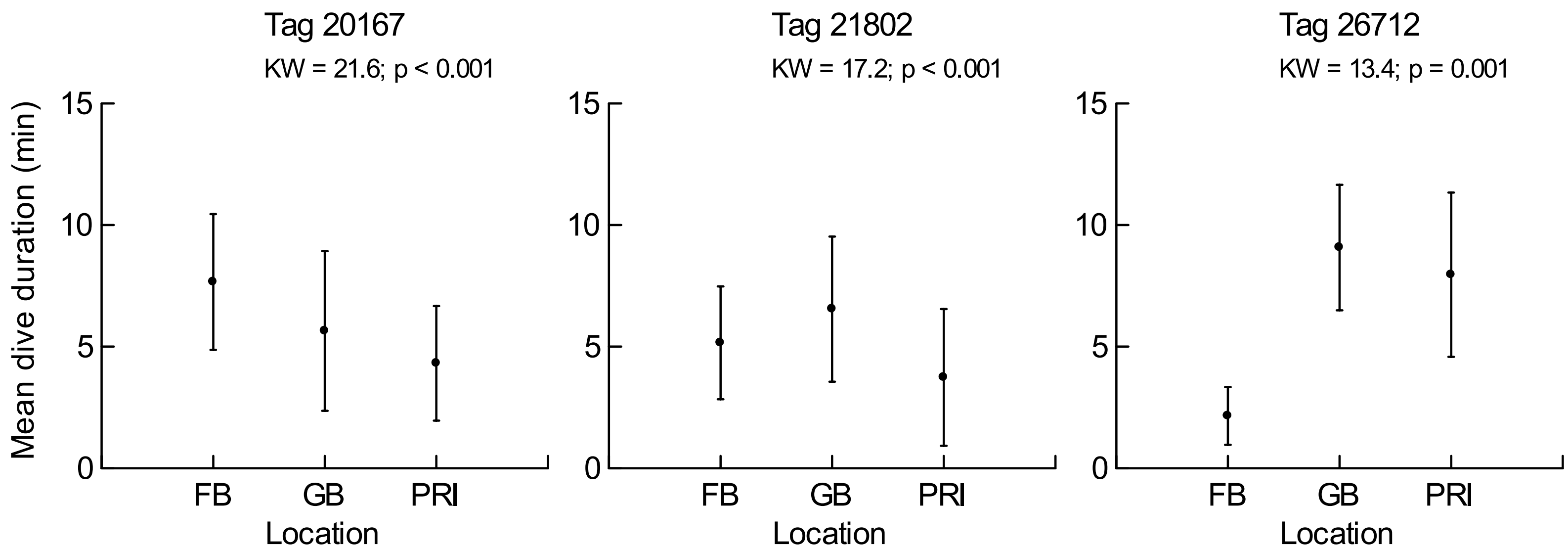

Figure 11. Plot of mean dive duration and SD as a function of location for four bowhead whales tagged with satellite-linked dive-recording instruments in 2003.

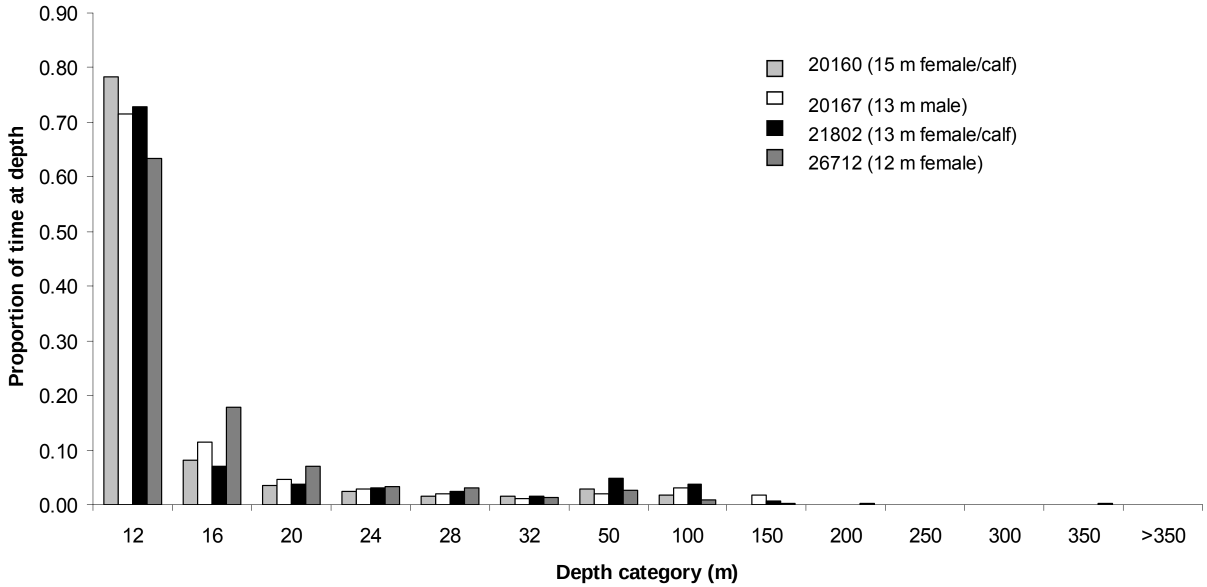

Figure 12. Plot of time-at-depth histograms for four bowhead whales tagged with satellite-linked dive-recording instruments in 2003, illustrating the proportion of time spent as a function of depth class.

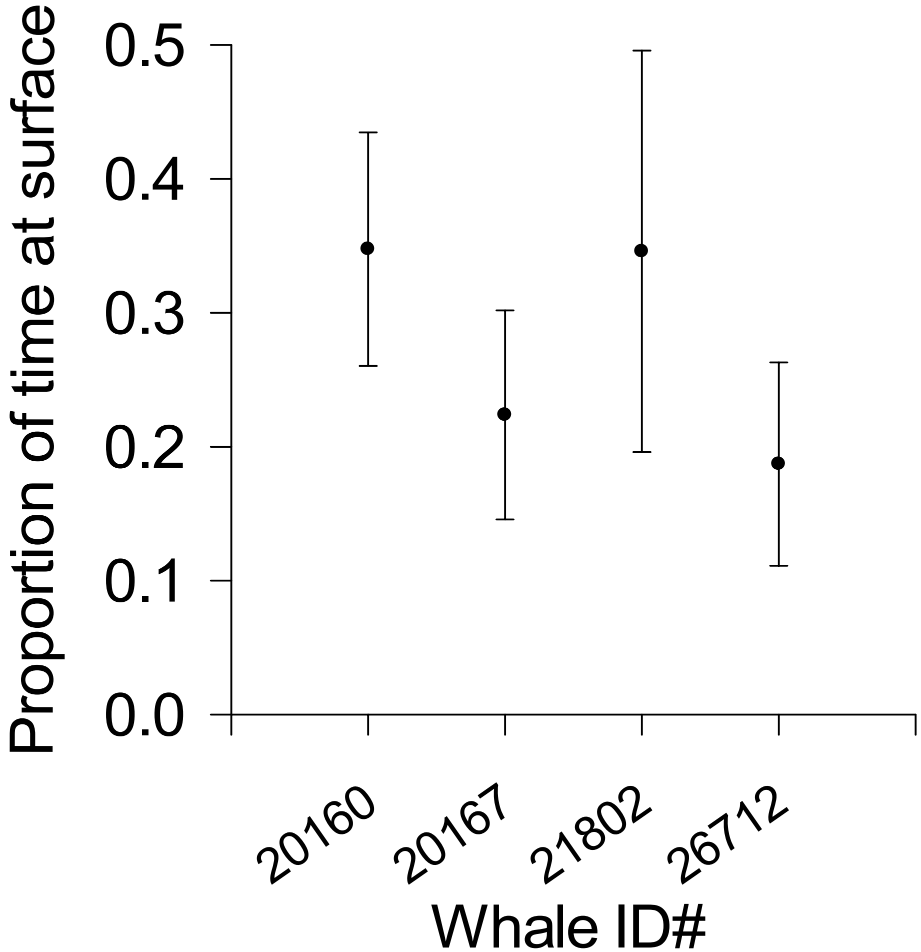

Figure 13. Plot of the mean proportion of time at surface and SD for four bowhead whales tagged with satellite-linked dive-recording instruments in 2003. KW = 93.0, p < 0.001

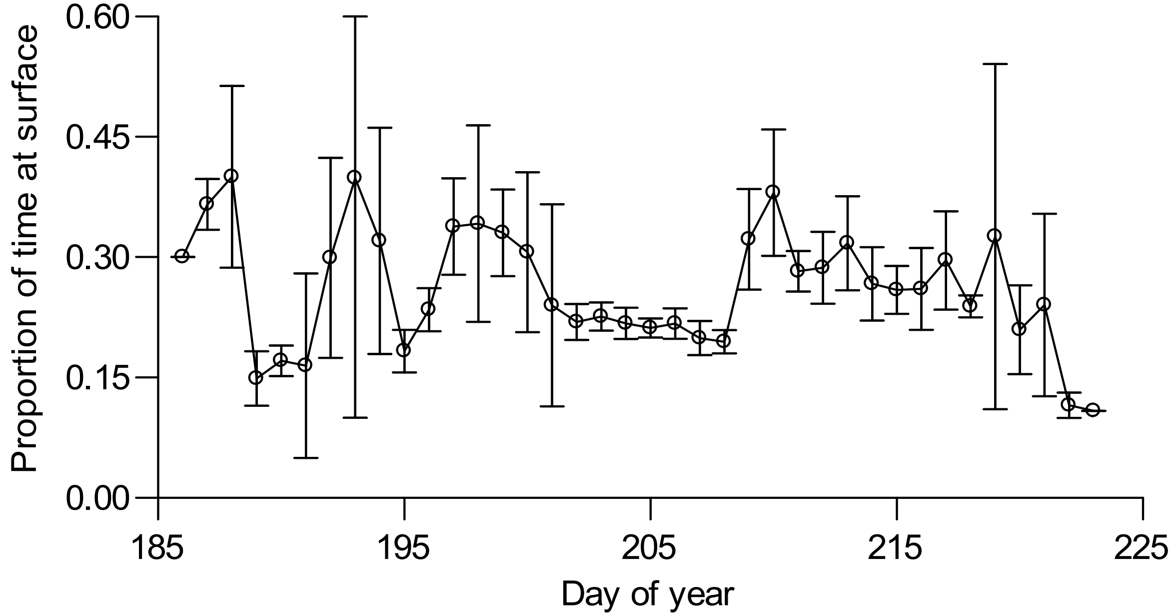

Figure 14. Plot of the mean proportion of time at surface and 95% confidence intervals for four bowhead whales tagged with satellite-linked dive-recording instruments in 2003. KW = 93.0, p < 0.001

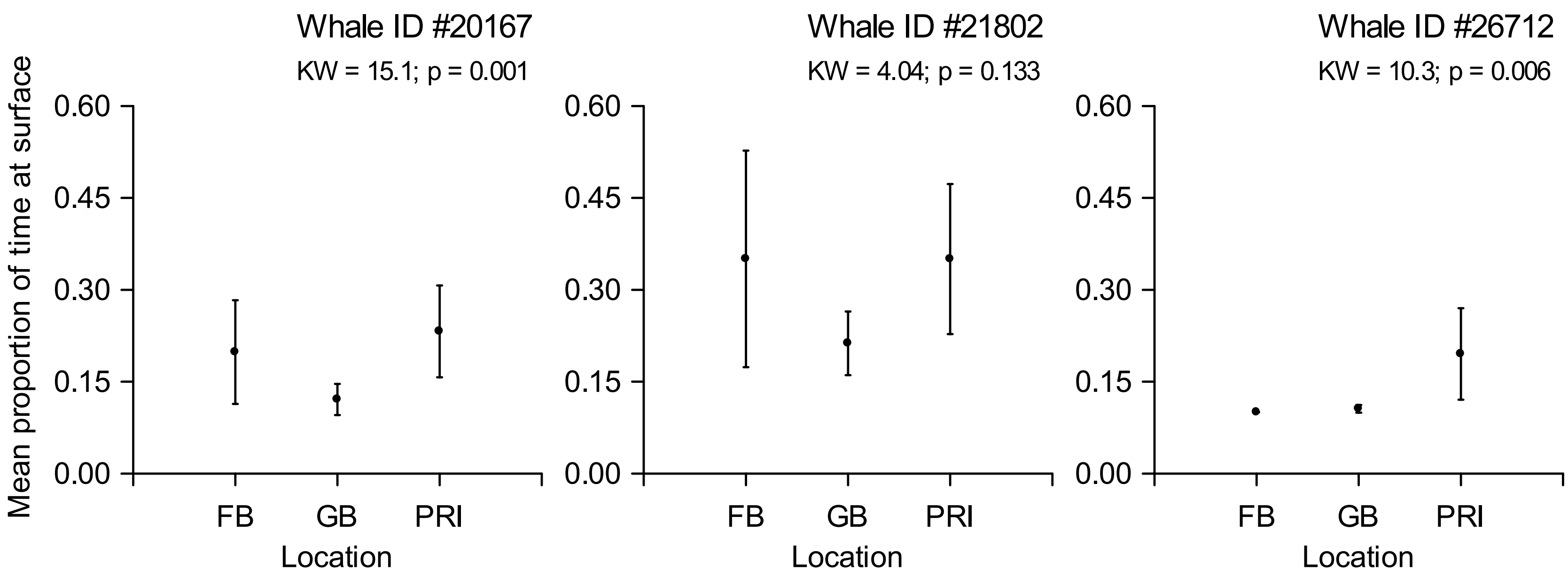

Figure 15. Plot of mean proportion of time at surface and SD as a function of location for four bowhead whales tagged with satellite-linked dive-recording instruments in 2003.

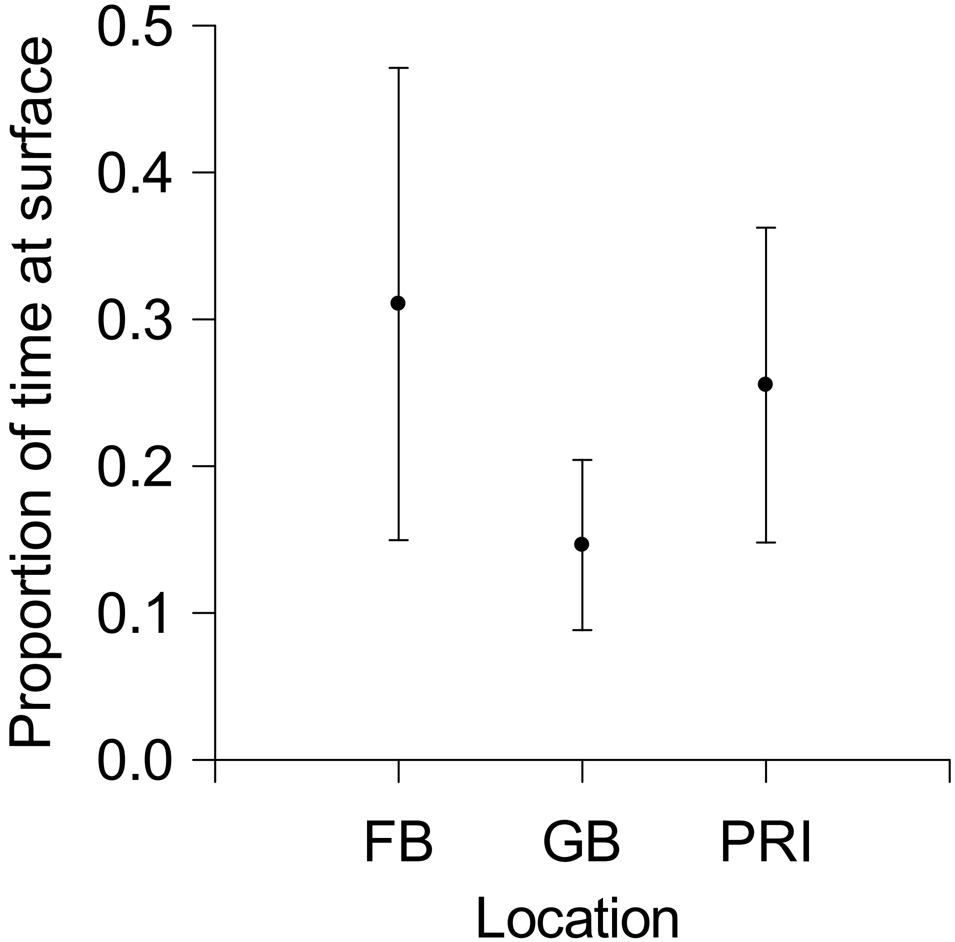

Figure 16. Plot of mean proportion of time at surface and SD as a function of location for data pooled for all four whales. Results of test for differences: for all three locations, KW = 18.6, $p < 0.001$; for FB vs PRI, MW = 8352, $p = 0.014$.

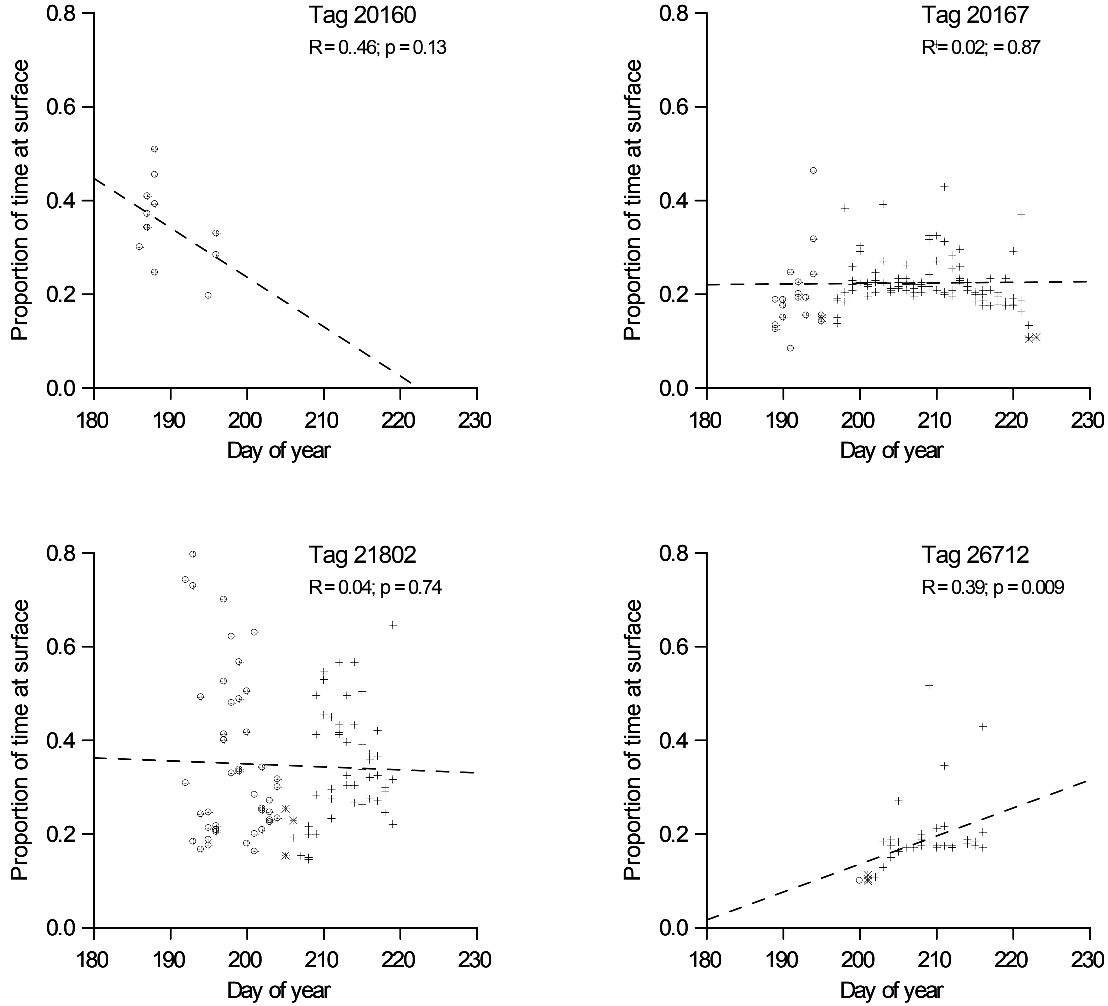

Figure 17. Plot of proportion-of-time at surface as a function of day of year for four bowhead whales tagged with satellite-linked dive-recording instruments in 2003. Symbols provide supplementary information on the geographic region that whales were located in: “o” = Foxe Basin, “x” = Gulf of Boothia and “+” = Prince Regent Inlet.