ARCTIC
VOL. 66, NO. 4 (DECEMBER 2013) P. 389–406

Dive Behavior of Eastern Chukchi Beluga Whales (*Delphinapterus leucas*), 1998–2008

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(*Received 2 January 2013; accepted in revised form 6 March 2013*)

ABSTRACT. We provide an exploratory description of the dive behavior of 23 beluga whales of the eastern Chukchi Sea stock, tagged with satellite-linked time and depth recorders at Point Lay, Alaska, between 1998 and 2007. Because of differences in how transmitters were parameterized, we analyzed data from tags deployed from 1998 to 2002 (*n* = 20 tags) and data from tags deployed in 2007 (*n* = 3 tags) separately. Using cluster analysis, we found three basic dive types in the 1998–2002 dataset. "Shallow" diving behavior was characterized by dives mostly 50 m in depth. "Intermediate" diving behavior was characterized by having one mode near the surface and a second mode near 250 m. "Deep" diving behavior was characterized by having one mode near the surface and a second mode more than 400 m from the surface. The average number of dives per hour ranged from 5.1 (SD = 2.1) to 9.8 (SD = 2.9) across dive types, with the fewest dives per hour in the deep diving category. In general, duration of dives ranged from 1 to 18 minutes; however, dives up to 21 minutes occurred in the deepest diving category. We found little evidence that dive behavior of the belugas in our sample varied by sex or age. In general, belugas dove more deeply in the eastern Beaufort Sea than in the western Beaufort or Chukchi Seas. The depths to which belugas most commonly dive in Barrow Canyon and along the Beaufort shelf break (200–300 m) correspond to the boundary where colder Pacific water overlies warmer Atlantic water, which is probably where Arctic cod (*Boreogadus saida*) are most dense. Diving depths within the Arctic Basin suggest that belugas are foraging mostly within the warm layer of Atlantic Water (~200–1000 m).

Key words: beluga whale, *Delphinapterus leucas*, Chukchi Sea, Beaufort Sea, dive behavior, Barrow Canyon

RÉSUMÉ. Nous dressons une description exploratoire du comportement de plongée de 23 bélugas du cheptel de l'est de la mer des Tchouktches dotés de marqueurs d'enregistreurs satellitaires de profondeur temporelle à Point Lay, en Alaska, entre 1998 et 2007. En raison des différences de paramétrage des transmetteurs, nous avons analysé séparément les données de marqueurs déployés de 1998 à 2002 (*n* = 20 marqueurs) et les données de marqueurs déployés en 2007 (*n* = 3 marqueurs). Grâce à une analyse par grappes, nous avons trouvé trois types de plongée fondamentaux dans l'ensemble des données de 1998 à 2002. Le comportement de plongée « en eau peu profonde » était principalement caractérisé par des plongées de 50 m de profondeur. Le comportement de plongée « intermédiaire » était caractérisé par un mode de plongée près de la surface et un autre mode à près de 250 m. Le comportement de plongée « en profondeur » était caractérisé par un mode de plongée près de la surface et un deuxième mode à plus de 400 m de la surface. Le nombre moyen de plongées à l'heure variait de 5,1 (écart-type = 2,1) à 9,8 (écart-type = 2,9) pour ce qui est de tous les types de plongée, la catégorie des plongées en profondeur ayant enregistré le moins grand nombre de plongées. En général, la durée des plongées durait de 1 à 18 minutes, mais cela dit, certaines des plongées en profondeur ont duré jusqu'à 21 minutes. Nous avons trouvé peu d'indices portant à croire que le comportement de plongée des bélugas de notre échantillon variait en fonction du sexe ou de l'âge. De manière générale, les bélugas plongeaient plus en profondeur dans l'est de la mer de Beaufort que dans l'ouest de la mer de Beaufort ou dans la mer des Tchouktches. Les profondeurs auxquelles les bélugas plongent le plus souvent dans le canyon Barrow et le long du rebord continental de Beaufort (de 200 à 300 m) correspondent à la limite où l'eau plus froide du Pacifique se superpose à l'eau plus chaude de l'Atlantique, là où la morue polaire (*Boreogadus saida*) est plus dense. Dans le bassin arctique, la profondeur des plongées suggère que les bélugas s'alimentent surtout dans la couche tempérée d'eau de l'Atlantique (~200 à 1 000 m).

Mots clés : béluga, *Delphinapterus leucas*, mer des Tchouktches, mer de Beaufort, comportement de plongée, canyon Barrow

Traduit pour la revue *Arctic* par Nicole Giguère.

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INTRODUCTION

Beluga whales (*Delphinapterus leucas*) are small cetaceans that live in seasonally ice-covered waters in the Arctic and subarctic regions of Alaska, Canada, and Russia; along the western coast of Greenland and the northern coast of Norway; and in the Svalbard archipelago. In Alaska, five stocks are commonly recognized: the Cook Inlet, Bristol Bay, eastern Bering Sea, eastern Chukchi Sea, and Beaufort Sea stocks (Frost and Lowry, 1990; O'Corry-Crowe et al., 1997, 2002).

The eastern Chukchi Sea stock is the focus of this report. Knowledge of this stock is based on data from aerial surveys conducted in the Chukchi Sea (e.g., DeMaster et al., 1998; Lowry and Frost, 2003) and tagging and harvest-related studies conducted at Point Lay, Alaska, where a subsistence harvest occurs each summer (Suydam et al., 2001). Satellite tagging studies conducted from 1998 to 2007 revealed that this stock winters in the Bering Sea and migrates into the Chukchi and Beaufort Seas each spring. After capture in June and July, tagged belugas migrated north and east through the northern Chukchi Sea and into the western Beaufort Sea (Suydam et al., 2001; Suydam, 2009). From mid-July to September, they rarely occurred in continental shelf waters (depth < 200 m) of the Chukchi Sea and ranged primarily along the shelf break (~200 m) and across deep waters (200–4000 m) of the central and eastern Beaufort Sea and the Arctic Ocean. All belugas that moved north of 75˚ N were large males, suggesting that adult males may use deeper water than adult females and immature animals (Suydam, 2009).

Most of the whales analyzed by Suydam (2009) were tagged with satellite-linked time and depth recorders (SLTDRs). Although the movements of these whales have been examined by Suydam et al. (2001) and Suydam (2009), their diving behavior has not. Here we provide an exploratory description of the dive behavior of 23 beluga whales tagged between 1998 and 2007 at Point Lay, Alaska.

METHODS

Capturing and Tagging Whales

We captured and tagged beluga whales in 1998, 1999, 2001, 2002, and 2007 after the annual community hunt in Kasegaluk Lagoon, near Point Lay. Native subsistence hunters use boats to direct belugas from the Chukchi Sea through a pass between barrier islands and into the shallow water of Kasegaluk Lagoon, where they are harvested (Neakok et al., 1985; Suydam, 2009). Belugas that enter the lagoon but escape the hunt are available for capture; however, ice conditions, weather, or limited availability of belugas prevented tagging in some years. Belugas were captured using hoop nets, stationary nets, or seine nets (Orr et al., 1998; Suydam et al., 2001; Suydam, 2009). In 1999, we tagged and then freed four whales that had become stranded during the drive hunt, but which were not harvested. Captured belugas were handled as described by Orr et al. (1998) and Suydam et al. (2001). We secured whales with a hoop net over their head and flippers and a padded rope placed around the caudal peduncle. The animals were held in water shallow enough that their dorsum was exposed. Whales were released within 20 to 60 minutes after capture. Most tagged belugas remained in Kasegaluk Lagoon for two to five days, although four whales (one in 1998 and the three in 2007) left the lagoon shortly after tagging.

Dive data from 23 of the 26 belugas that were tagged are analyzed here. Of the three tags not considered, one collected only location data and two transmitted for only five days each. The other tags were SLTDRs manufactured by Wildlife Computers (Redmond, WA, USA). Tags deployed in 1998 and 1999 (and one in 2001) used ST-10 transmitters, while most of those deployed in 2001 and 2002 used ST-16 transmitters. In 2007, we deployed newer SPLASH tags. Fourteen of the tags were glued to nylon belting in one of two configurations, saddle mount ($n = 7$) or side mount ($n = 7$). We also deployed nine tags with spider mount configurations (Table 1). Transmitters were attached with nylon or dacron pins approximately 0.33 m long (three pins for spider mounts or four for saddle and side mounts). The pins were inserted through the skin and blubber of the dorsal ridge or just anterior to the ridge (through holes made with a trocar) and fit through pre-cut holes in the belting attached to each transmitter or through adjustable loops of the spider mounts. Nylon or dacron washers and nuts screwed onto the pins held the transmitter to the back of each animal. More details on capture and tagging methods are provided in Suydam et al. (2001) and Suydam (2009).

Data Acquisition

Satellite locations were collected via the Argos data collection and location system (Fancy et al., 1988; Rodgers, 2001). Tag transmissions were collected by receivers onboard NOAA weather satellites and Doppler shift between transmissions was used to estimate tag locations. Location error was estimated by the Argos system and characterized by "location classes" (Argos, 2013). Location classes are only an approximate representation of location accuracy (e.g., Vincent et al., 2002). Instead of using only the locations representing the highest accuracy (2 or 3), we chose to use all available location classes (B, A, 0, 1, 2, 3) and a filter that removed velocities greater than a fixed threshold (McConnell et al., 1992). A threshold of 1.78 m/s was chosen after considering a variety of sources. Smith and Martin (1994) found belugas traveling at 1.4 m/s, Lydersen et al. (2001) documented 6 km/h (1.67 m/s) as a maximum sustained velocity, and Richard et al. (2001) documented velocities of 4.2 to 6.4 km/h (1.17 to 1.78 m/s), which included the fastest velocity observed in any of the studies.

Tags sampled pressure (i.e., depth) every 10 s, but because that sampling produced too much data to transmit,

TABLE 1. Beluga whales with satellite-linked time and depth recorders that are used in this analysis. All were captured at Point Lay, Alaska.

Year	ID #	Capture date	Sex	Age class	Color	Length (cm)	PTT[1]	Attachment type	Date of last transmission	Tag duration (days)[2]
1998	98-1	26 June	Male	Adult	White	440	11035	Saddle	8 July	13
	98-2	28 June	Male	Adult	White	432	2284	Saddle	12 July	15
	98-3	29 June	Male	Adult	White	398	11036	Saddle	10 October	104
	98-4	29 June	Male	Adult	White	415	2285	Saddle	28 September	92
	98-5	1 July	Male	Adult	White	414	2282	Saddle	29 August	60
1999	99-1	30 June	Male	Adult	White	418	11035	Side mount	24 September	87
	99-2	30 June	Female	Immature[3]	Gray	266	11036	Side mount	18 September	81
	99-3	30 June	Male	Adult	White	424	11037	Saddle	25 August	57
	99-4	30 June	Male	Adult	White	424	11041	Saddle	22 September	85
2001	01-1	3 July	Male	Adult	White	381	2093	Spider	9 August	38
	01-2	3 July	Female	Adult	White	359	2094	Spider	21 July	19
	01-3	5 July	Female	Immature	Gray	316	11038	Side mount	28 November	147
	01-4	5 July	Male	Immature	Gray	324	11041	Side mount	5 December	154
	01-5	5 July	Female	Immature	Gray	335	2280	Side mount	22 October	110
	01-6	7 July	Male	Adult	White	340	11037	Spider	16 November	133
	01-7	7 July	Male	Imm.	Lt. Gray	320	2281	Side mount	23 July	17
	01-8	7 July	Male	Adult	White	373	2282	Saddle	12 August	37
2002	02-1	7 July	Female	Immature	Gray	320	11036	Spider	13 September	69
	02-2	7 July	Male	Immature	Gray	276	11044	Spider	29 September	85
	02-4	8 July	Male	Immature	Gray	267	2088	Side mount	12 September	67
2007	07-1	1 July	Male	Adult	White	430	22149	Spider	3 December 2008	520
	07-2	1 July	Female	Adult	White	386	77015	Spider	12 November	135
	07-3	1 July	Female	Adult	White	398	36516	Spider	4 November	127

[1] Platform Transmitting Terminal number used for tag identification.
[2] Tag duration is the number of days from tag attachment to the last reception of a location that passed data screening.
[3] Age class is defined on the basis of color and length; immature whales are gray and generally under 350 cm.

tags had software onboard that summarized the information into histograms. Histograms covered 6 h intervals (bins) and were stored onboard the tag until they could be transmitted to a satellite. There were three histogram types: 1) dive depth histograms, which are a count of dives falling into each depth bin; 2) dive duration histograms, which are a count of dives falling into each time bin; and 3) time-at-depth histograms, which are presented as a proportion of the 6 h period spent in each depth bin. Threshold values for histogram bins are user defined and sometimes changed by year of deployment (Table 2). Bins accumulated data for four 6 h periods: dawn (0300 to 0900), day (0900 to 1500), dusk (1500 to 2100), and night (2100 to 0300). Hours are local time at Point Lay (GMT-10 h).

TABLE 2. Upper threshold limits (m) for depth and time at depth (TAD) and duration histogram bins for satellite tags deployed at Point Lay, Alaska, by year of deployment. The user defines a total of 14 histogram bins before the satellite-linked time and depth recorder is deployed; the last bin includes all data deeper than the deepest defined threshold.

	Depth and TAD (m)			Duration (min)		
Bin	1998	1999–2002	2007	1998–99	2002	2007
1	2[1]	4[2]	0[1]	1	1	0.5
2	4	8	10	3	2	1
3	6	12	50	6	3	1.5
4	10	28	100	9	4	2
5	26	52	200	12	5	3
6	50	100	300	15	6	4
7	100	152	400	18	8	5
8	150	200	500	21	10	6
9	200	252	600	24	12	7
10	250	300	700	24+	15	8
11	300	352	800		18	9
12	350	400	900		21	10
13	400	452	1000		25	20
14	400+	452+	1000+		25+	20+

[1] The minimum depth at which tag recorded dive data was 2 m.
[2] The minimum depth at which tag recorded dive data was 4 m.

Locating Dives

To relate dive behavior to bathymetry, we need to know where dives occurred. Locations were calculated whenever satellites received a tag transmission. However, dive data were collected within fixed 6 h intervals, with a time stamp denoting the starting hour and day of the interval. To assign a latitude and longitude to a particular dive bin, we used a correlated random walk model to estimate beluga location at the beginning of each 6 h period. The model was implemented using the software package "crawl" (Johnson et al., 2008) in R version 2.11.1 (R Development Core Team, 2007). The formulation was originally written for seals and included a stopping model that allows animals to haul out and stop moving. Because stopping was not identified in the

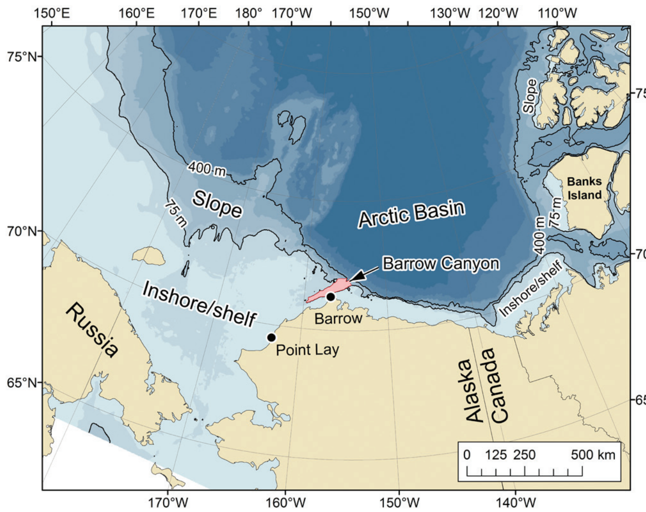

FIG. 1. Map of the study area and bathymetric regions used for analyses. Barrow Canyon (pink shading) is defined as the area between the bathymetric contours of 75 and 400 m, the deepest depth where we can know whether belugas reached the bottom (Table 4). We define areas with depths of less than 75 m as "Inshore/shelf," areas outside Barrow Canyon with depths of 75–400 m as "Slope," and areas with depths greater than 400 m as "Arctic Basin."

TABLE 3. Original and combined upper threshold limits (m) of depth and time-at-depth histogram bins for the combined 1998–2002 data set from belugas satellite-tagged at Point Lay, Alaska. The combined thresholds were used in the analyses.

Original thresholds (m)		
1998	1999–2002	Combined thresholds (m)
2		
4	4	
6	8	
10	12	10[1]
26	28	28
50	52	50
100	100	100
150	152	150
200	200	200
250	252	250
300	300	300
350	352	350
400	400	400
400+	452	400+
	452+	

[1] The minimum depth for dives to be considered was 4 m; hence, the first histogram bin spans from 4 to 10 m.

location data, and because we did not expect belugas to stop moving, this attribute of the model was disabled. The state-space formulation required prior knowledge of Argos error distributions for each location class. We parameterized this model with the same error distributions used by Johnson et al. (2008:1211), which are based upon the observations of Vincent et al. (2002).

Bathymetry

We assigned ocean depth to beluga locations by spatially joining locations to bathymetry data. Primarily we used the International Bathymetric Chart for the Arctic Ocean (IBCAO; Jakobsson et al., 2008), which covers latitudes north of St. Lawrence Island and was developed using multiple depth-sounding data sets. The IBCAO has a resolution of 2 km and was the only chart that covered all satellite locations in the Beaufort Sea. A few beluga locations ($n = 8$) fell south of the IBCAO grid in the Bering Sea, so we used the Alaska Ocean Observing System (AOOS) bathymetric grid for that region (Danielson et al., 2008). The AOOS bathymetry grid has a resolution of 1 km and was also developed using multiple depth-sounding data sets.

Partitioning the Study Area

We split the study area into four regions (Inshore/shelf, Barrow Canyon, Slope, and Arctic Basin; Fig. 1) on the basis of our knowledge of physical oceanography, the distribution of beluga whales, and how the satellite tags used in this study were programmed. In summer and early fall, the Alaska Coastal Current (ACC; Paquette and Bourke, 1974) carries relatively warm, fresh Alaska Coastal Water from the Bering Sea through Barrow Canyon into the Arctic Ocean (Pickart, 2004). The ACC extends eastward along the Beaufort slope and joins the Western Arctic Shelf Break Current (also known as the Western Arctic Boundary Current or the "Beaufort jet"; Pickart, 2004; Nikolopoulos et al., 2009). Under some conditions, the Beaufort jet may extend as far east as the Canadian Arctic Archipelago (von Appen and Pickart, 2012). Belugas are known to concentrate within Barrow Canyon and along the Beaufort Sea slope (Moore et al., 2000; Suydam et al., 2001; Suydam, 2009). While belugas also range offshore, over the Arctic Basin, satellite telemetry indicates higher use of the Beaufort slope and Barrow Canyon (Suydam et al., 2001; Suydam, 2009). The four study regions were therefore defined as follows: 1) Inshore/shelf regions were those less than 75 m deep. 2) Barrow Canyon: This bathymetric feature runs northeast-southwest offshore of Point Barrow. For our analyses, we considered only areas of the canyon between 75 and 400 m deep, since tags deployed before 2007 were set so that 400 m was the deepest depth where we knew that most belugas reached the bottom (Table 3). 3) Slope regions were those 75 to 400 m deep and outside of Barrow Canyon, and 4) Arctic Basin regions were those with depths greater than 400 m, the limit for most tags (Fig. 1).

Analyses for 1998–2002 Data

The tags deployed between 1998 and 2002 ($n = 20$) had similar settings and were combined for analysis. The bin definitions for depth and time-at-depth differed between 1998 and 1999–2002 (Table 2); for analysis, we combined these into a single definition (Table 3). Tags deployed between 1999 and 2002 required a beluga to dive at least 4 m for a dive to register; to make data comparable, all dives under 4 m were truncated from data collected in 1998. Bins with upper thresholds of 6 and 10 m from 1998 were combined into a single bin that spanned from 4 to 10 m. For 1999–2002, bins with thresholds of 8 and 12 m were combined into a single bin that spanned from 4 to 12 m, but for purposes of our analyses they were assumed to have an upper threshold of 10 m. For 1999–2002 data, dives deeper than 400 m were summed. The final definition had 11 bins (Table 3).

Cluster Analysis

We first used a k-means algorithm (Hartigan and Wong, 1979) within R to cluster depth histograms into similar groupings. This clustering approach minimizes the sum of squared errors (SSE) for a given number of centroids (i.e., groupings). In practice, as more centroids are fit to the data, total SSE declines until adding extra centroids has little to no effect. We sequentially fit 2 to 30 centroids to the data, one at a time, and calculated the drop in SSE as compared to SSE for 30 centroids. When adding a centroid resulted in less than a 1% drop in total SSE as compared to the total SSE for 30 centroids, we decided there were enough centroids (i.e., dive groupings) to describe variation in the data. To simplify the analysis, we examined three primary characteristics: the maximum depth bin used, the most common depth bin used (primary mode), and the second most common depth bin used (secondary mode). This method allowed us to identify depths that belugas may target and also prevented surface behavior from masking deeper diving behavior. For example, belugas that dive deeply may have to spend more time near the surface between dives. Therefore, a primary mode may occur at the surface while a secondary mode occurs at depth. We then calculated the average number of dives per hour (equal to the sum of dives during a 6 h period divided by 6), the mean dive duration histograms, and mean time-at-depth histograms for these groupings.

Statistical Tests

While cluster analysis is useful for summarizing diving behavior and illustrating common patterns in histogram shapes, statistical models are required for valid standard deviations, confidence intervals, and p-values. Although many dive records were collected (> 3000), these records were from a limited number of belugas ($n = 20$), so the records were not independent observations. Statistical models that account for repeated measures of the same individual are necessary to calculate correct variances and p-values. To account for repeated observations, each observation was indexed by time of collection and then modeled with a spatial power covariance structure (i.e., SP(POW); Schabenberger and Pierce, 2001; Littell et al., 2006; Kaps and Lamberson, 2009). This covariance structure is a generalization of the more commonly used first-order autoregressive (i.e., AR(1)) model. The AR(1) model assumes that all sampling intervals are equally spaced in time. The SP(POW) model accounts for the time elapsed between each pair of observations and therefore relaxes the requirement that data be sampled at equal intervals. If all time intervals are equal in duration, this model reduces to the AR(1) model. To account for a limited number of whales, individual whales were specified as random intercepts. All models were fit using Proc GLIMMIX in SAS/STAT software version 9.3 (SAS Institute Inc., 2011).

We modeled five different aspects of dive behavior taken from 6 h intervals: 1) depth of the deepest dive bin visited; 2) depth of the most common dive bin visited; 3) how often the most commonly visited dive bin included the seafloor; 4) average dive duration; and 5) maximum dive duration. When modeling the deepest and most common dive bins visited, we fitted data to a lognormal distribution to allow for positive skew. Binned histograms of dive data are often bimodal, with one mode occurring near the surface and the other at deeper depth. When the distribution of dives was bimodal, we considered only the deeper of the two modes when modeling the depth of the most common dive bin visited. We were not interested in surface behavior and limited analyses to depth bins more than 10 m deep. For modeling how often belugas visit the seafloor, we used logistic regression and coded dive records as "1" if the bin included the seafloor depth and "0" if it did not. Dive durations were measured as counts of dives falling into duration bins. When computing averages, we multiplied the count of dives for each histogram bin by the midpoint of the duration for that histogram bin, and then divided by the total count of dives. When computing maximum dive duration, we used the upper limit of the longest duration bin that was visited within each 6 h interval.

Explanatory variables, used in all analyses, included the additive effects of *sex* and *age* to account for differences in diving ability or dietary preference. We considered *time of day* (dawn, day, dusk, night) and *season* (summer or fall; not enough tags transmitted beyond November to allow other comparisons) to account for the possibility that beluga prey may migrate vertically within the water column as a function of daylight. The additive effect of season was used to account for the fact that the sun does not set at high latitudes during summer months. Histograms collected from June to August were classified as summer, and those collected from September through November as fall. We also included the additive effect of region (Inshore/shelf, Barrow Canyon, Slope, and Arctic Basin). Finally, we included the interactions *region*sex*, *region*age*, and *time of day*season*. Because the data set had only one adult female, we did not examine a *sex*age* interaction. The final model for each analysis was selected via backwards selection, in which we dropped variables one at a time until only statistically significant variables remained ($p \leq 0.05$).

Analyses for 2007 Data

Tags deployed in 2007 were examined separately because they were parameterized to target deeper diving behavior

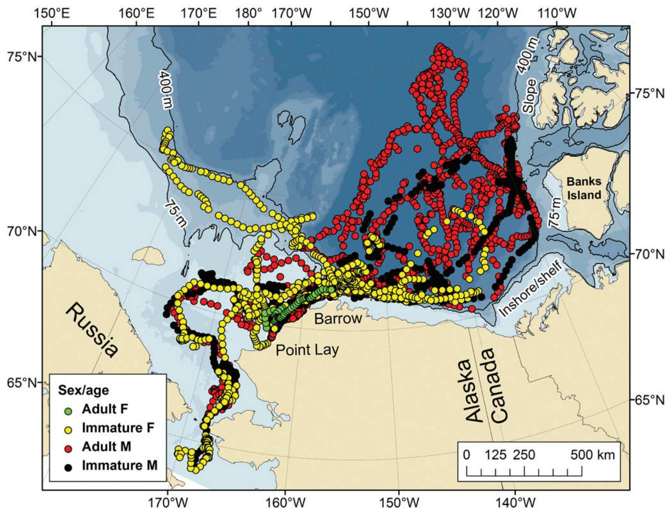

FIG. 2. State-space locations assigned to dive histograms for each sex and age class of beluga whales satellite-tagged at Point Lay, Alaska, in 1998–2002.

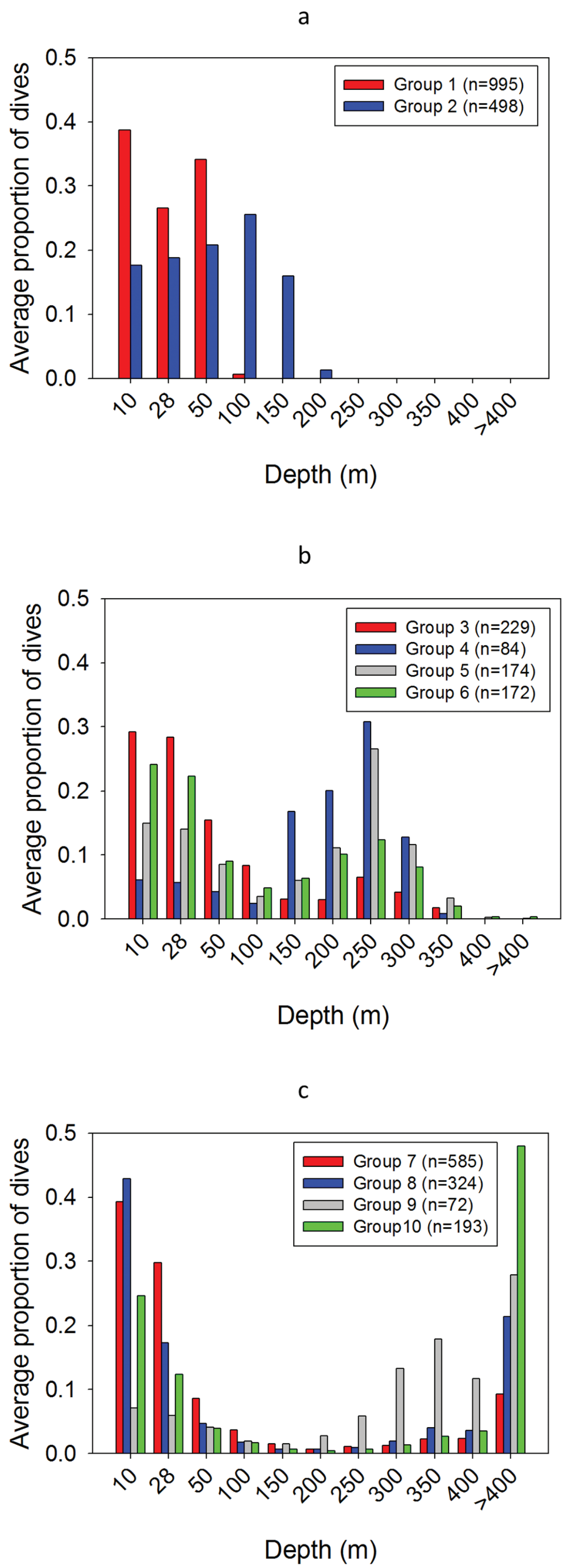

FIG. 3. Proportion of dives ($n = 3326$) that fall into depth bins for each grouping of beluga whales satellite-tagged at Point Lay, Alaska, in 1998–2002. The cluster analysis identified 10 groups; however, groups follow one of three general patterns: (a) "shallow" dives of 200 m or less; b) "intermediate" dives, which are generally 350 m or less in depth and have a mode near 250 m; and c) "deep" dives, which have a mode at depths greater than 400 m.

than those deployed between 1998 and 2002 (Table 2). Because there were only three tags in 2007, we limited our examination to descriptive statistics of diving behavior. However, these data allowed a better understanding of how deep belugas dove and the behavior of adult females.

RESULTS

1998–2002

For whales tagged during 1998–2002, a total of 3326 maximum depth histograms were collected: 688 from four immature males, 1536 from 11 adult males, 1033 from four immature females, and 69 from the single adult female. During the 3326 time periods for which we had maximum depth histogram data, there were also 2933 dive duration and 2914 time-at-depth histograms.

Adult males ranged farther north than other age/sex classes (Fig. 2; see also Suydam et al., 2001; Suydam, 2009). Therefore, a higher percentage of their dive histograms were from the Arctic Basin (57%) than was the case for immature males (39%) or immature females (20%) (Table 4). While few dive histograms for adult (6%) or immature (3%) males were located on the Slope, many dive histograms for immature females were located there (21%). All belugas had dive histograms within Barrow Canyon, ranging from 11% for adult males to 26% for adult females, and Inshore/shelf regions, ranging from 26% for adult males to 74% for adult females (Table 4).

Dive Depth Categories: When we used the k-means algorithm, approximately 94% of the variation in the data was explained by using ten dive groupings. Beyond ten dive groupings, each additional grouping resulted in a change in the total SSE of 1% or less. Dives in these ten groupings belonged to one of three general types (Fig. 3). The first type is shallow depth diving behavior (Fig. 3a), with

TABLE 4. Percentage (*n*) of maximum depth dive histograms located in each of four regions for each sex and age class of beluga whales satellite-tagged at Point Lay, Alaska, in 1998–2002. Percentages are column percentages.

Region[1]	Immature female (n = 4)	Immature male (n = 4)	Adult female (n = 1)	Adult male (n = 11)
Inshore/shelf	36% (373)	39% (267)	74% (51)	26% (405)
Barrow Canyon	23% (236)	20% (135)	26% (18)	11% (165)
Slope	21% (218)	3% (21)	–	6% (89)
Arctic Basin	20% (206)	39% (265)	–	57% (877)
Total	100% (1033)	100% (688)	100% (69)	100% (1536)

[1] Regions correspond to those presented in Figure 1.

TABLE 5. Dive statistics for the 10 dive groupings using the combined 1998–2002 data set for beluga whales satellite-tagged at Point Lay, Alaska.

Dive group[1]	Dive type[2]	N	Average degrees W longitude (SD)	Average no. of dives/h (SD)[3]	Average duration in min (range)	Average no. of dives/h to > 400 m (SD)
1	Shallow	995	162.8 (6.8)	8.1 (4.6)	3.4 (1-18)	0.0 (0)
2	Shallow	498	158.7 (6.7)	8.5 (2.7)	4.5 (1-18)	0.0 (0)
3	Intermediate	229	154.0 (8.3)	9.8 (2.9)	4.0 (1-18)	0.0 (0)
4	Intermediate	84	155.1 (5.4)	7.0 (2.3)	5.1(1-18)	0.0 (0)
5	Intermediate	174	157.8 (11.3)	7.2 (1.8)	4.7 (1-15)	0.0 (0.1)
6	Intermediate	172	154.3 (5.9)	8.1 (2.3)	4.3 (1-18)	0.0 (0.1)
7	Deep	585	143.1 (8.5)	8.6 (2.4)	4.1 (1-21)	0.7 (0.6)
8	Deep	324	140.4 (9.0)	6.5 (2.1)	3.8 (1-18)	1.3 (0.8)
9	Deep	72	145.5 (9.2)	5.9 (2.5)	4.6 (1-21)	1.5 (1.2)
10	Deep	193	137.7 (8.3)	5.1 (2.1)	4.1 (1-21)	2.3 (0.9)

[1] Dive groups were defined using the cluster analysis and correspond to groupings in Figures 3 and 4.
[2] Dive type is the classification presented in Figure 3.
[3] This column shows the average number and standard deviation of all dives within a histogram type.

most dives to less than 50 m (group 1) or 150 m (group 2). The second type is intermediate depth diving behavior, with one mode near the surface and a second mode near 250 m (groups 3–6) (Fig. 3b). The last type is deep diving behavior and includes a mode at depths greater than 400 m (groups 7–10). For dive groups 7 and 8, the primary mode is 10 m or more; for dive groups 9 and 10, the primary mode is more than 400 m (Fig. 3c).

The fewest dives per hour were found in three of the four deep diving categories (dive groups 8–10; Table 5). The average duration of dive groupings ranged from 3.4 to 5.1 min. While there was no obvious pattern in average duration of dives in relation to dive type, the range in dive durations was generally greater for deep dive types (i.e., dive groups 7–10). In general, dive duration ranged from 1 to 18 min; however, in three of the four deep diving types (dive groups 7, 9, and 10), dive durations ranged from 1 to 21 min (Table 5). Because dive depths were not directly linked to dive durations in the histogram bins, we cannot directly link longer dives to deeper dives. The average number of min/h spent near the surface in the 4–10 m depth bin ranged from 20.1 (SD = 6.8) to 36.9 (SD = 17.0) (Table 6). For deep dive types, the number of min/h spent in the greater than 400 m depth bin ranged from 2.9 (SD = 2.6) to 8.4 (SD = 4.0).

Shallow diving behavior was found mainly on the Inshore/shelf (71%), where the water is shallow (Fig. 4); however, shallow-type dives were also observed in the Barrow Canyon (19%), Slope (5%), and Arctic Basin (5%) regions, where the water is deep. Intermediate-type dives were found at similar proportions in the Arctic Basin (31%), Barrow Canyon (37%), and Slope (29%). A few intermediate dives were observed in Inshore/shelf regions (4%) near the boundaries of deeper regions. Because the Inshore/shelf region is less than 75 m deep, this finding is probably due to error in the bathymetric charts or in how dives were positioned. Deep diving behavior was observed mainly in the Arctic Basin (91%), but a small percentage of deep dives occurred over Barrow Canyon (3%), the Slope (6%), and the Inshore/shelf (1%) regions. Again, the presence of deep dives in the Inshore/shelf region was likely due to errors in bathymetric charts or Argos location error, or both.

Shallow dives were made by all sex and age classes: 49% of all dives made by immature males were shallow, as compared to 47% for immature females and 39% for adult males (Table 7). Deep diving behavior was most common among adult males, while intermediate dives were the least common. For adult males, 53% of all dives made were in the deep diving categories, compared to 29% for immature males and 17% for immature females. Only 9% of dives made by adult males were of intermediate depth, compared to 22% for immature males and 35% for immature females.

Factors Affecting Dive Depth and Duration: When examining the depth of the deepest dive bin visited during

TABLE 6. Average time (min/h) spent at depth for each dive grouping for beluga whales satellite-tagged at Point Lay, Alaska, in 1998–2002. For clarity, SD for each average is not shown; instead, the range of SD for averages is presented in the bottom row.

		Depth (m)										
Dive group[1]	Dive type[2]	10	28	50	100	150	200	250	300	350	400	> 400
1	Shallow	36.9	11.5	11.4	0.2	–	–	–	–	–	–	–
2	Shallow	25.0	9.2	10.7	9.5	5.1	0.4	0.1	–	–	–	–
3	Intermediate	30.2	10.7	5.7	4.0	2.4	2.4	3.0	1.2	0.3	–	–
4	Intermediate	20.1	3.4	3.3	6.0	10.2	7.9	7.5	1.7	0.1	–	–
5	Intermediate	23.7	5.5	3.6	5.5	5.3	6.1	7.8	2.0	0.5	0.1	–
6	Intermediate	27.2	8.4	3.6	4.6	5.0	4.9	4.3	1.6	0.3	0.1	0.1
7	Deep	33.4	8.8	3.0	2.4	1.8	1.6	1.6	1.5	1.5	1.3	3.0
8	Deep	32.5	4.5	2.2	2.5	2.2	1.9	2.3	2.2	2.4	2.0	5.4
9	Deep	21.8	3.1	2.9	4.1	4.0	3.9	5.0	5.3	4.6	2.3	2.9
10	Deep	27.4	3.2	2.1	3.0	2.7	2.5	2.6	2.5	2.8	2.8	8.4
Range of SD for averages		6.0–17.0	2.6–10.9	1.4–13.7	1.2–8.5	0.5–7.6	0.0–5.0	0.0–6.3	0.0–3.2	0.0–2.3	0.0–1.6	0.0–4.0

[1] Dive groups were defined using the cluster analysis and correspond with groupings in Figures 3 and 4.
[2] Dive type is a subjective classification, as presented in Figure 3.

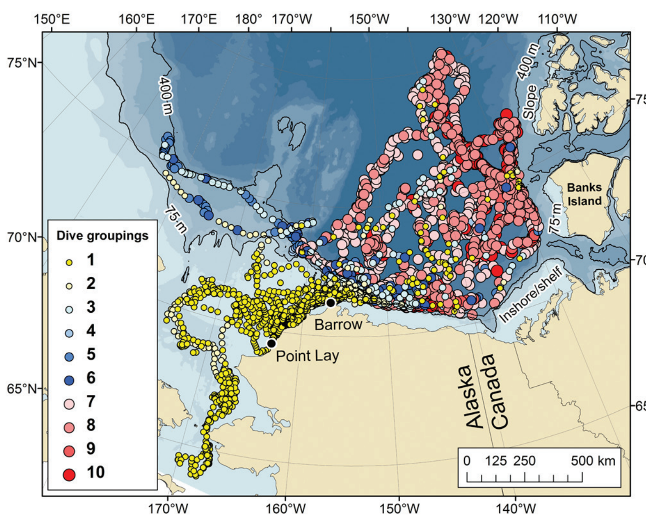

FIG. 4. Spatial distribution of dive groupings (n = 3326) for 20 beluga whales satellite-tagged at Point Lay, Alaska, in 1998–2002. Shallow dives (groups 1 and 2) are shades of yellow, intermediate dives (groups 3–6) are shades of blue, and deep dives (groups 7–10) are shades of red. Deep dives cannot occur on the shelf; however, both shallow and intermediate dives occurred within the Arctic Basin.

a 6 h period, we found no differences by *sex* (p = 0.94), *age* (p = 0.09), *time of day* (p = 0.54), or *season* (p = 0.19). The interaction *time of day*season* (p < 0.20) was insignificant, but the interaction *sex*age* (p = 0.06) was nearly significant. Statistically significant variables included *region* (p < 0.01) and the interaction *region*age* (p < 0.01). In general, the depth of the deepest dive bin used within a 6 h period was greater in regions with deeper water and was greater for immature belugas in Inshore/shelf and Barrow Canyon regions than for adults, but was similar for all age classes in the Slope and Arctic Basin regions (Fig. 5a). When examining the depth of the most commonly visited dive bin, we found no differences by *sex* (p = 0.44), *age* (p = 0.13), or *season* (p = 0.48). *Region* (p < 0.01) was a significant predictor and *time of day* (p = 0.06) was nearly significant. The interactions of *region*sex* (p < 0.01), *region*age* (p < 0.01), and *time of day*season* (p < 0.01) were all significant. Although the additive effects of *sex*, *age*, and *season* were not significant, their interactions were significant, indicating that there were effects of sex, age, and season in some regions or at some times of day, but they were not consistent across all regions or times of day. In general, the depth

TABLE 7. Percentage (number) of dive groupings attributed to each age and sex classification for beluga whales satellite-tagged at Point Lay, Alaska, in 1998–2002.

Dive group[1]	Dive type[2]	Immature female	Immature male	Adult male	Adult female
1	Shallow	30% (307)	31% (210)	28% (434)	64% (44)
2	Shallow	17% (180)	18% (125)	11% (168)	36% (25)
3	Intermediate	10% (106)	9% (63)	4% (60)	
4	Intermediate	5% (54)	2% (15)	1% (15)	
5	Intermediate	11% (113)	6% (44)	1% (17)	
6	Intermediate	9% (97)	5% (31)	3% (44)	
7	Deep	8% (80)	16% (108)	26% (397)	
8	Deep	3% (36)	9% (62)	15% (226)	
9	Deep	4% (39)	1% (9)	2% (24)	
10	Deep	2% (21)	3% (21)	10% (151)	
Total		100% (1033)	100% (688)	100% (1536)	100% (69)

[1] Dive groups were defined using the cluster analysis and correspond to groupings in Figures 3 and 4.
[2] Dive type is a subjective classification, as presented in Figure 3.

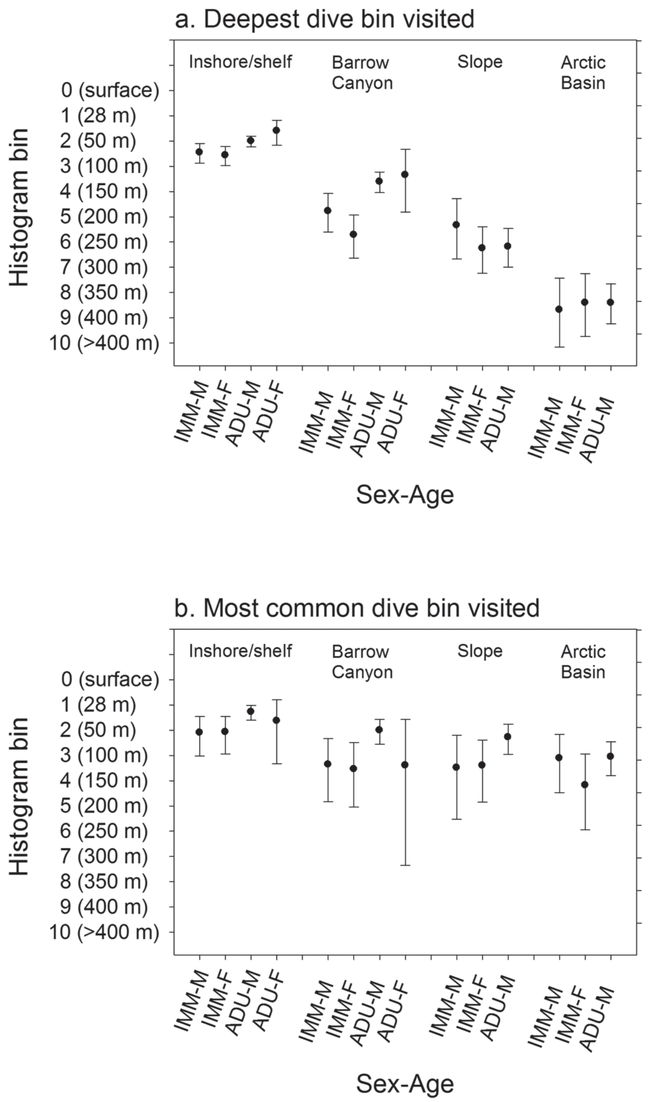

FIG. 5. Depth of (a) the deepest dive bin and (b) the most common dive bin visited during 6 h histogram periods for adult (ADU) and immature (IMM) male (M) and female (F) beluga whales satellite-tagged at Point Lay, Alaska, in 1998–2002. Means and 95% confidence limits are for bin values (i.e., values 1–10); upper depth thresholds are in parentheses for context.

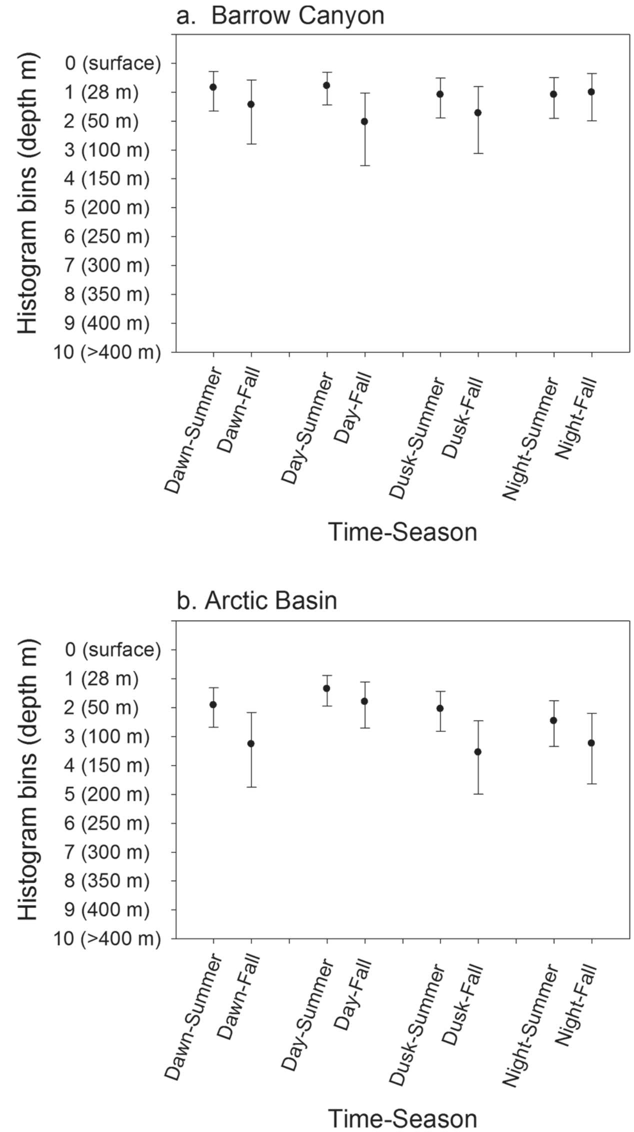

FIG. 6. Average depth of the most common dive bin visited during 6 h histogram bins differed significantly by time of day and season ($p < 0.01$). Here are two examples illustrating the effect of time of day and season for adult males in (a) Barrow Canyon ($n = 165$ histogram bins) and (b) the Arctic Basin ($n = 877$ histogram bins).

of the most commonly visited bin was greater in regions with deeper water (Fig. 5b). Again, adult belugas focused on shallower depths in the Inshore/shelf, Barrow Canyon, and Slope regions than immature belugas. In general, belugas focused on deeper depths within regions in the fall than in the summer (Fig. 6). For example, adult males in the Arctic Basin focused on histogram bin 2 (50 m) during dawn in summer and bin 3 (100 m) in fall (Fig. 6b). This relationship was not consistent across seasons or by time of day, which is why the interaction *time of day*season* was significant but the additive effect of *season* was not.

When examining how often the deepest mode during a 6 h period included the seafloor (Fig. 7), we found no differences by *sex* ($p = 0.57$), *age* ($p = 0.28$), *season* ($p = 0.48$), or the interactions of *region*sex* ($p = 0.50$) and *region*age* ($p = 0.53$). *Time of day* was borderline significant ($p = 0.06$). The final model included *region* ($p < 0.01$) and the interaction *time of day*season* ($p = 0.02$). The probability that the deepest mode in a dive histogram included the seafloor was 0.71 (SE = 0.03) in the Inshore/shelf, 0.48 (SE = 0.04) in Barrow Canyon, and 0.36 (SE = 0.05) in the Slope regions. The probability that belugas target the bottom by *time of day* and *season* differed by region. In summer, belugas frequented the seafloor less during the day in the Inshore/shelf and Barrow Canyon regions (Fig. 7a and b); however, there was considerable variability. The most distinct pattern occurred within the Slope region, where belugas dove to the bottom more often during the day in the fall. However, only nine observations of six belugas were made within this combination of *time of day*, *season*, and *region*. We were concerned that these might be outliers driving the significance of the *time of day*season* interaction. However, when we removed these nine observations, the *time*

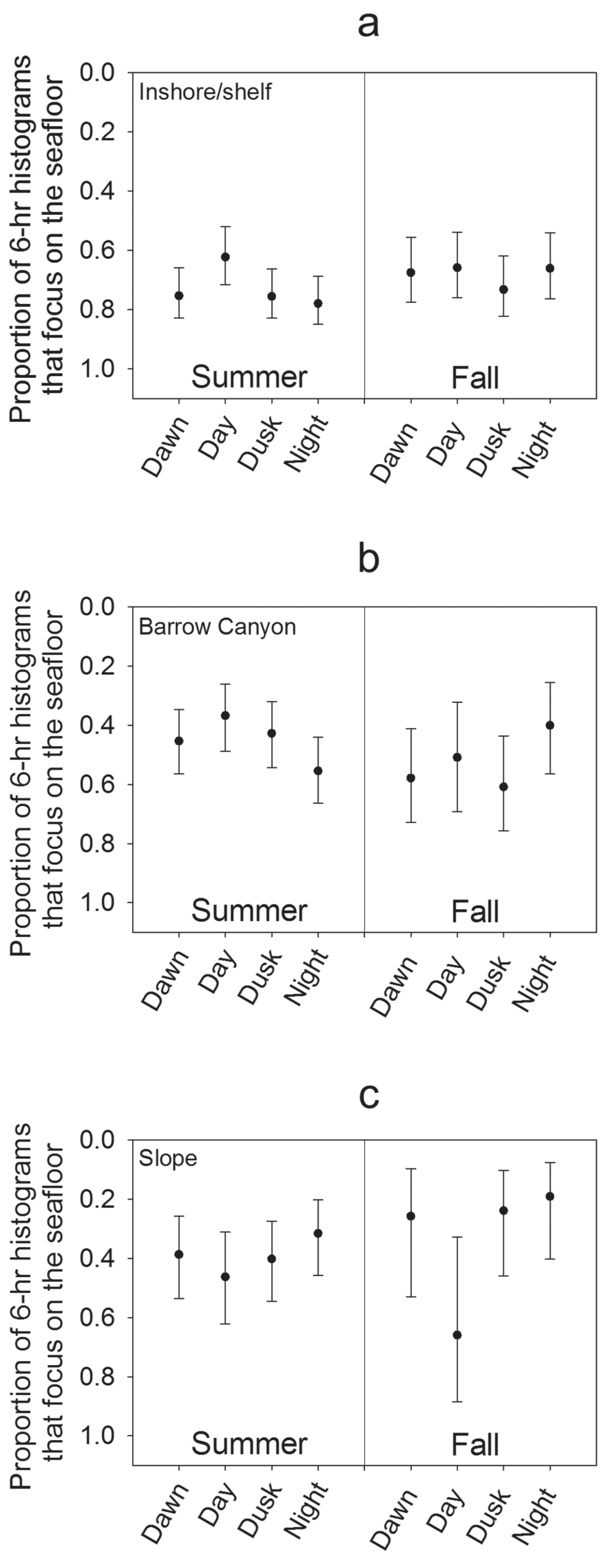

FIG. 7. Proportion of 6 h histogram bins where the most common depth of diving included the seafloor for a) Inshore/shelf, b) Barrow Canyon, and c) Slope regions, for beluga whales satellite-tagged at Point Lay, Alaska, in 1998–2002.

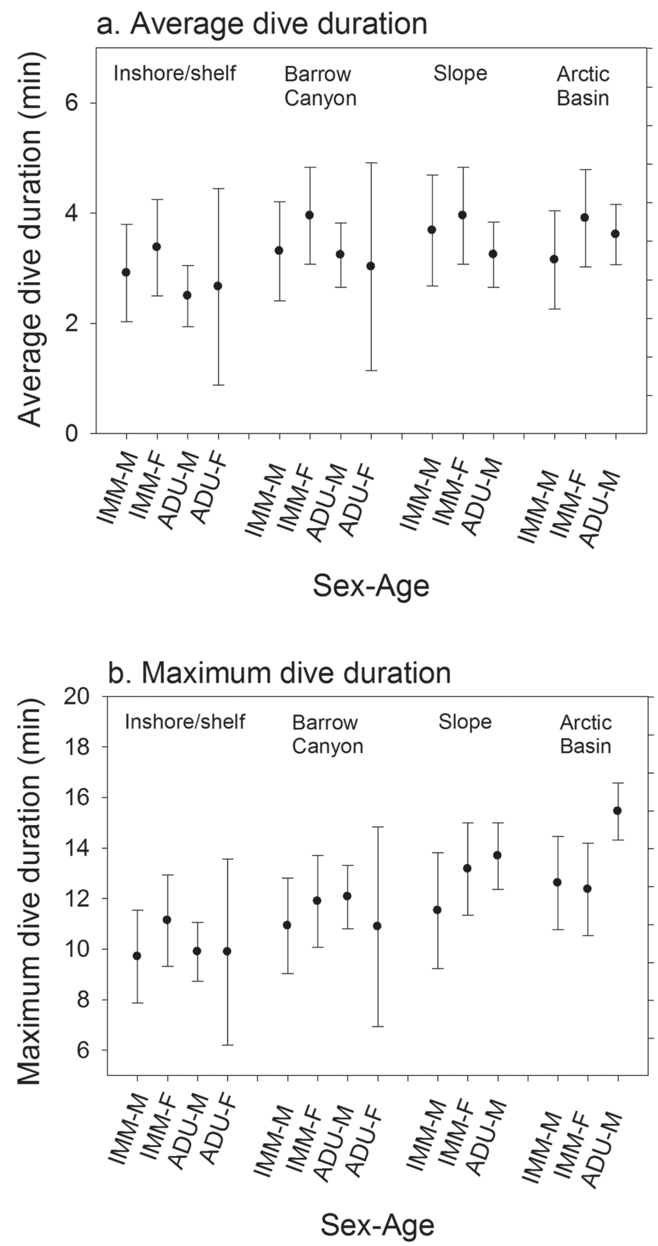

FIG. 8. Average (a) and maximum (b) dive duration (min) and 95% confidence intervals from 6 h dive histograms for adult (ADU) and immature (IMM) male (M) and female (F) beluga whales satellite-tagged at Point Lay, Alaska, in 1998–2002.

*of day*season* interaction was still statistically significant ($p = 0.01$).

The average duration of dives did not differ by *sex* ($p = 0.37$), *age* ($p = 0.61$), or the interaction of *sex*region* ($p = 0.48$). However, average dive duration did vary by *region* ($p < 0.01$) and the interaction of *region*age* ($p < 0.01$). Although these interactions were statistically significant, there are no consistent patterns to indicate that particular sexes or ages dive for longer durations (Fig. 8a). Furthermore, within regions, the difference between sex and age classes in dive duration was less than 1 min (range 43–55 sec). Average dive duration was longer in deeper water. In the Inshore/shelf region, average dive duration ranged from

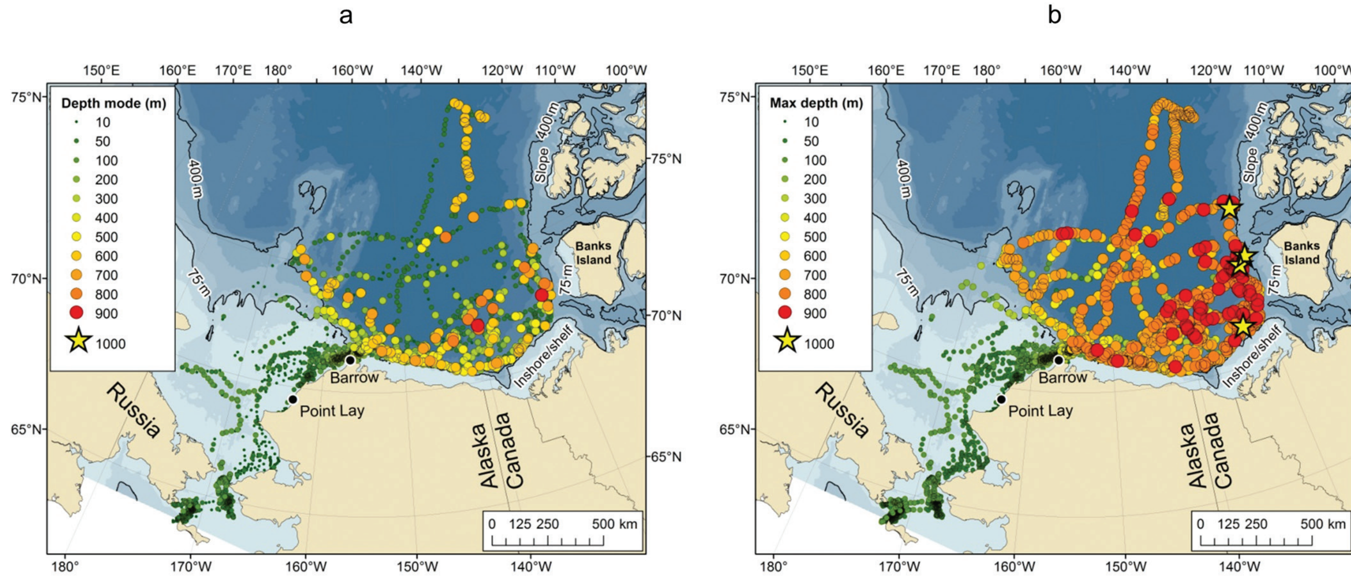

FIG. 9. Depth of (a) the most common dive bin and (b) the deepest dive bin visited during 6 h histogram periods (n = 2481) for three belugas satellite-tagged at Point Lay, Alaska, in 2007.

2.5 min for adult males to 3.4 min for immature females. In the Arctic Basin, average durations ranged from 3.1 min for immature males to 3.9 min for immature females.

The maximum duration of dives within a 6 h period did not differ by *sex* (p = 0.65) or *age* (p = 0.19), but it did vary by *region* (p < 0.01) and the interactions *region*sex* (p = 0.03) and *region*age* (p < 0.01). Although these interactions were statistically significant, there were no consistent patterns indicating that particular sexes or ages had longer maximum dive durations (Fig. 8b). As with average dive duration, maximum dive duration was longer in deeper water. In the Inshore/shelf region, the longest dives ranged from 9.7 min for immature males to 11.1 min for immature females. In the Arctic Basin, maximum durations ranged from 12.4 min for immature females to 15.5 min for adult males.

2007 Data

A total of 2481 maximum depth histograms were collected from belugas tagged in 2007, 1795 from an adult male (B07-1) and 686 from two adult females (B07-2 and B07-3; Table 1). Also collected were 1742 dive duration histograms and 1509 time-at-depth histograms.

The tag on the adult male (B07-1) transmitted for 521 days (1 July 2007 to 3 December 2008), collecting dive and location data for the entire winter of 2007. This tag was the first satellite transmitter to provide location and dive data for a beluga from the eastern Chukchi stock wintering in the Bering Sea. B07-1 was tagged at Point Lay on 4 July 2007. After migrating into the Beaufort Sea, B07-1 reached 74.86˚ N on 20 September and entered the Bering Sea, passing south of Little Diomede Island (65.75˚ N), on 20 December 2007. B07-1 wintered between Little Diomede Island and St. Lawrence Island and moved back into the Chukchi Sea on 23 May 2008. B07-1 ranged farther north in 2008 than in 2007, reaching 81.17˚ N on 11 August 2008. The whale returned to the northern Bering Sea on 23 November 2008 and remained within 130 km of Little Diomede Island until its tag stopped transmitting on 3 December 2008.

As expected, deeper diving was observed in regions with deeper water, such as the Arctic Basin (Fig. 9). As with belugas tagged during 1998–2002, deeper diving was more common in the Canadian Beaufort than in the Alaskan Beaufort (Fig. 9b). The four deepest dives, three for the adult male (B07-1) and one for an adult female (B07-2), fell into the 900–1000 m depth bin. All four deep dives occurred along the shelf break in the Canadian Beaufort Sea, west of Banks Island (Fig. 9b). Multiple dives to 900–1000 m never occurred within the same 6 h period. Two of the four deep dives may have been to the seafloor, as the seafloor depth was included within the depth bin. The dives occurred on 7 and 26 September in 2007 and on 13 and 22 September in 2008. Of the dives that included the 800–900 m depth bin, 77% (48 of 62) also occurred in September.

As in 1998–2002, depth data collected from tags deployed in 2007 were often bimodal. Usually the primary mode was at or near the surface and the secondary mode occurred at a deeper depth. We focused on the deeper of the two modes. The most common secondary mode was at 10–50 m in the Inshore/shelf, 200–300 m in Barrow Canyon, and 200 m along the Slope (Fig. 10). In the Arctic Basin, the most common secondary mode was at 50 m; however, 33% of histogram periods had secondary modes between 200 and 600 m. The deepest dive bins during a 6 h period ranged from 0 to 100 m for Inshore/shelf, 50 to 400 m for Barrow Canyon, 100 to 400 m for the Slope, and 0 to 1000 m for the Arctic Basin. In the Arctic Basin, 600–700 m was typically the deepest dive bin visited by all three individuals (Fig. 11).

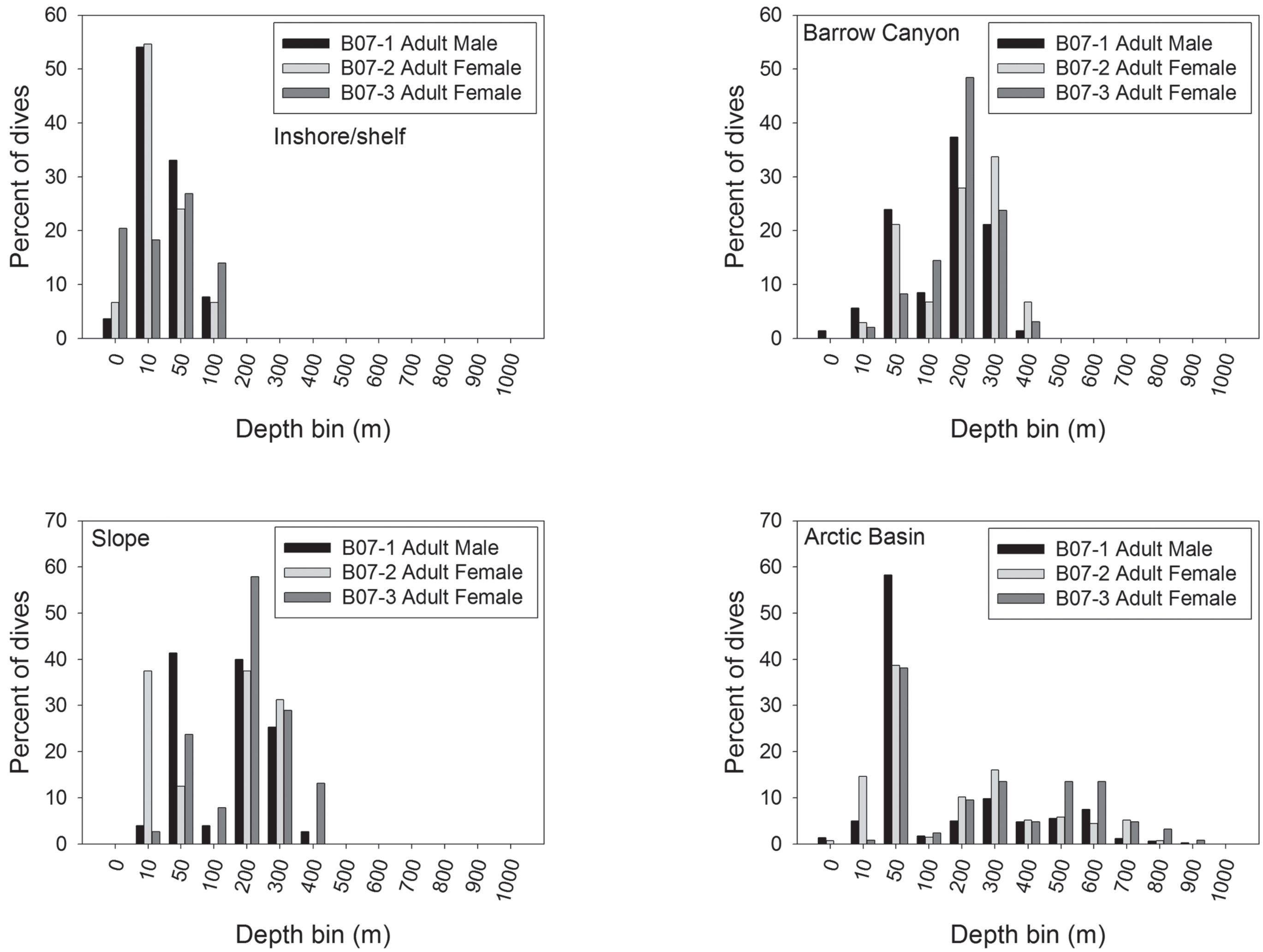

FIG. 10. Depth of the most common dive bin visited (n = 2481 bins) by three belugas satellite-tagged at Point Lay, Alaska, in 2007. For each region (Inshore/shelf, Barrow Canyon, Slope, or Arctic Basin), the number of dives falling into each depth bin is expressed as a percent of the total sample for each individual.

Like belugas tagged in 1998–2002, those tagged in 2007 spent approximately half of each hour near the surface for most dive histograms (first row in Table 8). New tag settings used in 2007 also allowed us to examine how much time whales spent at depths greater than 400 m. Across all histograms with dives deeper than 400 m, on average whales spent only 0.5 to 4.6 min per 6 h period below 400 m in 2007 (Table 8), compared to 0.1 to 8.4 min in 1998–2002 (Table 6).

The 2007 tags were programmed to include all dives longer than 20 minutes in the same bin. This bin included 5.2% of dives. The longest dives observed between 1998 and 2002 were in the 18–21 min bin and accounted for a similar percentage (4.9%) of all dives. Therefore, it is likely that there were few dives longer than 21 min for tags deployed in 2007. If we assume that all dives longer than 20 min in duration were exactly 21 min long, then the average duration of dives would be 7.7 (± 2.2 SD) min for the male B07-1, 7.1 (± 7.1) min for female B07-2, and 7.0 (± 2.1) min for female B07-3.

DISCUSSION

Clustering

Clustering provided a simple way to categorize 3326 histograms into 10 representative types, which provided an intuitive way to look at histograms by oceanographic region. We decided to stop adding clusters when the total SSE declined by less than 1% after a new addition. This rule was likely too strict, as we identified more dive groupings than necessary. Visual inspection of these 10 histogram types indicated they were variations on three themes: "shallow," "intermediate," or "deep" diving behavior (Fig. 3). However, if we had chosen to limit the number of clusters to three, we would have explained only 41% of the variation in the data. Using a stopping rule of less than 1% allowed us to explain 94% of the variation in the data and verify that we had not missed important groupings.

The utility of this approach for other studies will depend on how data are distributed. For example, if the total SSE continues to decline as centroids are added, there may not

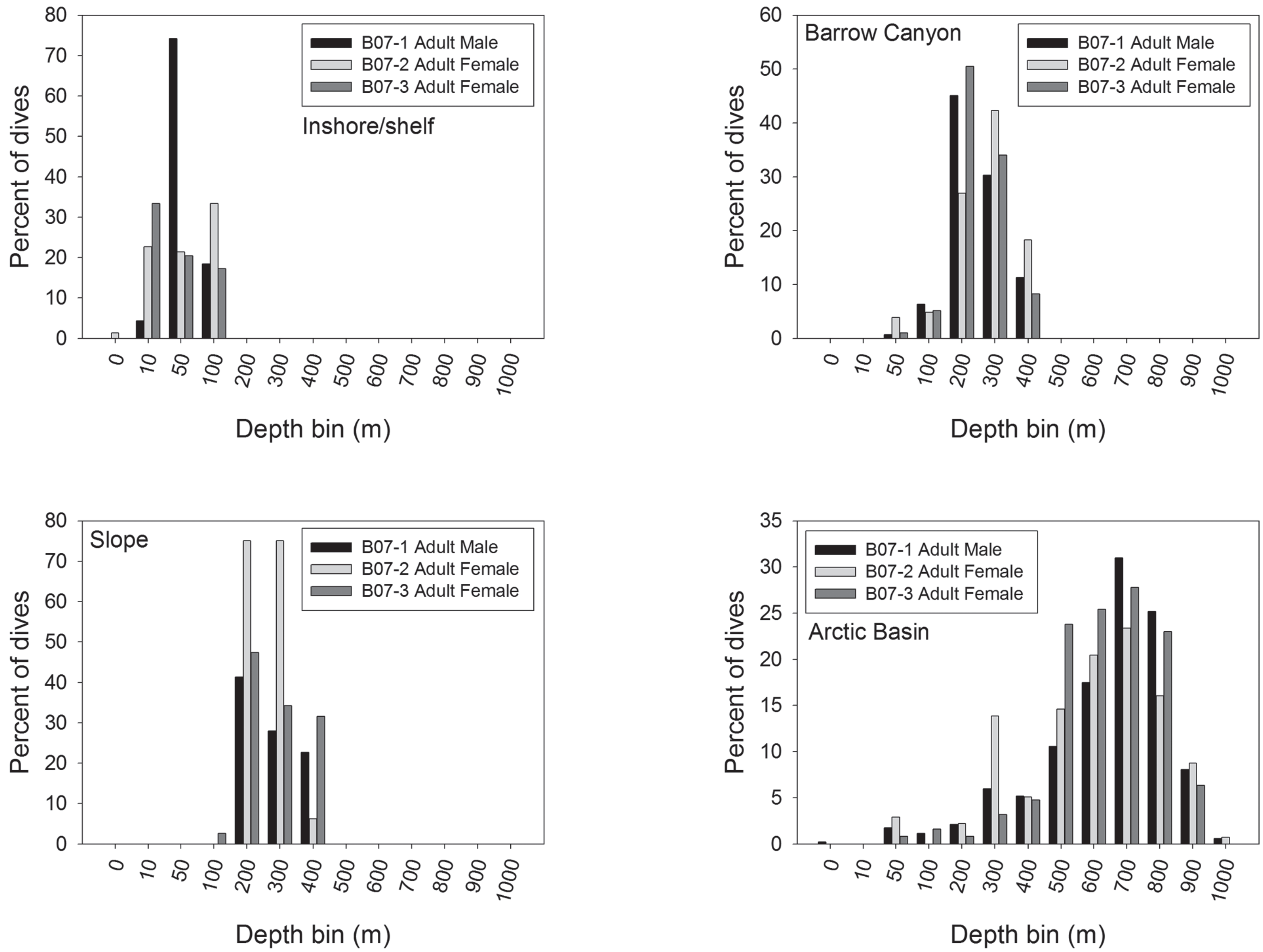

FIG. 11. Depth of the deepest dive bin visited (n = 2481 bins) by three belugas satellite-tagged at Point Lay, Alaska, in 2007. For each region (Inshore/shelf, Barrow Canyon, Slope, or Arctic Basin), the number of dives falling into each depth bin is expressed as a percent of the total sample for each individual.

be an obvious stopping point. Furthermore, while clustering reduces the amount of data to be considered, there is a chance that relevant differences in behavior could be grouped into the same clusters (e.g., Malcolm and Duffus, 2000). However, the large number of histograms, each with 14 bins, requires that the information be summarized in some fashion for interpretation.

Diving Depth

We found minor differences in diving depth by sex and age class. Similar proportions of shallow dives (i.e., ~40%–50%) were made by all sex and age classes except adult females, for which we have little data (Table 7). However, immature females had more intermediate dives and fewer deep dives than immature and adult males. Likewise, immature males had more intermediate dives and fewer deep dives than adult males (Table 7). However, the pattern of diving is confounded with beluga distribution patterns, and we cannot tell whether the depth to which belugas dive is determined by the region they frequent, or the region they frequent is determined by their diving ability. Adult males spent less time, indexed by the number of dive intervals available for analysis, in Barrow Canyon and Slope regions, where "intermediate dives" occur, and more time over the Arctic Basin region, where "deep dives" occur (Table 7).

Within Inshore/shelf and Barrow Canyon regions, immature belugas, both male and female, generally dove deeper than adults (Fig. 5), suggesting that age classes may use these regions differently. Within the Slope and Arctic Basin regions, however, dive behavior of immature and adult belugas was similar (Fig. 5). Belugas generally pass through Inshore/shelf regions and Barrow Canyon to reach the Slope and Arctic Basin regions (Suydam et al., 2001; Suydam, 2009). It is possible that adult belugas are mainly traveling through the Inshore/shelf and Barrow Canyon regions to reach feeding areas in the Slope and Arctic Basin regions. The best insights on diving ability come from tags deployed in 2007. Only three belugas were tagged in 2007: one adult male and two adult females. Four dives were recorded in the 900–1000 m depth bin, three for the adult male and one for an adult female. Adult females also made

TABLE 8. Average time (min/h and SD) spent at different depths (m) for histograms indexed by the maximum depth of diving during the 6 h histogram period for beluga whales satellite-tagged at Point Lay, Alaska, in 2007. For example, for a 6 h histogram with a maximum depth of 500 m, an average of 4.5 minutes (SD = 4.0) was spent at 400 m depth.

	Maximum depth (m) of dive during a 6 h period											
Depth (m)	10 (n = 83)	50 (n = 780)	100 (n = 237)	200 (n = 183)	300 (n = 189)	400 (n = 103)	500 (n = 89)	600 (n = 127)	700 (n = 195)	800 (n = 151)	900 (n = 53)	1000 (n = 3)
10	60 (0.1)	19.4 (10.8)	23.3 (11)	27.8 (11.9)	27.8 (9)	26 (8.4)	26.5 (8.6)	25.2 (8.3)	25.2 (7.8)	26.6 (7.6)	26.9 (5.2)	29 (9.9)
50	0 (0.2)	40.6 (10.8)	24.6 (12.3)	8.5 (7.1)	8.8 (6.9)	7.9 (5.1)	8.2 (5.2)	8.9 (5.7)	9.6 (6.4)	12 (6.1)	13 (5.6)	17.6 (6.8)
100	0 (0)	0 (0)	12.1 (11)	8.5 (7.9)	4.2 (4.3)	4.4 (3.2)	4.1 (3.5)	3.6 (3.6)	2.5 (1.4)	2.2 (1.5)	1.5 (0.8)	1 (1.2)
200	0 (0)	0 (0)	0 (0)	14.8 (10.8)	10.9 (7.6)	10.1 (6.6)	8.1 (5.1)	6.4 (4.4)	5.1 (4)	3.5 (2.6)	2.6 (1.3)	1.8 (1.6)
300	0 (0)	0 (0)	0 (0)	0 (0.1)	8.2 (7.5)	8.4 (5.4)	6.7 (4)	6.2 (4.3)	4.9 (3.5)	3.3 (2.2)	2.7 (1.5)	1.8 (1.6)
400	0 (0)	0 (0)	0 (0)	0 (0)	0 (0.1)	3.3 (4.4)	4.5 (4)	4.6 (2.6)	4 (2.5)	3.3 (2.1)	2.5 (1.2)	2.4 (2.6)
500	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1.8 (2.4)	3.9 (3.2)	4.2 (2.8)	3 (1.8)	2.6 (1.3)	1.8 (1.6)
600	0 (0)	0 (0)	0 (0)	0 (0.1)	0 (0)	0 (0)	0 (0)	1.1 (1.3)	3.3 (2.4)	2.7 (1.6)	2.5 (1.2)	1.4 (0.9)
700	0 (0)	0 (0)	0 (0)	0 (0)	0 (0.1)	0 (0)	0 (0)	0 (0.2)	0.8 (1.3)	2.7 (1.7)	2.7 (1.5)	1.2 (0.6)
800	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0.1)	0 (0.1)	0.7 (1)	2.4 (1.4)	1.2 (1)
900	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0.1)	0 (0)	0 (0)	0.5 (0.6)	0.6 (0)
1000	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)

numerous dives into the 800–900 m depth bin. We find no evidence to conclude that adult females do not dive as deeply as adult males.

The most comparable study is that of Richard et al. (1997), who tagged belugas from the Beaufort Sea stock (also known as the Mackenzie stock). This stock summers in and near the western Canadian Arctic Archipelago, including the Mackenzie River Delta, Amundsen Gulf, McClure Strait, Viscount Melville Sound, and shelf/slope waters west of Banks Island (Richard et al., 1997; Loseto et al., 2006; Asselin et al., 2011), and it partially overlaps the eastern Chukchi Sea stock in space and perhaps in time. Richard et al. (1997) found that male and female belugas dove to similar depths, but that only males ranged over deeper waters west of the shelf break. Both male and female belugas spent most of their time in medium-depth waters (15–600 m), where they typically dove to the bottom. Belugas in deep water (> 600 m) typically dove to 700–900 m; the deepest dive recorded was 1160 m (adult male). In deep water, dives were generally "V" shaped: belugas would dive to a maximum depth and then return immediately to the surface. It is likely that the deeper dives we observed were also "V" shaped, because belugas spent little time in the deeper depth bins (Tables 6 and 8).

Dive Duration

In general, belugas dove 5.1–9.8 times per hour. Fewer dives occurred during periods when belugas were diving to deeper depths (Table 5). The average duration of dives was very consistent across dive types (i.e., shallow, intermediate, and deep), although the longest dives (> 21 min) were observed during periods with the deepest dives.

Average dive duration ranged from 3.4 to 5.1 min (Table 5). After accounting for *region*, we found no significant relationship between *sex* or *age* and average or maximum dive durations. While there were some significant interactions between *region* and *age*, the effects on dive duration were slight. For example, although average duration had a significant interaction with *region*age*, it varied by less than a minute within regions (Fig. 8a). In general, average dive duration was fairly consistent across regions, sexes, and ages (Fig. 8a), while the maximum dive duration increased as depth increased (Fig. 8b).

Our findings generally agree with other studies of beluga dive behavior. Kingsley et al. (2001) found that most dives were shorter than 10 min in duration and that dive duration did not vary greatly with dive depth in Hudson Bay, where depth ranged from 40 to 400 m. Near Somerset Island, Canada, Martin and Smith (1999) observed a longer mean dive time (13.1 min) than we observed, but a similar maximum dive duration (22.9 min). For beluga whales near Devon Island, Canada, Heide-Jørgenson et al. (1998) found that most dives ranged from 9 to 18 min, which is also similar to the durations we observed (Table 5).

Segregation by Sex and Age

The effects of sex and age on diving behavior were slight and apparently confounded by water depth, region, or both. An understanding of how the eastern Chukchi Sea stock of beluga whales may or may not segregate spatially is critical to understanding differences in diving behavior. Segregation by sex and age is documented for other stocks of belugas; for example, beluga whales from the Beaufort Sea stock are known to segregate in the summer. In general, adult males spend more time under heavy sea ice near the Canadian Archipelago and offshore, younger males and females with older calves select habitats in open water near the ice edge, and young males and females with newborn calves select open water habitats near the mainland (Loseto et al., 2006).

Unfortunately, we have no information on how reproductive status may influence dive behavior. Females with calves may spend more time in shallower water; however, none of the females we tagged had dependent calves. Regardless, only three adult females were tagged during this study, so inferences regarding how reproductive status affects habitat use would be unreliable. There is no clear evidence that adult females from the eastern Chukchi Sea stock do not range as far north as adult males. To date, only adult males have ranged farther than 77˚ N. However, there are few data for adult males and females within the same year. While an adult male beluga (B07-1) ranged as far as 81.0˚ North latitude in 2008, this same beluga ranged only as far as 74.4˚ North in 2007, when both males and females were tagged. In 2007, B07-2 and B07-3, both adult females, ranged farther north than B07-1 (75.8˚ and 75.05˚ North, respectively). Unfortunately, tags on both females stopped transmitting in 2008, so we cannot compare their movements with the high-latitude movements of the adult male (B07-1) in 2008.

While immature females did not range as far north as adults, two immature males (B01-4 and B02-4) reached 76.0˚ North. It is unclear whether the patterns in dive behavior and movement should be attributed to annual variation in food availability or to behavior specific to sex and age class. In general, adult belugas were found more often over the Arctic Basin than immature belugas (Table 4, Fig. 2). Within the 1998–2002 sample, immature belugas occurred most commonly over the Inshore/shelf and Barrow Canyon regions (Table 4). Interestingly, immature males spent more time over the Arctic Basin (39% of histograms) than immature females (20% of histograms), but not as much time as adults (57% of histograms). Again, these results are largely confounded with the year of tagging because in many years only one age class or sex was tagged. Hence, separating the effects of annual variation from the effect of sex or age is not currently possible. In the future, tagging a mixture of sexes and ages within years will be necessary to clearly distinguish between the roles of sex, age, and annual variability in dive behavior.

Prey Availability and Physical Oceanography

An understanding of beluga diet would help us to interpret dive behavior. However, the diet of eastern Chukchi Sea beluga whales is not well known. Beluga stomachs from the subsistence harvest have been collected only from villages bordering the Chukchi Sea, and many of these stomachs were empty when the whales were harvested (Seaman et al., 1982; Quakenbush et al., in press). Hence, there is little information on diet either offshore or in the Beaufort Sea. However, both shrimp and echiurid worms occur commonly in stomachs from Point Lay and Barrow, suggesting that eastern Chukchi Sea belugas are often benthic feeders (Quakenbush et al., in press). Stomach contents also indicate that eastern Chukchi Sea belugas eat both saffron cod (*Eleginus gracilis*) and, to a lesser extent, Arctic cod (*Boreogadus saida*) (Seaman et al., 1982; Quakenbush et al., in press). While belugas from the Beaufort Sea stock eat Arctic cod more often than saffron cod (Loseto et al., 2009; Quakenbush et al., in press), we suspect that this fact more likely reflects availability of the two cod species, rather than resource partitioning between beluga stocks. We think it likely that belugas from the eastern Chukchi Sea stock forage on Arctic cod in the Beaufort Sea, much like belugas from the Beaufort Sea stock. Indeed, Arctic cod is known to be the predominant prey of belugas from a number of Arctic regions, including West Greenland (Heide-Jørgensen and Teilmann, 1994), the Barents and Kara Seas (Kleinenberg et al., 1964), and Svalbard (Dahl et al., 2000). Hence, on the basis of stomach contents and the diet of other beluga stocks, we would expect belugas to forage on the seafloor and in areas with high densities of Arctic cod.

We found that beluga whales often dove to the seafloor. The probability that the deepest mode in a dive histogram included the seafloor was 0.71 (SE = 0.03) in the Inshore/shelf, 0.48 (SE = 0.04) in Barrow Canyon, and 0.36 (SE = 0.05) in the Slope region. Other studies have indicated that diving to the seafloor, presumably for feeding, appears to be common for beluga whales. Richard et al. (1997) found that beluga whales in water 15–600 m deep often dove to the bottom within shelf waters in the eastern Beaufort Sea and within channels of the Canadian Archipelago. Heide-Jørgensen et al. (1998) found that beluga whales commonly dove to depths at or near the seafloor off the coast of Devon Island, Canada, where average maximum dive depths ranged from 483 to 665 m. Kingsley et al. (2001) found that belugas in Hudson Bay also commonly dove to the seafloor in waters up to 400 m deep. Martin and Smith (1999) found belugas diving to the bottom near Somerset Island, Canada, in water up to 400 m deep. Beluga whales we tagged spent 42% to 69% of the total dive time near the bottom, with shorter durations of bottom time at deeper depths. In addition to benthic organisms, such as shrimp and echiurids, Arctic cod are also known to sometimes concentrate near the seafloor. Near Barrow, Logerwell et al. (2011) found that Arctic cod was the most abundant fish species in bottom trawls, and Crawford et al. (2012) found high densities of Arctic cod near the bottom of Barrow Canyon.

Arctic cod may concentrate at hydrographic fronts, and the depth of these fronts generally corresponds to the depth of beluga dives within the Beaufort Sea. Hydrographic fronts are of known importance to marine mammals and birds, likely because they concentrate zooplankton, which in turn attract forage fishes (e.g., Hunt, 1991; Bost et al., 2009; Logerwell et al., 2011). In summer, the Alaska Coastal Current (ACC) carries Alaska Coastal Water (ACW) through Barrow Canyon. This current follows the Beaufort shelf break eastward and forms the western Arctic Shelf Break Current (Pickart, 2004; Nikolopoulos et al., 2009). Colder, saltier Pacific Winter Water (PWW) occurs both below and offshore of the Western Arctic Shelf Break Current, forming a distinct hydrographic front. Another front is located where PWW grades into warmer Atlantic Water (AW) around the 200–250 m depth (e.g., Pickart, 2004; Pickart et al., 2005; Nikolopoulos et al., 2009; von Appen and Pickart, 2012).

Near Prudhoe Bay, Moulton and Tarbox (1987) found higher densities of Arctic cod in the interface between warmer, fresher coastal water and colder, saltier water offshore (PWW). Similarly, Logerwell et al. (2011) found that along the eastern boundary of Barrow Canyon, Arctic cod (the most abundant fish species in bottom trawls) were more common in PWW. This finding may explain why beluga whales are sighted more frequently along the Beaufort slope than inshore (Moore et al., 2000) and may also explain why belugas commonly dove to the seafloor. Recently, Stafford et al. (2013) compared the strength of the ACC in Barrow Canyon with the density of beluga whales, as indexed by acoustic detections and counts from aerial surveys. They found that beluga group sizes were larger ($\mu = 2.9$ vs. $\mu = 6.8$) and belugas were acoustically detected during more hours of the day (4–6 h/d vs. 10–12 h/d) when the ACC was well defined and formed a stronger hydrographic front.

It is probable that the hydrographic front between colder PWW and warmer AW also has higher concentrations of Arctic cod. Near Barrow, Parker-Stetter et al. (2011) found higher densities of age 1+ Arctic cod in waters 100–500 m deep (i.e., Barrow Canyon and Slope regions) than in waters 40–100 m deep (i.e., the Inshore/shelf region). Figure 5b in Parker-Stetter et al. (2011) shows a layer of age 1+ Arctic cod centered on ~250 m that extends over the shelf break. Although characteristics of the water mass were not measured, this depth is generally the transition zone between colder PWW above and warmer AW below (Pickart, 2004; Pickart et al., 2005; Nikolopoulos et al., 2009; von Appen and Pickart, 2012). Crawford et al. (2012) found large shoals of Arctic cod within the upper part of the layer of AW, between 250 and 300 m, along the Beaufort continental slope. Approximately 46% of beluga dives over Barrow Canyon and 72% of dives over the Slope have a mode at ~250 m. Similarly, tags deployed in 2007 gave evidence that whales repeatedly dove to depths of 200–300 m in both Barrow Canyon and Slope regions (Figs. 10 and 11). Interestingly, such dives were also common over the Arctic Basin, suggesting that cod, or other forage species, may concentrate at this front throughout the Arctic Basin.

The deep dive type we most commonly observed in the eastern Arctic Basin was clearly deeper than the boundary between PWW and AW. Another front occurs at approximately 600–1000 m, where AW slowly grades into colder, more saline Deep Arctic Water (McLaughlin et al., 1996). Echo sounding studies in Amundsen Gulf have found aggregations of Arctic cod within AW in winter, often near the seafloor (Geoffroy et al., 2011). By the end of May, Arctic cod migrate out of Amundsen Gulf, presumably to deeper waters along the shelf break. The deepest dives we observed were in the 900–1000 m depth bin, which corresponds to the approximate lower limit of warm AW in this area (McLaughlin et al., 1996). However, it does not appear that whales were targeting this thermocline, as there were relatively few dives to that depth. Rather, it appears that whales were using the entire layer of AW within the Arctic Basin (Figs. 10 and 11).

Future studies of beluga whales would greatly benefit by deploying oceanographic tags capable of measuring conductivity (i.e., salinity), temperature, and depth. Oceanographic tags would help identify what features or water masses beluga whales are targeting for feeding. This information will improve our understanding not only of beluga behavior, but also of oceanography within Barrow Canyon and the Arctic Ocean, as belugas would effectively sample the water column as they travel and forage (Lydersen et al., 2002).

ACKNOWLEDGEMENTS

This project would not have been possible without the help and cooperation of the people and hunters of Point Lay. We especially thank Warren and Dorcus Neakok, Ben and Alice Neakok, Bill and Marie Tracey, Gordon Upicksoun, Thomas Nukapigak, Amos Agnasagga, Julius Rexford, and Danny Pikok. Many thanks to Charles Aniskette, Alvin Ashby, Vince Dollarhide, Leo Ferreira III, Nick Hank, Lauren Hansen, Rod Hobbs, Laura Hoberecht, Thomas Nukapigak, Jack Orr, Todd Robeck, Tracy Romano, Albert Simon, Heather Smith, Michelle Sparck, Suzann Speckman, Danny Susook, Bob Small, and Glenn and Kristina VanBlaricom for assisting with capture and tagging of whales. Logistical support was provided by Bill and Marie Tracey, Jack Taylor, Jerry Edwards, Julius Rexford, and Danny Susook in Point Lay and by Dave Ramey, Benny Achootchook, and Ambrose Leavitt in Barrow. Additional support and encouragement was received from Lloyd Lowry, Douglas DeMaster, Thomas F. Albert, Taqulik Hepa, Charles D.N. Brower, Dolores Vinas, Liza Delarosa, April Brower, and John Bengtson. Shawn Carey of NOAA and Pamela Clemens of the North Slope Borough administered the grants. Steve Okkonen and Kate Stafford provided helpful discussion on oceanography. Funding was provided by the Minerals Management Service, through the Coastal Marine Institute at the University of Alaska. The National Oceanic and Atmospheric Administration provided major funding to the Alaska Beluga Whale Committee through various grants (NOAA grant numbers NA67FX0197, NA9FX0128, NA17FX2593, and NA04NMF4390144). Funding and in-kind support were also provided by the Village of Point Lay; the North Slope Borough's Department of Wildlife Management, Grants Division, and School District; the National Marine Mammal Laboratory of the National Marine Fisheries Service; the Alaska Department of Fish and Game; the Minerals Management Service through the Coastal Marine Institute at the University of Alaska Fairbanks; and the Washington Cooperative Fish and Wildlife Research Unit at the School of Aquatic and Fishery Sciences, University of Washington. This research was conducted under Marine Mammal Protection Act permits (Nos. 782-1438 and 782-1719) issued to the National Marine Fisheries Service.

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