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Photo: Beluga whale tagging project in Cook Inlet, Alaska. From L to R: Monitoring the whale are Kristin Laidre and Rod Hobbs, restraining the fluke and assisting with the blood draw are Laura Hoberecht, Matt Eagleton, Bill Walker, Greg O'Corry-Crowe, Dan Vos, and Barbara Mahoney (standing). Photographer: Dana Seagars, NMFS-AKR.

MOVEMENT AND DIVE BEHAVIOR OF BELUGA WHALES IN COOK INLET, ALASKA

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ABSTRACT

Limited information exists on the foraging behavior of the endangered population of beluga whales (*Delphinapterus leucas*) in Cook Inlet, Alaska, especially during the winter months with heavy ice-cover. We used satellite telemetry to record the movement (n = 14) and diving (n = 11) behavior of whales across 3 years (1999-2003), including the winter months. Whales remained in Cook Inlet the entire time they were tracked. Mean dive depths across the entire tracking period ranged from 1.6 (SD ± 2.1) to 6.7 (SD ± 10.4) m and mean dive duration ranged from 1.1 (SD ± 1.3) to 6.9 (SD ± 9.5) minutes. Overall, dives were significantly shorter in the near-shore areas of Chickaloon Bay, Susitna Delta, Knik Arm, Turnagain Arm, and Trading Bay. This type of dive behavior, in combination with significantly slower transit rates suggests that whales are likely foraging in these areas. While belugas tended to prefer shallow inshore waters throughout the year, the presence of sea ice between December and May may prevent access to coastal areas. Preference for pack ice, despite the large proportions of Cook Inlet remaining ice-free, may be an indication of belugas attempting to access coastal areas despite increased ice concentration. With the declining abundance of Cook Inlet belugas, identifying potential foraging areas during ice-covered and ice-free periods is critical to the recovery of this endangered population.

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INTRODUCTION

Beluga whales (*Delphinapterus leucas*) in Cook Inlet are the most geographically and genetically isolated of the five stocks recognized around Alaska (O Corry-Crowe et al. 1997, Laidre et al. 2000). Their isolation, in combination with high site fidelity in summer (Rugh et al. 2000, 2005, 2010), makes them particularly vulnerable to both environmental (Moore et al. 2000) and anthropogenic impacts (Hill 1996). The population of Cook Inlet belugas declined by nearly 50% between 1994 and 1998 to an estimated 347 whales (Hobbs et al. 2000). Despite cessation of the Alaska Native subsistence hunt in 1999 of approximately 70 animals per year (Mahoney and Shelden 2000), the abundance estimates of belugas in Cook Inlet have remained low (321 and 340 animals in 2009 and 2010 compared to 653 in 1994) with no notable signs of recovery (Hobbs and Shelden 2008). In recognition of the low numbers of belugas remaining in Cook Inlet, the U.S. government listed this isolated population as endangered under the U.S. Endangered Species Act in October 2008.

The summer distribution and habitat of belugas has been well documented from annual aerial surveys (Rugh et al. 2000, 2004, 2005; Goetz et al. 2007, 2012). During this time, belugas concentrate in the upper reaches of the Inlet in shallow bays and river mouths where fish runs are abundant (Lensink 1961, Moore et al. 2000, Goetz et al. 2012). Prior to biologging technology, the winter distribution of Cook Inlet belugas was poorly understood and considered enigmatic. Calkins (1983) hypothesized that belugas left Cook Inlet during the winter, especially when heavy ice was present. Sporadic sightings outside of Cook Inlet have occurred in all seasons; however, these sightings of belugas are considered rare relative to the survey effort and hundreds of thousands of other cetacean sightings documented for the Gulf of Alaska and adjacent inside waters (Laidre et al. 2000).

In addition to sighting small, scattered pods of belugas during February-March 1997 surveys of Cook Inlet (Hansen and Hubbard 1999), numerous opportunistic sightings have been reported throughout the year (NMFS unpubl. data). Belugas were also observed every month except February during monthly aerial surveys conducted in 2001-2002, suggesting that at least part of the beluga population remains in the Inlet over winter (Calkins 1983). During these surveys, there were fewer beluga sightings in the winter (10 in January) than the summer (204 in

August), which may be linked to the inability of observers to detect belugas amongst heavy ice (Rugh et al. 2004).

Hobbs et al. (2005) provided the first evidence that belugas remain in Cook Inlet throughout the year and tend to disperse offshore into the deeper waters of the Inlet during the winter. While this study shed light on the location of Cook Inlet belugas during the winter, the dive behavior of these animals has yet to be well documented. A previous study utilized suction-cup attached VHF radio transmitters to characterize surfacing behavior and dive intervals in summer (Lerczak et al. 2000). While VHF telemetry provides general information on surfacing frequency and time spent below the surface it must be monitored from close range, and lacks the capability of remotely relaying detailed information on dive behavior. Biologging technology has proven to be a useful tool to monitor the movements and dive behavior of belugas in the high Arctic (Martin and Smith 1992, 1999; Heide-Jorgensen et al. 1998; Richard et al. 1998; Suydam et al. 2001). The decrease in tag size (mounted on the dorsal ridge) and increase in tag longevity (both battery life and attachment time) have facilitated the remote and continuous collection of data from individual whales for many months at a time.

In this study, biologging technologies were used to monitor the movements and dive patterns of belugas in Cook Inlet between 1999 and 2002. The goals were to examine movement and diving metrics such as transit rate, horizontal and vertical travel distances, and dive depth and duration to determine the preferred habitats and potential foraging locations of Cook Inlet belugas across two seasonal periods based on the presence of ice: June-November (summer and fall) and December-May (winter and spring).

METHODS

Tagging Protocol

Eighteen belugas were captured and tagged in three locations in upper Cook Inlet between 1999 and 2002 (Fig. 1). In 1999, one adult male was instrumented on 31 May at the mouth of the Little Susitna River. In September 2000 (n = 2) and August 2001 (n = 6), eight belugas were tagged in the vicinity of Eagle Bay, Knik Arm. A small female was tagged near the Little Susitna River in August 2001. During the end of July and beginning of August 2002 belugas were tagged at Little Susitna River (n = 2) and in Knik Arm (n = 6) (Table 1). Belugas were instrumented with either a satellite-linked time-depth recorder (Wildlife Computers Ltd., Redmond, WA) containing a Telonics ST-16 ARGOS transmitter (Telonics, Mesa, AZ) (ST-16, n = 11), a smart position or temperature transmitting tag (SPOT2, n = 2) (Wildlife Computers Ltd., Redmond, WA), or both (n = 5) (Table 1). Tags were programmed such that the ST-16 transmitted 24 hours a day while the SPOT2 tags transmitted every 10 days for 24 hours.

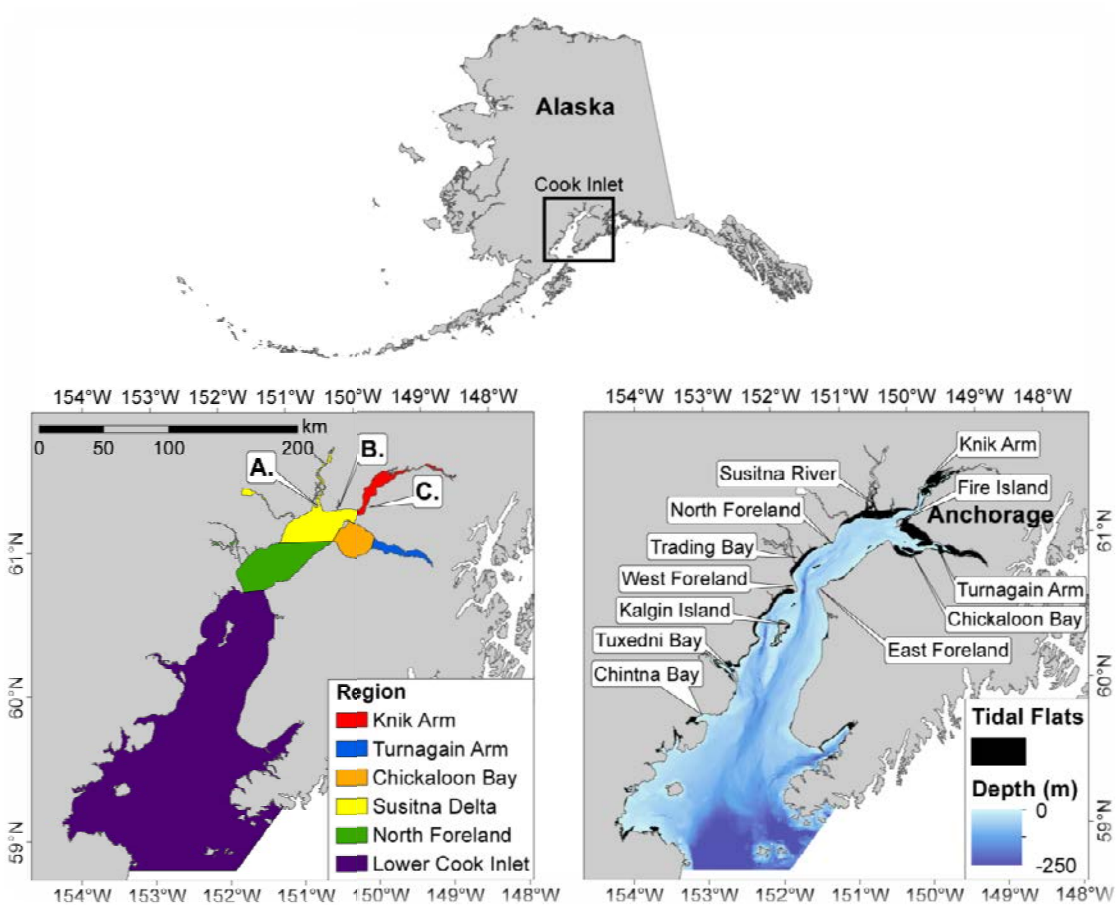

Figure 1. -- Cook Inlet, Alaska study area showing six defined regions and three tagging locations (A = Susitna River Delta, B = Little Susitna River, and C = Knik Arm near Eagle Bay) (left); Cook Inlet bathymetry and tidal flats (right).

Table 1. -- Tag type, location and physical characteristics of belugas tagged in Cook Inlet, Alaska, between 1999 and 2002.

Beluga ID	Tag type	Tag date	Tag location	Sex	Color	Length (cm)
CI-9901	ST-16	31 May 1999	Little Susitna River	M	White/gray	370
CI-0001	ST-16	13 Sept. 2000	Knik Arm	M	White	413
CI-0002	ST-16	13 Sept. 2000	Knik Arm	F	White/gray	272
CI-0101	SPOT2	10 Aug. 2001	Little Susitna River	F	Gray	257
CI-0102	ST-16[1]/SPOT2	11 Aug. 2001	Knik Arm	M	White	323
CI-0103	ST-16/SPOT2	12 Aug. 2001	Knik Arm	F	White	312
CI-0104[2]	ST-16[1]/SPOT2	13 Aug. 2001	Knik Arm	F	White	340
CI-0105	SPOT2	13 Aug. 2001	Knik Arm	F	White	357
CI-0106	ST-16/SPOT2	15 Aug. 2001	Knik Arm	F	White	401
CI-0107	ST-16/SPOT2	20 Aug. 2001	Knik Arm	M	White	442
CI-0201	ST-16	29 July 2002	Little Susitna River	M	White	412
CI-0202[2]	ST-16	30 July 2002	Little Susitna River	F	White/gray	341
CI-0203	ST-16	31 July 2002	Knik Arm	F	White	366
CI-0204[2]	ST-16	01 Aug. 2002	Knik Arm	F	White	379
CI-0205	ST-16	02 Aug. 2002	Knik Arm	M	White/gray	386
CI-0206	ST-16	03 Aug. 2002	Knik Arm	M	White/gray	353
CI-0207[2]	ST-16	03 Aug. 2002	Knik Arm	F	White	374
CI-0208	ST-16	04 Aug. 2002	Knik Arm	M	White/gray	376

[1] ST-16 did not transmit.
[2] Not included in analyses as tags transmitted < 1 day.

Using a modified encirclement technique, belugas were captured with set nets deployed from a boat (Ferrero et al. 2000). The tag deployed in 1999 was glued to a flexible rubber saddle with holes for attachment via pins. The tags deployed in 2000 incorporated two or three Monel cables into the epoxy casting, which were attached to the pins through the dorsal ridge of the whales with nuts and bolts. During the second half of 2001 and all of 2002, 3/8" pins with holes on either end for cable attachment were used.

Data Processing

Tracking Data

All data relayed via ARGOS were decoded using a DAP processor (Wildlife Computers). ARGOS data from the three belugas tagged with both SDR-T16 and SPOT2 transmitters were combined and sorted to maximize the quantity of location data. Location data were filtered using a basic speed filter of 15 km hr^{-1} to remove erroneous points (McConnell et al. 1992), based on the distribution of calculated speeds between ARGOS positions and the average known swimming speed of belugas (Richard et al. 2001b, Ezer et al.

2008). A land avoidance algorithm was developed and applied to these data to adjust positions from land to nearby water locations. Gaps in the data of longer than one day were removed to avoid errors associated with interpolating a track line far from any real ARGOS positions, thus dividing each animal's track into several segments. Using the 'CRAWL' package in *R* (Johnson 2011), we fit a continuous time-correlated random walk model to the ARGOS data in order to produce the most likely hourly position for each animal. This method takes into account the ARGOS error structure for each location class when interpolating the track (Johnson et al. 2008) and prevents unnecessary removal of lower location classes.

Kernel densities of the interpolated tracks were calculated in ArcMap (ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute) on the whole dataset and for two seasonal periods (June-November and December-May). Based on the average width of the narrowest parts of Cook Inlet (Knik Arm and Turnagain Arm), we used a 4 km search radius for all kernel density analyses. Because kernel analysis can be influenced by the number of animals in an area, we also produced graphics showing the sum of unique animals over the analysis extent. All kernel density surfaces were rescaled to values between 0 and 1 to facilitate comparison.

To provide a meaningful summary of tracking and diving metrics, we analyzed the data set as a whole to assess overall beluga behavior, and separately, as two seasonal periods, to assess beluga behavior in the presence and absence of ice. The two seasonal periods were based on the average significant appearance and disappearance of ice in northern Cook Inlet over a 17-year period (November 25 (SD ± 17 days) and April 9 (SD ± 18 days) between 1969 and 1985) (Mulherin et al. 2001). Using December as the cut-off between ice-covered and ice-free months in Cook Inlet, we divided the data into two equal time intervals: June-November and December-May. In addition, we divided the Cook Inlet study area into six analysis regions based on the geography of the inlet in order to create meaningful synthesis of beluga transit and dive behavior.

For each interpolated track data, we calculated mean transit rate (km hr^{-1}), maximum horizontal displacement, and the ratio of maximum horizontal displacement to total horizontal distance traveled for each individual and region in Cook Inlet. These values were calculated over the entire 4-year tracking period and for both 6-month periods. The ratio of maximum horizontal displacement to the total track length allowed us to assess the degree of directness or looping for each track. A paired *t*-test was used to assess difference in mean transit rates for each animal between the two seasonal periods and a two-factor ANOVA to examine differences in transit rate between regions and seasonal periods. To spatially depict areas of slow and fast transit rates, we used the hotspot analysis tool in ArcMap. This tool uses the Getis-Ord statistic, Gi*, to identify statistically significant spatial clusters of high values (hot spots) and low values (cold spots). The Gi* of the cell is the spatial average of the surrounding cells divided by the expected standard error. Extreme values of this statistic indicate more intense clustering around a location and measure the degree of deviation from a random distribution. The results from the hotspot analysis, *z*-scores, were transformed into a smooth surface using spatial averaging and were rescaled to values between -1 and 1 to accurately reflect hotspots (red) and low spots (blue).

Association with Sea Ice

The spatial distribution of sea ice concentration in Cook Inlet, computed twice a month between 1999 and 2003, was used to investigate beluga movements relative to average ice conditions. Ice concentration data were compiled from several imagery sources and downloaded from the National Ice Center (http://www.natice.noaa.gov/products/weekly_ products.html) and were converted from interchange file format to rasters using ArcMap. These data were delivered as polygons representing discrete ice concentration values: 0, 1, 13, 24, 35, 46, 57, 68, 79, 81, 91 and 92%. Ice data were re-categorized using definitions presented in the NOAA Observers Guide to Sea Ice (available at http://response.restoration.noaa.gov/book_shelf/ 695_seaice.pdf). Zero ice concentration was classified as ‘open water’, concentrations of 1, 13, and 24 were considered ‘very open pack’, concentrations of 35, 46, 57, and 68 were considered ‘open pack’, concentrations of 79 and 81 were considered ‘close pack’, and ice concentrations of 91 and 92 were considered ‘compact’ ice. The ice concentration value for each interpolated beluga location was extracted from the appropriate biweekly ice raster. To assess which ice type the majority of belugas inhabited, we examined the median ice concentration for all locations within the respective 2-week period relative to the proportion of ice types available in Cook Inlet for that period.

Six-hour Histogram Data

While all 11 tagged belugas instrumented with ST-16 tags transmitted histogram data on dive behavior, only six tags remained attached during both 6-month periods. We added 3 hours to the time of each 6-hour histogram to determine the midpoint and then used the interpolated track to calculate new positions based on time. All ST-16 tags had pressure transducers that sampled the depth of the whale at a resolution of 1 m. The dive data were summarized into bins representing 6 hours of behavior and transmitted via satellite. These data included the number of dives to depth and time spent in 14 depth categories (0-1, 1-2, 2-3, 3-4, 4-5, 5-10, 10-25, 25-50, 50-75, 75-100, 100-150, 150-200, 200-245, and > 245 m). Time at depth was reported as the number of 10-second intervals occurring within each depth bin; therefore, dive durations less than 10 seconds in a depth bin were potentially missed. In addition to depth bins, the number of dives was also compiled into 14 duration bins of 0-1, 1-2, 2-3, 3-4, 4-5, 5-6, 6-8, 8-10, 10-12, 12-15, 15-18, 18-21, 21-24, and > 24 minutes.

We calculated mean and maximum values for dive depth and duration across all 14 bins assuming that the maximum depth and duration occurred at the midpoint of each 6-hour interval. Values were calculated for each animal and region using all the data as well as two seasonal periods (June-November and December-May). A paired *t*-test was used to analyze differences in maximum and mean dive depth for the six animals that transmitted data across both 6-month periods. Because mean dive duration violated the assumptions of normality, we used a Wilcoxon test to access differences in dive duration between seasons. A two-factor ANOVA was used to examine differences in dive depth and duration across regions and seasons. Again, comparisons were made using dive data from the six belugas in which the tag relayed information for both 6-month periods.

Hotspot and kernel density analyses were used to identify regions of elevated diving activity. The hotspot analysis identifies spatial clusters of short and long duration dives, as well as large and small numbers of dives, independent of the number of whales while kernel density analysis calculates the density of dives on a continuous scale but is influenced by the number of whales.

In order to calculate the time spent diving relative to total time (or dive effort) for each beluga, we summed the time spent at depth across all 6-hour bins for each individual and divided by the total time accounted for by the 6-hour bins. Again, we used the hotspot analysis tool in

ArcMap to spatially depict clusters where belugas spent significantly more or less time at depth. The *z*-scores produced from this analysis were converted to a continuous surface using a 4 km search radius and rescaled from -1 to 1 to accurately portray hotspots and coldspots, respectively. Time spent diving was also examined across all regions and 6-month periods.

We classified beluga dives as benthic or pelagic by subtracting the bathymetric depth at the location of every dive from the midpoint of the depth bin. For example, if a dive occurred in 50 m of water and was recorded in the 5-10 m bin, then we subtracted -50 from -5.5 to get a value of 44.5. The resulting value provided a dive index with positive values representing midwater dives and negative values representing benthic dives. Because absolute values were not very informative due to errors in both the dive data and available bathymetry (3 arc sec coastal relief model obtained from http://www.ngdc.noaa.gov/mgg/coastal/coastal.html), we performed a hotspot analysis on the data to identify clusters of low values (areas where belugas were most likely diving to the bottom) and high values (areas where belugas were engaged in midwater diving). Because all dives occurring in areas that are exposed during low tide would result in a benthic classification by this method, areas overlapping with exposed tidal flats (as coded in the Environmental Sensitivity Index (ESI) for Cook Inlet) were excluded from this analysis.

In addition to classifying beluga dives, we examined the available bathymetry in Cook Inlet relative to the bathymetry at belugas dive locations. Again, due to unavoidable error associated with 6-hour binned data and the bathymetry, we categorized all bathymetric values within the extent of the beluga dive data and the bathymetric value associated with each dive into two classes: < 25 m (shallow) and > 25 m (deep). The cutoff value between deep and shallow was based on the median bathymetric value within the extent of the dive data, encompassing all but the southernmost region of Cook Inlet. We also examined the bathymetric value associated with all beluga dive locations according to both 6-month periods to determine if belugas prefer shallower or deeper areas of Cook Inlet during different times of year.

RESULTS

Tag Performance

Using a 15 km hr^{-1} basic speed filter on the ARGOS data reduced the number of locations by 31%, consistent with prior studies (Austin et al. 2003, Freitas et al. 2008). Removing gaps greater than 1 day further reduced the amount of data used in this analysis (Table 2). Although the tags transmitted for a total of 1,989 days (tag days), this was reduced to 1,479 analysis days (summed over 115 segments). The three animals transmitting with only SPOT2 tags (CI-0101, CI-0102, and CI-0105 - Table 2) contributed most to the discrepancy between tag and analysis days due to the programming of the tags (see Methods). Although four animals (CI-0102, CI-0106, CI-0201, and CI-0203) did not transmit during the December-May period, of the 1,479 total analysis days, 926 occurred in June-November and 552 in December-May. Total distance traveled (horizontal distance) was highly dependent on the number of analysis days and ranged between 493 and 15,689 km. The total vertical distance, assuming the animal traveled straight up and down during each dive, was also correlated with the number of analysis days and ranged between 41 and 944 km (Table 2). The number of 6-hour depth, duration, and time-at-depth histograms was nearly identical among belugas equipped with ST-16 tags (n = 11).

Table 2. --The number of segments and analysis days after removing data gaps greater than 1 day, horizontal and vertical distances traveled, and the number of histogram types (depth, duration, and time-at-depth (TAD) for belugas tagged in Cook Inlet between 1999 and 2002, overall and in two seasonal periods (June-November and December-May). Dash denotes no data.

Beluga ID	Tag days	Segments (*n*)	Analysis days: Overall	Analysis days: June-Nov.	Analysis days: Dec.-May	Horizontal dist. (km)	Vertical dist. (km)	6-hour histograms (*n*): Depth	6-hour histograms (*n*): Duration	6-hour histograms (*n*): TAD
CI-9901	108.2	5	103.0	102.8	0.1	4,715.4	193.4	398	398	407
CI-0001	111.6	1	111.5	77.8	33.6	9,610.7	518.0	440	442	438
CI-0002	126.3	1	126.3	78.0	48.2	10,193.1	605.6	487	475	481
CI-0101	121.5	8	5.6	4.8	0.8	528.6	-	-	-	-
CI-0102	106.8	8	5.6	5.6	0.0	493.0	-	-	-	-
CI-0103	128.9	17	21.8	21.6	0.2	824.3	41.6	45	49	51
CI-0105	138.6	23	14.9	10.3	4.6	1,277.7	-	-	-	-
CI-0106	104.1	2	94.7	94.7	0.0	5,943.8	390.1	371	370	368
CI-0107	200.5	1	200.3	101.9	98.4	15,699.9	1,386.6	796	798	797
CI-0201	94.0	3	91.5	91.5	0.0	4,097.9	152.0	352	351	356
CI-0203	23.2	1	23.2	23.2	0.0	1,228.0	205.6	88	88	89
CI-0205	241.2	10	215.8	111.8	104.0	8,169.2	792.8	767	755	762
CI-0206	230.6	18	200.6	104.7	95.8	8,321.3	913.4	755	757	744
CI-0208	293.4	17	264.7	98.0	166.7	10,191.9	1,946.1	940	944	937
Total	1,988.97	115	1,479.3	926.6	552.4	81,283.6	7,145.1	5,041	5,029	5,023

Distribution and Movements

By examining the interpolated tracking data for all whales overall and over two 6-month periods, we found that belugas spend most of their time in upper Cook Inlet, north of East Foreland and West Foreland (Figs. 1 and 2). During the 4 years of tagging data, three belugas ventured farther south than Kalgin Island with the farthest traveling animal reaching Tuxedni and Chinitna Bays in October. Approximately 63% of the tracking data occurred in June-November, with the greatest concentration occurring in northern Cook Inlet (Fig. 2). Kernel density plots show a clear pattern in the distribution of belugas (Fig. 3). In June-November, belugas spent the greatest amount of time in Knik Arm and Chickaloon Bay while in December-May the preferred areas are located farther south and encompass most of the area above East and West Foreland. Pooling all the data across the two 6-month periods and correcting for region area (Fig. 1) depicts where belugas spent most of their time: in Knik Arm, Turnagain Arm, Chickaloon Bay, and Susitna Delta regions (Table 3). Throughout the year, belugas spend over half their time in Knik Arm alone.

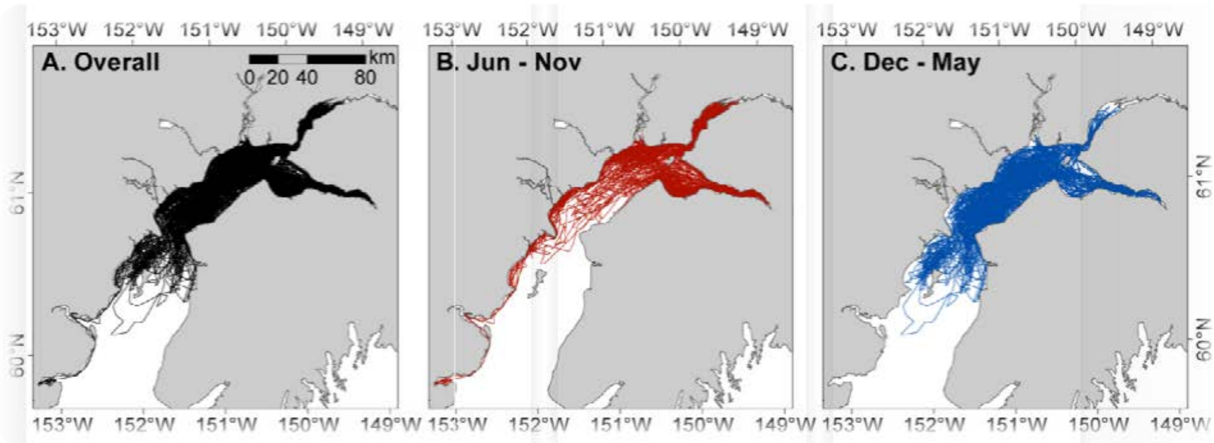

Figure 2. -- Tracklines (overall (A) and by two 6-month periods: June-November (B) and December-May (C)) from 14 belugas tagged in Cook Inlet, Alaska, 1999-2002.

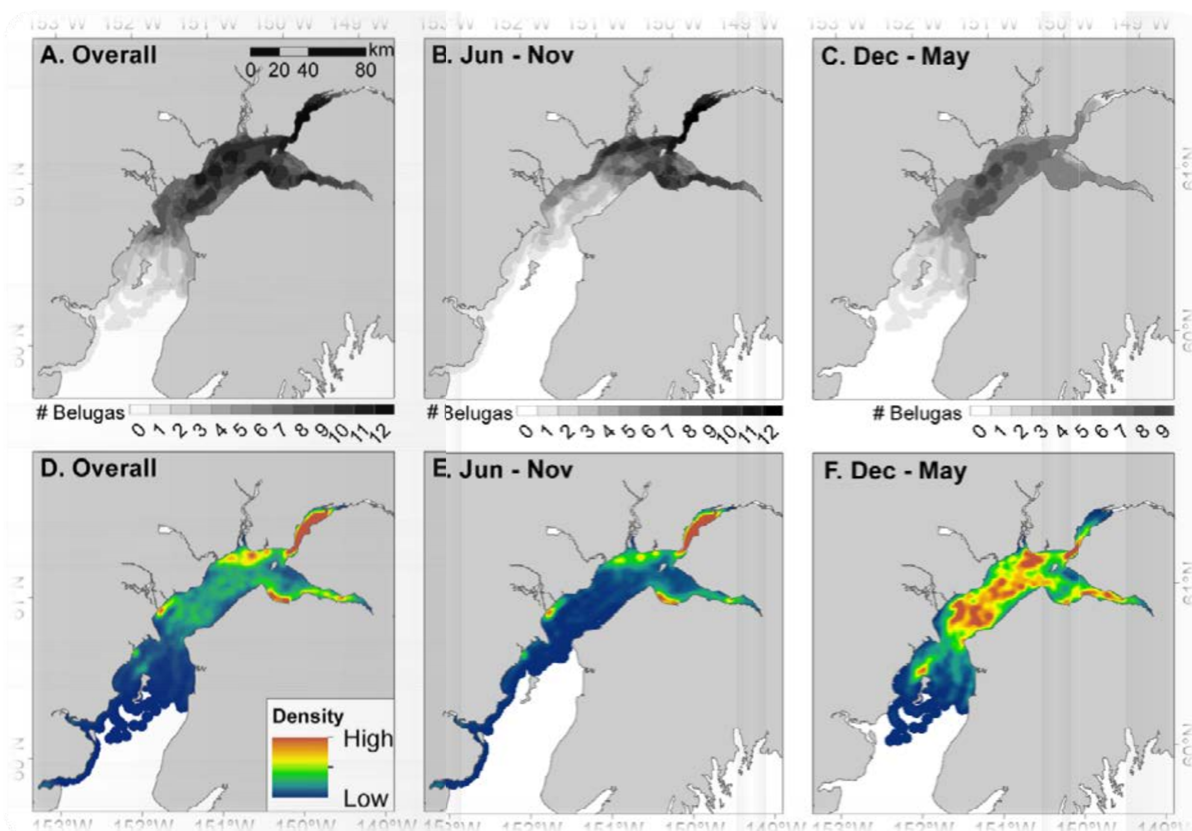

Figure 3. -- Number of belugas tagged in Cook Inlet, Alaska, 1999-2002 (A-C) and kernel densities of interpolated hourly positions (D-F) overall (A,D) and for two seasonal periods (June-November: B,E and December-May: C,F).

Table 3.-- Percentage of dives and time preset in each region for belugas tagged between 1999 and 2002, overall and in two seasonal periods (June-November and December-May), in six different regions of Cook Inlet. Proportions are corrected for region area.

	# dives (%)			Time present (%)		
Region	Overall	June-Nov.	Dec.-May	Overall	June-Nov.	Dec.-May
Knik Arm	52.5	64.6	11.7	53.8	65.8	13.0
Turnagain Arm	18.0	14.7	28.9	16.2	13.4	25.7
Chickaloon Bay	12.9	12.8	13.1	11.4	10.2	15.3
Susitna Delta	11.1	5.7	29.2	11.2	8.1	21.6
North Foreland	5.4	2.1	16.6	7.2	2.4	23.7
Lower Cook Inlet	0.2	0.1	0.4	0.2	0.1	0.6

Mean transit rate for all belugas was 2.8 (SD ± 2.4) km hr^{-1}, ranging from 1.6 (SD ± 2.0) km hr^{-1} to 4.3 (SD ± 3.1) km hr^{-1} among individuals (Table 4). Overall, belugas traveled significantly faster during December-May than June-November (paired *t*-test, $P < 0.001$). Transit rates in the six regions were also significantly different, both overall and by 6-month period (two-factor ANOVA, $P < 0.001$) (Table 5). Results from the hotspot analysis show that, regardless of the number of belugas, there are significant clusters of slow transit near the coast in Knik Arm, Chickaloon Bay, Susitna Delta, and Trading Bay and significant clusters of fast transit in areas away from the coast (Fig. 4). While there were clusters of slow transit in Trading Bay and Susitna Delta during both 6-month periods, the cluster of slow transit in Knik Arm during June-November shifted to Chickaloon Bay during December-May.

Average maximum straight line distance traveled from the first to the last position was 122 km, ranging from 35 to 242 km (Table 4). The ratio of maximum displacement to cumulative horizontal distance ranged from 0.01 to 0.08 with a mean of 0.04. There was no significant difference in either the mean maximum distance traveled or the mean ratio of max distance and total distance between 6-month periods for individual belugas.

Movement of belugas was influenced by the presence of ice in Cook Inlet during the winter (Fig. 5). Total ice cover in Cook Inlet was always less than 50% for every 2-week period. When ice was present, belugas were most commonly found in open pack ice (2002) and very open pack ice (2003). In 2002, belugas (n = 2) preferred open water only 2% of the time when ice was present in Cook Inlet as compared to 30% in 2003 (n = 3). Ice covered less than 10% of Cook Inlet on most occasions when belugas preferred open water.

Table 4. -- Mean transit rate, maximum displacement and the ratio of maximum displacement to total horizontal distance traveled for belugas tagged in Cook Inlet, Alaska, between 1999 and 2002, overall and in two seasonal periods (June-November and December-May). Dash denotes no data.

Beluga ID	Mean transit rate (km hr^{-1}) ± StDev Overall	June-Nov.	Dec.-May	Max displacement (km) Overall	June-Nov.	Dec.-May	Maximum displacement/ horizontal distance Overall	June-Nov.	Dec.-May
CI-9901	2.0 ± 2.1	2.0 ± 2.1	2.1 ± 1.6	87.04	87.04	7.07	0.02	0.02	0.93
CI-0001	3.8 ± 2.7	3.5 ± 2.7	4.3 ± 2.9	125.59	101.63	125.59	0.01	0.02	0.04
CI-0002	3.5 ± 2.5	3.4 ± 2.4	3.8 ± 2.5	192.85	165.90	192.85	0.02	0.03	0.05
CI-0101	4.3 ± 3.1	4.2 ± 3.1	5.5 ± 2.8	35.89	27.09	35.89	0.07	0.06	0.33
CI-0102	3.9 ± 2.9	3.9 ± 2.9	-	34.91	34.19	-	0.07	0.07	-
CI-0103	1.6 ± 2.0	1.6 ± 2.0	3.7 ± 2.5	67.35	67.35	8.48	0.08	0.08	0.46
CI-0105	3.8 ± 3.0	3.4 ± 3.0	4.8 ± 2.8	36.96	36.96	31.68	0.03	0.05	0.06
CI-0106	2.8 ± 2.6	2.8 ± 2.6	-	141.23	141.23	-	0.02	0.02	-
CI-0107	3.4 ± 2.8	2.9 ± 2.8	4.0 ± 2.7	173.32	72.22	173.32	0.01	0.01	0.02
CI-0201	2.1 ± 2.1	2.1 ± 2.1	-	241.66	241.66	-	0.06	0.06	-
CI-0203	2.3 ± 2.1	2.3 ± 2.1	-	135.82	135.82	-	0.11	0.11	-
CI-0205	1.7 ± 1.8	1.3 ± 1.7	2.1 ± 1.9	135.72	82.81	135.72	0.02	0.03	0.03
CI-0206	1.8 ± 1.9	1.4 ± 1.8	2.3 ± 2.0	145.10	145.10	137.88	0.02	0.05	0.03
CI-0208	1.7 ± 1.7	1.2 ± 1.6	2.0 ± 1.8	151.51	136.44	151.51	0.01	0.05	0.02
Mean	2.8 ± 1.0	2.6 ± 1.0	3.4 ± 1.3	121.78	105.39	100.00	0.04	0.05	0.20

Table 5. -- Mean transit rate, depth and duration for belugas tagged between 1999 and 2002, overall and in two seasonal periods (June-November and December-May) in six regions of Cook Inlet, Alaska.

Region	Mean transit rate (km hr^{-1}) ± StDev Overall	June-Nov.	Dec.-May	Mean depth (m) ± StDev Overall	June-Nov.	Dec.-May	Mean duration (minutes) ± StDev Overall	June-Nov.	Dec.-May
Knik Arm	2.1 ± 2.4	2.1 ± 2.4	2.4 ± 2.5	2.5 ± 4.5	2.5 ± 4.3	4.0 ± 7.7	1.7 ± 3.0	1.5 ± 2.0	6.0 ± 6.0
Turnagain Arm	3.0 ± 3.1	3.0 ± 3.1	2.9 ± 3.0	2.7 ± 4.9	1.9 ± 2.5	4.1 ± 7.2	1.9 ± 4.0	1.1 ± 1.6	3.3 ± 3.3
Chickaloon Bay	2.5 ± 2.1	2.5 ± 2.1	2.5 ± 2.1	3.4 ± 6.5	2.3 ± 3.6	6.9 ± 11.1	2.0 ± 3.9	1.3 ± 1.7	4.2 ± 4.2
Susitna Delta	2.3 ± 2.2	2.2 ± 2.1	2.5 ± 2.3	5.0 ± 9.6	3.2 ± 5.8	6.2 ± 11.2	4.2 ± 7.0	1.9 ± 2.5	5.6 ± 5.6
North Foreland	2.5 ± 2.3	1.9 ± 2.1	2.8 ± 2.3	7.8 ± 13.1	3.3 ± 6.1	9.7 ± 14.7	5.4 ± 7.9	1.3 ± 1.8	7.1 ± 7.1
Lower Cook Inlet	3.0 ± 2.4	2.3 ± 2.2	3.4 ± 2.4	7.2 ± 11.9	1.8 ± 3.3	10.2 ± 13.7	3.0 ± 4.8	1.3 ± 1.9	3.9 ± 3.9
Mean	2.6 ± 2.4	2.4 ± 2.4	2.7 ± 2.4	4.8 ± 8.4	2.5 ± 4.3	6.9 ± 10.9	3.0 ± 5.1	1.4 ± 1.9	5.0 ± 5.0

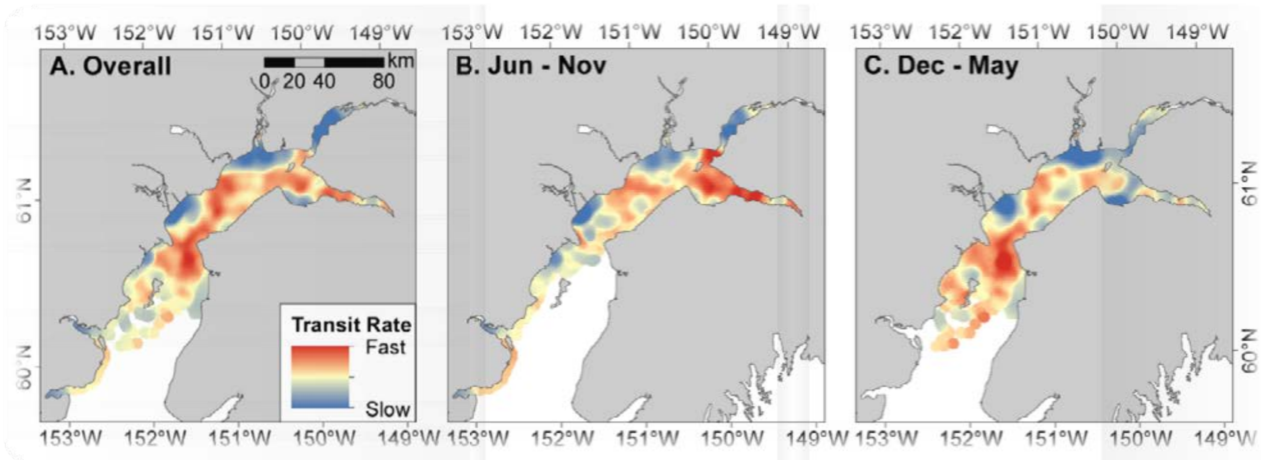

Figure 4. -- Hotspot analysis showing significant spatial clusters of slow (blue) and fast (red) transit rate for belugas tagged in Cook Inlet, Alaska, 1999-2002 (A. overall, B. June-November and C. December-May). Yellow areas are not significant.

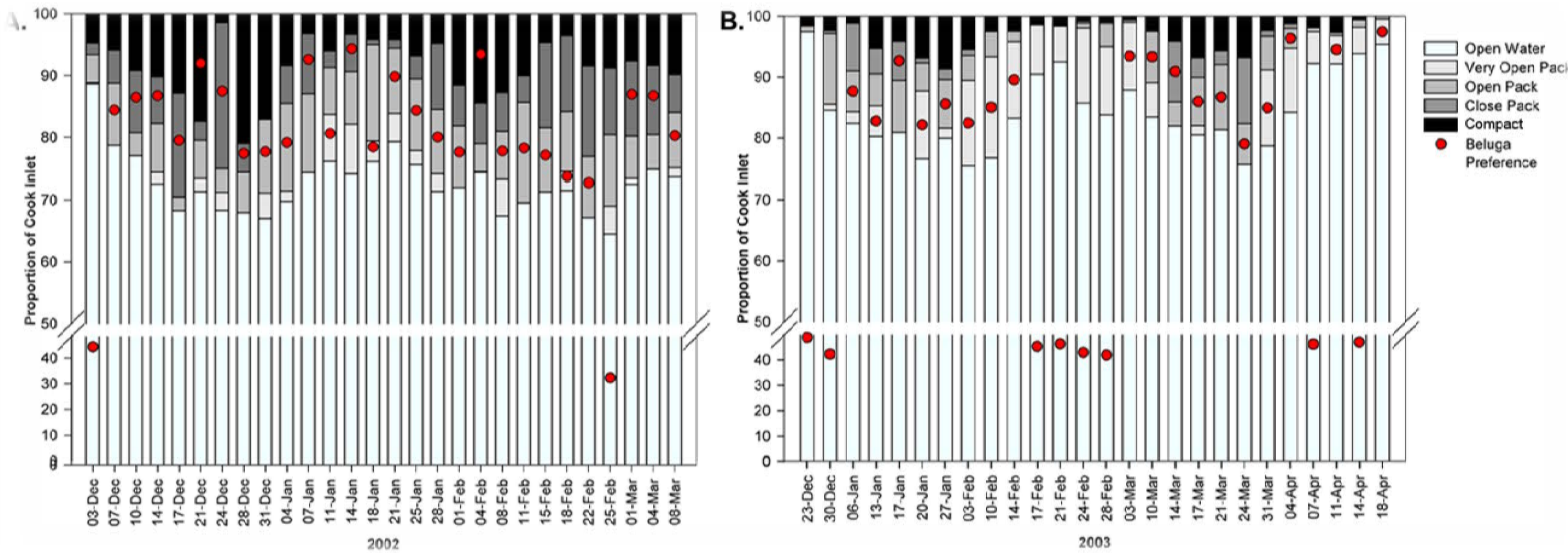

Figure 5. -- Biweekly proportion of ice type in Cook Inlet, Alaska, in 2002 (A) and 2003 (B) Red dots indicate ice-cover preferences of belugas tagged with satellite-transmitters during that period.

Dive Depth and Duration

The ratio of cumulative horizontal track length to total vertical dive distance ranged from 5.2 to 24.4 among belugas (Table 6). This ratio was significantly different between 6-month periods (paired *t*-test, $P < 0.01$) with animals in December-May having a lower ratio than in June-November. This pattern was driven by an increase in dive effort during December-May.

The number of dives recorded in each depth and duration bin varied by region and 6-month period (Figs. 6 and 7). No dives were recorded in the last two depth bins of the histogram data (150-200 and 200-250 m). Over 50% of the dives occurred in the first two depth (0-1 and 1-2 m) and duration bins (0-1 and 1-2 minutes) across regions and seasons. Deeper (5-50 m of water) and longer (> 21 minutes) dives were found in the Susitna Delta, North Foreland, and Lower Cook Inlet Regions. Deeper and longer dives were also more common in December-May than June-November.

Table 6. -- Ratios of the total horizontal distance to total vertical distance traveled and the amount of time spent diving to total time for belugas tagged in Cook Inlet between 1999 and 2002, overall and in two seasonal periods (June-November and December-May). Dash denotes no data.

	Horizontal distance/ vertical distance (m)			Time diving/total time (minutes)		
Beluga ID	Overall	June-Nov.	Dec.-May	Overall	June-Nov.	Dec.-May
CI-9901	24.4	24.3	-	15.6	15.6	-
CI-0001	18.6	21.3	15.0	24.3	21.8	30.5
CI-0002	16.8	25.7	11.4	28.6	27.7	30.1
CI-0103	19.8	19.4	-	17.4	17.4	-
CI-0106	15.2	15.2	-	23.8	23.8	-
CI-0107	11.3	14.3	9.9	26.6	24.1	29.1
CI-0201	27.0	27.0	-	15.8	15.8	-
CI-0203	6.0	6.0	-	24.4	24.4	-
CI-0205	10.3	12.1	9.4	18.3	16.5	20.6
CI-0206	9.1	14.1	7.5	20.5	15.2	26.6
CI-0208	5.2	11.3	4.4	21.9	16.6	25.1
Mean	14.9	17.3	9.6	21.6	19.9	27.0

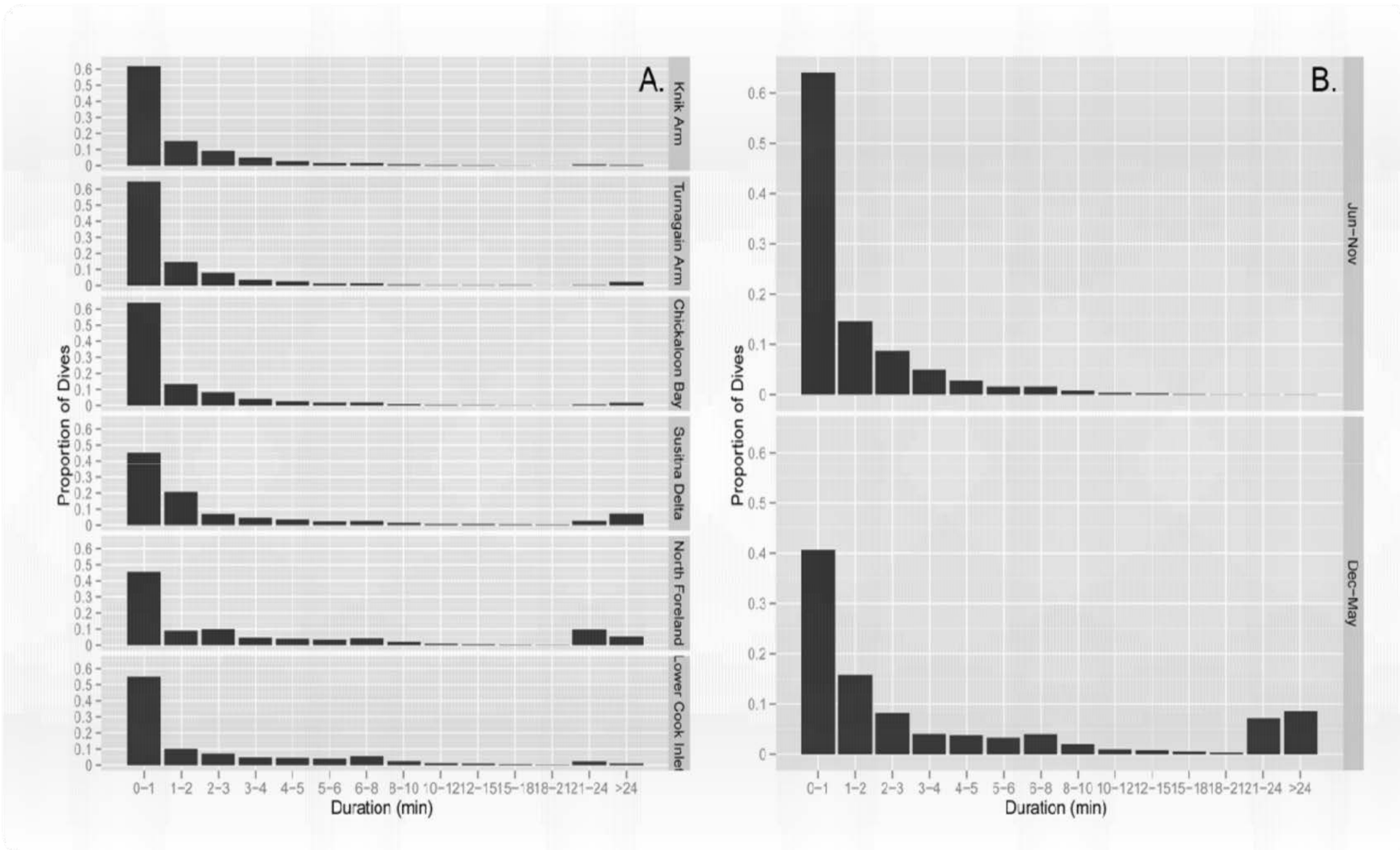

Figure 6. -- Proportion of dives in each duration bin in six regions of Cook Inlet (A) and two seasonal periods (June-November and December-May) (B) for belugas tagged between 1999 and 2002.

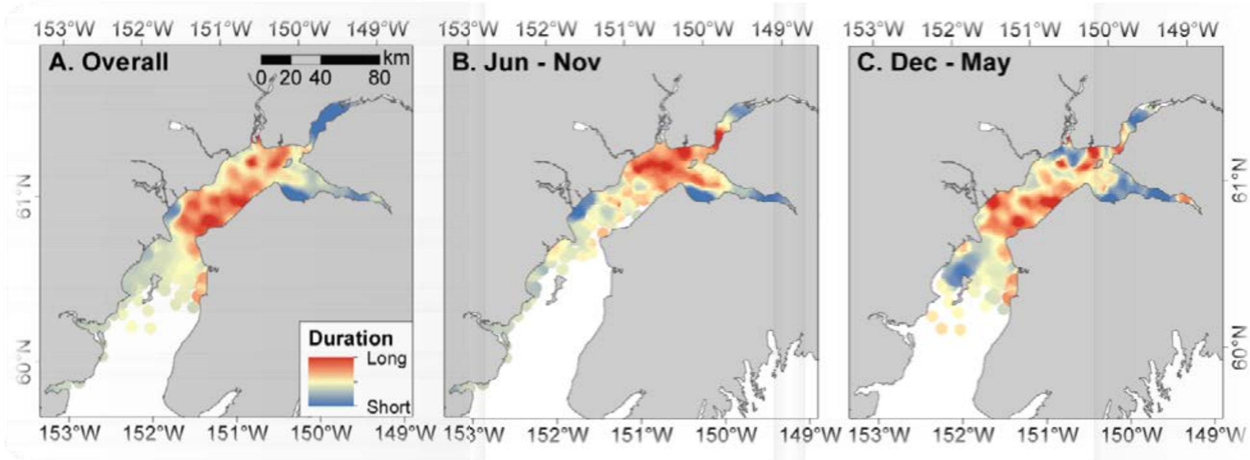

Figure 7. -- Hotspot analysis showing significant spatial clusters of short (blue) and long (red) dive duration for belugas tagged in Cook Inlet, Alaska, 1999-2002 (A. overall, B. June-November, and C. December-May). Yellow areas are not significant.

Mean dive depth for all belugas equipped with ST-16 tags (n = 11) was 4.21 (SD ±7.4) m and ranged from 1.6 (SD ± 2.1) to 6.7 (SD ± 10.4) m (Table 7). Average and maximum dive depths were significantly deeper in December-May than June-November (paired t-test, $P_{avgdepth}$ = 0.001, $P_{maxdepth}$ = 0.009). On average, belugas dived nearly three times deeper in December-May than June-November. Dive duration ranged from 1.1 (SD ± 1.3) to 6.9 (SD ± 9.5) minutes and averaged 2.48 (SD ± 3.37) minutes across all animals. Dives were significantly longer in December-May than June-November (Wilcoxon test, P = 0.028). With the exception of one beluga, maximum duration for all dives in both 6-month periods was greater than 24 minutes. Both dive depth and duration were significantly different across regions and seasonal periods (two-factor ANOVAs, P < 0.01; Table 5). In December-May, dives were significantly deeper and longer than in June-November across all regions (t-tests, P < 0.01). Dives occurring in the North Foreland and Lower Cook Inlet regions had the deepest mean depths while those in the North Foreland and Knik Arm regions had the longest mean duration (Table 5).

Table 7. -- Maximum and mean dive depth and duration for belugas tagged in Cook Inlet between 1999 and 2002, overall and in two seasonal periods (June-November and December-May). Dash denotes no data.

Beluga	Maximum depth (m)			Mean depth (m) ± StDev			Maximum duration (minutes)			Mean duration (minutes) ± StDev		
ID	Overall	Jun-Nov	Dec-May	Overall	Jun-Nov	Dec-May	Overall	Jun-Nov	Dec-May	Overall	Jun-Nov	Dec-May
CI-9901	62.5	62.5	-	3.0 ± 6.7	3.0 ± 6.7	-	>24	>24	-	3.1 ± 3.4	3.1 ± 3.4	-
CI-0001	62.5	62.5	62.5	3.1 ± 6.0	2.2 ± 4.3	6.8 ± 9.6	>24	>24	>24	1.5 ± 2.1	1.2 ± 1.5	2.7 ± 3.3
CI-0002	125.0	62.5	125.0	5.8 ± 10.3	3.2 ± 4.3	12.3 ± 16.1	>24	>24	>24	3.1 ± 4.2	2.4 ± 3.5	4.6 ± 5.3
CI-0103	62.5	62.5	-	3.2 ± 5.3	3.2 ± 5.3	-	13.5	13.5	-	1.1 ± 1.3	1.1 ± 1.3	-
CI-0106	62.5	62.5	-	3.2 ± 4.7	3.2 ± 4.7	-	>24	>24	-	1.4 ± 1.9	1.4 ± 1.9	-
CI-0107	125.0	62.5	125.0	6.7 ± 10.4	3.6 ± 5.3	11.4 ± 13.9	>24	22.5	>24	2.2 ± 2.8	1.5 ± 1.7	3.2 ± 3.7
CI-0201	37.5	37.5	-	1.6 ± 2.1	1.6 ± 2.1	-	>24	>24	-	1.2 ± 1.6	1.2 ± 1.6	-
CI-0203	125.0	125.0	-	7.3 ± 9.7	7.3 ± 9.7	-	>24	>24	-	1.7 ± 1.7	1.7 ± 1.7	-
CI-0205	125.0	62.5	125.0	3.5 ± 7.4	1.9 ± 3.5	6.0 ± 10.5	>24	>24	>24	6.9 ± 9.5	1.3 ± 1.5	14.2 ± 10.5
CI-0206	125.0	62.5	125.0	3.6 ± 8.2	1.6 ± 2.5	6.5 ± 11.7	>24	>24	>24	1.4 ± 1.7	1.0 ± 1.2	1.9 ± 2.2
CI-0208	175.0	62.5	175.0	5.3 ± 10.5	2.2 ± 2.9	6.5 ± 12.1	>24	>24	>24	3.8 ± 6.8	1.2 ± 1.4	4.9 ± 7.8
Mean	98.9	65.9	122.9	4.2 ± 7.4	3.0 ± 4.7	8.2 ± 12.3	-	-	-	2.5 ± 3.4	1.6 ± 1.9	5.2 ± 5.5

Hotspot analysis on the duration of dives showed that belugas dived consistently longer in most mid-inlet areas between East Foreland and West Foreland and Fire Island. This pattern changed between seasonal periods with clusters of elevated dive rate located farther north in June-November than December-May (Fig. 8B-C). Clusters of short duration dives were located near the coast in both seasonal periods, primarily in Knik Arm, Turnagain Arm, Chickaloon Bay, and the Susitna Delta regions. These same regions had clusters of large numbers of dives (Fig. 9). Coldspots, or clusters of low dive numbers, were located between North Foreland and the Susitna Delta. This pattern of cold and hotspots was not consistent between seasons (Fig. 9B-C). In June-November, the dive rate in the Susitna Delta was low, while in December-May, this was the predominant area where large numbers of dives were clustered.

Analysis of dive density revealed the same spatial pattern as the hotspot analysis, providing independent verification of the location of important areas. To ensure these patterns were not driven by the behavior of a single animal, we created a map showing the number of unique animals that passed through each cell. More than one beluga was present in nearly all areas north of East and West Foreland. In Knik Arm there were not only significant clusters of dive activity but also the highest density of dives during June-November (Fig. 9D-I). Similarly, in Susitna Delta the largest density and clusters of dive activity occurred in December-May. Although only three animals contributed to the density of dives just north of Kalgin Island (Fig. 9I), the number of belugas present at any given location did not appear to bias the results of the kernel density (Fig. 9D-F). The proportion of dives across the two 6-month periods was distributed differently across regions (Table 3); in December-May, most dives occurred in the Turnagain Arm, Susitna Delta and North Foreland regions while in June-November, nearly 66% were located in Knik Arm.

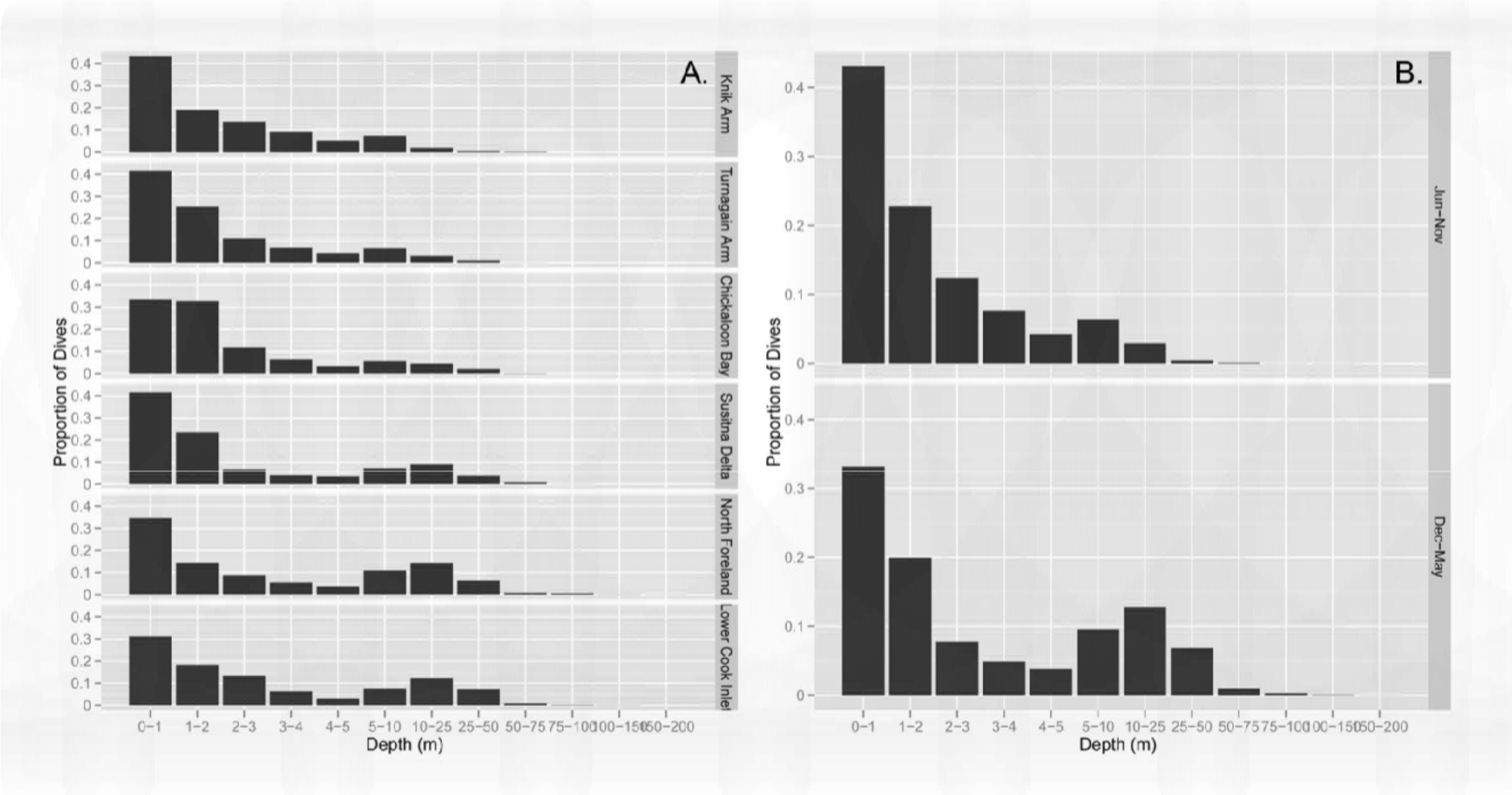

Figure 8. -- Proportion of dives in each depth bin in six regions of Cook Inlet (A) and two seasonal periods (June-November and December-May) (B) for belugas tagged between 1999 and 2002.

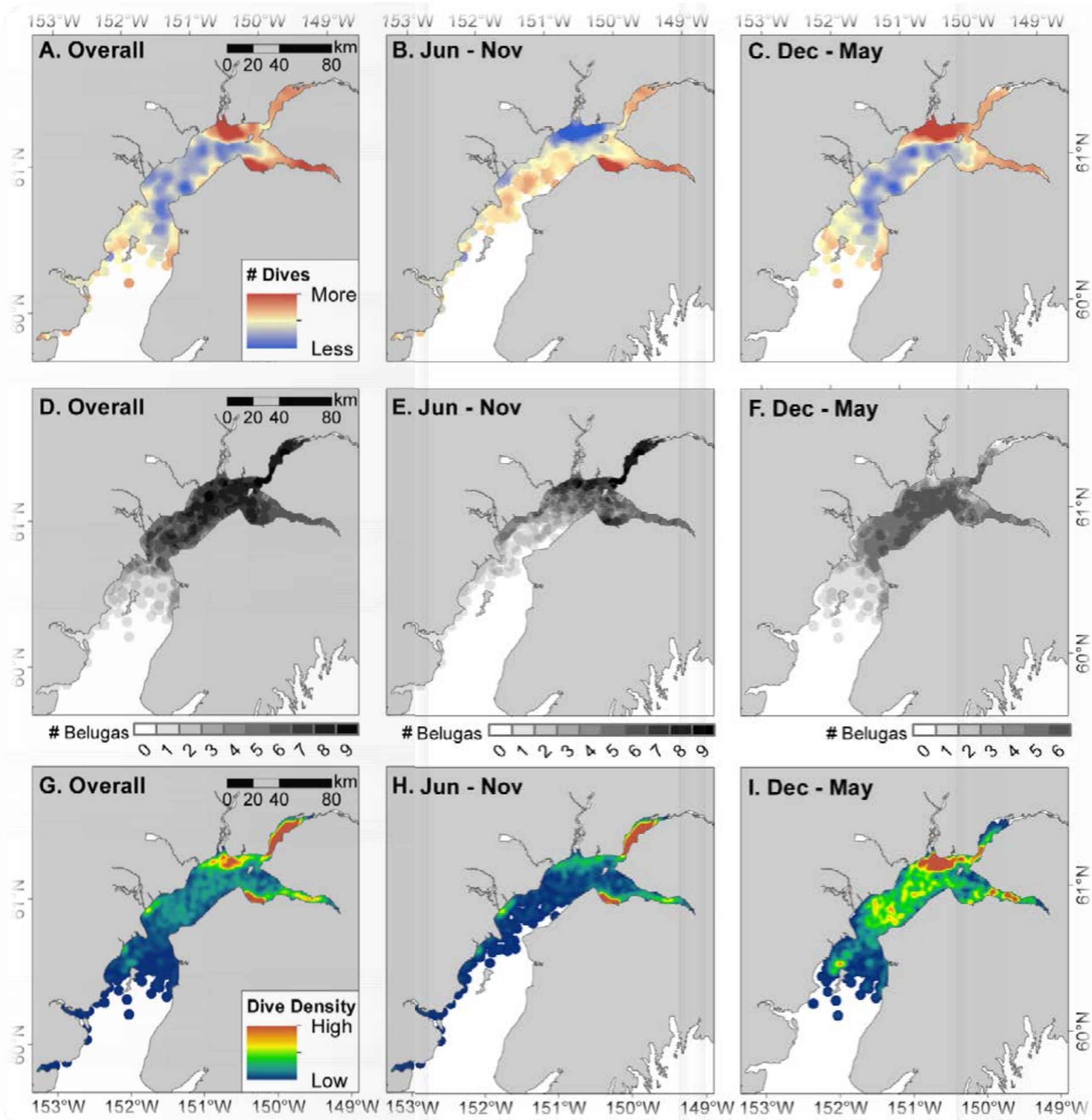

Figure 9. -- Hotspot analysis showing significant spatial clusters of less (blue) and more (red) dives (A-C), number of diving belugas (D-F), and kernel densities of dives (G-I) for belugas tagged in Cook Inlet, 1999-2002 - overall (A,D, and G), June-November (B, E, and H), and December-May (C, F, and I). Yellow areas are not significant.

Pelagic dives were significantly clustered in offshore areas while benthic dives were clustered in upper Cook Inlet, near the coast (Fig. 10A). While this pattern was consistent across seasonal periods, there was a greater clustering of pelagic dives south of North Foreland in December-May (Fig. 10C). These clusters aligned with the deeper bathymetric channels that span the inlet lengthwise from the Gulf of Alaska (Fig. 1B). There was no significant difference in the proportion of benthic or pelagic dives between seasons for individual whales (paired t-test, $P > 0.05$). While results from the two-factor ANOVA also showed no significant difference in the proportion of benthic and pelagic dives between seasonal periods in the six different regions, the overall proportion of benthic dives between regions was significant (two-factor ANOVA, $P < 0.001$). Overall, pelagic dives were more common than benthic dives across all regions in Cook Inlet; however, when benthic dives did occur, they were concentrated in Knik Arm, Turnagain Arm, and Chickaloon Bay (Table 8).

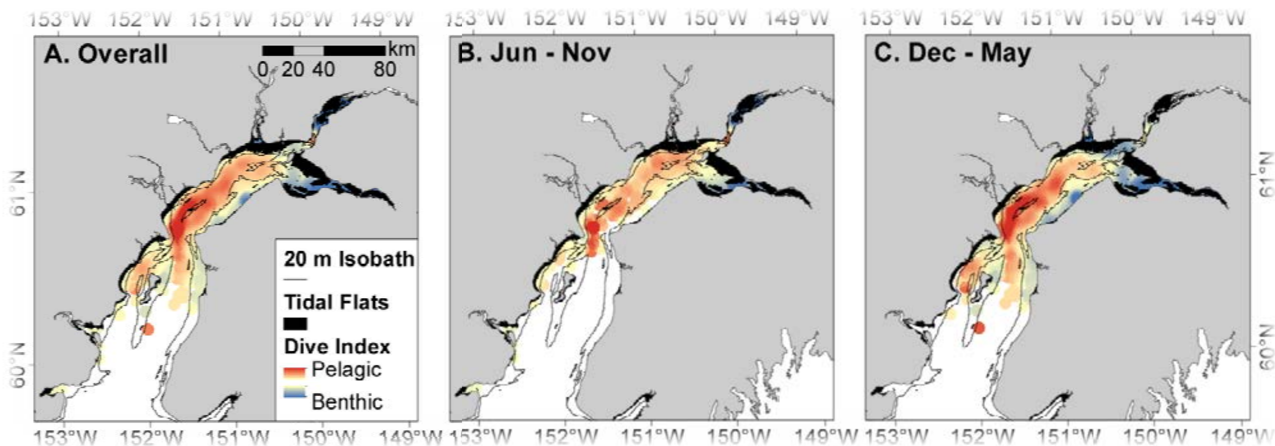

Figure 10. -- Hotspot analysis showing significant spatial clusters of benthic (blue) and pelagic (red) dives for belugas tagged in Cook Inlet, Alaska, 1999-2002 (A. overall, B. June-November and C. December-May). Yellow areas are not significant.

Table 8. -- Ratios of benthic dives to total dives and time diving to total time for belugas tagged between 1999 and 2002, overall and in two seasonal periods (June-November and December-May) in six regions of Cook Inlet.

	Benthic dives/total dives			Time diving/total time		
Region	Overall	June-Nov.	Dec.-May	Overall	June-Nov.	Dec.-May
Knik Arm	21.9	22.6	12.3	20.1	20.1	20.3
Turnagain Arm	44.6	41.0	50.2	19.8	18.8	21.3
Chickaloon Bay	27.7	25.6	31.2	22.4	21.3	25.2
Susitna Delta	16.0	10.5	19.0	21.2	18.2	25.0
North Foreland	12.6	8.1	13.8	25.5	18.3	28.1
Lower Cook Inlet	14.5	8.6	15.9	24.5	16.4	28.3
Mean	22.9	19.4	23.7	22.3	18.9	24.7

Generally, the proportion of shallow and deep bathymetric depths at dive locations matched the total proportion of shallow and deep bathymetric depths available for each region (Fig. 11A). In other words, in most regions, belugas did not show a preference for diving in shallow or deeper areas. Belugas were, however, diving deeper in Chickaloon Bay and North Foreland and shallower in lower Cook Inlet than would be expected given the available bathymetry. In comparing the bathymetric depth at each dive between seasons, we found that belugas prefer deeper water (> 25 m) in December-May and shallower water (< 25 m) in June-November across all seasons (Fig. 11B). Water depths do not exceed 25 m in the Turnagain Arm region; therefore, all belugas constrained to shallow water when occupying this region.

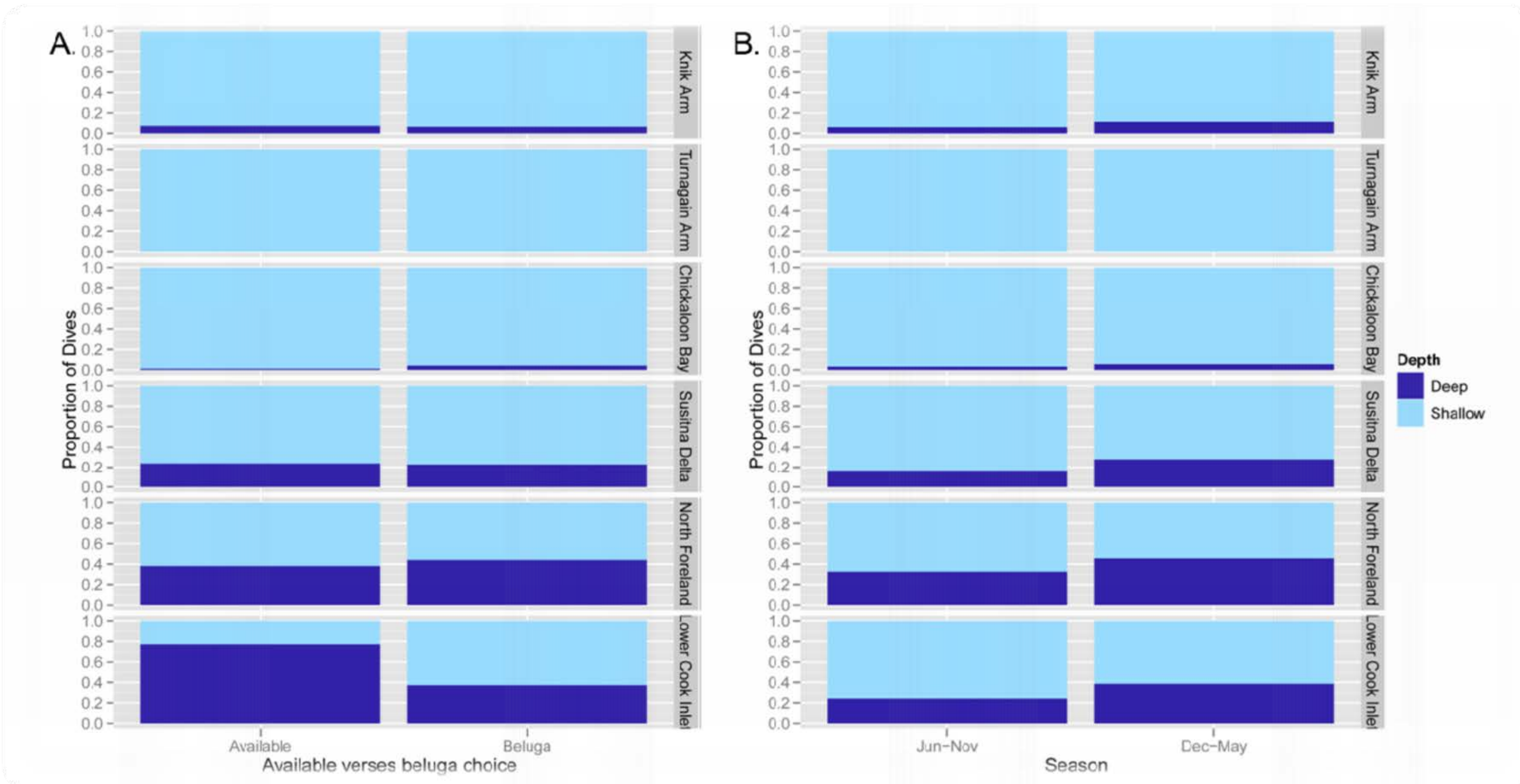

Figure 11. -- Available bathymetry in Cook Inlet, Alaska relative to bathymetry at beluga dive locations within six regions of Cook Inlet (A); bathymetric depth at beluga dive locations in two season periods (June-November and December-May) in six different regions of Cook Inlet (B). Depths were classified as shallow (< 25 m) and deep (> 25 m).

Dive Effort

On average, belugas spent 21.6% of their time diving, ranging from 15.6% to 28.6% for all tagged animals (Table 6). In December-May, belugas spent significantly more time diving than in June-November (paired *t*-test, $P < 0.01$). Similar to both dive depth and duration, the proportion of time spent diving across the 14 depth bins varied by region and season (Fig. 12). Over 50% of the dive effort occurring in the Knik and Turnagain Arm, Chickaloon Bay, and Susitna Delta regions was 2 m or shallower (Fig. 12A). In North Foreland and Lower Cook Inlet, belugas spent a larger proportion of time diving in water between 5 and 25 m. A similar pattern emerged between seasons; belugas spent a relatively greater proportion of time diving deeper in December-May than June-November (Fig. 12B). Regardless of depth, overall dive effort was significantly different across regions and seasons (two-factor ANOVA, $P < 0.001$) with the greatest proportion of dive effort in the North Foreland and Lower Cook Inlet regions (Table 8). The diving effort was significantly higher in December-May than in June-November (paired *t*-test, $P = 0.02$).

Hotspot analysis revealed that when belugas are diving, there are clusters of more time at depth in mid-Inlet waters, north of Chickaloon Bay and in the North Foreland and Lower Cook Inlet regions (Fig. 13A). Most of Trading Bay as well as the Susitna Delta, Knik and Turnagain Arm, and Chickaloon Bay regions showed clusters of less time spent at depth (i.e., coldspots of dive effort). These patterns drastically changed between seasons; in June-November, clusters of high dive effort were primarily north of East and West Foreland, with the greatest concentration located north of Chickaloon Bay while in December-May high dive effort was concentrated farther south, primarily mid-inlet, east of Trading Bay (Fig. 13B-C).

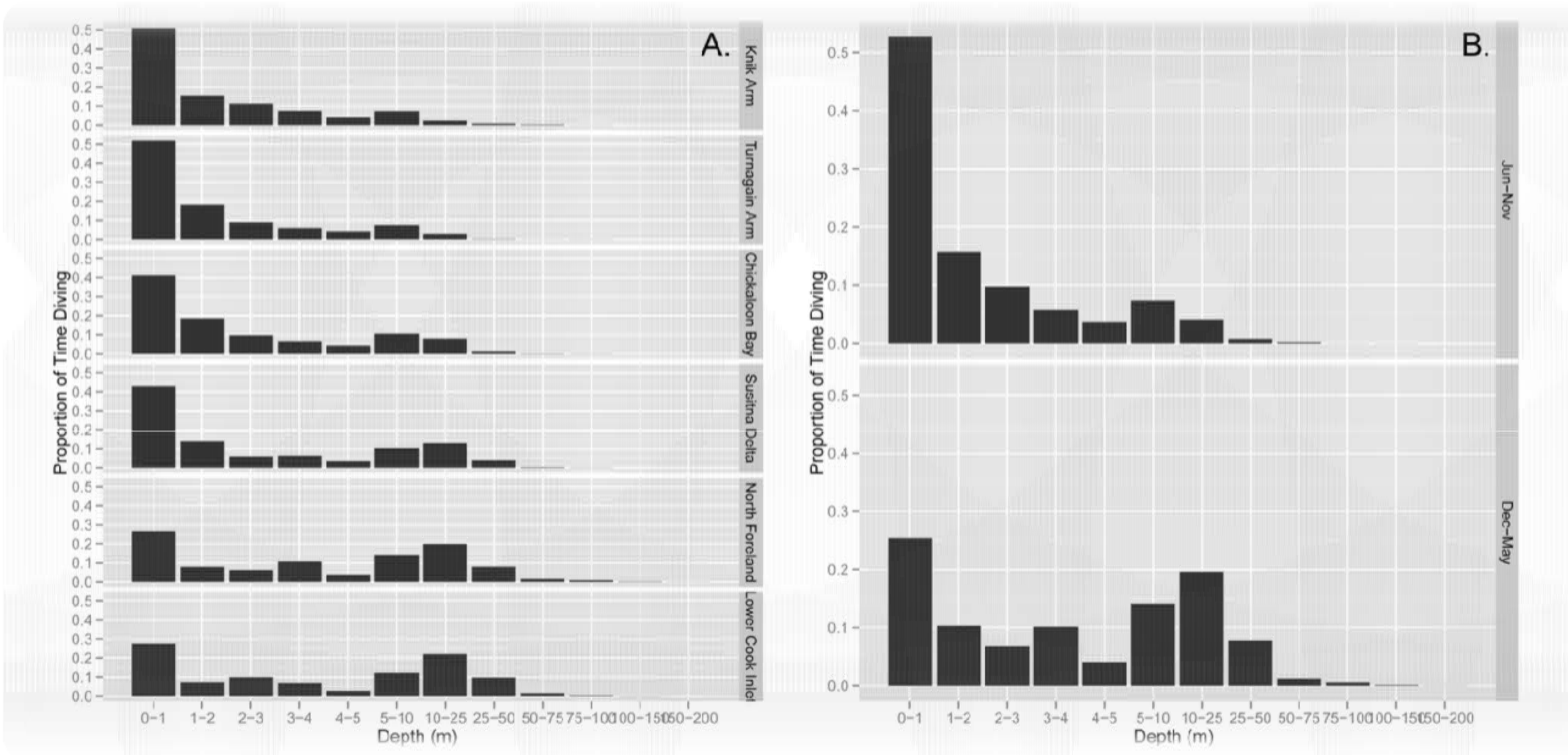

Figure 12. -- Proportion of time spent diving in each depth bin in six regions of Cook Inlet (A) and two seasonal periods (June-November and December-May) (B) for belugas tagged between 1999 and 2002.

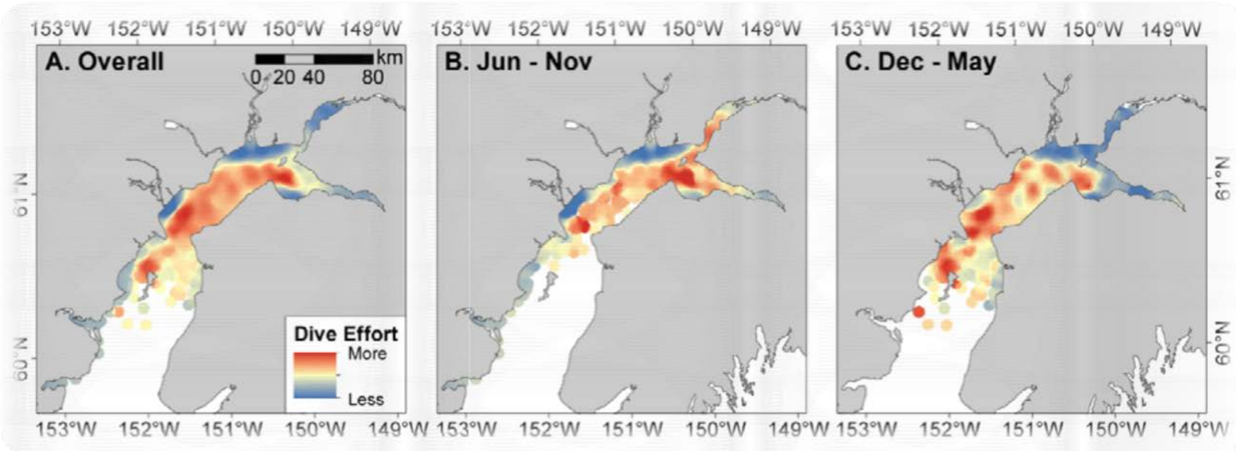

Figure 13. -- Hotspot analysis showing significant spatial clusters of less (blue) and more (red) dive effort for belugas tagged in Cook Inlet, Alaska, 1999-2002 (A. overall, B. June-November and C. December-May). Yellow areas are not significant.

DISCUSSION

We analyzed data from 14 tagged belugas across 4 years to study the movement and dive behavior of the endangered Cook Inlet population with a particular focus on preferred habitat and foraging locations. While belugas were once common in the nearshore waters of the southern inlet, only one or two beluga groups have been found in lower Cook Inlet since the mid-1990s (Rugh et al. 2000, 2005). The range contraction of Cook Inlet belugas, coincident with declining abundance, may have resulted in the current occupation of areas in northern Cook Inlet where tidal flats create more efficient foraging habitat (Rugh et al. 2010).

The movements are consistent with the hypothesis that belugas from the Cook Inlet remain in the inlet year-round (Hobbs et al. 2005). Similarly to other populations of belugas that do not make annual long distance migrations between summering and wintering grounds (Richard et al. 1998, 2001a,b; Martin and Smith 1999; Suydam et al. 2001), Cook Inlet belugas exhibit year-round fidelity. The average ratio of maximum travel distance to total horizontal distance traveled for all animals was 0.04 indicating that belugas in Cook Inlet show high site fidelity. While this ratio was higher in December-May, differences were not significant and were most likely due to belugas traveling farther to avoid fast ice or to locate prey when concentrated fish runs were absent.

While the limited sample size of this study may not fully characterize the movement (n = 14) and dive behavior (n = 11) of the entire population, we are confident that the general patterns presented in this paper accurately reflect beluga behavior in Cook Inlet. Our results corroborate the findings of Hobbs et al. (2005) in which belugas spent more time offshore between East and West Forelands and Fire Inland during the winter. This is likely due to a decrease in fish runs at the river mouths and the formation of ice which begins in early December (Mulherin et al. 2001). Ice extent and thickness peaks in mid-February and breaks up between March and May. During colder winters, ice may extend into the lower Inlet approaching the Gulf of Alaska (Mulherin et al. 2001). The large amounts of freshwater entering Knik Arm and Turnagain Arm contribute to relatively high concentrations of ice in these areas over the winter. While belugas have entered areas with ice cover as dense as ~100% (Suydam et al. 2001) in the Arctic, whales typically retreat from dense sea ice to loose pack ice in the winter where predicable cracks and leads form (Heide-Jørgensen et al. 2002). The belugas in our study showed a similar trend and spent most of their time in each 2-week period outside the compact ice. In 2002 and 2003, belugas showed a preference for open pack ice (40-50% cover) and very open pack ice (10-30% cover).

In addition to sea ice, tides may influence beluga movements (Kleinenberg et al. 1964, Caron and Smith 1990). Cook Inlet exhibits one of the most extreme tidal cycles in the world with tidal variation ranging from 6 to 9.5 m and currents often greater than 6.2 m s^{-1} (Moore et al. 2000). During low tide, large tidal flats become exposed in much of northern Cook Inlet (Fig. 1B). During flood tide, belugas move into the upper reaches of the inlet, following narrow channels between the exposed tidal flats, and they depart during ebb tide (Moore et al. 2000). Using two of the same animals included in this study, Ezer et al. (2008) showed significant correlations when comparing beluga movements in upper Cook Inlet with tidal change and currents; both animals took advantage of the high tide to swim to shallow areas that are otherwise inaccessible. While we did not specifically analyze beluga movement relative to the tidal cycle in this study, animations of the interpolated tracks (http://www.ccpo.odu.edu/~tezer/CI/Beluga_Weekly_anim.gif accessed 10 January 2012) show movements into and out of the northern reaches of Knik Arm and Turnagain Arm, corresponding with the tidal cycle.

In the June-November belugas spent the highest proportion of time in the Chickaloon Bay, Knik Arm, and Turnagain Arm regions; however, in December-May, belugas drastically reduced their time in the Knik Arm region and increased time spent in the Susitna Delta and North Foreland regions. This same pattern was observed for the number of dives in which belugas dive substantially more in the Knik Arm region during June-November. Irrespective of region and seasonal period, belugas spent the greatest amount of time in the coastal areas of Knik Arm, Turnagain Arm, Susitna Delta, Chickaloon Bay, and Trading Bay. These areas also coincided with slower transit rate, presumably indicative of increased foraging success. Robinson et al. (2010) found transit rate to be the best single predictor of foraging success among several diving and movement parameters, consistent with other studies linking transit rate and foraging success (Crocker et al. 2006, Tinker et al. 2007, Villegas-Amtmann et al. 2008, Kuhn et al. 2009). Clusters of fast transit rate linked slow transit areas and identified probable routes between foraging areas (Robinson et al. 2010). With known eulachon and salmon runs, Susitna Delta, Chickaloon Bay, Knik and Turnagain Arm, and the west side of the upper inlet have been previously identified as beluga feeding hotspots in summer and fall (NMFS 2008). Goetz et al. (2012) identified these same areas as important summer habitat based on physical and environmental parameters; belugas were not only most likely to occur in these areas but also to be present in larger groups.

The coastal areas of Chickaloon Bay, Knik Arm, Turnagain Arm, and Trading Bay are areas where belugas performed intense, short duration dives during June-November. In the Susitna Delta region, belugas were diving less frequently in June-November but for longer periods of time. This discrepancy is likely due to the bathymetric differences between regions; bottom depths in Knik Arm, Turnagain Arm, and Chickaloon Bay are predominantly < 25 m while ~20% of the Susitna Delta is > 25 m deep. There is a marked difference in the number of dives occurring in the Susitna Delta between the two seasonal periods; the number of dives occurring in this region in December-May was nearly double that in June-November. This pattern is most likely driven by a combination of belugas spending more time at the surface in June-November and less overall time in Knik Arm and Turnagain Arm in December-May due to sea ice.

Previous studies have found that belugas spent most of their time in shallow estuaries where surfacing times are particularly long (Martin and Smith 1992, Heide-Jorgensen et al. 2001, Lydersen et al. 2001). The precision of the dive recorders used in our study may be insufficient to record all dives in extremely shallow water; therefore, the number of dives recorded in coastal areas may be underrepresented. As a result, dive effort (or the proportion of time spent diving relative to total time) was the highest in mid-inlet, in deeper waters, and lowest in areas where belugas spent the majority of their time and were traveling the slowest. While it is certainly possible that the total amount of time spent diving in deeper water is greater than the sum of all shallow dives near the coast, the higher density of dives in coastal areas makes this scenario unlikely. Dive effort in shallow, coastal areas was confounded by depth sensor limitation and the summary of dive data into 6-hour periods. Although overall effort may be biased downward, there were far more dives in the nearshore shallow regions where belugas are known to feed: Susitna Delta, Knik Arm, Turnagain Arm, and Chickaloon Bay. Dives in these areas were also shorter in duration possibly due to limitations imposed by the bathymetry. These results are consistent with findings in Western Hudson Bay where belugas performed shorter duration dives in riverine waters as compared to deeper marine waters (Martin et al. 2001). In shallow, coastal areas where prey are readily accessible near the surface, belugas have little incentive to dive.

Belugas are known to be exceptional divers and routinely reach depths of > 650 m in the Arctic Ocean (Shaffer et al. 1997, Heide-Jorgensen et al. 1998, Martin et al. 1998, Martin and Smith 1999). Such dives are assumed to represent foraging behavior (Martin and Smith 1992, 1999). It is important to note belugas in Cook Inlet are obviously constrained by the depth of the Inlet, which, on average, reaches approximately 60-73 m (Bouma et al. 1977, Muench et al. 1978). In the southern Inlet, a 100 m deep channel extends northward until bifurcating around Kalgan Island, forming two shallow channels (Moore et al. 2000) (Fig. 1B). Belugas move to these deeper waters in December-May and dive deeper, but typically do not reach the bottom. Pelagic dives were clustered in these deeper waters while benthic dives were clustered nearshore and in the shallow regions of northern Cook Inlet. More dispersed movements into the middle inlet and deeper and longer dives in December-May may represent a different foraging tactic, where whales find prey in deeper waters, after seasonal salmon runs have ceased. During this time, belugas are opportunistic feeders, most likely feeding on demersal or pelagic fish species. Depending on the life stage, potential prey items are likely to include flatfish, cod, sculpin, pike, grayling, and walleye pollock (Klinkhart 1966, Clausen 1981, Seaman et al. 1982, Haley 1986, Perez 1990, NMFS 2008).

The area just north of Kalgin Island is thought to be an important area for belugas in the winter during maximum ice extent (Hansen and Hubbard 1999). The combination of bathymetric channels and currents create small-scale eddies which concentrate nutrients and may provide refuge for anadromous fish. While only three belugas visited the area just north of Kalgin Island in December-May, they spent a relatively long time in the area. Slow speeds and increased dive effort in combination with the unique oceanography of areas near Kalgin Island may indicate important winter foraging area for belugas when anadromous fish runs are not present in northern Cook Inlet.

The movement and dive behavior of belugas in Cook Inlet indicate that prey availability was not the only factor driving their foraging. While many rivers in southern Cook Inlet sustain large salmon runs, belugas rarely traveled to these areas. Hazard (Hazard 1988) hypothesized that foraging success of belugas is higher near river mouths that concentrate prey than in open bays. This is further supported by studies in Bristol Bay where belugas appear to prefer specific streams based on the configuration of the channel (Frost et al. 1983). The combination of narrow passageways and shallow waters most likely makes foraging in these areas more efficient.

Using 14 years of aerial survey data, Goetz et al. (2012) identified Chickaloon Bay, Knik Arm, and the Susitna Delta as areas with high probability of beluga presence during the summer. However, in this study, the Susitna Delta region is more important during the winter (December-May). This discrepancy is most likely due to aerial survey design. Because surveys were flown at low tide to minimize search area, belugas were not likely to be present in Knik Arm where water is too shallow or has completely receded. Our study identified Knik Arm as a highly important area for belugas based on several behaviors: increased time spent in area, slow transit rate, and increased number of shallow and short duration dives. These behaviors were present across seasons despite limited access to due to the tidal cycle in the summer and the heavy ice in the winter. While the importance of Knik Arm is not clearly understood, according to traditional ecological knowledge, belugas travel in Knik Arm to avoid killer whales and to use the sheltered bays as nursery grounds (Huntington 2000).

Larger sample sizes are necessary to confirm that the observed tracking and diving behaviors are representative of the population. However, because belugas are found in large groups in the upper inlet during summer, we can assume that the behavior of a few tagged individuals may be representative of the behavior of a larger group. Belugas in Cook Inlet displayed clear variation in movement patterns and dive behavior in different regions and seasons. Independent of region, belugas made significantly shorter and shallower dives and traveled significantly slower in June-November than in December-May, indicating an increase in foraging activity in summer and fall. Our results are consistent with findings that belugas sustain themselves over the winter when less prey is available by building up fat reserves throughout the summer (Huntington 2000). Across seasons, the dive and tracking metrics summarized in this study identify coastal areas near the Susitna Delta, Chickaloon Bay, Knik Arm, Turnagain Arm, north Kalgin Island, and Trading Bay as important habitat and possible foraging areas. Though belugas tend to prefer the coastal shallow waters of upper Cook Inlet, their behavior is strongly influenced by tides and sea ice during the winter. As a result, managers should be careful to protect not only shallow coastal habitat but also mid-inlet areas that act as important corridors when belugas transit between preferred habitat or when heavy ice prevents access to inshore waters.

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