



## Movements of beluga whales (*Delphinapterus leucas*) in Bristol Bay, Alaska

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### ABSTRACT

We describe the annual distribution of beluga whales (*Delphinapterus leucas*) in Bristol Bay, Alaska, using data from 31 satellite-linked transmitters during 2002–2011. Bristol Bay has one of the largest and best studied Pacific salmon (*Oncorhynchus* spp.) fisheries in the world, allowing us to link the seasonal distribution of belugas to that of salmon. During salmon migrations, beluga movements were restricted to river entrances. Belugas generally did not relocate to different river entrances or change bays during peak salmon periods. However, the location of belugas was not related to the number of salmon passing counting towers, suggesting that belugas were either selecting locations that were good for catching salmon or there were simply more salmon than belugas needed to supply their nutritional needs. The distribution of belugas expanded after salmon runs ended, and was greatest in winter when belugas ranged beyond the inner bays, traveling as far west as Cape Constantine. Belugas continued to frequent the inner bays in winter whenever sea ice conditions allowed, *e.g.*, when winds moved sea ice offshore; however, they were never located south of the southern ice edge in open water or outside of Bristol Bay.

**Key words:** Bristol Bay, Nushagak Bay, Kvichak Bay, beluga, white whale, *Delphinapterus leucas*, diet, lattice-based density, utilization distribution, *Oncorhynchus* spp., salmon.

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; the western coast of Greenland; the northern coast of Norway; and the Svalbard archipelago. Populations are typically named after where they summer and, in Alaskan waters, five populations are commonly recognized by their summer ranges: Cook Inlet, Bristol Bay, eastern Bering Sea, eastern Chukchi Sea, and Beaufort Sea (Frost and Lowry 1990; O'Corry-Crowe *et al.* 1997, 2002).

The focus of this manuscript is the Bristol Bay population. The Bristol Bay population is largely restricted to an estuarine system characterized by large tidal

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fluctuations, turbid water, and large tidal flats/sandbars. This population appears to be stable or increasing; aerial counts of belugas in Bristol Bay increased by 4.8% per year between 1993 and 2005 (Lowry *et al.* 2008) and the population is believed to number ~3,000 animals (Allen and Angliss 2012).

Belugas in Bristol Bay are generalist predators and consume a wide variety of invertebrates, including shrimp (order Decapoda), isopods (order Isopoda), and polychaete worms (class Polychaeta), and fishes, such as flatfish (family Pleuronectidae), sculpin (family Cottidae), and lamprey (family Petromyzontidae) (see review in Quakenbush *et al.* 2015). However, in spring and summer their primary prey are fish that spawn in high densities, especially rainbow smelt (*Osmerus mordax*) and salmon (*Oncorhynchus* spp.), including sockeye (*O. nerka*), coho (*O. kisutch*), Chinook (*O. tshawytscha*), chum (*O. keta*), and pink (*O. gorbuscha*) salmon. When ice cover on the rivers breaks up, typically in April, belugas move up the rivers in pursuit of spawning rainbow smelt. The smelt runs end in late May and beluga diet shifts to outmigrating salmon smolt (*i.e.*, juvenile salmon that hatch and live 1–3 yr in freshwater before migrating to the ocean), which are believed to be the highest density prey until late June, when beluga diet shifts to adult salmon returning to spawn. The occurrence of salmon in the stomachs of belugas is directly correlated with their abundance; sockeye salmon are the main salmonid found in beluga stomachs during the first 3 wk of July, after which other species, such as coho or pink salmon, predominate until the end of August when salmon are no longer spawning (Brooks 1955, Lowry *et al.* 1986).

Bristol Bay has the largest commercial sockeye salmon fishery in the world; between 1992 and 2011, an average of 25.3 million sockeye salmon were commercially harvested annually (Jones *et al.* 2013). Indeed, the commercial value of sockeye salmon is the reason why studies of beluga diet and movements were initiated in 1954. There was concern that belugas were consuming too many salmon smolt and limiting salmon populations (Brooks 1955). Prior to the passage of the U. S. Marine Mammal Protection Act of 1972 (MMPA; 16 USC §1361 *et seq.*), the Alaska Department of Fish and Game investigated the efficacy of reducing predation of salmon smolt by hazing belugas with small boats during 1956–1959 and in 1965, by using charges of dynamite in 1960, and by broadcasting killer whale (*Orcinus orca*) calls over underwater speakers from 1965 to 1968 and in 1970 (Brooks 1955; Lensink 1961; Fish and Vania 1971; ADF&G, unpublished data). Due to the commercial importance of salmon in Bristol Bay, the timing and magnitude of adult salmon migrations are particularly well studied, allowing us to link the seasonal distribution of belugas to the seasonal abundance of salmon. Unfortunately, little is known about beluga diet or distribution in fall and winter, or how sexes may distribute themselves differently.

In this manuscript we provide a description of the annual distribution of beluga whales tagged with satellite-linked transmitters in Bristol Bay, Alaska, and describe how movements vary when adult salmon are migrating. Although the general distribution of belugas in Bristol Bay was known from prior studies in the spring and summer (*e.g.*, Brooks 1955; Lensink 1961; Frost *et al.* 1984, 1985), this is the first description of beluga distribution in this region based upon data from satellite telemetry, and the first to describe fall and winter distribution. We first examine movements relative to seasons and sex, then focus on movements during the adult sockeye salmon migration.

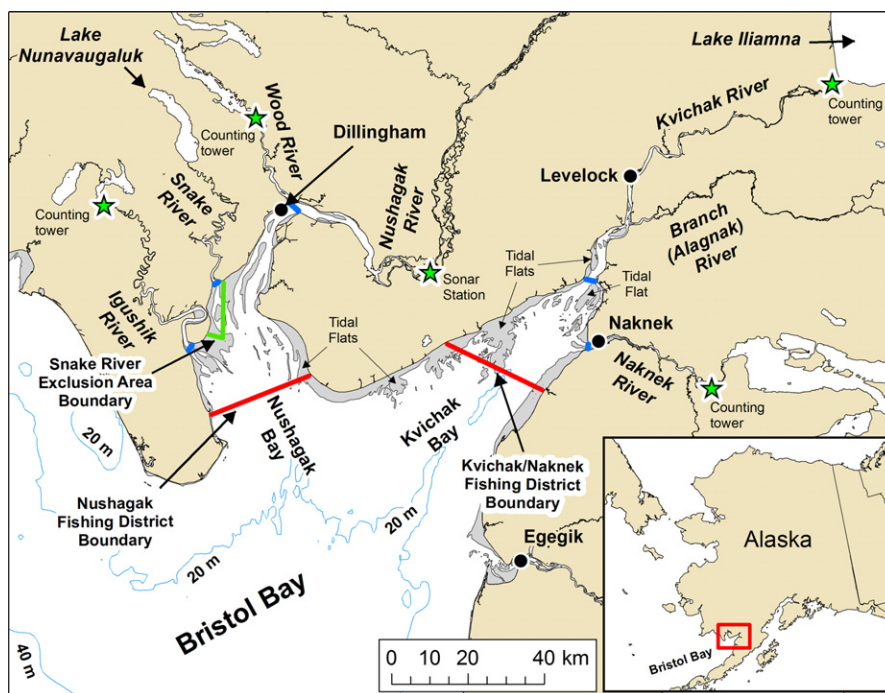
## MATERIALS AND METHODS

*Study Area*

Bristol Bay is located in southwestern Alaska (Fig. 1). The inner bay includes Kvichak and Nushagak Bays, which are the outlets of the Kvichak and Nushagak Rivers. Bristol Bay is generally shallow; depths within Kvichak and Nushagak Bays rarely exceed 25 m. At the towns of Dillingham and Naknek tides are in excess of 10 m and large mudflats (Fig. 1) are exposed at low tide.

*Tagging Data and Location Processing*

Belugas were captured in shallow water in Kvichak and Nushagak Bays (Fig. 1, Table 1) by surrounding whales with a large mesh seine net. We tried to capture whales longer than 8.5 ft (259 cm), which would be independent of their mothers and  $>2$  yr of age (Vos 2003, Suydam 2009), and did not tag females with dependent calves. Once captured, we secured whales by placing a padded rope around the caudal peduncle and a hoop net over their head and flippers (Orr *et al.* 1998). The animals were held in water shallow enough that their ventrum rested on the bottom but their



*Figure 1.* Bristol Bay, Alaska. Mudflats (gray areas) are exposed at low tide and the boundaries of commercial fishing districts are shown in red; fishing districts are upriver of boundary lines. The Snake River Exclusion Area, an area where commercial fishing is not allowed, is shown in green. Stars indicate counting towers or sonar stations where adult salmon are counted (*i.e.*, where escapement is documented). River entrances are marked with blue lines.

Table 1. Satellite transmitters deployed on beluga whales between 2002 and 2011 in Bristol Bay, Alaska.

Year	ID	Sex	Length (cm)	Color	Tag type	Site	Date deployed	Date last transmission	Days with locations
2002	Beluga02-1	F	289	White-gray	SDR-16	Kvichak Bay	18 May 2002	29 September 2002	117
2002	Beluga02-2	M	293	Gray-white	SDR-16	Kvichak Bay	19 May 2002	29 September 2002	114
2002	Beluga02-3	M	298	White-gray	SDR-16	Kvichak Bay	19 May 2002	18 September 2002	25
2002	Beluga02-4	F	293	Gray-white	SDR-16	Kvichak Bay	20 May 2002	8 September 2002	42
2002	Beluga02-5	M	345	White	SDR-16	Kvichak Bay	20 May 2002	16 August 2002	38
2003	Beluga03-1	M	418	White	SDR-16	Kvichak Bay	9 May 2003	12 June 2003	3
2003	Beluga03-2	F	325	White	SDR-16	Kvichak Bay	10 May 2003	9 August 2003	40
2003	Beluga03-5	M	371	White	SDR-16	Kvichak Bay	13 May 2003	5 September 2003	60
2006	Beluga06-1	F	295	White	SDR-16	Nushagak Bay	8 September 2006	20 September 2006	20
2006	Beluga06-3	F	310	White-gray	SDR-16	Nushagak Bay	10 September 2006	1 January 07	44
2006	Beluga06-4	M	361	White	SPLASH	Nushagak Bay	10 September 2006	15 September 2006	14
2006	Beluga06-5	M	366	White	SPLASH	Nushagak Bay	10 September 2006	27 January 2007	126
2008	Beluga08-1	F	310	Gray	SPLASH	Nushagak Bay	17 May 2008	29 October 2008	58
2008	Beluga08-2	F	305	White-gray	Mk10 GPS	Nushagak Bay	17 May 2008	18 November 2008	101
2008	Beluga08-3	F	335	Gray-white	Mk10 GPS	Nushagak Bay	18 May 2008	4 December 2008	95
2008	Beluga08-5	F	312	Gray	SPLASH	Nushagak Bay	19 May 2008	20 December 2008	100
2008	Beluga08-6	M	411	White	Mk10 GPS	Nushagak Bay	19 May 2008	9 January 09	115
2008	Beluga08-7	F	320	White	SPLASH	Nushagak Bay	20 May 2008	29 November 2008	76
2008	Beluga08-8	M	254	Gray	SPLASH	Nushagak Bay	20 May 2008	1 December 2008	80
2008	Beluga08-9	F	274	Gray	Mk10 GPS	Nushagak Bay	20 May 2008	25 November 2008	74
2008	Beluga08-10	F	?	Gray-white	Mk10 GPS	Nushagak Bay	21 May 2008	20 September 2008	40
2008	Beluga08-11	M	257	Gray-white	Mk10 GPS	Nushagak Bay	17 September 2008	4 March 2009	89
2008	Beluga08-12	M	328	White	SPLASH	Nushagak Bay	19 September 2008	9 February 2009	39
2008	Beluga08-13	F	342	White	Mk10 GPS	Nushagak Bay	20 September 2008	5 April 2009	90
2008	Beluga08-14	M	396	White	Mk10 GPS	Nushagak Bay	20 September 2008	24 April 2009	107
2008	Beluga08-15	F	272	Gray-white	SPLASH	Nushagak Bay	21 September 2008	11 June 2009	113
2008	Beluga08-16	M	384	White	Mk10 GPS	Nushagak Bay	21 September 2008	12 August 2009	125
2008	Beluga08-17	F	340	White	Mk10 GPS	Nushagak Bay	21 September 2008	26 January 2009	57
2008	Beluga08-18	M	269	Gray	Mk10 GPS	Nushagak Bay	24 September 2008	27 January 2009	37
2011	Beluga11-1	F	335	White	SPLASH	Nushagak Bay	18 May 2011	25 November 2011	54
2011	Beluga11-2	F	259	Gray	SPLASH	Nushagak Bay	20 May 2011	19 September 2011	75

dorsum was exposed. Transmitters were attached with three (for spider mounts) or four (for saddle and side mounts) nylon or Dacron<sup>2</sup> pins, approximately 0.33 m long; pins were 6.5 mm in diameter in 2002, 2003, and 2006, and 9.5 mm in diameter after 2006. Pins were inserted through the skin and blubber of the dorsal ridge or just anterior to it (through holes made with a trocar) and fitted through precut holes in the belting of each transmitter or through adjustable cable loops of the spider mounts. Whales were released within 20–120 min after capture depending on whether health assessment sampling was conducted in addition to tagging.

All transmitters were produced by Wildlife Computers (Redmond, WA). Between 2002 and 2011, 31 tags were deployed (Table 1). Tags deployed in 2002 and 2003 were SDR-16 transmitters. In 2006, deployed tags were a mix of SDR-16 and SPLASH transmitters. In 2008 and 2011, deployed tags were SPLASH or MK10 GPS transmitters. The two tags deployed in 2011 were both SPLASH transmitters. Tag programming changed throughout the study. Prior to 2008, tags were programmed to transmit during all hours of all days. In 2008, tags were set to transmit all hours of every other day. In 2011, one tag transmitted all hours of every day and one tag transmitted all hours of every other day.

The utility of the location data was limited. We received an average of 6.4 locations per day (mode = 1 per day) and transmissions were often clustered in time. Furthermore, transmitters programmed to transmit every other day created problems for some analytical methods and prevented us from examining small-scale movements. For example, belugas in Bristol Bay are known to move up and down rivers with the tides (Frost *et al.* 1985). However, we did not receive enough satellite locations from any transmitter to reliably reconstruct the path of movement within days and therefore cannot address movements relative to tidal state. In general, there were not enough locations to generate reliable track lines or analyze movements with state-space or use first passage time models. Hence, we focused on larger-scale seasonal movements and analytical methods that do not rely upon track data.

Satellite locations were collected *via* the Advanced Research and Global Observation Satellite (ARGOS) data collection and location system (Fancy *et al.* 1988, Rodgers 2001). Location error is estimated by the ARGOS system and characterized by “location classes” (see the ARGOS User’s Manual for a complete description; available at <http://argos-system.org/manual/>). Location classes are only an approximate representation of location accuracy (*e.g.*, Vincent *et al.* 2002). When processing the location data, we first used a filter that removed locations resulting in 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 1.67 m/s as a maximum sustained velocity, and Richard *et al.* (2001) documented velocities of 1.17 to 1.78 m/s, which included the fastest observed velocity in any of the studies. After filtering the data, we removed locations that fell on land. We then selected the highest quality location per day to represent the daily location of each whale. When locations were tied in quality, we used the location that was closest to 0 GMT, which corresponds to approximately 1330 local sun time.

<sup>2</sup>Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

### *Environmental Data*

We defined five seasons based upon our prior knowledge of sea ice, fish migration, beluga movements, and beluga diet.

*Winter season (15 December–15 April)*—This is generally the period when rivers are frozen and sea ice is commonly found within Bristol Bay. Few, if any, belugas are harvested at this time and their winter diet is unknown. While the date of freeze-up is highly variable, the date of “ice out” on the rivers is fairly constant. Belugas are typically first seen moving up the Naknek River (Fig. 1) in April. Between 2002 and 2009, local observers reported belugas were first spotted moving up the Naknek between 10 and 29 April ( $\bar{x}$  = 18 April).

*Smelt/smolt season (16 April–22 June)*—This is the period between when rivers become ice-free and sockeye salmon begin to migrate into the bay to spawn. Belugas are known to move up rivers at this time and are known to consume rainbow smelt and outmigrating salmon smolt (Brooks 1955). Because of the commercial value of adult sockeye, most studies focus on sockeye smolt. During the study period, sockeye smolt were studied in the Kvichak and Wood Rivers. The Snake River does not have a significant run of salmon (Rowse and Kaill 1983). Although the Igushik and Nushagak Rivers have significant sockeye runs, smolt migrations have not been studied there.

In general, river systems with many lakes, such as the Naknek and Wood river systems, have more prolonged migratory periods than those with fewer lakes, such as the Kvichak River (*e.g.*, see fig. 6 in Rogers 1988). On the Kvichak River, most smolt migrate within a week-long period in late May. Between 2008 and 2012, the median date of the smolt migration ranged from 27 May to 1 June (Wade *et al.* 2013). Smolt typically migrate on the Naknek River between mid-May and July, with multiple peaks (*i.e.*, multiple modes in abundance) between late May and mid-June (*e.g.*, Russell and McCurdy 1972, Bue 1986, Rogers 1988, Crawford and Cross 1995). Smolt runs in the Wood River occur later than in other rivers in Bristol Bay, typically beginning in late May and extending through the third week of August. Migration peaks at various times between late June and mid-July (Nelson 1965).

Based upon stomach samples collected in the Naknek River, Brooks (1955) believed that belugas first migrated up the rivers in spring to prey upon rainbow smelt. Belugas then switched to salmon smolt as they became available. When smolt were no longer available, belugas switched back to rainbow smelt until adult salmon began to migrate up the rivers to spawn. Because rainbow smelt and salmon smolt are available at the same time, prior to when adult salmon migrate, we combined the two time periods into the “smelt/smolt” season.

*Sockeye season (23 June–23 July, Fig. 2)*—Sockeye salmon are counted annually from towers on the Kvichak, Wood, Igushik, and Naknek Rivers (Anderson 2000). Sockeye are also counted annually on the Nushagak River at a sonar station (Crawford and Fair 2003). Smaller numbers of Chinook and chum salmon also migrate up rivers at this time, but are only counted on the Nushagak River (Fig. 2). We refer to this period as the “sockeye season” because the vast majority of fish are sockeye salmon; however, belugas may also consume Chinook in both the Kvichak and Nushagak drainages and chum salmon in the Nushagak drainage at this time.

*Pink and coho season (24 July–31 August)*—Pink and coho salmon generally spawn in late summer, after sockeye have spawned (Fig. 2). Pink salmon follow a strict 2 yr life cycle, creating even and odd year populations. In Bristol Bay, the population that spawns in even years is substantial while the odd year population is very low

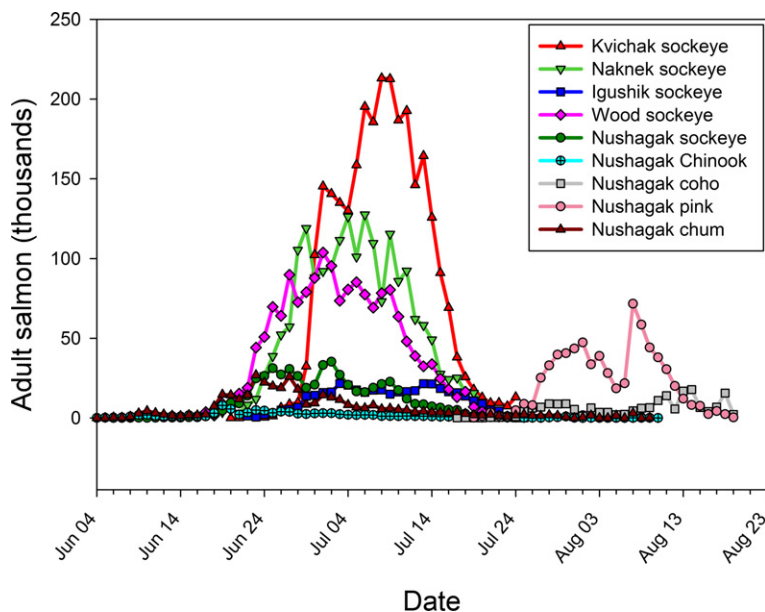


Figure 2. Average daily escapement (*i.e.*, fish that escape fisheries to spawn) of sockeye, coho, Chinook, chum, and pink salmon between 2002 and 2011. For pink salmon, only even-year averages are shown. Note that escapement of coho, chum, and pink salmon are not monitored within Kvichak Bay.

(Table 2). Coho salmon return in significant numbers annually. At this time, there is also a late season chum run in the Kvichak drainage. While the late season run of chum salmon is largely unstudied, it is well-known to sport fishing lodges in the area, and based upon commercial catch data (Table 2) spawning chum salmon likely occur in significant numbers.

*Post-salmon season (1 September–14 December)*—Virtually all adult and juvenile salmon have completed their migrations by the end of August. Because few belugas are harvested in the fall, their diet at this time is mostly unknown.

### Statistical Analyses

*Seasonal movements*—To identify time periods when belugas may be located in different areas or move differently within Bristol Bay, we examined three metrics related to location and movement. First, belugas are known to sometimes congregate near river entrances (Goetz *et al.* 2007, 2012; Ashford *et al.* 2013; Ezer *et al.* 2013). Hence, we modeled the distance to the nearest river entrance as a function of season and the sex of belugas. For each beluga whale location, we calculated travel distances (not straight line distances) to the entrances of the Kvichak, Naknek, Igushik, Snake, and Wood/Nushagak Rivers because these are the river entrances that contained beluga locations during the study period. Travel distances calculated using “gdistance” (<http://cran.r-project.org/web/packages/gdistance/index.html>) in R version 3.0.2 (R Core Team 2013). This package calculates distances and routes on a geographical grid. Distances are calculated between nodes, and paths must travel from node to

Table 2. Commercial catch of salmon by fishing district (Kvichak/Naknek or Nushagak) 2002–2011. Averages are for 2002–2011, however, the average for pink salmon only includes even years. Data are taken from Jones *et al.* (2013).

District	Year	Sockeye	Chinook	Coho	Chum	Pink
Kvichak/ Naknek	2002	1,418,938	969	0	19,180	10
	2003	3,348,504	567	42	34,481	24
	2004	4,715,070	1,360	2,142	29,972	7,749
	2005	6,728,469	1,377	3,314	204,777	32
	2006	7,151,741	2,333	5,163	457,855	25,149
	2007	9,022,511	1,484	2,180	383,927	9
	2008	10,381,844	1,307	7,055	237,260	20,682
	2009	8,514,944	974	732	255,520	23
	2010	10,858,209	369	1,006	330,342	8,237
	2011	9,016,321	2,693	633	205,789	13
	10 yr average	7,115,655	1,343	2,227	215,910	12,365
Nushagak	2002	2,839,424	39,473	93	276,777	204
	2003	6,665,965	42,615	583	740,311	188
	2004	6,104,048	96,534	47,706	458,902	26,150
	2005	7,096,031	62,308	42,456	966,050	554
	2006	10,876,552	84,881	44,385	1,240,235	39,011
	2007	8,404,111	51,473	29,578	953,275	384
	2008	6,903,157	18,670	76,668	492,341	138,284
	2009	7,730,168	24,287	35,004	744,083	320
	2010	8,424,030	25,580	69,186	509,628	1,289,970
	2011	4,886,552	29,811	4,613	340,881	257
	10 yr average	6,993,004	47,563	35,027	672,248	298,724

node. We allowed belugas to move from each node to any one of the nearest 24 nodes. The grid had 100 m spacing between nodes and no nodes were on land. This spacing was sufficient to allow node connections for belugas in narrow rivers.

Second, we modeled distance (kilometers) between sequential locations, which we term “displacement distance” as a function of season and sex. Note that displacement distance represents how the general location of individual whales shifted, not the true distance whales traveled. Because some transmitters were programmed to transmit every other day and the displacement of an animal may be dependent upon the amount of time elapsed, we limited the data set to locations collected every other day, allowing us to use data from all whales in the analysis.

Third, we examined the proportion of whale locations falling within Nushagak and Kvichak Bays by season and sex. Belugas may move between Kvichak and Nushagak Bays during the ice-free seasons. When sea ice is present, belugas remain within greater Bristol Bay, but are often outside of Kvichak and Nushagak Bays. As such, we limited this analysis to the ice-free seasons. We examined how the proportion of locations in each bay varied by season and sex.

Both the distance to the nearest river entrance and displacement distance were log transformed and modeled using linear mixed models. Models were fitted using Proc GLIMMIX in SAS (SAS Institute Inc. 2011). We used a hierarchical model structure to account for how beluga locations were collected; we tagged a relatively small number of belugas and then each beluga was located (*i.e.*, measured) repeatedly. We modeled individual belugas as a random intercept and accounted for repeated



measurements by fitting a spatial power model to the residual error. The spatial power model (Schabenberger and Pierce 2001, Littell *et al.* 2006, Kaps and Lamber-son 2009) is an extension of the AR(1) model that does not require intervals between observations (*i.e.*, locations) be of equal length. By fitting individual belugas with random intercepts, we account for unequal sample sizes per individual when estimating population-level parameters. We examined nine different models that represented how belugas may move differently by season and/or sex (Tables 3, 4). Models were ranked using AIC (Burnham and Anderson 2004) and the best approximating model (*i.e.*, the model with the lowest AIC) was used for inference.

To model the proportion of observations in each bay we coded locations within Kvichak Bay as “1” and locations within Nushagak Bay as “0.” We then modeled the proportion using a binomial error distribution and a logit link in Proc GLIMMIX. As with the other models, we assumed that individual belugas were random effects and modeled temporal autocorrelation with a spatial power model. Generalized linear mixed models that do not assume normal error distributions and identity link functions are fitted with quasi-likelihoods in Proc GLIMMIX, not with maximum likelihood, so we did not use AIC to compare models. Instead, we fitted the data to each time period and used the model to test for differences by sex and season. In effect, we used the statistical model to estimate valid *P*-values while accounting for a limited number of tagged whales and temporally correlated data.

*Movements relative to sockeye salmon escapement*—Escapement is the number of fish that escape commercial and subsistence fisheries, and other sources of predation, such as belugas, to spawn. Escapements of adult sockeye salmon are counted daily on all rivers with significant sockeye runs (Fig. 1). For the period starting on 1 June (before the sockeye runs began) and ending when the sockeye runs ceased, we examined the same three metrics detailed above; specifically, we modeled (1) the distance belugas were located from the nearest river with salmon as a function of the total number of salmon (in thousands) counted daily within that river, (2) the distance between beluga locations (displacement) as a function of the daily count of salmon in the nearest river with sockeye, and (3) the choice of bay as a function of the daily count of salmon in the nearest river with sockeye. We expected that the belugas would be located closer to river entrances and have smaller displacement distances when escapement was higher. Likewise, we expected that the proportion of locations in each bay would vary as a function of escapement, such that belugas would be more likely to move between bays when escapement decreased where they were located. Salmon are believed to require 1–4 d to pass from the open bays to where they are counted upriver. To account for this, we modeled each river separately and included lags of 0, 2, 4, 6, 8, and 10 d. Because large numbers of salmon may provide more food than belugas can consume, we also included a binary variable that was equal to 0 if no salmon were counted or 1 if any salmon were counted. In effect, we asked if belugas simply respond to sockeye salmon being present. This variable was also lagged. As with the analyses above, models were fit with belugas as random intercept and a spatial power model was used to account for autocorrelated errors within each beluga.

*Utilization distributions*—To visualize the distribution of belugas we calculated the utilization distributions (*i.e.*, probability densities) of belugas within the study area for each season by sex. Utilization distributions were calculated using the lattice-based approach of Barry and McIntyre (2011). Most kernel methods estimate density in unconstrained space, not accounting for areas where animals cannot enter. When locations cluster along shorelines or in rivers, positive density typically falls in areas that should have zero density, such as land. Typical approaches to estimating kernel

Table 3. Models used to examine how far belugas are located from river entrances. Individual belugas were fitted as random intercepts and autocorrelated errors were fit with a spatial power covariance structure. The most parsimonious model is denoted by bold font and  $\Delta\text{AIC} = 0$ .

Model	Model groupings	-2LogL	AIC	$\Delta\text{AIC}$
1	Null (intercept only)	4,349.39	4,355.39	138.26
2	Sex	4,350.21	4,356.21	139.08
3	Winter, Non-winter	4,242.39	4,248.39	31.26
4	<b>Winter, Smelt/smolt, Salmon, Post-salmon</b>	<b>4,211.13</b>	<b>4,217.13</b>	<b>0.00</b>
5	Winter, Smelt/smolt, Sockeye, Pink/Coho, Post-salmon	4,213.5	4,219.5	2.40
6	Winter, Smelt/smolt, Sockeye, Pink/Coho (even years), Coho (odd years), Post-salmon	4,214.4	4,220.4	3.30
7	Winter, Smelt/smolt, Salmon+Sex, Post-salmon	4,212.9	4,218.9	1.78
8	Winter, Smelt/smolt, Sockeye+Sex, Pink/Coho (even years)+Sex, Coho (odd years)+sex, Post-salmon	4,211.17	4,217.17	0.04
9	Winter+Sex, Smelt/smolt+Sex, Sockeye+Sex, Pink (even years)+Sex, Coho (even and odd years)+Sex, Post-salmon+Sex	4,214.6	4,220.6	3.42

Table 4. Models used to examine the distance between sequential locations (displacement) of belugas by time of year. Individual belugas were fitted as random intercepts and autocorrelated errors were fit with a spatial power covariance structure. The most parsimonious model is denoted by bold font and  $\Delta\text{AIC} = 0$ .

Model	Model groupings	-2LogL	AIC	$\Delta\text{AIC}$
1	Null (intercept only)	4,397.4	4,403.4	91.6
2	Sex	4,398.4	4,404.4	92.7
3	Winter, Non-winter	4,344.8	4,350.8	39.0
4	<b>Winter, Smelt/smolt, Salmon, Post-salmon</b>	<b>4,305.73</b>	<b>4,311.73</b>	<b>0.0</b>
5	Winter, Smelt/smolt, Sockeye, Pink/Coho, Post-salmon	4,307.4	4,313.4	1.6
6	Winter, Smelt/smolt, Sockeye, Pink/coho (even years), Coho (odd years), Post-salmon	4,307.9	4,313.9	2.2
7	Winter, Smelt/smolt, Salmon+Sex, Post-salmon	4,307.2	4,313.2	1.4
8	Winter, Smelt/smolt, Sockeye+Sex, Pink/coho (even years)+Sex, Coho (odd years)+sex, Post-salmon	4,308.52	4,314.52	2.8
9	Winter+Sex, Smelt/smolt+Sex, Sockeye+Sex, Pink (even years)+Sex, Coho (even and odd years)+Sex, Post-salmon+Sex	4,310.7	4,316.7	5.0

densities first estimate the density in unconstrained space, clip areas that are unavailable to the animal, and then renormalize the density so it sums to one. The approach of Barry and McIntyre (2011) starts with a grid of evenly spaced nodes; nodes are connected to adjacent nodes to form a spatial lattice. Density is estimated using a random walk process, where the length of the random walk,  $k$ , controls the smoothness of the density. Specifically, animal density is estimated as the probability density of the length- $k$  random walk on the lattice. At  $k = 0$ , the density is equal to the original observations. As  $k$  increases, density diffuses from node to node. An obvious advantage to this model is that density must follow linkages between nodes and, therefore, is not allowed to fall on land or cross impassable barriers, such as peninsulas. As a smoothing parameter,  $k$  is analogous to the bandwidth of kernel methods (e.g., Wor-ton 1989) and, as with kernel methods, cross-validation can be used to estimate  $k$ . We used the `latticeDensity` package (Barry and McIntyre 2011) in R to estimate  $k$  with cross-validation and to estimate lattice-based densities of belugas.

Choosing the spacing between nodes is a tradeoff between computational efficiency and the ability for the lattice to fit into bays and rivers. Computing requirements are not trivial for models with many nodes; however, if node spacing is too great, the lattice will not extend into bays and rivers. During ice-free periods, we spaced nodes 800 m apart. During the winter season, when belugas range over a larger area, we spaced nodes 1,200 m apart. This is analogous to estimating density within 800 m and 1,200 m pixels.

To account for possible differences in density due to differing duty cycles, we fitted the separate utilization distributions to locations from transmitters with 1 d and 2 d duty cycles. We then weighted the density layers by how many locations were in them, summed the layers to generate a single density layer for each season, and normalized the layers such that the density summed to 1.

## RESULTS

Between 2002 and 2011, 31 belugas of known sex were tagged in Bristol Bay (Table 1). Tagged whales ranged in length from 254 cm to 418 cm. Based on a length threshold of 288.5 cm (Suydam 2009), 24 were adults and 6 were likely juveniles, and one was of unknown age (Table 1).

*Distance from river entrances*—The distance (kilometers) each beluga was from the nearest river entrance was calculated for 31 whales on a total of 2,168 d. The best approximating model indicated that distance to river entrances differed by season but not sex (Table 3); furthermore the model pooled the sockeye, pink, and coho seasons into a single “salmon” season. On average, belugas were farthest from the nearest river entrance in winter ( $\bar{x} = 46.0$  km), were closer to river entrances during the smelt/smolt ( $\bar{x} = 13.6$  km) and post-salmon ( $\bar{x} = 14.6$  km) seasons, and were closest during the combined salmon seasons ( $\bar{x} = 8.6$  km) (Fig. 3).

The only model within 2 AIC of the best approximating model had similar support ( $\Delta = 0.04$ ) and suggested that male belugas may be closer to river entrances during the sockeye season ( $\bar{x} = 6.4$  km, 95% CL = 4.4–9.2) than females ( $\bar{x} = 9.6$  km, 95% CL = 7.5–12.4) and farther from river entrances during the even-year pink/coho season ( $\bar{x} = 10.1$  km; 95% CL = 7.0–14.4) than females ( $\bar{x} = 8.1$  km, 95% CL = 6.2–10.5) (Table 3, Model 8). However, during the even-year pink/coho season, the confidence intervals for each sex overlapped the mean of the opposite sex, suggesting the effect was largely limited to the sockeye season.

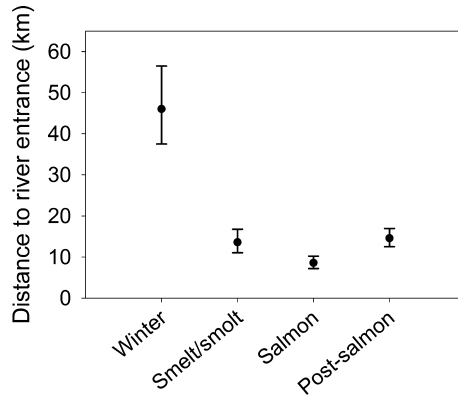


Figure 3. Average distance (km) from river entrances of beluga whales by season in Bristol Bay, Alaska, 2002–2011. Error bars are 95% confidence intervals.

*Average displacement*—Displacement (distance between sequential locations) was calculated for 1,478 location pairs collected from 30 belugas. The best approximating model indicated that displacement of belugas differed by season, but not by sex (Table 4, Model 4). Displacement was greatest during the winter ( $\bar{x} = 20.0$  km) and the least during the pooled salmon seasons ( $\bar{x} = 5.6$  km). Displacement was higher during the smelt/smolt ( $\bar{x} = 11.5$  km) than the post-salmon ( $\bar{x} = 9.2$  km) seasons (Fig. 4). Two other models were within 2 AIC of the best approximating model. The first model (Table 4, Model 7,  $\Delta = 1.4$ ) suggested that sexes may show different displacement rates, however, the difference between males ( $\bar{x} = 6.22$  km, 95% CL = 4.6–8.3) and females ( $\bar{x} = 6.24$  km, 95% CL = 5.1–7.6) was minimal (*i.e.*, ~40 m on average) and confidence limits overlapped, suggesting that this model was only within 2 AIC of the best approximating model because it differed by a single parameter. As a model selection criterion, AIC penalizes the log likelihood of the model by two times the number of parameters. Hence, when adding a single parameter to a

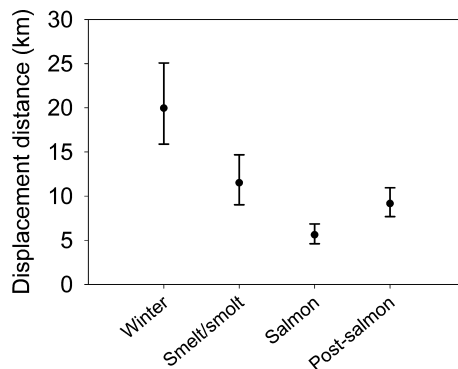


Figure 4. Average distance (km) between sequential locations with 2 d intervals (displacement distance) of beluga whales by season in Bristol Bay, Alaska, 2002–2011. Error bars are 95% confidence intervals.

model, there is often a decrement of  $\sim 2$  AIC units if the model likelihood is unchanged. Hence, the AIC score of Model 7 is spurious. The second model within 2 AIC of the best approximating model (Table 4, Model 5,  $\Delta = 1.6$ ) suggested that displacement was slightly higher during the even-year pink/coho season ( $\bar{x} = 6.7$  km, 95% CL = 5.5–8.3) than during the sockeye season ( $\bar{x} = 5.7$  km, 95% CL = 4.5–7.1). Again, confidence limits of each season overlapped the mean of the other season, so the effects are weak.

*Proportion of locations in Nushagak and Kvichak Bays*—We only considered the ice-free seasons in this analysis because belugas spent much of their time outside of Kvichak and Nushagak Bays in winter. We included 1,766 locations, representing 31 belugas, in this analysis. During the smelt/smolt season and sockeye seasons, the proportion of beluga locations was approximately equal between bays for both sexes (Table 5). Sample sizes were too low during the odd-year coho migration to discern how belugas were distributed or if there were differences by sex ( $n = 3$  females and 2 males). During the even-years when both pink and coho spawn, males were evenly distributed between bays, however, females shifted their distribution towards Nushagak Bay. Ninety-one percent of locations from nine female belugas were located within Nushagak Bay at this time (Table 5) and of the two female belugas that started the season in Kvichak Bay, both switched to Nushagak Bay before the pink/coho season was complete. Belugas of both sexes were more likely to be found in Nushagak Bay during the post-salmon season (Table 5).

*Movements between bays*—We found that belugas often move between Kvichak and Nushagak bays. During the smelt/smolt season 10 of 22 (46%) belugas switched bays at least once. A similar percentage of belugas switched bays during the salmon seasons; 7 of 19 (37%) switched bays at least once during the sockeye season, 5 of 14 (36%) during the even year pink/coho migration, and 2 of 4 (50%) during the odd year coho migration. After the salmon migrations were complete, belugas moved more widely and 20 of 29 (69%) switched bays at least once.

In general, belugas did not switch bays during the peak of the salmon migration. Of the seven belugas switching bays during the sockeye season, three switches occurred between 23 and 25 June (*i.e.*, before the peak sockeye migration; Fig. 2) and three occurred between 18 and 20 July (*i.e.*, after the peak sockeye migration; Fig. 2). Of three switches made before the peak sockeye migration, all were by females, two were from the Kvichak to the Nushagak and the third was from the Kvichak to the Nushagak and back to the Kvichak. Of switches made after the peak sockeye migration, two of three were made by females and all were from the Kvichak to the Nushagak. Only one beluga switched bays during the peak sockeye migration; an immature female moved from the Nushagak to the Kvichak.

Of the five belugas switching bays during the even-year pink and coho season, one was made by a female moving from the Kvichak to the Nushagak on 31 July (*i.e.*, before the peak of the pink salmon migration; Fig. 2). The remaining switches were made between 16 and 28 August (*i.e.*, after the peak of the pink salmon migration; Fig. 2) by three males and one female. Three of these were movements from the Kvichak to the Nushagak. Only four belugas were tracked during the entire odd-year coho season. Of these, one male and one female (50%) switched bays in 2003, which was a year with low numbers of harvested coho (Table 2). Neither beluga tagged in 2011 switched bays.

*Winter movements*—Of the 14 tags that transmitted during the winter season (4 in 2006/2007 and 10 in 2008/2009), only four tags, all deployed in 2008, lasted until spring. None of the tags deployed in 2006 transmitted past January

Table 5. Proportion of beluga whale locations in Kvichak and Nushagak Bays by season and sex. The model used to calculate *P*-values assigned whales a random intercept and accounted for temporal autocorrelation using a spatial power model. Significant percentages and *P*-values are in bold. Due to small sample sizes, we did not estimate *P*-values by sex for the odd year coho season.

Season	Bay	Statistic	Male	Female
Smelt/smolt (15 April–22 June)	Kvichak Bay	<i>n</i> (observations)	( <i>n</i> = 9 whales) 52	( <i>n</i> = 13 whales) 119
		Percent	59.8%	63.3%
		<i>n</i> (observations)	35	69
		Percent	40.2%	36.7%
		Difference by bay	<i>P</i> = 0.98	<i>P</i> = 0.82
Sockeye salmon (23 June–23 July)	Kvichak Bay	<i>n</i> (observations)	( <i>n</i> = 7 whales) 43	( <i>n</i> = 12 whales) 67
		Percent	48.9%	38.7%
		<i>n</i> (observations)	45	109
		Percent	51.1%	61.9%
		Difference by bay	<i>P</i> = 0.45	<i>P</i> = 0.32
Coho salmon (odd years) (23 July–31 August)	Kvichak Bay	<i>n</i> (observations)	( <i>n</i> = 2 whales) 2	( <i>n</i> = 3 whales) 15
		Percent	12.5%	37.5%
		<i>n</i> (observations)	14	25
		Percent	87.5%	62.5%
		Difference by bay	NA	NA
Pink and coho salmon (even years) (23 July–31 August)	Kvichak Bay	<i>n</i> (observations)	( <i>n</i> = 5 whales) 57	( <i>n</i> = 9 whales) 15
		Percent	57.6%	9.0%
		<i>n</i> (observations)	42	152
		Percent	42.4%	91.0%
		Difference by bay	<i>P</i> = 0.86	<i>P</i> < 0.05
Post-salmon (1 September–14 December)	Kvichak Bay	<i>n</i> (observations)	( <i>n</i> = 12 whales) 91	( <i>n</i> = 16 whales) 124
		Percent	21.1%	26.2%
		<i>n</i> (observations)	341	349
		Percent	78.9%	73.8%
		Difference by bay	<i>P</i> < 0.01	<i>P</i> < 0.01

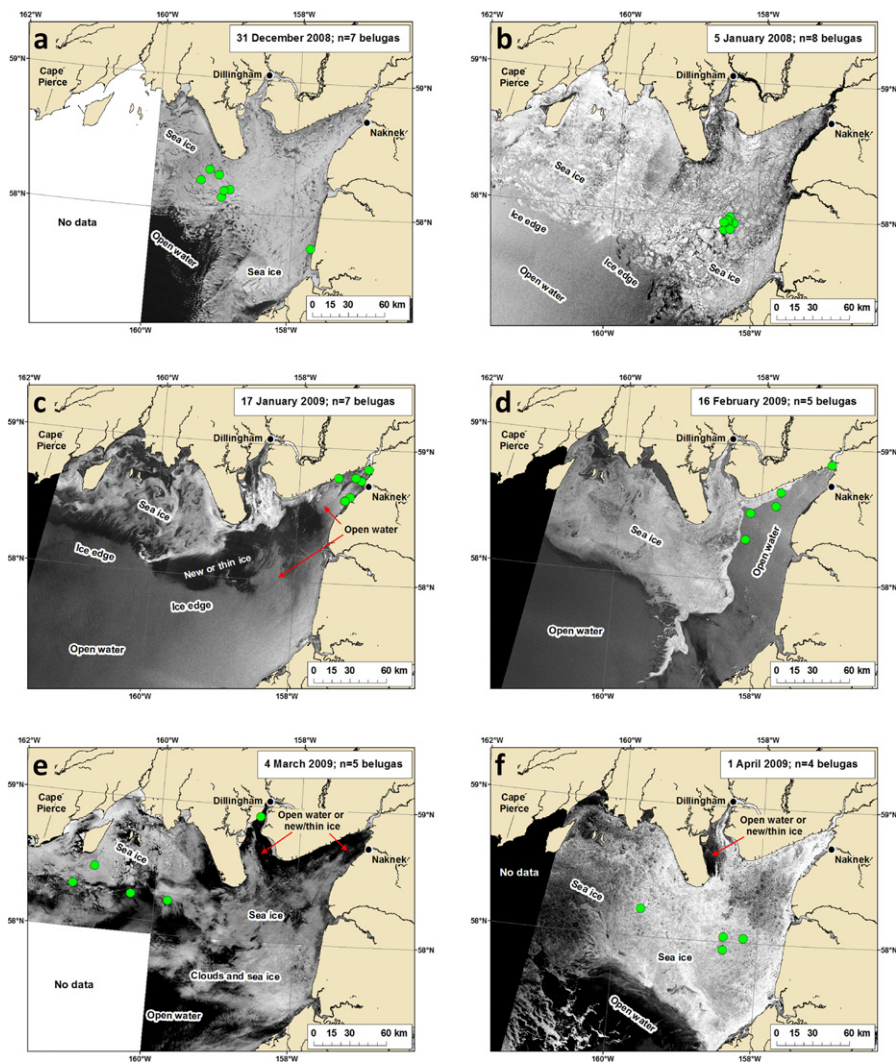


Figure 5. Winter distribution of belugas (green dots) and sea ice for a sample of dates in 2009. Imagery in parts (a) and (e) are MODIS data (<https://earthdata.nasa.gov/>). All other imagery is PALSAR data available through the Alaska Satellite Facility (<https://www.asf.alaska.edu/>).

in the first winter of their deployment (Table 1). Hence, our results are largely limited to movements in the winter of 2008/2009. Bristol Bay is at the southern extent of winter sea ice in the Bering Sea, where the distribution of sea ice is largely wind dependent and changes rapidly (Neibauer and Schell 1993). In the winters of 2006/2007 and 2008/2009 belugas ranged outside of Nushagak and Kvichak Bays and, in March of 2009, a beluga traveled as far west as Cape Pierce (Fig. 5). However, belugas continued to periodically move into inner

Nushagak and Kvichak Bays throughout the winter (Fig. 5c, d, e). Although belugas could be found within the inner bays in any month during the winter season, fewer belugas used the inner bays in February and March. All 14 tagged belugas used the inner bays in December, after the post-salmon season. Nine of 11 used the inner bays in January, 4 of 7 in February, and 1 of 5 in March. In early April, three of four belugas used the inner bays, prior to the spring melt. Although tagged belugas often moved into the inner bays when open water or thin ice was present, they did not use ice-free waters south of the ice edge (Fig. 5a, b, f).

*Movements relative to daily sockeye escapement*—When sockeye salmon were spawning, we found that belugas either aggregated near the Snake River or the Kvichak River entrance (see *Utilization distributions* below). Only a single beluga was located in the Igushik River while sockeye were spawning. Hence, we focused our escapement analyses on how far beluga locations were from the Snake and Kvichak River entrances, as these were the main places belugas appeared to aggregate. When modeling beluga movements as a function of sockeye escapement, we related distance from the Snake River as a function of sockeye escapement in the combined Nushagak and Wood Rivers, as it appears belugas intercept sockeye that are bound for the Nushagak and Wood Rivers near (upstream from) the Snake River (see *Utilization distributions* and Discussion).

*Distance from river entrances as a function of sockeye escapement*—In Nushagak Bay, the most parsimonious model for the distance belugas were from the Snake River included not the number of sockeye salmon, but simply if sockeye were being detected at counting stations upstream, with a 2 d lag ( $P < 0.001$ ). Belugas were an average of 22.9 km (95% CI = 16.0–32.8) from the Snake River in June, prior to salmon spawning. This distance declined to an average of 12.9 km (95% CI = 9.1–18.3) when sockeye salmon were being detected, with a 2 d lag. A model with no lag also fit the data reasonably well ( $\Delta\text{AIC} = 1.19$ ). The distance belugas were from the Snake River was also significantly related to the number of salmon detected with a 2 d lag ( $P < 0.005$ ); however, this model received little support ( $\Delta\text{AIC} = 7.46$ ). A model including sex effects was within 2 AIC units of the best approximating model, however, confidence limits on the effect overlapped zero and the effect had a  $P$ -value of 0.9.

In Kvichak Bay, the most parsimonious model for the distance belugas were from the Kvichak River included not the number of sockeye salmon, but simply if sockeye were being detected at counting stations upstream, with no lag ( $P < 0.001$ ), and included an additive effect of sex ( $P < 0.05$ ). Female belugas were generally farther from the river entrance than males. In June, prior to when sockeye salmon were detected at the counting tower on the Kvichak River, female belugas were an average of 24.5 km (95% CI = 18.6–32.3) from the river entrance while males were 14.0 km (95% CI = 9.6–20.5) away. When salmon were detected at the counting station on the Kvichak, females were within 13.0 km (95% CI = 9.5–17.8) of the river, while males were within 8.9 km (95% CI = 5.5–14.5) of the river. The distance belugas were from the Kvichak River was also significantly related to the number of salmon detected with a 4 d lag ( $P < 0.02$ ); however, this model received little support ( $\Delta\text{AIC}=19.6$ ).

*Displacement as a function of sockeye escapement*—In Nushagak Bay, the most parsimonious model indicated that the distance between sequential beluga locations was dependent upon whether or not sockeye were being detected on the Wood or Nushagak Rivers with no time lag ( $P < 0.001$ ). Sequential beluga locations were 36.7 km



apart (95% CI = 23.1–58.1) in June, prior to the sockeye runs. This distance declined to an average of 11.9 km (95% CI = 8.1–17.6) when sockeye salmon were being detected. A model including sex effects was within 2 AIC units of the best approximating model, confidence limits on the effect overlapped zero and the effect had a  $P$ -value of 0.79. The distance belugas were from the Snake River was also significantly related to the number of salmon detected with a 2 d lag ( $P < 0.02$ ); however, this model received little support ( $\Delta\text{AIC} = 22.0$ ).

In Kvichak Bay, the most parsimonious model indicated that the distance between sequential beluga locations was dependent upon whether or not sockeye were being detected at counting stations upstream, with no lag ( $P = 0.02$ ), and included an additive effect of sex ( $P = 0.08$ ). Locations of female belugas were generally farther apart than those for males. In June, prior to when sockeye salmon were detected at the counting tower on the Kvichak River, sequential locations of female belugas were an average of 23.9 km (95% CI = 16.7–34.2) apart while those for males were 13.1 km (95% CI = 7.7–22.5) apart. When salmon were detected at the counting station on the Kvichak, the distance between locations declined to 14.6 km (95% CI = 10.0–21.2) for females and 10.2 km (95% CI = 5.4–19.1) for males. Although the effect of sex had a relatively large  $P$ -value ( $P = 0.08$ ), the next best approximating model without a sex effect was 2.4 AIC units greater. The distance between sequential locations was also significantly related to the number of sockeye counted with a 4 d lag ( $P < 0.04$ ); however, this model received essentially no support ( $\Delta\text{AIC} = 11.5$ ).

*Proportion of locations in Nushagak and Kvichak Bays as a function of sockeye escapement*—There was no detectable relationship between the probability that belugas shifted from Nushagak Bay to Kvichak Bay and daily sockeye escapement ( $P = 0.71$ ). Likewise, there was no relationship between the probability that belugas shifted from Kvichak Bay to Nushagak Bay and daily sockeye escapement ( $P = 0.72$ ).

*Utilization distributions (lattice-based density)*—We used 2,168 locations from 31 beluga whales to calculate utilization distributions. We pooled sexes when calculating utilization distributions during the smelt/smolt, odd-year coho, post-salmon, and winter seasons. There was no evidence that beluga distribution differed by sex during the smelt/smolt, post-salmon, and winter seasons, and there were also not enough data to test for differences by sex during the odd-year, coho only season. However, we found evidence that males and females may distribute themselves differently during the sockeye and even-year pink/coho seasons, leading us to fit separate utilization distributions for males and females for those seasons.

As noted above, belugas ranged into outer Bristol Bay during the winter season, but were also found within the inner bays (*i.e.*, Nushagak and Kvichak) (Fig. 6a). During the smelt/smolt season, belugas shifted their distribution to the northern shore of Bristol Bay. At this time, the distribution of tagged belugas extended up the Kvichak, Nushagak, Wood, Snake, and Igushik Rivers (Fig. 6b). When adult sockeye salmon begin to migrate, most belugas moved to one of two areas, the entrance of the Kvichak River, near King Salmon Creek, or the extensive mudflats near the entrance of the Snake river (Fig. 6c). The main difference between males and females was that some females used the area near Etolin Point during the sockeye season; 4 of 12 (33%) females (two in 2002, one in 2003, and one in 2008) used the area around Etolin Point while sockeye were spawning. Although none of the seven tagged males used Etolin Point at this time, all four females also used the areas near King Salmon Creek or the mudflats near the entrance of the Snake River. The distribution of male belugas was similar during the even-year pink/coho season as during the sockeye

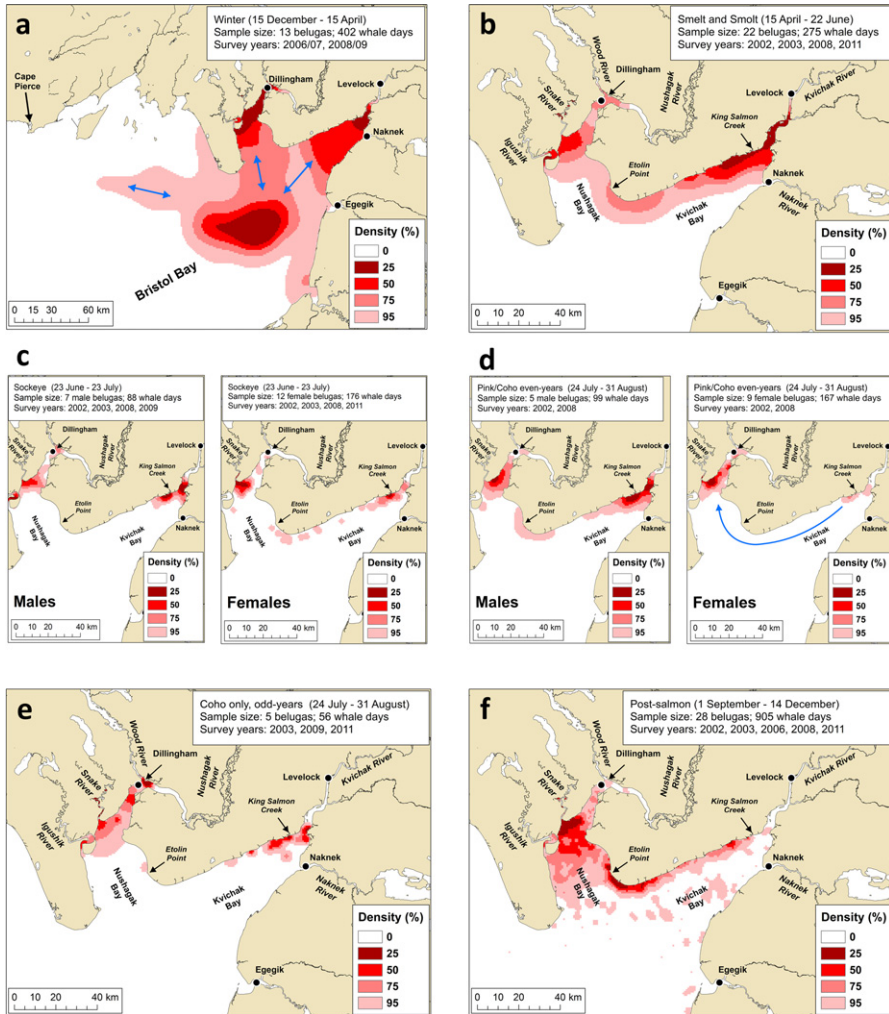


Figure 6. Utilization distributions for beluga whales in Bristol Bay, Alaska, during the (a) winter, (b) smelt/smolt, (c) sockeye, (d) even-year pink/coho, (e) odd-year, coho only, and (f) post-salmon seasons. Blue arrows show the general movement of belugas within seasons. Whale days are the sample size of days with whale location data.

season; however, female belugas moved from Kvichak Bay into Nushagak Bay without using the Etolin Point area (Fig. 6d). During odd-years, when only coho spawn, the distribution of tagged belugas was more widespread (Fig. 6e). Although the areas near the entrance of the Snake River and King Salmon Creek were still characterized by high density, tagged belugas were also more likely to be found in the Igushik and Snake rivers, and upstream from Dillingham. After the adult salmon migration was complete, the distribution of belugas widened greatly (Fig. 6f); high use areas included the region surrounding Etolin Point and, again, the mudflats near the entrance of the Snake River.

## DISCUSSION

*Limitations of satellite tags*—A variety of factors may influence the interpretation of data from satellite tagging studies. In this study, we analyzed data from 31 belugas out of a population of ~3,000 animals (Allen and Angliss 2012). Most belugas were tagged in the spring and most were tagged in Nushagak Bay. While it is possible this may have biased our conclusions about use of the two bays, we found that belugas often moved between Nushagak and Kvichak Bays. Every beluga tagged in the Kvichak ( $n = 8$ ) moved to Nushagak Bay at least once and only two whales tagged in the Nushagak ( $n = 23$ ) did not move to the Kvichak at some time. Therefore, we think it unlikely that the location of tagging biased our results.

A more serious problem is caused by freshwater discharge from rivers. The satellite tags used in this study rely on a drop in voltage between two diodes on the body of the tag to trigger a transmission. When the tag breaks the surface, voltage between the diodes declines and the tag transmits. A similar voltage drop occurs when the tag encounters fresh water; consequently, tags in freshwater may sense dry conditions and transmit while underwater. Tag settings varied by year, but most tags were limited to  $\leq 250$  transmissions per day. Tags were programmed to transmit every 91 s when they sense dry conditions and, if they began to transmit underwater, would reach transmission limits within approximately 6.5 h after the start of each day. Furthermore, transmissions are no longer synchronized with surfacing events in freshwater. For a transmission to reach an ARGOS satellite, the whale must be at the surface when the tag transmits. Hence, daily transmission limits and the likelihood that the most transmissions will occur when the whale is underwater may negatively bias in the number of locations received in regions with fresh water. Consequently, belugas may range farther upstream or spend more time in the upper bays and rivers than tagging data indicate.

To explore how freshwater may bias our understanding of the distribution of belugas from telemetry data, we calculated utilization distributions from aerial survey data collected by Lowry *et al.* (2008) between 1993 and 2005 during the adult sockeye migration. While the 95% density isopleth is very similar between the tag and aerial survey data, and both methods identify high use areas near the Snake River and King Salmon Creek, the aerial survey data show more use above Dillingham, near the confluence of the Nushagak and Wood Rivers (Fig. 7). This discrepancy is not due to our use of only one location per day when modeling beluga distribution. In the raw satellite location data, only 0.01% (174 of 14,138 locations) occurs north of 59°N (approximately 4 km south of Dillingham). In contrast, aerial surveys found belugas above 59°N in every survey year (1993, 1994, 1999, 2000, 2004, and 2005), accounting for 23% of all groups sighted and 17% of all belugas counted. Hence, it appears that belugas use the upper bays and rivers more than expected based upon the satellite location data, probably due to freshwater confusing tag sensors.

We expect our understanding of beluga distribution, based upon satellite tags, to be most biased in the spring, when belugas are known to move up the rivers to feed on salmon smolt and rainbow smelt, and least biased in the fall and winter, when belugas move farther offshore where water is saltier. We received no satellite locations above Levelock on the Kvichak River or from the Branch (Alagnak) River (Fig. 1). However, our own observations and those of subsistence hunters confirm that belugas often range many kilometers above Levelock in spring, when they are also found in the lower Branch River. Belugas are also known to move up and down the rivers in

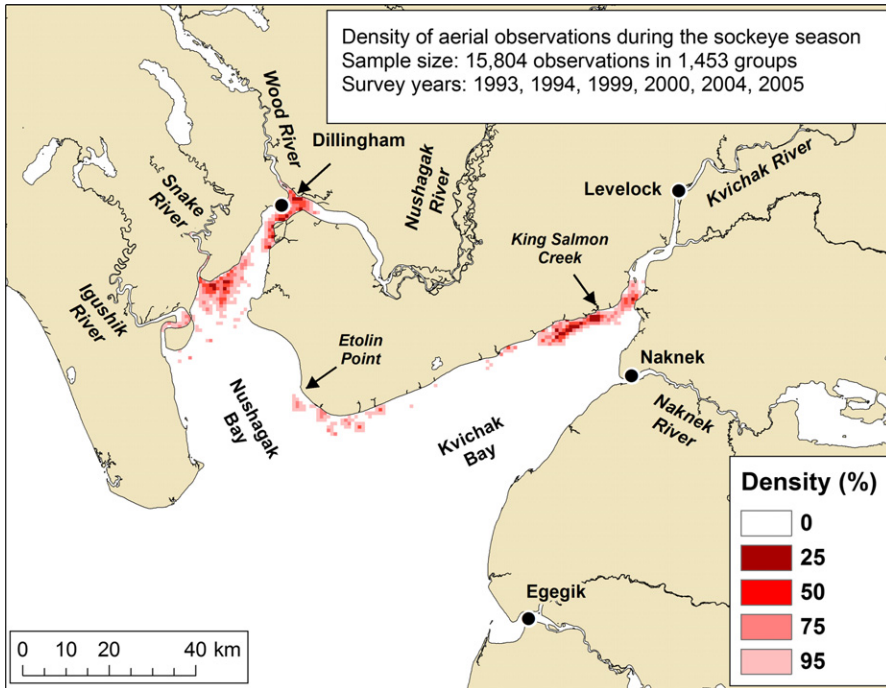


Figure 7. Utilization distribution derived from aerial survey counts of belugas during the sockeye season between 2002 and 2008 (data from Lowry *et al.* 2008). Compare with Figure 6c.

spring, coming upstream with the flood tide and going downstream with the ebb tide (*e.g.*, Lensink 1961, Frost *et al.* 1985). On average, we received only 6.4 locations per day from tags, and these locations were often close in time. As such, examining movements on fine time-scales was not possible.

Clearly these issues need to be addressed in future tagging studies where belugas may use fresh waters. Improved programming or tag design will allow a better understanding of the distribution of belugas in Bristol Bay and may allow the collection of more detailed movement data. While some tags were programmed to transmit for 2 h and then turn off for 2 h, thereby more evenly distributing transmissions throughout the day, all tags still had daily transmission limits that will be exceeded when tags enter fresh water. Factory recommendations are to use a default “dynamic” setting that automatically adjusts the amount of voltage drop that is necessary for a tag to transmit. However, this threshold can be manually set. Perhaps adjusting the threshold value such that a larger drop in voltage is necessary for a tag to transmit will allow tag sensors to correctly detect when the tag is at the surface. Tag engineers warn us that manually setting the voltage thresholds may result in having fewer transmissions in general. If the locations we receive are better distributed such a trade-off may be worthwhile.

*Distribution during the non-salmon seasons*—Belugas are known to move into the inner bays and up rivers when ice begins to break-up. Prior to the adult salmon migration, Brooks (1955) and Lensik (1961) found that belugas moved up the rivers,

preying predominantly upon rainbow smelt and, later, salmon smolt. Our data generally show this pattern; with the density of beluga locations highest in inshore areas and in the river systems in spring (Fig. 6b).

The distribution of belugas shifted to Nushagak Bay after the salmon runs were complete. Few beluga stomachs have been collected in autumn, limiting our knowledge of what belugas are eating. Stomach contents from a female beluga, harvested near Dillingham in October 2003, included rainbow smelt, saffron cod (*Eleginus gracilis*), isopods (*Saduria entomon*), unidentified species of rock sole (*Lepidopsetta* sp.), and shrimp (order Decapoda). Such prey are likely found throughout Bristol Bay and we do not know why both male and female belugas were more likely to be found in Nushagak Bay after the salmon runs are complete.

Belugas are not believed to be common in the inner bays in winter, but are sometimes sighted there when sea ice allows. Bristol Bay is on the southern edge of maximum sea ice extent in the Bering Sea (Neibauer and Schell 1993); here the ice is highly fragmented and, due to winds, open water may exist in the inner bays during any month (Fig. 5). Although belugas were not found in open water south of the ice edge (Fig. 5a, b, f), they were also not observed deep within the inner bays when there was no open water or thin ice. Perhaps belugas avoid the inner bays when heavier sea ice is present due to the risk of entrapment. We only have one winter with an adequate sample size ( $n = 10$  belugas; 2008/2009) limiting our understanding of this time period. Tagging studies continue in Bristol Bay, and a more detailed examination of beluga movements relative to sea ice is warranted.

*Beluga whales and salmon*—Belugas are well-known consumers of adult salmon (Brooks 1955, Seaman *et al.* 1982, Lowry *et al.* 1986). If belugas preferentially consume adult salmon when they are available and salmon are not equally available in all habitats, this preference should manifest as habitat selection. Using satellite telemetry, we found that belugas used specific locations and restricted their movements when adult salmon return to Bristol Bay to spawn. In general, whales selected either the entrance to the Kvichak River, especially near King Salmon Creek, or the entrance to the Snake River. Whales restricted their distribution at this time (Fig. 4) and generally did not switch between bays during the peak of salmon migration.

We found limited evidence that male and female belugas distribute themselves differently during the sockeye season in Kvichak Bay, both in our coarse seasonal analysis (Table 3, 4) and within our focused examination of daily sockeye escape-ment. The main difference between males and females in Kvichak Bay was that some females used the area near Etolin Point during the sockeye season; 4 of 12 (33%) females (two in 2002, one in 2003, and one in 2008) used the area around Etolin Point while sockeye were spawning (Fig. 6c). None of the seven tagged males used Etolin Point at this time. With that said, all four females also used the area near King Salmon Creek near the Kvichak River or the mudflats near the Snake River and this is why we did not detect a difference in the proportion of locations within each bay as a function of sex (Table 5).

The effects of sex were more evident during the even-year pink and coho salmon runs. While male belugas remained equally distributed during the even-year pink salmon runs, the distribution of tagged females shifted to Nushagak Bay (Table 5; Fig. 6d). Only one of nine tagged females was not in the Nushagak during the peak of the pink salmon run. Although differential movements of male and female belugas could be spurious and due to small sample sizes, this is unlikely. The binomial

probability of finding eight of nine females in Nushagak Bay if they were randomly distributed is only 0.02. Likewise, the probability of finding only two of three males in the Nushagak if the true probability is equal to that of females ( $8/9 = 0.89$ ) is 0.01. Using a chi-square test, the probability that males are distributed the same as females is only 0.052 ( $\chi^2 = 3.76$ ). While all statistical tests are suspect when sample sizes are small, there are some biological reasons that females may relocate to Nushagak Bay when pink salmon run.

Average even-year harvest of pink salmon is typically an order of magnitude higher in Nushagak Bay than Kvichak Bay (Table 2). Females may relocate to Nushagak Bay because female groups may include calves or young belugas that cannot consume large salmon. Belugas swallow their prey whole (Brooks 1955, Quakenbush *et al.* 2015) and younger belugas are limited to smaller prey by the size of their esophagus (Fay 1971). Many Chinook, and some chum and coho salmon, may be too large for smaller belugas to eat, thereby limiting the suitability of some adult salmon as prey even when they are available. Belugas wean sometime during their second year. Calves do not eat salmon at all during their first year; Brooks (1955) found that calves of the year ate mostly small bottomfish and shrimp while yearlings mainly ate smaller fish and few adult salmon. Lowry *et al.* (1986) found no salmon in the stomach of a calf (length = 187 cm) found in the Snake River on 1 July 1982, during the sockeye run. Stomach contents of this calf mostly consisted of rainbow smelt. Pink salmon are the smallest salmon in Bristol Bay, averaging 1.6 kg in the 2002–2011 commercial harvest (Jones *et al.* 2013). In contrast, sockeye ( $\bar{x} = 2.7$  kg), chum ( $\bar{x} = 3.0$  kg), coho ( $\bar{x} = 3.2$  kg), and, especially Chinook ( $\bar{x} = 7.0$  kg), are much larger. While the youngest female belugas in our study were likely  $>2$  yr of age and independent of their mothers (Suydam 2009), they may have associated with maternal groups that included calves and yearlings. If so, the females may have moved to Nushagak Bay to provide feeding opportunities for younger belugas, such as smaller pink salmon and/or because there are alternative food sources for calves.

Males may have no reason to relocate to Nushagak Bay during the pink runs, because salmon are still available in Kvichak Bay. There is a well-known, but unstudied, August run of chum salmon in the Kvichak and Branch (Alagnak) Rivers and, while the run of Kvichak pink salmon is relatively small, thousands of fish are still present (Table 2). Brooks (1955) sampled belugas on the Kvichak River in early August of 1954. Of 17 belugas with food in their stomachs, 65% contained pink salmon and 41% contained chum salmon. Even though the main Chinook and sockeye runs were over, 5% of stomachs contained Chinook and 35% contained sockeye. As such, males may have no reason to move to the Nushagak River.

In both Nushagak and Kvichak Bays, belugas apparently target migrating salmon in the bays and not farther upstream in the rivers. Salmon may be easier for belugas to catch in the bays where water is turbid and there are extensive mudflats. Mudflats may aggregate migrating salmon and, perhaps, salmon cannot visually avoid belugas in turbid water. The main use area identified by tags in Nushagak Bay is located northeast of the entrance to the Snake River where there are extensive mudflats. Belugas are known to feed on sockeye in the Snake River. Lowry *et al.* (1986) found a dead subadult beluga approximately 3 km upstream from the river entrance that had been feeding on sockeye. However, Lake Nunavaugaluk, at the head of the Snake River (Fig. 1), has historically poor salmon production and escapement. Escapement studies conducted between 1962 and 1982 found that an average of only 12,000 sockeye adults return to the Snake River, annually (Rowse and Kaill 1983). In contrast, average annual escapement on the combined Wood and Nushagak Rivers is over 2

million sockeye (Jones *et al.* 2013). Because the main use area is on the mudflats northeast of the Snake River, we suspect that belugas are likely intercepting salmon heading to the Wood or Nushagak rivers.

Because there are so few spawning salmon in the Snake River, the Alaska Department of Fish and Game has closed the area near the entrance of the Snake River to commercial fishing in an attempt to foster the establishment of a larger salmon population there (Snake River Exclusion Area; Fig. 1). Consequently, there may be fewer disturbances here during the commercial fishing season. However, most of the area used by belugas is outside of the Snake River Exclusion Area (Fig. 6, 7) and local fishermen report belugas foraging around boats, suggesting that the distribution of belugas is not primarily determined by disturbance.

Daily escapement counts of sockeye salmon explained little of the variation in beluga distribution. Models relating beluga distribution to whether or not sockeye salmon are detected at counting towers/sonar stations fit the data much better than those using the actual number of salmon counted. Likewise, time lags were largely insignificant. In effect, belugas simply restricted their movements when sockeye were being detected at counting towers and sonar stations. Although salmon are believed to move upriver within 2–4 d of leaving the bays, there is likely variation in when salmon are available to belugas and also in how belugas respond to salmon density. We suspect that the number of salmon available to belugas in the open bays is related to escapement in a more complex fashion than simple time lags.

This manuscript highlights how difficult it is to relate the movements of a marine mammal to prey resources. Although belugas changed their distribution when salmon were running, we found no relationships between which bay belugas chose and the magnitude of escapement. While the main salmon runs are well monitored in Nushagak Bay, not all fisheries are monitored every year and only sockeye runs are monitored in Kvichak Bay. Hence, even though fisheries are probably better monitored in Bristol Bay than any other place that belugas range in Alaska, large gaps in our knowledge of the size and timing salmon fisheries still exist. Of course, escapement counts are only indices of the number of salmon available and the timing of availability. Even relatively small runs of salmon may provide more fish than belugas can consume. During the study period, the average annual escapement count was 8.7 million fish (all species). Brooks (1955) conservatively estimated that an adult beluga consumed approximately five salmon (all species) per day. If there are approximately 2,500 subadult and adult belugas, then we would expect them to consume approximately 750,000 salmon if they were available for 60 d. This is approximately 9% of the average annual escapement value. However, escapement is the count of salmon that passed the counting stations having already escaped commercial and subsistence fishing and also beluga predation, and these numbers do not include any salmon species in the Kvichak drainage except sockeye. As such, 8.7 million fish is a gross underestimate of how many fish are potentially available to belugas. If harvested fish are also available for belugas in addition to commercial fishing boats, then there was an annual average of 21 million fish potentially available to belugas during the study period (of which belugas would require only 3.5%). While the accuracy of such a calculation is dubious, it generally illustrates how many adult salmon are available in Bristol Bay and why we might not expect belugas to respond to the number of fish in a particular run.

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