Diet of Beluga Whales, *Delphinapterus leucas*, in Alaska from Stomach Contents, March–November

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ABSTRACT—At least five stocks of beluga whales, Delphinapterus leucas, *are found in Alaska waters: Beaufort Sea, eastern Chukchi Sea, eastern Bering Sea, Bristol Bay, and Cook Inlet. The two northernmost stocks (Beaufort Sea and eastern Chukchi Sea) are highly migratory; the two southernmost stocks (Bristol Bay and Cook Inlet) are nonmigratory. Little is known about the seasonal movements and distribution of the eastern Bering Sea stock. Beluga populations in Alaska are thought to be stable or increasing, except for the Cook Inlet stock which is listed as endangered under the Endangered Species Act.*

We analyzed stomach contents from beluga whales collected between the months of March and November taken in subsistence harvests, from belugas found dead, and from belugas collected for research. We describe prey species and their percent frequency of occurrence (% FO) as well as potential biases from the seasonality of prey relative to the timing of sampling, and differential feeding and digestion. Diet was highly variable among stocks. The predominant fish species of the Beaufort Sea stock was Arctic cod, Boreogadus saida *(21% FO), although shrimp (60% FO) and smoothskin octopus,* Benthoctopus leioderma *(42% FO) were found more frequently. Although the eastern Chukchi Sea stock ate more saffron cod,* Eleginus gracilis *(7% FO) than Arctic cod (3% FO), shrimp (73% FO) and echiurids (27% FO) were more prevalent than fish. The eastern Bering Sea stock had the most diverse diet, and dominant fish species included saffron cod (95% FO), rainbow smelt,* Osmerus mordax *(62% FO), several species of sculpin (Family Cottidae) and flatfish (Family Pleuronectidae), both at 48% FO, and Arctic cod at 43%. Dominant invertebrates included shrimp (86% FO), with polychaetes, isopods, bivalves, amphipods, and echiurids ranging from 29 to 38% FO. Pacific salmon,* Onchorhyncus *spp., predominated over cod in Bristol Bay (81% FO) and Cook Inlet (67% FO) beluga stocks, and invertebrates appeared to be less prevalent prey. In Bristol Bay, smelt were also eaten more often (43% FO) than cod (3% FO), while in Cook Inlet cod were eaten more often (39% FO) than smelt (11% FO). Invertebrates were common in the diet of all Alaska beluga stocks and shrimp (mostly from the family Crangonidae) were the most prevalent.*

Introduction

At least five stocks of beluga whales, *Delphinapterus leucas*, occur in the waters of Alaska (Fig. 1). These stocks were tentatively identified by their summer distributions (Frost and Lowry, 1990; Richard et al., 2001), and were later confirmed genetically (O'Corry-Crowe et al., 1997, 2002, 2010). The distribution of beluga whales in Alaska is discontinuous from Yakutat Bay[1, 2] to Cook Inlet to Bristol Bay. The entire area from Bristol Bay northward and eastward to Canada is used by belugas; the Bering and Chukchi seas are used year-round and the Beaufort Sea is used in summer (Frost and Lowry, 1990).

Beluga whales in Alaska appear to follow one of two life history strategies: migratory and nonmigratory. Migratory stocks use shallow nearshore and deepwater offshore habitats (Hazard, 1988; Frost and Lowry, 1990), and include the eastern Chukchi Sea stock (population size ~4,000 (Allen and Angliss, 2011)) and the Beaufort Sea or Mackenzie stock (population size ~39,000 (Harwood et al., 1996; Allen and Angliss, 2011)).

Nonmigratory stocks use shallow, estuarine habitats year-round and include the Bristol Bay and Cook Inlet stocks. The Bristol Bay population is increasing (Lowry et al., 2008) and is estimated to be ~3,000 (Allen and Angliss, 2011). Local sightings and satellite telemetry confirm that belugas occur in Bristol Bay in all months of the year (Harrison and Hall, 1978; Frost and Lowry, 1990; Lensink[3]; Quakenbush and Citta[4]; Quakenbush[5]).

The population in Cook Inlet is estimated to be 312 whales and appears to be decreasing at 1.6% per year (Hobbs et al., 2015). The population declined dramatically between 1994 and 1998 (Hobbs et al., 2000) and the stock was determined to be depleted under the Marine Mammal Protection Act in 2000 (NOAA, 2000); the original cause of the decline is believed to be overharvest. Between 1999 and 2006 the harvest was restricted to five

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[1]There is a small group of <20 belugas that appear to be resident in Yakutat Bay, a deepwater fiord (Laidre et al., 2000; Allen and Angliss, 2011)

[2]O'Corry-Crowe, G., W. Lucey, C. Bonin, E. Henniger, and R. Hobbs. 2006. The ecology, status and stock identify of beluga whales, *Delphinapterus leucas*, in Yakutat Bay, Alaska. Rep. to U.S. Mar. Mamm. Comm., NMFS-YSB-YTT, 22 p.

[3]Lensink, C. J. 1961. Status report: beluga studies. Alaska Dep. Fish Game, Juneau. Unpubl. rep., 38 p.

[4]Quakenbush, L., and J. Citta. 2006. Fall movements of beluga whales captured in the Nushagak River in September 2006. Unpubl. rep. to Alaska Beluga Whale Committee, P.O. Box 69, Barrow Alaska 99723, 9 p.

[5]Quakenbush, L., Alaska Dep. Fish Game, 1300 College Road, Fairbanks. Unpubl. data.

belugas, and after 2006 no harvest has been allowed.

In October 2008, the Cook Inlet beluga whale population was listed as endangered under the Endangered Species Act (NOAA, 2008). Aerial surveys (1994–2011) and satellite telemetry (1999–2002) have shown that Cook Inlet beluga whales remain in the Cook Inlet area all year (Rugh et al., 2000, Hobbs et al., 2005). Except for Cook Inlet belugas, the other four beluga stocks in Alaska continue to be harvested for subsistence by coastal indigenous people and harvests are sustainable (Allen and Angliss, 2011). The Beaufort Sea stock is also harvested in Canada during summer; most of the Alaska harvest of this stock occurs during the spring migration.

The eastern Bering Sea beluga stock is found in the Yukon-Kuskokwim Delta area and in Norton Sound in summer. Aerial surveys conducted there provide a population estimate of ~18,000 (Allen and Angliss, 2011). The winter range of the eastern Bering Sea stock is unknown; therefore it is not known whether this stock is migratory.

Throughout their range, belugas feed on a variety of fish and invertebrates, often on prey that form concentrations such as schooling fish and shrimp (Seaman et al., 1982). Beluga whale diet has been described in Canada (Doan and Douglas, 1953; Sergeant, 1973; Vladykov[6]), Russia (Kleinenberg et al., 1964; Tomlin, 1967), and Svalbard and northwestern Europe (Lono and Oynes, 1961). In Alaska, information on beluga whale diet is limited to one published paper by Seaman et al. (1982) describing stomach contents from 119 beluga whales from six locations in the Bering and Chukchi seas but none from Cook Inlet. Additional Bristol Bay diet information was recorded in unpublished Alaska Department of Fish and Game (ADFG) reports (Brooks[7, 8]; Lensink[3]; Klinkhart[9]; Vania[10]) and by Frost et al. (1984).

Information collected since Seaman et al. (1982) from Kotzebue Sound is provided in an unpublished report by Lowry et al.[11] Based on traditional ecological knowledge, Huntington et al. (1999) described the diet of belugas in the nearshore areas of the eastern Bering Sea, Kotzebue Sound, and the eastern Chukchi Sea to include a variety of prey items, but primarily fish. Cook Inlet beluga prey have been indirectly described by relating whale movements to seasonal fish runs in a publication on traditional ecological knowledge from the beluga hunters of Cook Inlet (Huntington, 2000) and in published and unpublished reports (Fall et al., 1984; Hobbs et al.[12]).

This paper provides: 1) an updated description of the diet of beluga whales in Alaska using identifiable prey items found in their stomachs between 1954 and 2012, and 2) a comprehensive description of diet from stomach contents of Cook Inlet beluga whales.

Methods

Data included in this study came from the stomachs of beluga whales: 1) harvested for subsistence, 2) found dead, and 3) collected for published (Frost et al., 1984) and unpublished ADFG diet studies (Brooks[7, 8]; Lensink[3]; Vania[10]; Lowry et al.[11]; and ADFG[13]). We assigned each beluga to a stock based on collection timing and location (Fig. 1). Collections were made between March and November.

Stomachs and stomach contents were handled in several ways: 1) stomachs were collected whole and frozen, 2) stomach contents were removed and frozen, or 3) stomach contents were removed and placed in 10% formalin. In the laboratory, contents were weighed to the nearest 0.1 g and then rinsed with fresh water on a 1.0 mm sieve stacked on a 0.5 mm sieve. For frozen whole stomachs, all parts of the stomach were opened and rinsed over sieves so that all otoliths, fish bones, and cephalopod beaks that tend to adhere to the stomach lining were collected. In some cases, incomplete stomachs or a subsample of contents were collected, and in other cases prey items were identified visually in the field without collecting the stomach; these were noted by individual beluga in the database. Prey items were sorted into major taxonomic groups and identified to the lowest taxonomic level.

Fish were tabulated by counting whole fish when present and by adding the maximum count of left or right otoliths plus half of the count of otoliths that could not be identified as left or right. Lengths of otoliths that did not appear degraded were measured to the nearest 0.1 mm. Otolith lengths were converted to fish lengths using conversion equations (e.g., Frost and Lowry, 1981; Seaman et al., 1982; Harvey et al., 2000) when possible. Converted lengths are considered minimum lengths because erosion of the otoliths caused by digestion is expected to decrease otolith length and because some equations are known to have poor correlations (Harvey et al., 2000).

Cephalopods were identified by their beaks (Clarke, 1986). We used the maximum count of upper or lower beaks to determine the number consumed. The lower beak hood lengths

[6]Vladykov, V. D. 1946. Etudes sur les mammiferes aquatiques. IV. Nourriture du marsouin bloc ou beluga (*Dephinapterus leucas*) du fleuve Saint-Laurent. Dep. Pech., Quebec, 129 p.

[7]Brooks, J. W. 1954. Beluga. *In* 1954 Annual Rep., Alaska Dep. Fish Game, Juneau, p. 51–57.

[8]Brooks, J. W. 1955. Beluga. *In* 1955 Annual Rep., Alaska Dep. Fish Game, Juneau, p. 98–106.

[9]Klinkhart, E. G. 1966. The beluga whale in Alaska. Alaska Dep. Fish Game Rep., 11 p.

[10]Vania, J. 1967. Beluga. *In* 1966 Annual Rep., Alaska Dep. Fish Game, Juneau, p. 21–24

[11]Lowry, L. F., K. J. Frost, and G. A. Seaman. 1986. Investigations of belukha whales in coastal waters of western and northern Alaska. Part III. Food habits. Final Rep. U.S. Dep. Commer. NOAA, Anchorage, from Alaska Dep. Fish Game, 24 p.

[12]Hobbs, R. C., K. E. W. Shelden, D. J. Vos, K. T. Goetz, and D. J. Rugh. 2006. Status review and extinction assessment of Cook Inlet belugas (*Delphinapterus leucas*). U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Alaska Fish. Sci. Cent. Proc. Rep. 2006-16, 74 p.

[13]Alaska Dep. Fish Game. Unpubl. data on file at 1300 College Road, Fairbanks, AK 99701.

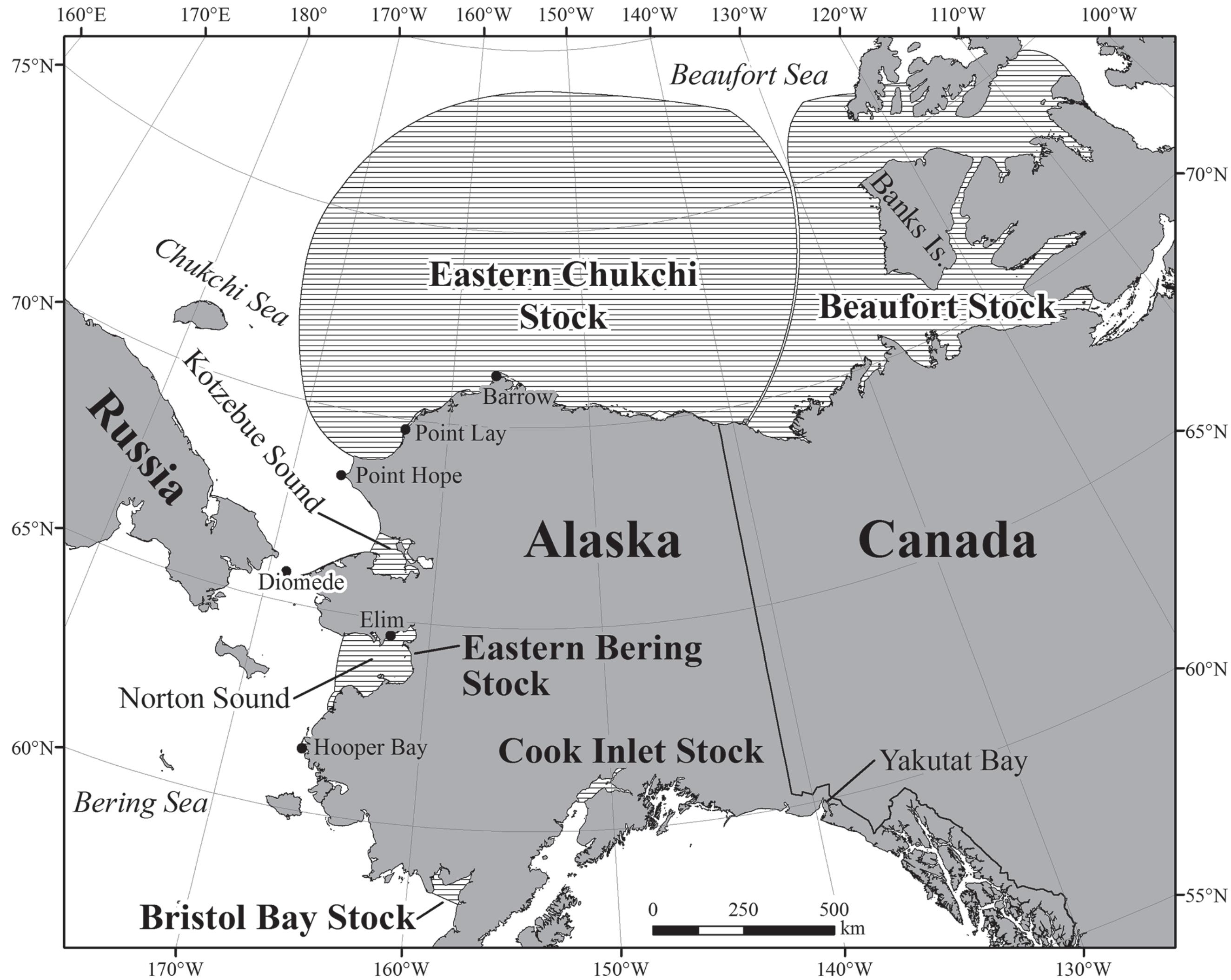

Figure 1.—Known summer areas used by five stocks of beluga whales in Alaska and the area within Kotzebue Sound where stock assignment is unclear. Belugas from the Beaufort Sea stock are harvested at Diomede and Point Hope while on spring migration and harvested in Canada in summer.

were measured to the nearest 0.1 mm and used to estimate cephalopod total body weight using an equation for a closely related species, *Octopus vulgaris* (Clarke, 1986).

For 17 stomachs from Cook Inlet beluga whales between 1992 and 2001, only a subsample of the stomach contents was collected, and only fresh or slightly digested material was identified. Few otoliths were recorded in these samples, but, diagnostic bones of fish were identified by Pacific Identifications Inc.[14], Victoria, British Columbia, Canada. No invertebrate prey items were recorded or identified.

We present fish prey in beluga stomachs as the percent number (% N) of fish by taxon by beluga whale stock. We determined the total number of fish identified in all fish taxa for all stomachs of that stock of beluga whale and then calculated the percentage of the total represented by each taxon. For example, if we estimated 100 individual fish from fish taxon A (e.g., saffron cod, *Eleginus gracilis*) and 300 fish from all fish taxa in all stomachs sampled from that beluga stock, then the % N of taxon A (saffron cod) for that stock was 100/300 or 33%. For invertebrates, % N was not calculated because we often could not determine the number of individuals from the parts available.

[14]Mention of trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA.

The percent frequency of occurrence (% FO) is provided for all major prey types and was calculated for each stock as the number of stomachs containing that prey type divided by the total number of stomachs that contained any prey. For example, if 100 stomachs contained prey of any kind and 75 of those stomachs contained parts of echiurid worms, the % FO of echiurids would be 75%. Due to differential digestion rates, volume measurements were not considered representative of the true volume of prey consumed and were not analyzed.

Results

Our dataset includes 365 beluga whale stomachs, 233 of which had never been reported before, and 132 from unpublished ADFG reports. Stomachs from the ADFG studies included 22 collected in 1982 at Elephant Point (Eschscholtz Bay) in Kotzebue Sound (Lowry et al.[11]) and 109 collected in Bristol Bay during 1954 and 1955 (Brooks[7, 8]), 1965 and 1966 (Vania[10]), and in 1982 and 1983 (Frost et al., 1984), and one collected in Cook Inlet (Baxter and Baxter[15]). Of the 365 stomachs, 82 were empty (22%) or contained only nonfood items and 283 (78%) contained prey remains (Table 1).

Stomachs were collected from Cook Inlet to Barrow from 217 beluga whales harvested for subsistence, 102 collected for research, 41 found dead, and for 5 animals for which the type of death was not recorded. Most of the whales found dead were in Cook Inlet (n = 30; 73%).

Prior to 1982, beluga whales regularly occurred and were harvested in Kotzebue Sound. After 1982, occurrence became irregular and infrequent, and it is not known to what stock these belugas belonged. For this study, we considered stomachs collected from belugas in Kotzebue Sound to be Kotzebue Sound belugas, even though some of them may have been from other stocks.

Table 1.—Number of stomachs analyzed from Alaska's beluga whales belonging to five stocks and from a Kotzebue Sound population collected between 1954 and 2012.

	Number of Stomachs				
Stock ID	Total	Empty (%)	Month	Range of years	No. of years
Beaufort Sea	62	0 (0)	4–6	1983–2003	5
Eastern Chukchi Sea	67	37 (55)	6–8	1983–2010	13
Kotzebue Sound	29	7 (24)	6,7,10	1982–2008	3
Eastern Bering Sea	39	7 (18)	5–7,9,10	1993–2012	12
Bristol Bay	115	14 (12)	5–8,10	1954–2011	11
Cook Inlet	53	17 (32)	3–11	1961, 1992–2010	17
Total	365	82 (22)	3–11	1954–2012	30

For all locations in Alaska, a minimum total of 37 fish species and 40 invertebrate species were identified in beluga whale stomachs (Table 2, 3). Other species may have been present that we were not able to identify. Nonfood items included sand, pebbles, wood and other vegetation, kelp, feathers, and a piece of bone.

Beaufort Sea Stock

We analyzed stomach contents from 62 beluga whales from the Beaufort Sea stock collected between 1983 and 2003 at Point Hope and Diomede (Table 1). All were collected during April, May, and June. Sex was reported for all but one (19 males and 42 females) and length was reported for all but two. The mean length for males was 355 cm (range 203–462) and for females 332 cm (range 240–396) (Table 4). Twenty-one stomachs (34%) contained a minimum total of 418 fish of at least eight different species from five families (Table 2). The predominant species was Arctic cod, *Boreogadus saida*, which comprised 82% N and 21% FO (Table 2) and one stomach contained otoliths from 190 Arctic cod. Forty-one stomachs (66%) contained only invertebrates.

Otoliths from six fish species were measured to estimate the sizes of fish eaten. The largest fish were Arctic staghorn sculpin, *Gymnocantheus tricuspis*, with an estimated mean length of 17.9 cm (range 16.1–18.9), followed by shorthorn sculpin, *Myoxocephalus scorpius*, at 16.2 cm (range 12.1–18.5; Table 5). Arctic cod were next in estimated length (mean 14.2 cm, range 8.2–21.2) followed by walleye pollock, *Theragra chalcogramma*, and saffron cod, which were similar in estimated length at 10.7 cm (range 8.2–12.3) and 10.3 cm (range 7.6–16.3), respectively. Pacific sand lance, *Ammodytes hexapterus*, were the smallest with a mean length of 9.9 cm (range 8.1–11.3; Table 5).

Most stomachs (n = 57; 92%) contained invertebrates that represented 16 species from multiple taxonomic groups: predominately shrimp (60% FO), cephalopods (52% FO), echiurids (19% FO), and amphipods (11% FO; Table 3). Shrimp included at least five species from at least three families. All cephalopods were octopus (n = 358), 266 (74%) of which were identified as smoothskin octopus, *Benthoctopus leioderma* (Table 3). Three that were not identified to species were of the same genus and 89 were only recorded as octopus. The number of octopus per stomach ranged from 0 to 144 individuals, with two stomachs having >100 lower or upper octopus beaks each. Based upon 35 measurable beaks of 107 beaks present in a beluga stomach harvested near Point Hope in 1997, the average estimated weight per octopus was 1,015 g (SD = 442, range 140–1,965). The average estimated weight per octopus, calculated from 50 of 144 octopus beaks in a beluga whale harvested near Little Diomede in 2003, was 881 g (SD = 415, range 155–1,965).

Eastern Chukchi Sea Stock

Stomachs from 67 beluga whales from the eastern Chukchi Sea stock were collected between 1983 and 2010 (Table 1). Most (58 or 87%) were collected near Point Lay during June and July, and most (37 or 55%) were

[15]Baxter, R., and S. Baxter. 1961. Cook Inlet data report series 61-1, stream surveys west side Cook Inlet –1961. Alaska Dep. Fish Game, Homer, 43 p. + 10.

Table 2.—Percent number and percent frequency of occurrence of fish identified from stomach contents of beluga whales collected in Alaska by location, 1954–2012. Percent number is the number of fish from a taxa divided by the total number of all fish eaten (x 100). Percent frequency of occurrence is the number of stomachs that contained a fish taxon divided by the total number of stomachs that contained prey (x100).

	1983–2003 Beaufort		1983–2010 E. Chukchi		1982–2008 Kotzebue		1993–2012 E. Bering		1954–2005 Bristol Bay		2002–2010 Cook Inlet	
	Percent number n = 21	Percent frequency n = 62	Percent number n = 9	Percent frequency n = 30	Percent number n = 21	Percent frequency n = 22	Percent number n = 21	Percent frequency n = 21	Percent number n = 99	Percent frequency n = 100	Percent number n = 17	Percent frequency n = 18
Stomachs that contained fish (%)		34		30		95		100		99		94
Taxon — Stomachs that contained only fish (%)		8		7		5		10		76		50
Fishes												
All Petromyzontidae, lamprey spp.							<1	19	<1	3		
Arctic lamprey, *Lethenteron camtschaticum*							<1	19				
All Clupeidae					<1	5	1	24				
Pacific herring, *Clupea pallasii*					<1	5	1	24				
All Catostomidae											1	6
Longnose sucker, *Catostomus catostomus*											1	6
All Osmeridae	<1	2	7	3	3	55	14	67	16	43	12	11
Pond smelt, *Hypomesus olidus*									<1	1		
Rainbow smelt, *Osmerus mordax*			7	3	3	55	13	62	2	5		
Eulachon, *Thaleichthys pacificus*											12	11
Capelin, *Mallotus villosus*							<1	24				
All Salmonidae							<1	10	83	81	38	67
Dolly Varden, *Salvelinus malma*									<1	1		
Pink salmon, *Oncorhynchus gorbuscha*									<1	18		
Coho salmon, *Oncorhynchus kisutch*							<1	5	<1	10	21	28
Chinook salmon, *Oncorhynchus tshawytscha*									<1	3	2	11
Chum salmon, *Oncorhynchus keta*							<1	5	<1	15	8	17
Sockeye salmon, *Oncorhynchus nerka*									58	55		
All Gadidae	86	23	40	13	95	95	78	100	<1	3	42	39
Arctic cod, *Boreogadus saida*	82	21	7	3	–	–	29	43				
Saffron cod, *Eleginus gracilis*	1	5	20	7	94	95	48	95	<1	2	26	22
Walleye pollock, *Theragra chalcogramma*	3	3					<1	10			10	17
Pacific cod, *Gadus macrochephalus*											1	6
All Gasterosteidae, stickleback spp.	<1	2							<1	3		
All Cottidae	9	5			1	9	4	48	<1	6	1	6
Arctic staghorn sculpin, *Gymnocanthus tricuspis*	1	3					<1	5				
Sculpin species, *Hemilepidotus* spp.							<1	5				
Pacific staghorn sculpin, *Leptocottus armatus*											1	6
Belligerent sculpin, *Megalocottus platycephalus*							<1	19				
Shorthorn sculpin, *Myoxocephalus scorpius*	7	3					<1	14				
Sculpin species, *Myoxocephalus* spp.							<1	14				
Ribbed sculpin, *Triglops pingelii*							<1	5				
Sculpin species, *Triglops* spp.							3	5				
All Agonidae, poachers							<1	5				
All Liparidae							<1	14				
Variegated snailfish, *Liparis gibbus*							<1	14				
All Zoarcidae			13	3			<1	5				
Canadian eelpout, *Lycodes polaris*			13	3			<1	5				
All Stichaeidae					<1	5	<1	38	1	7	1	6
Stout eelblenny, *Anisarchus medius*							<1	5				
Slender eelblenny, *Lumpenus fabricii*					<1	5	<1	38				
Slender eelblenny or snake prickleback, *Lumpenus* spp.											1	6
All Ammodytidae	3	8	13	3	<1	5	<1	24				
Pacific sand lance, *Ammodytes hexapterus*	3	8	13	3	<1	5	<1	24				
All Pleuronectidae							2	48	<1	10	3	11
Pacific halibut, *Hippoglossus stenolepis*							<1	5				
Flathead sole, *Hippoglossoides elassodon*							<1	5				
Starry flounder, *Platichthys stellatus*											1	6
Northern rock sole, *Lepidopsetta polyxystra*							<1	14				
Unidentified rock sole, *Lepidopsetta* spp.									<1	1		
Longhead dab, *Limanda proboscidea*							<1	29				
Yellowfin sole flounder, *Limanda aspera*											2	11
Arctic flounder, *Pleuronectes glacialis*							<1	14				
All Unidentified fish	1	5	27	13			<1	14	<1	3	2	11
Minimum no. of fish species eaten (total = 37)	8		5		6		25		14		12	
Minimum no. of fish eaten	418		15		1,354		5,781		26,721		106	

empty. The other nine stomachs were from belugas harvested near Barrow in June, July, and August, none of which were empty. Although it is not entirely clear whether belugas near Barrow in summer belong to the Beaufort Sea or eastern Chukchi Sea stock, movements from satellite telemetry data suggest they are more likely to be eastern Chukchi Sea belugas (Fig. 1; Richard et al., 2001; Suydam et al., 2001).

Sex was known for all 67 belugas; 36 were males and 31 were females (Table 4). Mean body length for males (n = 26) was 390 cm (range 280–478) and for females (n = 25) was 349 cm (range 253–410). At least five species of fish from four families (Table 2), and 15 species of invertebrates from nine taxonomic groups were identified (Table 3). Of the 30 stomachs that contained food items nine (30%) contained fish for which the most prevalent species was saffron cod (7% FO).

Otoliths from three fish species were measured to estimate the sizes of fish

Table 3.—Percent frequency of occurrence of invertebrates identified from stomach contents of beluga whales collected in Alaska by location, 1954–2012. Percent frequency of occurrence is the number of stomachs that contained an invertebrate taxon divided by the total number of stomachs containing prey (x100).

	Percent frequency of occurrence					
	1983–2003 Beaufort *n* = 62	1983–2010 E. Chukchi *n* = 30	1982–2008 Kotzebue *n* = 22	1993–2012 E. Bering *n* = 21	1954–2005 Bristol Bay *n* = 100	2002–2010 Cook Inlet *n* = 18
Stomachs containing invertebrates (%)	92	93	95	90	24	50
Taxon — Stomachs containing only invertebrates (%)	66	70	5	0	1	6
Invertebrates						
All Porifera			5	5		6
All Polychaeta	5	17		38		11
Polynoidae		7		24		
Nereididae, *Nereis* spp.		7		10		
Pectinariidae				5		
All Bivalvia			5	33	3	
Astartidae, Astarte spp.				5		
Myidae				5		
Clinocardiinae, *Serripes groenlandicus*				5		
Tellinidae, *Tellina* spp.				5		
All Cephalopoda	52	10	5	10		
Squid, *Gonatus* spp.		3				
Minimum number of squid		3				
Octopus	42	7	5			
Benthoctopus leioderma, smoothskin octopus	8	3				
Benthoctopus spp.	2					
Minimum number of octopi	358	4	1			
All Gastropoda		7	36	10		
Polinices spp.			27			
All Cirripedia, barnacles	2					
All Mysidae			14	24		6
Mysis oculata				24		
Neomysis rayii				19		6
Neomysis spp.			14			
All Isopoda		3	36	38	4	
Saduria entomon			18	33	3	
Saduria spp.		3	18		1	
All Amphipoda	11	7	41	29		11
Ampeliscidae, *Ampelisca* spp.	2					
Byblis spp.	3					
Lysianassidae, *Orchomene* spp.						6
Uristidae, *Anonyx* spp.	2					
Senticaudata						
Anisogammaridae, *Anisogammarus pugettensis*	2					
Calliopiidae		3				
Gammaridae	3		14	5		
Gammarus spp.	2	3	27	19		
Melitidae, *Melita* spp.				5		
All shrimp	60	73	86	86	21	39
Caridea		3		29		17
Hippolytidae	2					
Eualus spp.	2					
Crangonidae	8	30		19		
Argis dentata	3					
Argis lar	3	3		5		
Argis spp.	13	30				
Crangon alaskensis or septemspinosa			32	29		6
Crangon franciscorum						6
Crangon spp.	11		59	10	2	6
Sclerocrangon boreas	2	23		5		
Pandalidae, *Pandalus* spp.	3					
All crabs	2	3		14	1	6
Majidae				5	1	
Oregoniidae, *Chionoecetes bairdi*						6
Chionoecetes opilio		3				
Hyas lyratus	2					
All Sipuncula		3				
All Echiuridae	19	27	5	29		6
All Bryozoa				10		
Clypeasteroida, sand dollar	2					
All Ascidiacea, tunicates		7		14		
Chelysoma spp.		3				
Pelonaia corrugata		7		5		
All unidentified invertebrates	3	10				6
Minimum no. of species eaten (total = 40)	16	15	9	22	4	8

eaten. The largest fish were saffron cod with an estimated mean length of 13.6 cm (range 6.5–20.7), followed by Pacific sand lance at 10.1 cm (range 9.7–10.5; Table 5). The otoliths from two Canadian eelpout, *Lycodes polaris*, were also measureable, but because no size or weight conversions have been developed for this species, fish size could not be estimated (Table 5).

Of the 30 stomachs that contained food items, 21 (70%) contained only invertebrates (Table 3). Shrimp occurred most often (73% FO), followed by echiurid worms (27% FO), polychaetes (17% FO), and cephalopods (10% FO).

Between 1989 and 2010, 13 of 28 stomachs (46%) were reported to contain sand or "mud balls" but no food. Whether the mud was ingested incidentally or intentionally is unknown; however, stomachs with food usually had only minor amounts of nonfood items like sand and wood. In 2012, we examined stomach contents from two of the belugas harvested at Point Lay on 30 June 2009 where the contents appeared to be mostly fine grain sand; however, we found evidence of both fish and invertebrate prey. The first stomach was that of a white female and contained 3.9 kg of sand and parts of 63 tunicates (3 *Pelonaia corrugate*, 10 *Chelysoma* spp., and 50 unidentified to species), parts of at least 53 shrimp (all from the family Crangonidae, including 26 *Sclerocrangon boreas*), and 11 polychaetes (8 *Nereis* spp. and 3 from the family Polynoidea). The second stomach, that of a white-gray male, contained 2.1 kg of sand, and parts of 17 tunicates (7 *Pelonaia corrugate*, and 10 unidentified), at least 15 crangonid shrimp (including 5 *Sclerocrangon boreas*), and 4 otoliths; two each from saffron cod and Pacific sand lance. It is possible that stomachs visually inspected in the past and thought to contain only mud balls also contained invertebrates and otoliths mixed with the mud.

Table 4.—Sex and body length for some Alaska beluga whales belonging to five stocks and from a Kotzebue Sound population analyzed for stomach contents collected between 1954 and 2012.

Stock Location	Sex			Male body length (cm) *n*; mean (SD) range	Female body length (cm) *n*; mean (SD) range
	Male	Female	Unknown		
Beaufort Pt. Hope, Diomede	19	42	1	19; 355 (68.7) 203–462	41; 332 (32.0) 240–396
Eastern Chukchi Barrow, Pt. Lay	36	31	0	26; 390 (49.5) 280–478	25; 349 (30.9) 253–410
Kotzebue Escholtz Bay, Kotzebue	14	13	2	3; 304 (44.7) 257–345	5; 346 (27.5) 297–363
Eastern Bering Elim, Koyuk, Unalakleet, Hooper Bay	14	14	11	13; 389 (66.2) 279–475	9; 351 (66.9) 238–414
Bristol Bay	31	55	27	29; 333 (78.6) 187–470	47; 317 (49.2) 193–387
Cook Inlet	20	21	10	8; 391 (72.7) 256–463	15; 337 (67.1) 160–391

Kotzebue Sound

We analyzed stomach contents from 29 beluga whales harvested in Kotzebue Sound; 22 were harvested in June 1982 (two (9%) were empty), six were harvested in July 2007 (five (83%) were empty), and one was harvested in October 2008 (with food) (Table 1). Of 27 belugas where sex was known, 14 were males and 13 were females. Body lengths of three males averaged 304 cm (257, 310, and 345 cm) and five females averaged 346 cm (range 297–363) (Table 4). In 1982, stomach contents were identified and counted only from subsamples. For the more recent stomachs, all were analyzed completely but only two had contents. The only stomach with prey in 2007 contained a single gastropod operculum. The one stomach collected in 2008 contained both fish and invertebrates.

Of the 22 stomachs from Kotzebue with food, 21 contained fish (Table 2). At least six species of fish were identified representing six families. Saffron cod (95% FO) and rainbow smelt, *Osmerus mordax,* (55% FO) were most prevalent, followed by sculpins (9% FO). Pacific sand lance; Pacific herring, *Clupea pallasii*; and slender eelblenny, *Lumpenus fabricii*, were each represented at 5% FO (Table 2). Saffron cod were also numerically dominant; 1,279 of 1,354 (94% N) total fish eaten were saffron cod (Table 2).

Otoliths from 23 saffron cod were measured to estimate the average fish length at 23.8 cm (range 7.4–41.9; Table 5). One otolith from a Pacific sand lance provided a length estimate of 15.0 cm and two otoliths from rainbow smelt estimated fish lengths at 12.2 cm (range 11.1–13.2). One otolith from a slender eelblenny was measured but no conversion was available.

All but one stomach with food contained invertebrates (n = 21; 95%); including at least nine species. Shrimp was the dominant group (86% FO) followed by amphipods (41% FO); gastropods and isopods were represented equally at 36% FO (Table 3).

Eastern Bering Sea Stock

Stomach contents from 39 belugas from the eastern Bering Sea stock were collected between 1993 and 2012 during May (n = 17), June (n = 7), July (n = 1), September (n = 2), October (n = 9), and month unknown (n = 3). Seven of the 39 (18%) stomachs, six of which were collected in mid-June 1995, were empty (Table 1). Of 28 belugas where sex was known, the sex ratio was even at 14 each. Body length of 13 males averaged 389 cm (range 279–475), and nine females averaged 351 cm (range 238–414) (Table 4).

Stomachs from 11 beluga whales harvested near Elim in 1996 were only visually inspected and are not included in Tables 2 or 3: those stomachs contained saffron cod, and one also contained rainbow smelt. One of the 11 stomachs (9%) contained invertebrates, which were only identified as shrimp.

Of the 21 stomachs with food that were fully analyzed all contained cod: saffron cod (95% FO), Arctic cod (43% FO), and walleye pollock (10% FO; Table 2). In addition to cod, the overall fish diet by % FO included rainbow smelt (62%), several species of flounder and sculpin (both at 48%), slender eelblenny (38%), Pacific sand lance; capelin, *Mallotus villosus*; and Pacific herring (all at 24%); Arctic lamprey, *Lethenteron camtschaticum* (19%); snailfish (14%); and two species of salmon (coho, *Oncorhynchus kisutch*; and chum, *O. keta,* each at 5%). Nine stomachs contained evidence of >100 individual saffron cod (range 121–474). Overall, a minimum of 25 species of fish from 12 families were identified (Table 2).

Table 5.—Mean, standard deviation (SD), and range of otolith lengths (mm), fish length (cm), and weight (g) of fish collected from beluga whale stomachs. Fish length and weight were converted from equations or measured directly from whole fish.

Fish	Beluga stock	*n*	Mean otolith length in mm (SD) range	Mean fish length in cm (SD) range	Mean fish weight in g (SD) range	Source of equation
Clupeidae						
Pacific herring	E. Bering	18	4.9 (0.5) 4.0–5.8	24.1 (2.8) 19.1–28.5	228.6 (85.5) 99.4–388.3	Harvey et al., 2000
Osmeridae						
Pond smelt	Bristol Bay	2	2.7 (0.4) 2.4–3.0			No conversion available
Rainbow smelt	Kotzebue	2	4.4 (0.6) 4.0–4.8	12.2 (1.5) 11.1–13.2	14.1 (5.6) 10.1–18.0	Harvey et al., 2000
	E. Bering	233	5.0 (1.0) 2.0–9.5	13.9 (2.8) 5.7–25.9	24.6 (19.1) 1.1–162.6	Harvey et al., 2000
	Bristol Bay	6	5.0 (1.8) 1.4–6.2	13.7 (5.0) 4.1–17.0	27.0 (15.7) 0.4–41	Harvey et al., 2000
	Bristol Bay	2		19.6 (2.8) 17.6–21.5	67.3 (30.1) 46.0–88.6	Length measured Weight Harvey et al., 2000
	Bristol Bay	1			53.1 (NA)	Measured
Eulachon	Cook Inlet	4	4.3 (0.3) 3.9–4.5	17.4 (1.2) 15.7–18.5	51.2 (10.5) 36.4–60.6	Harvey et al., 2000
Capelin	E. Bering	5	2.5 (0.3) 2.3–3.0	12.4 (0.9) 11.6–14.0	15.6 (4.0) 12.3–22.4	Harvey et al., 2000
Salmonidae						
Coho salmon	Cook Inlet	10	4.9 (0.2) 4.5–5.2			
	Cook Inlet	3		62.1 (2.6) 58.3–64.1	3,124 (357) 2,747–3,476	Measured
Chum salmon	Cook Inlet	4	5.4 (0.2) 5.2–5.5			
	Cook Inlet	5		60.0 (3.8) 56.0–65.0	2,989 (600) 2,275–3,661	Measured
Sockeye salmon	Bristol Bay	2	5.4 (1.6) 4.3–6.5	64.4 (13.4) 54.9–73.8	3,478 (2,493) 1,715–5,240	Measured
Gadidae						
Arctic cod	Beaufort	84	5.9 (1.3) 3.0–8.9	14.2 (2.9) 8.2–21.2	24.6 (16.0) 2.8–78.3	Frost and Lowry, 1981
	E. Bering	467	5.9 (0.5) 4.7–7.3	14.5 (1.0) 11.9–17.6	21.5 (5.3) 10.5– 41.4	Frost and Lowry, 1981
Saffron cod	Beaufort	4	5.9 (2.2) 4.4–9.1	10.3 (4.0) 7.6–16.3	9.7 (12.4) 2.6–28.2	Frost and Lowry, 1981[1]
	E. Chukchi	2	7.4 (5.1) 3.8–11.0	13.6 (10.0) 6.5–20.7	30.5 (40.7) 1.7–59.3	Frost and Lowry, 1981[1]
	Kotzebue	23	12.1 (5.2) 4.3–20.1	23.8 (11.3) 7.4–41.9	151.6 (142.7) 2.4–522.7	Frost and Lowry, 1981[1]
	E. Bering	558	10.3 (2.2) 4.9–17.6	19.3 (4.8) 8.4 – 36.0	56.9 (41.7) 3.7–329.2	Frost and Lowry, 1981[1]
	Bristol Bay	1	4.2 (NA)	7.2 (NA)	2.3 (NA)	Frost and Lowry, 1981
	Cook Inlet	3	11.5 (3.3) 7.7–13.4	18.9 (6.2) 11.8–22.6	77.6 (55.8) 13.1–111.3	Harvey et al., 2000
Walleye pollock	Beaufort	3	5.0 (1.0) 3.9–5.7	10.7 (2.2) 8.2–12.3	8.1 (4.1) 3.5–11.3	Frost and Lowry, 1981
	E. Bering	1	4.2 (NA)	8.9 (NA)	4.5(NA)	Frost and Lowry, 1981
Cottidae						
Arctic staghorn sculpin	Beaufort	4	5.6 (0.3) 5.1–5.8	17.9 (1.2) 16.1–18.9	56.8 (11.3) 40.7–66.3	Seaman et al., 1982[2]
Belligerent sculpin	E. Bering	7	6.8 (0.7) 6.2–7.8	23.0 (2.7) 20.5–26.9	125.2 (45.0) 84.9–194.3	Seaman et al., 1982[2]
Shorthorn sculpin	Beaufort	17	5.1 (0.5) 4.1–5.7	16.2 (2.0) 12.1–18.5	43.0 (14.3) 17.0–62.1	Seaman et al., 1982[2]
	E. Bering	4	6.1 (0.6) 5.4–6.6	20.2 (2.3) 17.3–22.1	83.7 (27.8) 50.6–106.8	Seaman et al., 1982[2]
Stichaeidae						
Stout eelblenny	E. Bering	1	1.4 (NA)			No conversions available
Slender eelblenny	Kotzebue	1	2.2 (NA)			No conversions available
	E. Bering	9	2.5 (0.3) 2.1–2.9			No conversions available
Liparidae						
Variegated snailfish	E. Bering	2	2.7 (0.1) 2.6–2.8			No conversions available
Zoarcidae						
Canadian eelpout	E. Chukchi	2	5.9 (0.5) 5.5–6.2			No conversions available
Ammodytidae						
Pacific sand lance	Beaufort	3	1.9 (0.4) 1.5–2.3	9.9 (1.6) 8.1–11.3	3.9 (1.7) 2.2–5.5	Harvey et al., 2000
	E. Chukchi	2	2.0 (0.1) 1.9–2.1	10.1 (0.6) 9.7–10.5	4.0 (0.6) 3.6–4.5	Harvey et al., 2000
	Kotzebue	1	3.2 (NA)	15.0 (NA)	12.0 (NA)	Harvey et al., 2000
	E. Bering	1	1.7 (NA)	8.9 (NA)	2.8 (NA)	
Pleuronectidae						
Longhead dab	E. Bering	3	3.1 (0.6) 2.5–3.6			No conversions available
Arctic flounder	E. Bering	3	4.3 (0.2) 4.1–4.4			

[1]There are two different length regressions in Frost and Lowry (1981) for this species depending on otolith size.
[2]The length and weight regressions from Seaman et al. (1982) are the same for all Cottidae species.

The average estimated lengths of fish, from largest to smallest, was Pacific herring (24.1 cm, range 19.1–28.5); belligerent sculpin, *Megalocottus platycephalus* (23.0 cm, range 20.5–26.9); shorthorn sculpin (20.2 cm, range 17.3–22.1); saffron cod (19.3 cm, range 8.4–36.0); Arctic cod (14.5 cm, range 11.9–17.6); rainbow smelt (13.9 cm, range 5.7–25.9); and capelin (12.4 cm, range 11.6–14.0). Walleye pollock and Pacific sand lance each had one otolith with an estimated fish length of 8.9 cm. Otoliths were measured for several other species for which conversions were not available to estimate length (Table 5).

Of the 21 stomachs that contained food items, 19 (90%) contained invertebrates. At least 22 species of invertebrates were represented, of which shrimp was predominant at 86% FO followed by polychaetes and isopods at 38% FO each, then bivalves at 33% FO, echiurids and amphipods at 29% FO each, mysids at 24% FO, crab and tunicates at 14% FO; gastropods, cephalopods, and bryozoans were each represented at 10% FO (Table 3).

Three of the belugas, whose stomach contents are included above, were caught in the same net near Elim, in Norton Sound, on 30 Sept. 2000. One was an adult male (357 cm) and two were smaller females (238 and 245 cm). All three stomachs contained Arctic cod and saffron cod, but the male had also eaten two adult salmon (one coho and one chum); the female stomachs had no salmon but contained other smaller fish (e.g., slender eelblenny, smelt, sculpin) and the larger female's stomach also contained shrimp and cephalopods.

Six stomachs were collected on 27 Oct. 2012 in Hooper Bay, one white male and five females (one white, three white-gray, and one dependent calf). These belugas were part of a larger group of about 80 belugas that hunters noted were after fish, possibly cod (Simon[16]). Five of these stomachs contained a wide variety of fish and invertebrates (Table 6). The sixth stomach, from the calf, was empty.

Table 6.—Number and type of prey identified from stomach contents of five belugas from the eastern Bering Sea stock collected in Hooper Bay, Alaska, on 27 October 2012.

	Beluga stomach				
Taxon — Gender / Color	1 Male White	2 Female White	3 Female White-gray	4 Female White-gray	5 Female White-gray
Fishes					
All Petromyzontidae, lamprey spp.					
Arctic lamprey, *Lethenteron camtschaticum*	3		2	2	11
All Osmeridae					
Rainbow smelt, *Osmerus mordax*	41	174	128	200	203
Capelin, *Mallotus villosus*		4	9	7	1
All Gadidae					
Arctic cod, *Boreogadus saida*	78	347	399	440	380
Saffron cod, *Eleginus gracilis*	181	242	390	83	147
All Cottidae					
Sculpin species, *Hemilepidotus* spp.		1			
Belligerent sculpin, *Megalocottus platycephalus*		4	9	4	5
Sculpin species, *Myoxocephalus* spp.	1	2			2
All Liparidae					
Variegated snailfish, *Liparis gibbus*		1	4	1	
All Zoarcidae					
Eelpout species, *Lycodes spp.*			2		
All Stichaeidae					
Stout eelblenny, *Anisarchus medius*				1	
Slender eelblenny, *Lumpenus fabricii*	1	1	1	4	1
All Ammodytidae					
Pacific sand lance, *Ammodytes hexapterus*		1	2	1	2
All Pleuronectidae					
Longhead dab, *Limanda proboscidea*		4	2	2	1
Arctic flounder, *Pleuronectes glacialis*		1	3		
All Unidentified fish				4	
Minimum no. of fish eaten	305	782	951	749	753
Invertebrates					
All Polychaeta					
Polynoidae	18	11	19	8	8
Nereididae, *Nereis* spp.	11			2	
All Bivalvia		3			
All Mysidae					
Mysis oculata	1	9	12	10	9
Neomysis rayii		5	3	2	1
All Isopoda					
Saduria entomon	1	3	4	1	1
All Amphipoda					
Gammaridea	3				
Gammarus spp.			10		5
Melitidae, *Melita* spp.		1			
All shrimp					
Crangon alaskensis or septemspinosa	1	50	60	40	35
Shrimp spp.	20				
All Ascidiacea, tunicates					
Pelonaia corrugata		1			
Minimum no. of taxon eaten	13	20	18	18	16

Bristol Bay Stock

Stomach contents from 115 beluga whales from the Bristol Bay stock were collected between 1954 and 2011 in May (n = 25), June (n = 31), July (n = 32), August (n = 26), and October (n = 1). Of the 115 stomachs, 14 (12%) were empty (Table 1). Of the 101 stomachs that contained prey 100 (99%) contained fish. One beluga stomach from August 2010 was only visually inspected and is not included in Table 2; this stomach was reported to be full of adult coho salmon.

The dominant fish family was Salmonidae (81% FO and 83% N), with all five salmon species identified (Table 2). Sockeye, *Oncorhynchus nerka*, was the most prevalent species (55% FO and 58% N) followed by pink, *O. gorbuscha*, (18% FO), chum (15% FO), coho (10% FO), and Chinook, *O. tshawytscha*, (3% FO). Osmeridae, the smelt family, was the only other prevalent family (43% FO), with rainbow smelt the majority by species. Although Table 2 shows rainbow smelt only representing 5% FO of the 43% FO of all smelt, most smelt were not reported by species in the early data. It is likely that the majority of these

[16]Simon, A., Native Village of Paimiut, P.O. Box 91, Hooper Bay, AK 99604. Personal observ.

unidentified smelt were rainbow smelt as they are the predominant species in Bristol Bay. Evidence of more than 300 smelt per stomach was found in seven stomachs (range 368–710 individuals). Other stomachs with large numbers of fish included 14 stomachs with >500 salmon smolts (range 531–2,798) and four stomachs with seven or more adult sockeye salmon (range 7–9).

At least 14 different species from eight fish families were represented in Bristol Bay beluga stomachs during this time (Table 2). The lengths of two sockeye salmon were measured at 54.9 and 73.8 cm. The lengths of two rainbow smelt were measured at 17.6 and 21.5 cm, whereas the lengths of six rainbow smelt estimated from otoliths averaged 13.7 cm (range 4.1– 17.0) (Table 5).

Of the 101 stomachs that contained prey, 24 stomachs (24%) contained invertebrates from at least four species from four taxonomic groups. Shrimp was the most dominant invertebrate (21% FO), followed by isopods (4% FO) and bivalves (3% FO). A few shrimp were identified as crangonids, however, most were recorded only as shrimp (Table 3).

Cook Inlet Stock

A total of 53 stomachs were analyzed from Cook Inlet (Table 1); however, stomachs collected between 1992 and 2001 (n = 24) were analyzed separately from stomachs collected between 2002 and 2012 (n = 28). Contents were only visually inspected and not quantified during the earlier time period, whereas entire stomachs were analyzed and all identifiable prey items enumerated during the later time period. The contents of one stomach from one female beluga killed near the mouth of the Katnu River in 1961 was reported by Baxter and Baxter[17] to include Dolly Varden, *Salvelinus malma;* Pacific staghorn sculpin, *Leptocottus armatus*; "gray sand shrimp" (likely a crangonid shrimp species), and other unidentifiable fish remains. Only data from complete stomachs collected from 2002 to 2012 appear in Tables 2 and 3.

Stomachs from the earlier time period (1992–2001) were collected between April and October; 7 of the 24 (29%) were empty. Eulachon, *Thaleichthys pacificus*, and Chinook salmon were the only prey identified to species during this time period. No invertebrates were reported in those stomachs with prey, however, cursory visual inspections could have missed invertebrate remains. We believe that invertebrates were part of the diet during this time period, but they were not identified or reported. Empty stomachs occurred in summer and fall. Of the 24 belugas sampled, 16 belugas were harvested, 5 were found dead, and for 3 the cause of death was unrecorded.

Twenty-eight stomachs analyzed during 2002–2012 were collected between March and November. Ten of 28 stomachs (36%) were empty; one collected in June, two in August, two in September, four in October, and one in November. Of the 18 stomachs with food 17 (94%) contained fish remains and 9 (50%) contained invertebrates (Tables 2, 3). Three beluga whales were harvested, 24 were found dead, and for one the type of death was unrecorded. A minimum of 12 fish species and 8 invertebrate species were identified (Tables 2, 3).

The 12 fish species represented seven families (Table 2). Salmon (67% FO), cod (39% FO), smelt (11% FO), and flounder (11% FO) were most prevalent (Table 2). Salmon that could be identified to species included coho (28% FO, 21% N), chum (17% FO, 8% N), and Chinook (11% FO, 2% N). Cod species included saffron cod (22% FO, 26% N), walleye pollock (17% FO, 10% N), and Pacific cod, *Gadus macrochephalus* (6% FO, 1% N). Eulachon (11% FO 12% N) was the only smelt identified, and yellowfin sole, *Limanda aspera* (11% FO, 2% N) and starry flounder, *Platichthys stellatus* (6% FO, 1% N) were the only flounders. One longnose sucker, *Catostomus catostomus*, was the only freshwater fish found.

Salmon were the largest fish eaten by Cook Inlet beluga whales. Coho salmon averaged 62.1 cm (range 58.3–64.1) in length, and chum salmon averaged 60.0 cm (range 56.0–65.0) (Table 5). Other fish in which lengths could be estimated included saffron cod (18.9 cm, range 11.8–22.6), and eulachon (17.4 cm, range 15.7–18.5) (Table 5). For three beluga whale stomachs that were relatively full when collected one contained 12 whole coho salmon (27.8 kg), the second had five whole chum salmon (15.6 kg), and the third had three whole coho salmon and two partially digested salmon of unidentified species (15.0 kg).

Shrimp, polychaetes, and amphipods made up the bulk of the invertebrate prey. Of the 18 stomachs that contained prey, 9 (50%) contained eight species of invertebrates, predominantly shrimp (39% FO), followed by polychaetes and amphipods, each represented at 11% FO (Table 3).

Discussion

Data Limitations

Diet studies using stomach contents have well known biases (Tollit et al., 2010; Bowen and Iverson, 2012). Stomach contents represent some portion of an individual's most recent feeding activity. Small and soft parts digest more quickly and completely (Sheffield et al., 2001), which in our dataset could result in an under-representation of prey such as polychaetes and salmon smolts. Hard parts (e.g., otoliths and cephalopod beaks) can remain in the stomach longer and can accumulate through several feedings (Jobling and Breiby, 1986), which can result in an over-representation of prey such as saffron cod (large otoliths) and octopus (beaks tend to adhere to stomach lining and are resistant to digestion: Pitcher, 1980; Bigg and Fawcett, 1985). Stomachs collected from belugas found dead may be less likely to contain prey than harvested belugas; if the animals were sick or injured they may not have been feeding normally prior to death. Because most of the nonharvested belugas came from Cook Inlet, this concern mostly applies to that stock.

In addition to biases due to differential feeding and digestion, seasonality of prey (relative to the time of sampling), individual prey preferences, and perhaps other factors we have not identified may also affect results of diet studies. For example, adult salmon runs occur at specific times of year, and some species are available over a longer period of time than others. Many of the stomachs we examined were from belugas harvested by subsistence hunters. Thus, the timing of sample collection was often linked to the timing of subsistence activities.

Depending upon when stomachs are collected, what is present (or not present) in them will vary. If no stomachs were collected during a particular time of year, prey species specific to that time of year would be missing from our analysis. Samples from the subsistence harvest were collected in spring, summer, and fall when people hunt, and samples from belugas found dead were collected in summer and fall when people are most likely to observe and respond to them. Furthermore, there appears to be considerable variation in diet among individuals. For example, the three belugas that were caught in the same net on the same night near Elim in the eastern Bering Sea each contained different food items.

In spite of such biases, stomach contents collected from the harvest and from belugas found dead provide valuable information regarding prey consumed (often identified to species), and the number and frequency of their occurrence. With adequate samples sizes, stomach content data provide valuable information about the diet of each stock. Other methods of diet analysis (e.g., stable isotopes and fatty acids) result in qualitative information regarding trophic level and general categories of prey. Quantitative information from these indirect approaches require complete prey libraries (often difficult to obtain) in order to interpret diet to the species level (Budge et al., 2006; Newsome et al., 2010).

Non-feeding Periods

Beluga whales in some areas of Alaska are known to eat large amounts of fish in spring and summer, although it is not known if other activities take precedence over feeding during this time or how much feeding occurs in winter. Most stomachs (66%) collected from Point Lay (eastern Chukchi Sea stock) were empty. These belugas were harvested in June and July when migrating, molting, calving, or other behavior may have been more important than feeding. Histological studies of liver and pancreas tissue from belugas harvested at Point Lay indicated that they were likely fasting prior to harvest (Woshner, 2000). Belugas may fast during the annual skin molt.

Another reason belugas may have empty stomachs, in addition to illness or injury, may be due to the avoidance of marine mammal-eating killer whales, *Orcinus orca*. Belugas harvested in Kotzebue Sound in July 2007 were believed to be avoiding killer whales because they would not leave shallow water even while being approached by boats to be hunted; five of six stomachs examined were empty, and one contained only one operculum from a gastropod. Belugas sometimes regurgitate food when being chased (Quakenbush[5]), which could result in empty stomachs at the time of sampling.

In Bristol Bay, Lensink[3] found that in early June, beluga stomachs were mostly empty. Six stomachs collected during 6–15 Jun. 1959 and 1960 were empty except for a few shrimp fragments, indicating there may be a period of reduced feeding after salmon smolts migrate to sea and before adult salmon are available. Lensink[3] also reported that eight beluga stomachs collected during 11–25 Sept. 1959 and 1960 contained only small quantities of shrimp, small flatfish, and a lamprey, possibly indicating another reduced feeding period after adult salmon runs end in the fall. Very few stomachs were collected in fall and winter for any beluga stock in Alaska.

Comparison with Other Studies

Prior to this study, Seaman et al. (1982) provided the most complete information on beluga whale diet in Alaska. At the time it was published, diet data for Cook Inlet belugas were not available. Our study identified 34 fish prey to species, one sculpin to genus, *Hemilephidotus*, and two that could only be identified to family; Gasterosteidae (sticklebacks), and Agonidae (poachers). Fish eaten by belugas in our study that were not found by Seaman et al. (1982) included Arctic lamprey, pond smelt, *Hypomesus olidus*; eulachon, capelin, five species of Pacific salmon, Pacific cod, walleye pollock, poachers, variegated snailfish, eelblenny, and Pacific sand lance. We did not identify any whitefish, *Coregonus* sp., in our study, which were found by Seaman et al. (1982) and by Huntington (2000). While Seaman et al. (1982) reported the general categories of flatfish and sculpin as prey; we identified seven flatfish and six sculpin to species (Table 2). Two of the species identified in our study alone were found exclusively in Cook Inlet: eulachon and Pacific cod.

Although capelin are sometimes observed in large concentrations near Point Lay and Barrow and are likely important to belugas wherever they are available (Suydam[17]) we only found them in five stomachs from the Eastern Chukchi Sea stock, and they were not found by Seaman et al. (1982). Capelin may be an example of a prey species that has a strong regional and seasonal component that our opportunistic collection regime does not often detect.

We identified invertebrates that were not found by Seaman et al. (1982), including several additional taxa of amphipods, shrimps, crabs, and bivalves. Our findings relative to cephalopods were similar in that more octopus than squid was eaten (Table 3). Some of the invertebrates found in beluga stomachs could be due to secondary ingestion, because sculpin and saffron cod eat shrimp, amphipods, crabs, and polychaetes. Seaman et al. (1982) considered octopus, shrimp, and some-

[17]Suydam, R., North Slope Borough, P.O. Box 69, Barrow, AK 99723. Personal observ.

times isopods to be directly consumed by belugas.

By looking at stomachs with no fish remains (n = 65), we found that polychaetes, gastropods, cephalopods, isopods, amphipods, shrimp, echiurids, and tunicates were present and were likely ingested directly as prey by beluga whales. Echiurid setae are commonly found in beluga stomachs, appear to be resistant to digestion, and may have delayed passage through the stomach. Evidence of echiurids was found in stomachs from all stocks, except Bristol Bay, in this study.

Our findings that the predominant fish species of the Beaufort Sea stock was Arctic cod was also found by Loseto et al. (2009) using fatty acid analysis. Overall however, we found invertebrates in more stomachs than fish; 66% of all stomachs contained invertebrates only. Loseto et al. (2009) did not find invertebrates to be important prey relative to the importance of Arctic cod.

Regional Differences

Stocks were sampled during different seasons making seasonal comparisons difficult. A comparison of the overall diet of the different stocks, however, showed that the northernmost migratory stock (Beaufort Sea) predominantly fed on shrimp (60% FO), octopus (42% FO), and Arctic cod (21% FO). The eastern Chukchi Sea stock fed mostly on shrimp (73% FO), echiurids (27% FO), polychaetes (17% FO), and saffron cod (7% FO). The eastern Bering Sea stock and Kotzebue belugas fed mostly on saffron cod (both 95% FO) and shrimp (both 86% FO). Six other invertebrate taxa were notable for the eastern Bering stock; polychaetes and isopods each at 38% FO, bivalves at 33%, echiuriids and amphipods each at 29% FO, and crabs and tunicates each at 14% FO. In addition to shrimp, four other invertebrate taxa were prominent for Kotzebue belugas; amphipods (41% FO), gastropods and isopods each at 36% FO, and mysids at 14% FO. The two nonmigratory stocks (Bristol Bay and Cook Inlet) were the stocks in which most salmon were found, but they also ate smelt, cod, and shrimp; although invertebrates appeared to be much less important compared to the other stocks (Table 3).

Prior to 2002, Cook Inlet beluga stomachs were not completely analyzed, and therefore less information is available for this time period, especially regarding invertebrate prey. Although Chinook salmon was identified in one of the earlier stomach samples and subsistence hunters reported 19 adult Chinook salmon in one harvested beluga (Huntington, 2000), we only identified Chinook salmon in two stomachs sampled after 2002 (n = 18). The main Chinook salmon runs in Cook Inlet occur April–July (Barrett et al.[18, 19]; McKinley and Fleischman[20, 21]). Six of the 18 stomachs we analyzed after 2002 were collected during this time period, and therefore could have contained Chinook salmon.

Otoliths of all species of salmon are small and degrade easily, making identification of salmon to species more difficult. Similarly, in Bristol Bay where all five salmon species are available, Chinook salmon were the least represented in the beluga diet, but again this may be due to the difference in the timing of collections relative to timing of specific salmon runs.

Other Differences

In addition to the seasonality of prey availability, prey size may also influence diet. Beluga whales swallow their prey whole (Brooks[8]; this study), thus smaller (i.e., young) belugas are limited by the size of their esophagus to smaller prey (Fay, 1971). Brooks[8] found that unweaned calves ate small bottomfish and shrimp. Yearlings mainly ate smaller fish and few adult salmon. Therefore, 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.

Our sample sizes of beluga sex and length, and fish length did not allow us to analyze diet by beluga sex or age class, although subadult belugas have been found to eat more invertebrates, while adult females ate smaller fish and adult males ate larger fish (Seaman et al., 1982).

On the other hand, all sizes of belugas likely eat salmon smolts during smolt migration to the sea. Although not represented in any samples, salmon smolts are known to be important to Bristol Bay belugas in the spring (Brooks[7, 8]) and may be important to Cook Inlet belugas as well.

Prior to 2002 in Cook Inlet, more beluga stomachs were collected from harvested animals, while after 2002, more stomachs were collected from stranded animals due to the restricted harvest. No invertebrates were recorded in the earlier sample of Cook Inlet beluga stomachs. This is most likely due to an artifact of the field methods used to determine diet. Stomach contents appeared to have been examined in a more cursory fashion that may have resulted in invertebrate prey items being missed. Although not detecting invertebrates in the earlier stomach samples does not necessarily change the number of fish species eaten, it does indicate the difference in the methods used to analyze diet could have influenced the fish results as well. Seasonal distribution of stomachs was similar for both time periods.

Beluga distribution within Cook Inlet has been shifting to the upper Inlet from a broader distribution that more regularly included the lower (Kachemak Bay) and the mid-inlet (Rugh et

[18]Barrett, B. M., F. M. Thompson, and S. N. Wick. 1984. Adult anadromous fish investigations: May–October 1983. Sustina Hydro Aquatic Studies. Rep. No. 1. Alaska Dep. Fish Game, Anchorage.

[19]Barrett, B. M., F. M. Thompson, and S. N. Wicks. 1985. Adult salmon investigations: May–October 1984. Susitna Aquatic Studies Program. Rep. No. 6. Alaska Dep. Fish Game, APA Doc. No. 2748, Anchorage.

[20]McKinley, T. R., and S. Fleischman. 2010a. Stock assessment of late-run Chinook salmon in the Kenai River, 1999–2006. Alaska Dep. Fish Game, Fishery Data Series No. 10-96, Anchorage.

[21]McKinley, T. R., and S. Fleischman. 2010b. Stock assessment of early-run Chinook salmon in the Kenai River, 1999-2006. Alaska Dep. Fish Game, Fishery Data Series No. 10-19, Anchorage.

al., 2000). Belugas used to feed on herring in Kachemak Bay prior to the late 1920's when herring declined there (Rounsefell, 1930). In April, hunters from Nanwalek would harvest belugas when they fed on herring in Halibut Cove within Kachemak Bay (Rounsefell, 1930; Stanek, 1994). The distributional shift to the upper Inlet could be due to fewer belugas available to fill the historic habitat, the upper Inlet becoming better habitat, or the lower Inlet becoming poorer habitat. Fewer fish, however, does not explain why belugas use the Kenai River less than in the past, because salmon runs there are believed to be at least as large as those in the Susitna River in the upper Inlet (McKinley and Fleischman[20,21]). Other activities, such as a commercial beluga harvest in the 1960's (Mahoney and Shelden, 2000) and increased boat traffic, may be factors in the decline in use of the Kenai River area.

The two nonmigratory stocks, Cook Inlet and Bristol Bay, have several things in common that may allow them to be resident year-round. Both regions are large, tidally influenced estuarine systems with multispecies salmon runs and shallow-water habitat for escape from killer whales. Both regions also have an abundance of smelt, although eulachon in Cook Inlet may be more seasonally restricted than rainbow smelt in Bristol Bay.

The tides in both areas keep the sea ice broken all winter, which allows belugas access to the bays, but the floating ice restricts killer whale access in winter. Beluga whales do not have a dorsal fin (an advantage for surfacing in sea ice), and they can swim and feed in very shallow, muddy water (<1 m). These adaptations and their distribution may serve as defenses against killer whales (Frost and Lowry, 1990). Killer whales appear to avoid ice likely because their large dorsal fin limits their ability to surface and breathe in broken ice covered water (Matthews et al., 2011; Higdon et al., 2012). The migratory stocks of belugas may rely on sea ice as escape habitat while the resident stocks may rely on shallow water. In addition to food, habitat selection may also involve molting and calving areas, protection from killer whales, and human activity.

Although the eastern Bering Sea stock also has access to large multispecies salmon runs in summer in the Yukon-Kuskokwim Delta and Norton Sound areas, these areas freeze more completely in winter due to weaker tides that are unable to keep the ice broken. It is not clear why more salmon were not found in stomachs of belugas from the eastern Bering Sea, but it may be due to timing of harvests and the importance of commercial fishing in the area. Some hunters may be fishing instead of pursuing belugas at a time when salmon may be an important prey item. It is clear that the migratory stocks of belugas take advantage of the seasonal abundance of forage fish nearshore in summer.

Beluga whales were harvested regularly and in significant numbers in Kotzebue Sound prior to 1982 (e.g., Eschscholtz Bay belugas from Seaman et al.[22] came from this harvest). After 1983, 10 or fewer belugas have been harvested in the sound in most years (Frost and Suydam, 2010). However, two unusual events have occurred resulting in high harvests, one in 1996 and another in 2007. The belugas harvested in 1996 were genetically similar (using mtDNA) to those harvested in the late 1970's and early 1980's; however, those harvested in 2007 were not (O'Corry-Crowe[23]).

Few belugas have been seen or harvested near Kotzebue in recent years; however, in July 2007 a large group (~150) of mostly adult male belugas went deep into Kotzebue Sound, and many were harvested. The genetic (mtDNA haplotypic) composition of this group was distinct from all previously sampled beluga whale groups from Kotzebue Sound. As a group, the whales harvested in 2007 had very strong genetic similarities (mtDNA and nDNA) to the Beaufort Sea stock. Genetic analysis is ongoing to determine whether the 2007 belugas were from the Beaufort Sea stock, were a mix of two or more stocks of whales, or were from a previously unidentified stock (O'Corry-Crowe[23]).

Interspecies Overlap in Diet

Interspecies overlap in fish prey is most likely to occur among belugas and seals, although other possibilities include Steller sea lions, *Eumetopias jubatus,* and harbor porpoises, *Phocoena phocoena*, in some areas. The Beaufort Sea, eastern Chukchi Sea, and eastern Bering Sea beluga stocks likely overlalp with ringed, *Pusa hispida*, and spotted, *Phoca largha,* seals, for all fish species (Gol'tsev, 1971; Bukhtiyarov et al., 1984; Quakenbush et al.[24, 25]) and with bearded seals, *Erignathus barbatus*, for Pacific sand lance, Arctic cod, saffron cod, sculpins, eelblenny, and flatfish (Kosygin, 1971; Lowry et al., 1980; Antonelis et al., 1994; Quakenbush et al.[26]). In Bristol Bay, the most abundant seals are spotted and harbor, *Phoca vitulina*, seals and in Cook Inlet, only harbor seals are present. Overlap with fish species important to humans is also possible for the eastern Bering Sea, Bristol Bay, and Cook Inlet stocks where commercial and subsistence fisheries for herring and salmon exist.

Interspecies overlap for invertebrate prey is most likely to occur among

[22]Seaman, G. A., K. J. Frost, and L. F. Lowry. 1985. Investigations of belukha whales in coastal waters of western and northern Alaska. Part I. Distribution, abundance and movements. U.S. Dep. Commer., NOAA, OCSEAP Final Rep. 56:153–220 (avail. from NOAA-OMA-OAD, Alaska Office, 701 C. Street, P.O. Box 56, Anchorage, AK 99513).

[23]O'Corry-Crowe, G., Fl Atl. Univ., Harbor Br., 5600 U.S. 1 North, Fort Pierce, FL 34946. Personal commun., July 2012.

[24]Quakenbush, L., J. Citta, and J. Crawford. 2009. Biology of the spotted seal (*Phoca larga*) in Alaska from 1962 to 2008. Prelim. Rep. Natl. Mar. Fish. Serv., Natl. Mar. Mammal Lab., Seattle, 66 p.

[25]Quakenbush, L., J. Citta, and J. Crawford. 2011a. Biology of the ringed seal (*Phoca hispida*) in Alaska, 1960–2010. Final Rep. Natl. Mar. Fish. Serv., Natl. Mar. Mammal Lab., Seattle, 72 p.

[26]Quakenbush, L., J. Citta, and J. Crawford. 2011b. Biology of the bearded seal (*Erignathus barbatus*) in Alaska, 1960–2009. Final Rep. Natl. Mar. Fish. Serv., Natl. Mar. Mammal Lab., Seattle, 71 p.

Table 7.—Fish and invertebrate prey diversity by stock of beluga whales in Alaska.

Stock	No. fish species	No. invertebrate species	Month
Beaufort	8	16	4–6
E. Chukchi	5	15	6–8
Kotzebue	6	9	6,7,10
E. Bering	25	22	5–7, 9,10
Bristol Bay	14	4	5–8, 10
Cook Inlet (<2002)	2	0[1]	4–10
Cook Inlet (>2002)	12	8	3,6–9,11

[1]No invertebrates were recorded during this time period likely due to field methods.

belugas and both Pacific walrus, *Odobenus rosmarus*, and bearded seals for many benthic invertebrates. Only the Cook Inlet stock is exempt from such overlap as walruses and bearded seals are not found there. Invertebrate taxonomic groups of importance to belugas that are also eaten by walrus and bearded seals include polychaetes, gastropods, bivalves, octopi, mysiids, isopods, amphipods, shrimp, crabs, echiuriids, and ascidians (Lowry et al., 1980; Fay, 1982; Quakenbush et al.[26]).

Diversity and Amount of Prey

The greatest diversity of fish prey was found in the eastern Bering Sea stock where 25 species of fish were eaten, followed by Bristol Bay with 14 species and Cook Inlet with 12 species (Table 7). The greatest diversity of invertebrates was also found in the eastern Bering Sea stock where 22 species were found followed by the Beaufort Sea stock with 16 species and the eastern Chukchi stock with 15 species.

Although we did not often determine the total amount of a prey item eaten by individual beluga whales, there were a few instances of whole fish (e.g., 12 whole coho salmon weighing 27.8 kg), numbers of otoliths (e.g., otoliths indicating a total of 951 fish eaten including 128 rainbow smelt, 390 saffron cod, and 399 Arctic cod, Table 6), and numbers of octopus beaks (e.g., > 144 for an estimated total weight of 127 kg) that suggest prey numbers and volumes consumed can be large. Such numbers indicate that, at least seasonally, beluga whales eat substantial amounts of food.

In summary, beluga whale diets in Alaska waters varies somewhat by stock, with the northernmost stocks feeding mostly on shrimp, octopus, and Arctic cod. To the south, saffron cod replaces Arctic cod and octopus is no longer prevalent. In the two most southern stocks, Arctic and saffron cod are largely replaced by salmon and smelt (rainbow smelt in Bristol Bay and eulachon in Cook Inlet). Shrimp are common prey for all beluga stocks in Alaska. Beluga whales swallow their prey whole, thus size of prey may be related to beluga size (i.e., age) although there also may be individual preferences. Younger belugas may be more limited in prey available to them. Our results may be influenced by biases due to stomach content analyses, nonrandom hunting affecting our sample of stomachs, seasonal changes in prey availability, lack of samples during winter, and other factors. Very little is known about what and how much beluga whales eat during winter and whether accumulating fat stores in summer and fall is important for survival.

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