

# Segregation of Beaufort Sea beluga whales during the open-water season

L.L. Loseto, P. Richard, G.A. Stern, J. Orr, and S.H. Ferguson

**Abstract:** Population segregation by habitat use occurs because energy requirements and survival strategies vary with age, sex, size, and reproductive stage. From late summer to early fall in 1993, 1995, and 1997, relative length (age), sex, and reproductive status of satellite-tagged beluga whales (*Delphinapterus leucas* (Pallas, 1776)) in the eastern Beaufort Sea were tested for habitat segregation. We used (i) resource selection function models to evaluate how belugas used areas of varying sea ice concentration and shelf habitat and (ii) distance analysis to measure the selection of areas varying in distance to mainland and island coastlines. Resource selection functions and distance analysis established that habitat selection differed with length, sex, and reproductive status of whales: (i) females with calves and smaller males selected open-water habitats near the mainland; (ii) large males selected closed sea ice cover in and near the Arctic Archipelago; and (iii) smaller males and two females with calves (not newborn) selected habitat near the ice edge. The segregation of habitat use according to sex, age, and reproductive status relates to the different resources required at different life stages and may represent characteristics of beluga social structure. We discuss our results in the context of two common sexual segregation hypotheses and conclude that summer habitat segregation of belugas reflects differences in foraging ecology, risk of predation, and reproduction.

**Résumé :** La ségrégation dans les populations d'après l'utilisation de l'habitat se produit à cause de besoins énergétiques et de stratégies de survie qui varient en fonction de l'âge, du sexe, de la taille et de l'état reproductif. Nous avons vérifié la ségrégation d'habitat en fonction de la longueur relative (âge), du sexe, et de l'état reproductif chez des bélugas (*Delphinapterus leucas* (Pallas, 1776)) munis d'une étiquette-satellite dans l'est de la mer de Beaufort de la fin de l'été au début de l'automne en 1993, 1995 et 1997. Nous employons (i) des modèles de fonction de sélection des ressources pour évaluer comment les bélugas utilisent les différentes zones d'accumulation de glace de mer ainsi que les habitats de banquise et (ii) une analyse de distance pour mesurer la sélection des zones situées à des distances diverses de la côte du continent ou des îles. Les fonctions de sélection des ressources et l'analyse de distance montrent que la sélection d'habitat varie en fonction de la longueur, du sexe et de l'état reproductif. En effet, (i) les femelles avec petits et les mâles de plus petite taille choisissent les habitats d'eau libre près du continent, (ii) les mâles de grande taille choisissent une couverture fermée de glace de mer dans l'archipel Arctique ou les environs et (iii) les mâles plus petits et deux des femelles (avec des petits non nouveau-nés) préfèrent l'habitat près de la marge de la glace. La ségrégation de l'utilisation de l'habitat en fonction du sexe, de l'âge et de l'état reproductif s'explique par les besoins différents en ressources aux divers stades du cycle et peut refléter les caractéristiques de la structure sociale des bélugas. Nous comparons l'appui que donnent nos résultats à deux hypothèses communes de la ségrégation sexuelle et nous concluons que la ségrégation dans l'habitat d'été des bélugas traduit des différences dans l'écologie de la recherche de nourriture, le risque de prédation et la reproduction.

[Traduit par la Rédaction]

## Introduction

Population segregation by habitat use occurs because energy requirements and survival strategies vary with age, sex, size, and reproductive stage. Sexual segregation can be defined as the selection of different habitats or locations by

gender (Conradt 1998). Some studies have found sexual segregation to be driven by body size dimorphism (Ruckstuhl and Neuhaus 2002; Bowyer 2004), where males and females within a species have different resource demands related to size. Differences in reproductive condition may also lead to segregation (Stevick et al. 2002). Sexual segregation has been documented in sexually dimorphic mammals (Ralls 1977; Bonenfant et al. 2004; Bowyer 2004), including marine mammals (Stewart 1997; Austin et al. 2006). For example, in the dimorphic northern elephant seal (*Mirounga angustirostris* (Gill, 1866)), males are up to 10 times the size of females and, as a result, are assumed to require different feeding strategies, resources, and habitat use to maintain this size difference (Le Boeuf et al. 2000). Among cetaceans, sexual segregation occurs in both mysticetes (e.g., Atlantic humpback whale, *Megaptera novaeangliae* (Borowski, 1781); Stevick et al. 2003) and odontocetes (e.g., bottlenose dolphin, *Tursiops truncatus* (Montagu, 1821); Conner et al. 1999).

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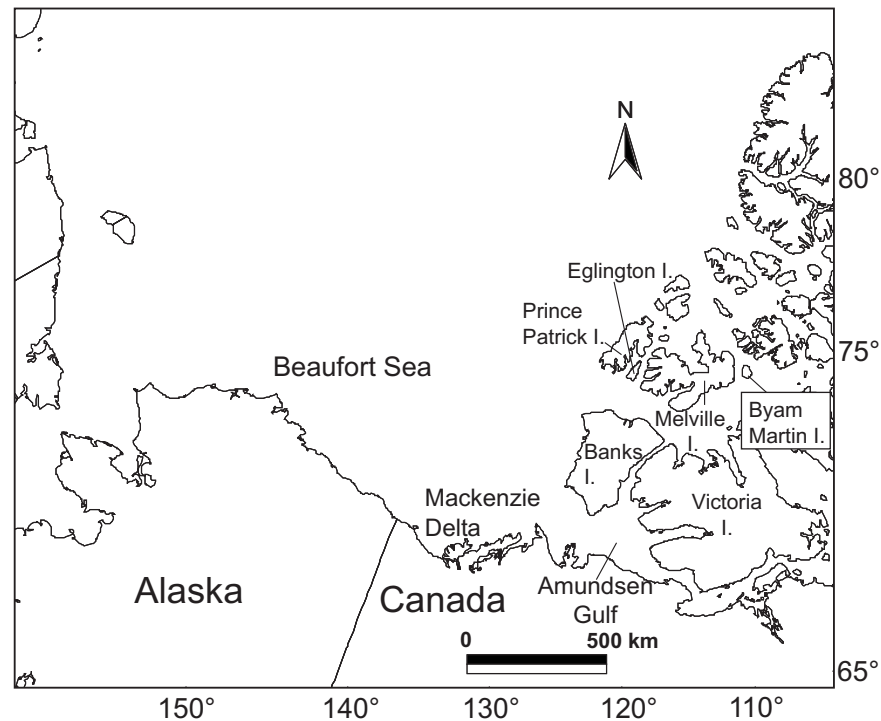
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**Fig. 1.** Area used by Beaufort beluga whales (*Delphinapterus leucas*) during late summer and early fall. Beluga capture occurred in the Mackenzie Delta during July in 1993, 1995, and 1997.



Beluga whales (*Delphinapterus leucas* (Pallas, 1776)) are sexually size dimorphic, with males being larger than females, on average (Harwood and Smith 2002). Observations of segregation by sex and age class have been reported for populations that summer in estuaries of the Canadian High Arctic and eastern Hudson Bay (Smith et al. 1994). However, no quantitative assessments accompanied these observations. Smith et al. (1994) observed adult nursing females and older female offspring near shore in the estuaries, while large males formed large pods (10 to 15 individuals) that spent little time in the estuaries.

Every spring the eastern Beaufort Sea beluga population migrates from the Bering Sea to summer in the eastern Beaufort Sea. The summer harvest of Beaufort beluga whales by communities of the Inuvialuit Settlement Region (Northwest Territories, Canada) is an important component of the Inuvialuit subsistence lifestyle (Usher 2002). The Beaufort beluga whale population is one of the world's largest, with a minimum estimate of 20 000 individuals (Harwood et al. 1996). At present there is no indication of population decline.

During the summer, some males spend time north of the Mackenzie Delta, in the Arctic Archipelago, and most females remain close to the mainland shoreline and in Amundsen Gulf (Richard et al. 2001). Why this population segregates by summering habitat and how factors such as resource use and availability, predator avoidance, and foraging behaviour affect habitat selection are unknown. Barber et al. (2001) suggested that sea ice and bathymetry are important habitat features to consider when investigating beluga habitat use. Recent changes in climate have affected sea ice characteristics including sea ice thickness (Yu et al. 2004), extent (Johannessen et al. 2004), and concentration (Barber

and Hanesiak 2004), necessitating an understanding of sea ice as a habitat resource for beluga whales to evaluate possible impacts of environmental change.

Here we examine the segregation of Beaufort beluga whales by summer habitat using satellite tracking data collected in 1993, 1995, and 1997. We consider how Beaufort beluga whales selectively use habitat relative to sex, age, and reproductive status according to (i) resource selection functions (Arthur et al. 1996) of sea ice concentration and shelf habitat and (ii) distance to island and mainland coastlines.

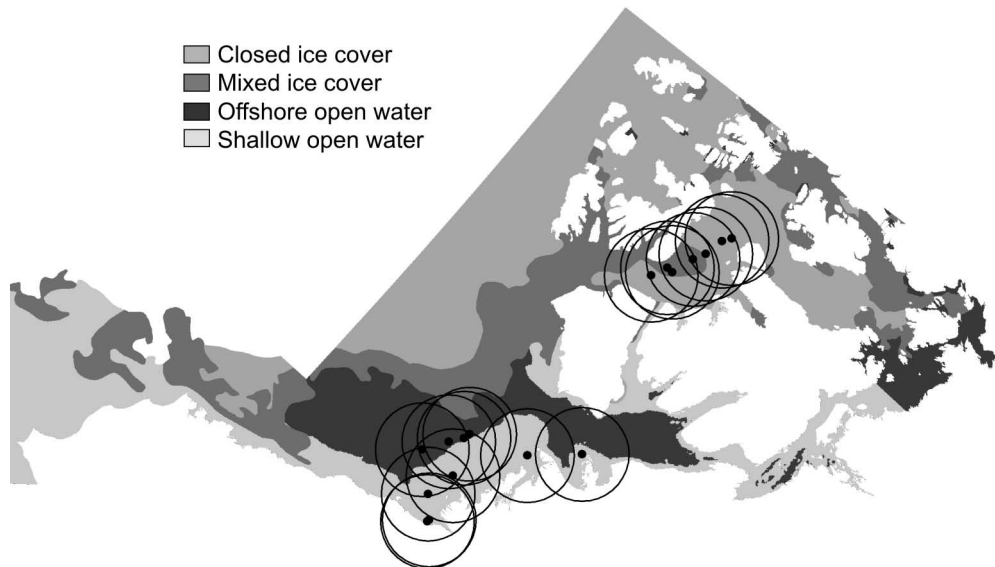
## Materials and methods

### Tagging and satellite telemetry

Three, thirteen, and eight beluga whales were captured in the Mackenzie Delta, Northwest Territories, Canada (Fig. 1), and tagged with satellite transmitters in 1993 (10–19 July), 1995 (3–16 July), and 1997 (26 July – 1 August), respectively (see Table 1) (Richard et al. 2001). Whales were captured and tagged using techniques approved by the Department of Fisheries and Oceans Canada Animal Care Committee, described in Orr et al. (2001). Briefly, a whale is selected and herded to shallow waters (approx. 2 m depth) by boats. A seine net is then deployed that encircles the whale, and people in zodiac boats remove the whale from the net and secure it using tail ropes and a hoop net. After the whale is secured, size measurements are taken and satellite-linked transmitter tags are placed. The tags are positioned onto the dorsal ridge with surgical nylon pins (6 mm diameter) that are fastened with washers secured through the skin and blubber of the dorsal ridge (Orr et al. 2001).

Deployed tags transmit location data when the whale surfaces, exposing the tag antenna to satellites in the area (Richard

**Fig. 2.** Example habitat map (week of 15 August 1995) used to determine use and availability of four habitat types: offshore open water, mixed ice cover, closed ice cover, and shallow open water. Median daily locations (•) and buffers (radius = 95th percentile of daily distance travelled) indicate habitat available to whales (see Materials and methods).



et al. 2001). Transmissions from tags were received by ARGOS satellites that estimate the precision of the point location of transmission and provide a quality index termed location class. All location classes were used to derive beluga tracks after filtering locations to remove outliers (Richard et al. 2001). We removed low-quality locations having errors greater than 1 km to use a swim speed filter calculated using good-quality locations (less than 1 km error). All available daily locations ( $n = 9565$ ) from the filtering were then reduced to median daily locations for each animal ( $n = 1099$ ).

#### Habitat classification

Four habitat categories were chosen based on sea ice cover and water depth for the 3 years (1993, 1995, and 1997) and 2 months (July and August) of tracking. Weekly composite sea ice charts were obtained from Environment Canada's Canadian Ice Service (<http://ice-glaces.ec.gc.ca>) as digital layers and imported into ArcView<sup>®</sup> 3.3 (Environmental Systems Research Institute, Inc., Redlands, California). These charts provide weekly polygons of sea ice cover categories (in tenths) within the study area. Based on previous findings that belugas from several populations spent the majority of their time in either open water or closed ice (Barber et al. 2001), we grouped ice cover into three categories: open water (sea ice concentrations of 0/10 to 1/10), mixed ice (sea ice concentrations of 2/10 to 8/10), and closed ice (sea ice concentrations of 9/10 to 10/10). In addition, we classified shelf and non-shelf habitat according to a 200 m water depth threshold (Macdonald et al. 1989). Combining our sea ice categories with shelf categories resulted in four habitat groupings: open water–off shelf (hereafter, offshore open water), mixed ice–off shelf (mixed ice), closed ice–off shelf (closed ice), and open water–shelf (shallow open water). Little or no ice was present in the shelf zone over the duration of the study, so the habitat groupings mixed ice–shelf and closed ice–shelf were not considered.

#### Resource selection function analysis

Resource selection function analysis provides a means to evaluate whether the use of habitats by wildlife is selective, thus demonstrating a preference for a particular habitat and the resources associated with it (Manly et al. 1993). Selection is defined as the use of particular habitat types more often than would be expected if all habitat types were used randomly and in proportion to their availability (Johnson 1980). Resource selection indices are calculated for each habitat category from the ratio of percent used to percent available; the entire set of indices (ratios) is collectively termed the “resource selection function” (Manly et al. 1993). The resource selection function estimates the probability a habitat category will be selected relative to the probability of selecting other habitats based on availability.

Resource selection function analysis is problematic where habitat changes temporally (e.g., seasonal sea ice) or where animals undertake long-distance movements resulting in different mixtures of habitat available over time and space (Manly et al. 1993). Arthur et al. (1996) developed an iterative method for the estimation of the maximum likelihood of the resource selection function to control for changing habitat availability. This method has been successfully used to evaluate habitat use at the seasonal scale in polar bears (*Ursus maritimus* Phipps, 1774) (Ferguson et al. 2000) as well as at the finer scale of daily habitat selection in woodland caribou (*Rangifer tarandus caribou* (Gmelin, 1788)) (Rettie and Messier 2000).

Habitat use was defined for each beluga daily median location by assigning 100% to the habitat at that location and 0% to the other habitat categories. Habitat availability was defined by the percentage of each habitat category inside a buffer circle around the median location for the previous day for the individual beluga (Fig. 2). The buffer circle radius (137.2 km) was determined by calculating the 95th percentile of daily distance travelled for all individuals and was

used for all point location buffers, as recommended by Rettie and Messier (2000). Within the buffer, any area occupied by land was removed from the proportion of habitats available. For each animal, maximum-likelihood estimates of the habitat selection function were obtained using the iteration method proposed by Arthur et al. (1996). The selection indices were calculated as follows:

$$[1] \quad w_k = \frac{\sum_{i=1}^D O_{ik}}{\sum_{i=1}^D \frac{A_{ik}}{\sum_{j=1}^H A_{ij} b_j}}$$

$$[2] \quad b_k = \frac{w_k}{\sum_{j=1}^H w_j}$$

where  $k$  is the habitat category from the set  $j = 1$  to  $H$ ,  $O_{ik}$  is the proportion of habitat type  $k$  used on day  $i$  (either 0 or 1),  $A_{ik}$  is the proportion of habitat type  $k$  available on day  $i$ ,  $b_k$  is the estimated selection index for habitat type  $k$ , and  $D$  is the number of days the animal was located. The value 0.25 (or equal probability of use for four habitat categories, 1/4) was used for all  $b_j$  in the first step of the iteration. Next, eq. 2 was used to calculate the new values for  $b_j$  and the process was repeated. Values for selection indices were then standardized by returning the  $b_j$  indices to the first equation to continue the iteration. The iteration stopped when values of  $b_j$  stabilized, i.e.,  $b_j = w_j$  for all  $j$ .

### Distance analysis

Distances to the mainland and island coastlines were calculated to provide an additional confirmatory test of the results of the resource selection function analysis. First, median daily locations for whales in all 3 years were combined to estimate home range using the kernel 95% home range method of the Animal Movement extension to ArcView (Worton 1989; Hooge and Eichenlaub 1997). Within this home range, 1099 random points (equal to the number of actual locations) were generated. The shortest distance to the coastline of the mainland and the shortest distance to the coastline of one of six islands (Banks, Melville, Victoria, Prince Patrick, Eglington, and Byam Martin) (Fig. 1) were determined for all randomly generated and actual point locations.

### Statistical analysis

We used a multivariate analysis of variance to determine whether habitat use was significantly different from random. Multiple dependent variables were synthetic values derived from the differences between the selection indices ( $b_j$ ) for the habitat types (e.g., synthetic variable =  $b_j$  mixed ice –  $b_j$  closed ice) and the mean vector of contrasts was compared with a vector of 0 (Arthur et al. 1996). The use of synthetic variables allows for the comparison of habitat use relative to availability between habitat pairs (Arthur et al. 1996). When habitat use was significantly different from random, habitat

categories were ranked according to the mean selection indices ( $b_j$ ) and compared using univariate paired  $t$  tests (Arthur et al. 1996).

We tested for effects of gender and year whales were tagged on habitat use with a multivariate analysis of variance. Next, we tested for the effects of length (proxy for age) and reproductive status along with year. We reorganized the age and reproductive status combinations into three categories: (1) females with calves, (2) juveniles, and (3) adults. Adult males were defined as whales greater than the asymptotic length of 420 cm (Luque and Ferguson 2006). Two females without calves were present; the one larger (373 cm) than those with calves was placed into the adult category, and the female at 302 cm was classified as a juvenile based on models of individual growth rates for the Beaufort Sea population (Luque and Ferguson 2006). The effects of age–reproductive class and year were assessed with multivariate analysis of variance as described above.

Cluster analysis was used to objectively group individual whales based on similarity of habitat selection indices ( $b_j$ ) (PROC CLUSTER, SAS<sup>®</sup> version 8, SAS Institute Inc., Cary, North Carolina). The complete cluster method was the unpaired group mean and the distance measure was the Euclidean distance (Romesburg 1984). Groups were defined based on discontinuities in the  $F$  values (SAS Institute Inc. 1989). Analysis of variance was used to test for differences among the groups identified by the cluster analysis.

As a secondary assessment of the resource selection results, we tested for differences in distances to the mainland and islands among the groups identified using cluster analysis. Differences between group locations and random point locations were tested by analysis of variance with Dunnett's post hoc test (Sokal and Rohlf 1981).

## Results

### Habitat selection indices

Beluga habitat use was not random because resource selection indices for the four habitat types were not equally probable (i.e.,  $b_j$  values were different from 0.25) (Table 1). Habitat selection was significantly different from random ( $F_{[3,19]} = 16.98$ ,  $P < 0.01$ ). Offshore open water was used most often ( $\bar{x} b_j = 0.37$ ,  $\sigma = 0.04$ ), more than mixed ice and shallow open water ( $P = 0.02$ ;  $P < 0.001$ ). The second most selected habitat category was closed ice ( $\bar{x} b_j = 0.28$ ,  $\sigma = 0.04$ ), which was used significantly more than shallow open water ( $P = 0.048$ ).

### Grouping according to sex, length, and reproductive class

According to the multivariate analysis of variance, males and females did not select habitat differently from one another, and there was no significant difference in habitat selection among the 3 years (Table 2). In the second analysis, habitat use differed for age (length) and reproductive groups (Table 2). Owing to these differences in habitat selection, we used a cluster analysis to objectively group belugas into more meaningful groups.

Three groups of belugas were identified by the cluster analysis (Tables 3 and 4). A discriminant function analysis described dispersion among the three groups (Fig. 3). Factor

**Table 1.** Resource selection functions ( $b_j$  values) for beluga whales (*Delphinapterus leucas*) captured in 1993, 1995, and 1997 in the eastern Beaufort Sea, Canada.

Year	Tag ID	Sex*	Adult length (cm)	Calf length (cm)	No. of days transmitted	Habitat category $b_j$ values				Cluster group
						Offshore open water	Mixed ice	Closed ice	Shallow open water	
1993	17002	M <sup>c</sup>	457		11	0.12	0.32	0.53	0.037	2
	17005	M <sup>c</sup>	442		61	0	0.71	0.29	0	2
	17009	F <sup>a</sup>	302		14	0.66	0	0	0.34	1
1995	17001	M <sup>c</sup>	427		27	0.52	0.17	0.31	0	3
	17002	M <sup>a</sup>	404		28	0.72	0	0	0.28	1
	17003	M <sup>c</sup>	432		17	0.02	0.2	0.75	0.04	2
	17004	M <sup>a</sup>	373		24	0.5	0.04	0.14	0.31	1
	17005	M <sup>a</sup>	353		23	0.42	0.2	0.16	0.23	1
	17007	F <sup>c</sup>	373		26	0.38	0.34	0	0.27	1
	17008	Fc <sup>b</sup>	361	182 <sup>†</sup>	9	0.64	0	N/A <sup>‡</sup>	0.36	1
	8754	Fc <sup>b</sup>	363	217	23	0.35	0	N/A	0.65	1
	17010	M <sup>a</sup>	399		26	0.35	0.39	0.21	0.04	3
	17011	M <sup>a</sup>	402		25	0.22	0.25	0.46	0.07	2
	17012	M <sup>a</sup>	404		30	0.15	0.32	0.31	0.22	3
	17013	M <sup>a</sup>	402		30	0.13	0.31	0.52	0.03	2
	17014	Fc <sup>b</sup>	340	223	30	0.18	0.36	0.23	0.23	3
	1997	2118	Fc <sup>b</sup>	374	? <sup>§</sup>	27	0.34	0.14	0.51	0
10692		Fc <sup>b</sup>	338	243	33	0.55	0.19	0	0.25	1
10693		M <sup>a</sup>	395		48	0.41	0.11	0.34	0.14	3
8754		M <sup>a</sup>	405		50	0.3	0.26	0.33	0.11	3
8755		M <sup>a</sup>	400		58	0.64	0.08	0	0.28	1
25846		M <sup>a</sup>	374		46	0.56	0.16	0.19	0.08	1
8757		M <sup>a</sup>	379		37	0.35	0.14	0.39	0.11	3
8758		M <sup>c</sup>	421		46	0.3	0.08	0.54	0.09	3

\*M, male; F, female; Fc, female with calf; superscripts a, b, and c correspond to the MANOVA groups juvenile, female with calf, and adult.

<sup>†</sup>Neonate.

<sup>‡</sup>Habitat categories not available.

<sup>§</sup>Length unknown.

**Table 2.** Results from multivariate analysis of variance of habitat selection indices (four habitats) for 24 beluga whales from the eastern Beaufort Sea: (1) effects of year, gender, and their interaction and (2) effects of year and age-reproductive class.

Tests among habitat selection indices and explanatory factors	df	F	P
Test 1			
Year	8, 26	1.217	0.33
Gender	4, 13	1.641	0.22
Interaction	8, 26	1.66	0.16
Test 2			
Age-reproductive class	8, 28	2.756	0.02
Year	8, 28	1.048	0.43

1 explained 94% of the variation and was principally explained by the closed ice habitat. In the first cluster, both offshore and shallow open water habitat categories were used more often than expected based on availability ( $\bar{x} b_j$  values = 0.55 and 0.28, respectively; Table 4). This group was composed of 10 individuals: five females (three with calves) and five males in the smaller length range (353 to 404 cm; Table 3). The second cluster selected the closed ice habitat, followed by the mixed ice habitat ( $\bar{x} b_j = 0.53, 0.34$ ). This group was made up of five males; three were

**Table 3.** Number and length of beluga whales captured from the eastern Beaufort Sea according to sex and reproductive class.

Cluster group	Number of whales (length range in cm)		
	Males	Females with calves	Females without calves
1 (open water)	5 (353–404)	3 (338–363)	2 (302–373)
2 (closed ice)	5 (402–457)	0	0
3 (ice edge)	7 (379–427)	2 (340–374)	0

**Note:** Groupings are based on similarity of resource selection functions (see Materials and methods).

the largest of all the tagged whales. The final cluster selected the offshore open water ( $\bar{x} b_j = 0.35$ ) and closed ice habitats ( $\bar{x} b_j = 0.34$ ) more often than expected based on availability (Table 4). Examination of movement patterns illustrated that belugas followed the ice edge. This third group was composed of two females with calves and seven males that ranged in length from 379 to 427 cm (Table 3).

**Distance analysis**

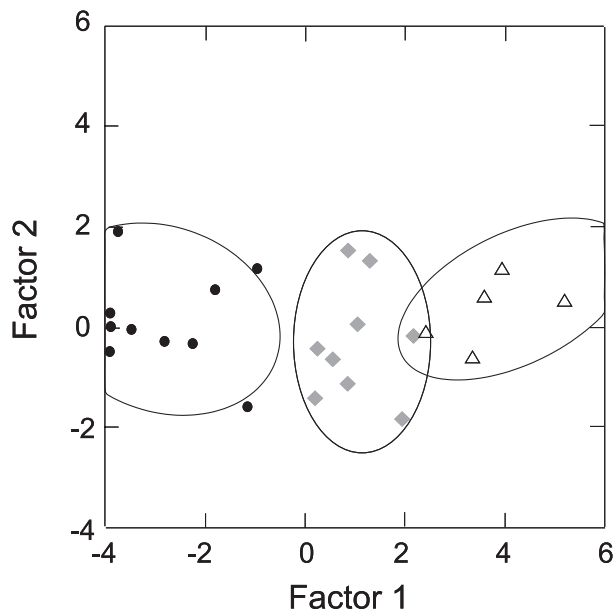
Analysis of variance tests for the distance to the mainland and island coastlines revealed the three cluster groups and the control group (random point locations) were significantly different (Table 4). Post hoc tests revealed whales that selected heavy ice concentration were the farthest from

**Table 4.** Beluga whales clustered into three groups based on habitat selection by sex and length ( $F_{[8,32]} = 7.6$ ,  $P < 0.0001$ ).

Cluster group	Habitat categories ( $b_j$ values)				Distance (km)	
	Offshore open water	Mixed ice	Closed ice	Shallow open water	Mainland	Islands
Group 1 (open water)	0.55 (0.04)	0.12 (0.04)	0.04 (0.02)	0.28 (0.03)	264 (10)	824 (23)
Group 2 (closed ice)	0.1 (0.04)	0.34 (0.07)	0.53 (0.06)	0.04 (0.01)	402 (16)	306 (36)
Group 3 (ice edge)	0.35 (0.04)	0.21 (0.03)	0.34 (0.04)	0.1 (0.03)	255 (10)	308 (23)
Random control (distance analysis)					424 (7)	752 (16)

**Note:** Values are means with SE in parentheses. Distance to the mainland and island coastlines differed among the three groups and a control group (random points) (mainland:  $F_{[3,2176]} = 86.6$ ,  $P < 0.001$ ; island:  $F_{[3,2176]} = 114.7$ ,  $P < 0.0001$ ).

**Fig. 3.** Results of discriminant function analysis of beluga selection indices ( $b_j$  values) for four habitat categories demonstrate groupings derived by the cluster analysis. The first group selected open water (●), the second group selected closed ice (△), and the third group selected ice edge habitat (◆).



the mainland and the closest to the islands, and their distances were not different from distances to the mainland coastline generated from random points. Whales that selected open water and ice edge habitats were closer to the mainland coast and were not significantly different from one another (Table 4). Whales farthest from the islands were those that selected open water, and their distances were not different from those generated from random points (Table 4). Whales that selected ice edge habitat and those that selected heavy ice concentration had similar distances to the island coastlines.

## Discussion

Habitat selection by beluga whales during the open-water season was affected by age and reproductive status, not individually but in concert. Sexual segregation refers to different habitat use by each sex (Conradt 1998); however, here three groups emerged that were not defined by sex alone. Sexual segregation into three groups occurs in other odontocetes such as northern bottlenose whales (*Hyperoodon ampullatus* (Forster, 1770)) (Gowans et al. 2001). In some cases sexual

segregation results from complex social structures; for example, in sperm whales (*Physeter macrocephalus* L., 1758), females, calves, and immature whales form long-term, multi-year associations (Christal and Whitehead 2001). In contrast, adult male sperm whales are often solitary and form temporary, loose aggregations (Whitehead and Weilgart 2000). Intraspecific segregation can be a consequence of different requirements within the population that vary over space and time (Stevick et al. 2002). Here, resource selection functions quantified habitat use and subsequent analysis revealed segregation, but why belugas segregate and what specific habitat attributes were selected is unclear. Two common explanations for sexual segregation are the predation risk hypothesis and the forage selection hypothesis, which are presented here to assist in the interpretation of the observed Beaufort beluga whale segregation.

### Sexual segregation hypotheses

The predation risk hypothesis postulates that predator avoidance behaviour by reproductive females will result in the geographic segregation of sexes by habitat use (Main et al. 1996). Predators of Beaufort beluga whales include humans, polar bears, and killer whales (*Orcinus orca* (L., 1758)). There is also the potential for infanticide (calf killing) by adult beluga males, which occurs in some marine mammals such as bottlenose dolphins (*Tursiops* sp.) (Patterson et al. 1998) and polar bears (Derocher and Wiig 1999). The basis of the predation risk hypothesis is habitat selection to avoid mortality by predation, but in a more general framework the hypothesis could be expanded to include abiotic causes of mortality, such as drowning caused by ice entrapment or mortal injury from sea ice.

The forage selection hypothesis relates to size dimorphism and maintaining a larger body mass by foraging more or on different-quality food, resulting in differential habitat use (Clutton-Brock et al. 1982; Conradt 1998). This hypothesis in its simplest form addresses energy requirements related to size but could be broadened to include the unique energy demands of pregnant or lactating females (Loudon 1985). Next, we discuss our findings of beluga segregation into three groups — those in open water near mainland, those in ice-covered areas in and near the Arctic Archipelago, and those selecting ice edge habitat — in the context of these two general hypotheses.

### Habitat selection: open water near mainland

The selection of open-water habitat near the mainland shore by females with calves and small males lends support to the predation risk hypothesis. Females invest 2–3 years of

traveling with their offspring (Caron and Smith 1990), likely avoiding habitats associated with predation and mortality risk. Use of open-water regions would reduce the risk of polar bear predation and avoid the risk of ice entrapment. Shallow open water could provide refuge from killer whale predation because the large size of these predators would inhibit their mobility in shallow waters. Physiological constraints of calves such as lung capacity or dive depth limitations may also restrain movement into regions of extensive sea ice cover. The small males in this group are likely immature whales that may also be avoiding mortality risks associated with sea ice or aggression by large males (Scott et al. 2005). On the other hand, they may be part of a social unit with the females and calves, not having made a transition to adult male behaviour and associated habitat use. Segregation of females with calves and immature whales from adult males is common in marine mammals such as sperm whales (Christal and Whitehead 2001). If this group represents a social unit, perhaps the immature males are participating in the protection of offspring, which is thought to be an important factor in the formation of whale social groups (Whitehead 2003).

#### **Habitat selection: ice-covered areas in and near the Canadian Arctic Archipelago**

This group consisted of large males, including the three largest, that selected closed ice and mixed ice habitat closest to island coastlines. Spatial and temporal segregation of older adult males from females and immature whales occurs in belugas (Smith et al. 1994) and other odontocetes such as bottlenose whales (Gowans et al. 2001). It is unknown whether large beluga males travel together as a unit or remain solitary during the summer, similar to adult male sperm whales (Whitehead and Weilgart 2000). Habitats selected by large male belugas have both predation and ice entrapment risks, thus segregation is not explained by mortality or predation avoidance.

In the summer, closed or mixed ice often overlies deeper areas of the Beaufort Sea and the Arctic Archipelago. Since these males were the closest to the island coastlines of the Arctic Archipelago, likely either ice cover or deep water was being selected. If habitats are selected for feeding, then belugas could be feeding on Arctic cod (*Boreogadus saida* (Lepechin, 1774)) under the ice (Gradinger and Bluhm 2004), or they may be feeding on the rich benthic food available from the deep-water environment. Therefore, use of these high-risk habitats likely offers energy benefits to support the greater growth and biomass necessary for the development of dimorphism, a scenario that supports the forage selection hypothesis. Adult males from the Chukchi Sea beluga whale population also enter heavy sea ice over deep sea regions, for reasons that are unclear (Suydam et al. 2001). If the sea ice provides an important feeding resource, then the predicted loss of ice cover with climate change may affect the energy requirements of large adult males.

#### **Habitat selection: ice edge**

The third beluga group selected the ice edge regions (off-shore open water, closed ice cover). This group was close to both mainland and island coastlines, suggesting habitat use was not related to coastlines. Ice edge areas are highly pro-

ductive zones providing seasonal food for marine birds and mammals (Moore et al. 2000; Harwood and Smith 2002). Therefore, this habitat is likely selected for feeding, supporting the forage selection hypothesis of segregation. The seven males in this group were generally smaller than those selecting ice cover and larger than immature males selecting open-water habitats. Perhaps these males have passed an age or maturity threshold that enables them to leave their maternal groups and protective habitats to explore more productive regions. They may represent an intermediate stage, such as subadult males that segregate from their maternal groups and remain separate from large adult males owing to social structure or physiological demands. Formation of subadult male social groups occurs in northern bottlenose whales and some bottlenose dolphins (Smolker et al. 1992; Gowans et al. 2001), and in sperm whales subadult males form loose associations or remain solitary (Christal et al. 1998).

Two females with calves were also present in this group. This does not necessarily suggest that subadult males and females form semipermanent social groups. Selection of ice edge habitats by these females is likely risky relative to selection of open-water habitats; however, their calves were not newborns, so susceptibility to predators may have been reduced. These females may represent a segment of the population with older calves that are ready to begin interacting with males again and are prepared to mate during winter. Without tracking data for the calves, it is not known whether they still accompanied their mothers once leaving the estuary of capture. Also, we cannot assess whether these females consistently used ice edges from year to year regardless of reproductive stage.

The two segregation hypotheses evaluated are not mutually exclusive (Bleich et al. 1997), and our data were inadequate to conclusively test between the two. Our results illuminate the factors responsible for beluga segregation based on habitat selection. Beluga habitat segregation according to age and reproductive class demonstrates the different resource needs of individuals and the various habitats that can provide these resources. Our results provide the first quantitative report of habitat segregation that may represent beluga social structure. Previous observations of beluga sexual segregation in northern Canada (Smith et al. 1994) and Greenland (Heide-Jorgensen and Lockyer 2001) did not quantify the segregation relative to habitat selection. The lack of beluga segregation and social structure studies is largely due to the difficulty in observing Arctic marine mammals. In addition, little is known about beluga life stages, body growth dynamics, and maternal development, resulting in the difficulty in identifying age structure and reproductive status. Our study demonstrates that protecting beluga whale habitat requires understanding the needs of various age, sex, and reproductive groups and the different habitats they select.

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