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Food consumption, growth and reproduction of Belugas (*Delphinapterus leucas*) in human care

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Summary

This report describes the body measurements, weight changes and food consumption of 9 Belugas housed at Vancouver Public Aquarium between 1967 and 1991. Females' body growth leveled off at around 300 cm and 7 years, while males continued to grow until at least 14 years. Annual food consumption seems to be related to sex and age as well as to social group changes and feeding techniques. After reaching sexual maturity at about 7 years, males ate less than in the remainder of the year during August and September, the season in which they were sexually active. The females which were sexually approached also reduced their intake during those months. Belugas of 200 kg were found to eat around 4.5%, those of 1400 kg 1.2% of their body weight per day in water with average annual water temperatures between 10 and 12°C. A significant negative correlation was found between average monthly water temperature and average daily food intake per month. This relationship and water temperatures in the Belugas' distribution areas were used to calculate that a wild adult female Beluga of 600–700 kg may eat around 4900 kg of fish per year (8.144.000 Kcal/year). The passage time of carmine red dye through gastrointestinal tract was on average 4.5 hrs.

Keywords: Beluga, *Delphinapterus*, energetics, food consumption, reproduction, growth, food passage time.

Introduction

Belugas (*Delphinapterus leucas*) are medium-sized toothed whales which inhabit arctic and sub-arctic waters (Stewart & Stewart, 1989) and experience lower water temperatures than most other toothed whales. They are adapted to maintain a constant core temperature of around 37°C in this cold environment by having a thick dermis and a thick insulating blubber envelope. However, they use much energy to keep their core temperature stable. Because the Beluga is one of the most abundant odontocetes in arctic waters (Fay, 1979), it probably has a relatively large impact on its prey populations.

For the management of Beluga populations in the wild, information is needed about population size, age composition and sex ratio, seasonal distribution, diet, energy requirements relative to seasonal prey distribution and density, and competition with other marine mammals and fisheries. This information could facilitate prey management to allow target numbers of Belugas to survive in particular geographical areas.

The seasonal movements of Belugas have been described by Tomilin (1957), Kleinenberg *et al.* (1964), Sergeant & Brodie (1969a), Sergeant & Hoek (1973), Braham & Krogman (1977), Fraker *et al.* (1978), Harrison & Hall (1978), Fraker & Fraker (1979), Seaman & Burns (1981), Finley *et al.* (1982) and Krogman & Carrol (1982). Belugas usually feed in waters above the continental shelf (Fay, 1979).

As prey Belugas in the Saint Lawrence estuary (temperate water) take mainly Cod (*Gadus morhua*), Pollock (*Pollachius vireus*), Herring (*Clupea harengus*), Capelin (*Mallotus villosus*) and Smelt (*Atherina presbyter*), and to a lesser extent Sculpin (*Myoxocephalus scorpius*), polychaetes, cephalopods and crustaceans. These prey types and their proportions in the diets of different Beluga sex and age classes in various seasons have been described by Vladykov (1946), Kleinenberg *et al.* (1964) and Seaman *et al.* (1982). In the arctic waters the major food species of Belugas is the Polar or Arctic cod (*Boreogadus saida*), a fish which is frequently associated with the ice edge (Sergeant, pers. comm.). In arctic waters Belugas probably also eat a lot of benthic invertebrates, because Belugas can

Table 1. Details of the studied Belugas at Vancouver Public Aquarium

Animal code	Sex	Birth date	Origin	Arrival date
D1	♀	1961	King Salmon, Alaska	09-1967
D2	♂	1966	King Salmon, Alaska	09-1967
D3	♀	1970	Churchill river, Manitoba	29-07-1976
D4	♀	1975	Churchill river, Manitoba	29-07-1976
D5	♂	1977	Born at Vancouver Aquarium	13-07-1977
D6	♀	1979	Churchill river, Manitoba	17-07-1985
D7	♂	1982	Churchill river, Manitoba	17-07-1985
D8	♂	1981	Churchill river, Manitoba	15-08-1990
D9	♀	1986	Churchill river, Manitoba	15-08-1990
D10	♂	1986	Churchill river, Manitoba	15-08-1990

dive to considerable depth to reach the bottom (Martin & Smith, 1992).

At present it is impossible to measure energetic requirements of odontocetes in the wild. Energetic studies on wild Belugas are particularly difficult due to the ice and weather conditions, and the continuous darkness of the arctic winter in some parts of the distribution area (Brodie, 1982). While the Beluga is a widely kept toothed whale, little is published from captive studies about its food requirements (Doidge, 1990a). Sergeant (1969) calculated food intake to body weight ratios for some Belugas, but the weights he used were estimated, the water temperature was not reported, and food intakes were not averaged over long periods. Since 1974 the Vancouver Public Aquarium has recorded food intake, body weight and morphological measurements of their Belugas as well as environmental parameters such as water temperature. The present study analyses this information for husbandry and wildlife management purposes.

Materials and Methods

Study animals

The study was conducted on the 10 Belugas described in Table 1 housed at Vancouver Public Aquarium. Age estimates are based on the colour, size and weight of the animals (Sergeant, 1973). The younger the animal on arrival, the more accurate the age estimate is. Some of the age estimates for animals that were older than 3 years on arrival (D1 and D8) may be 1 year off to either side of the actual age.

Study area

At the Vancouver Public Aquarium (123° 10′ West longitude, 49° 11′ North latitude) the animals were kept in the B.C. Tel pool (elliptical, 11 m × 5.5 m; depth: 4.8 m) and during illness and pool maintenance in an adjoining pool (7.5 m × 4.5 m; depth: 3 m) until 31 May 1990. The water temperature, which was influenced by the sea temperature, was measured each day. The daily temperature varied between 7.5 and 16.9°C during the study period, while the annual average water temperature varied between 10.5 and 12.4°C. Salinity varied between 1.8 and 2.8% and the free chlorine level fluctuated between 0.28 and 0.90 mg/l.

After 31 May, 1990 the animals were housed in the Arctic Canada pool (11 m × 5 m; depth: 6.5 m) and in a 3 m deep adjacent medical pool. In addition the animals could be kept in a research pool (15 m × 15 m; depth: 3 m). The water was chilled and the temperature was kept between 10 and 11.5°C. The salinity varied between 2.5 and 2.7%, and the free chlorine level fluctuated between 0.38 and 0.64 mg/l.

Food

The animals were fed 3 to 5 times a day. Until mid 1974 the diet consisted of around 90% Herring (*Clupea harengus*) and 10% Surf Smelt (*Hypomesus pretiosus*). In the second half of 1974 the diet consisted of 90% Herring and 10% Mackerel (*Scomber scombrus*). Starting in 1975 the diet was changed to about 75% Herring, 15% Mackerel and 10% squid (*Loligo* spp.). The squid was sometimes replaced by Whiting (*Merlangius merlangus*). The percentages are based on weight, and there were small variations in the percentages of the different species given to individuals. Vitamins were added to the fish, after it had been defrosted. All food was given during training and show sessions, and as a rule, feeding was stopped when the animals stopped swallowing their food immediately. Individual food records per day were kept from 1974. The present study is based on the food intake data between 1974 and 1991.

Body weight and length
The animals were weighed on arrival at the Aquarium, and usually when they were transported between pools. Because of the different frequencies of transports and lengths of time the whales were at the Aquarium, some animals were weighed more often than others. Body length measurements were taken irregularly, and not always simultaneously with weight measurements.

Sexual behaviour
When sexual behaviour was observed by the trainers, this was registered on the food record sheets. Sexual behaviour is defined as attempts or acts of intromission by the males toward the females.

Passage time of food through gastrointestinal tract
To measure the passage time of food through the gastrointestinal tract, a gelatine capsule containing 6 g of carmine red dye was added to the animal's normal feed between 09.30 and 11.10 hrs. The animal was then kept under constant observation until red dye was seen in the faeces. Tests were conducted twice on 2 animals (D8, an approximately 650 kg, 11-year-old male and D6, an approximately 600 kg, 13-year-old female), in November 1992 and 3 times on 7-year-old male D10 and 14-year-old female D6 in September 1993.

Results

Growth
The body length of 4 male Belugas in this study increased from about 130 cm at birth to about 450 cm when 14 years old (Fig. 1A). However, length at the same age differed substantially; for instance D2 and D7 were 380 and 340 cm when both were 8 years old. The same is true for the females (Fig. 1B), although females remained smaller than males when adult. Individual Belugas reached their maximum lengths at different ages.

Until the age of about 2 years, individuals of both sexes weighed about the same (Fig. 2). Thereafter, males were heavier than females of the same age.

Annual food consumption
Male D7's average daily food intake increased from 8 kg when he was 4 years old to 14 kg when he was 7 years old (Fig. 3A). D2's daily food intake increased from 15.5 kg when he was 8 years old, to 19.5 kg when he was 13 years old. This animal decreased his intake during the second part of his 10th year and the first half of his 11th year. This reduction in food intake occurred simultaneously with changes in the social composition of the group; D2 lost his partner, was introduced to a new partner, and he was moved to a holding pool next to the Killer whale (*Orcinus orca*) pool for part of the year. Animal D10 ate 12.5 kg/day when he was 4 years old, in his first year at the aquarium. Animal D8 ate 13 kg/day when he was 10 years old (Fig. 3A).

Female D4's average daily food intake increased from 7 kg when she was 2 years old to 11 kg when she was 9 years old (Fig. 3B). D6's daily food intake increased from 9 kg when she was 7 years old, to 13 kg when she was 12 years old. D3's daily food intake increased from 10.5 kg when she was 7 years old, to 12 kg when she was 21 years old. Animal D9 ate 11 kg/day when she was 5 years old. Animal D1 ate between 14 and 15 kg/day when she was 13 and 14 years old.

Seasonal food intake fluctuations and sexual behaviour
During his 10th year, male D8 became sexually active in August. In that month he (Fig. 4A) and 5-year-old female D9 ate less than usual (Fig. 4C). This was the first full calender year after male D8 arrived. A year later he again reduced his food intake in August and September (Fig. 4B).

During his 7th year, male D7 became sexually active in September, and ate less than usual (Fig. 4D). That same month and year, 19-year-old female D3 and 10-year-old female D6 also reduced their intake (Figs 4E & F).

Male D2 showed little sexual behaviour and no seasonal depression of food intake.

Food consumption relative to body weight
The few available data show that average daily food intake over a calender year per kg of body weight is dependent on the actual body weight (Fig. 5). The larger the animal, the smaller the relative food intake. Animals of 200 kg eat on average around 4.5% of their body weight per day, whereas animals of 1400 kg need only 1.2%. These percentages should be evaluated in relation to the water temperature. Here, average annual water temperatures were between 10.5 and 12.4°C.

Influence of water temperature on food intake
In non-pregnant female D3, daily food intake was recorded over 15 years (Fig. 3B), while her body weight remained fairly constant (from 600 kg to around 700 kg). Because in these years the average monthly water temperature varied from about 8°C to 16°C it was possible to correlate monthly food intake and water temperature for one adult individual. This is shown in Fig. 6 (Pearson correl. coeff.: $r = -0.32$, $P<0.005$, $N = 158$). Low water temperatures lead to increased food intake by this individual.

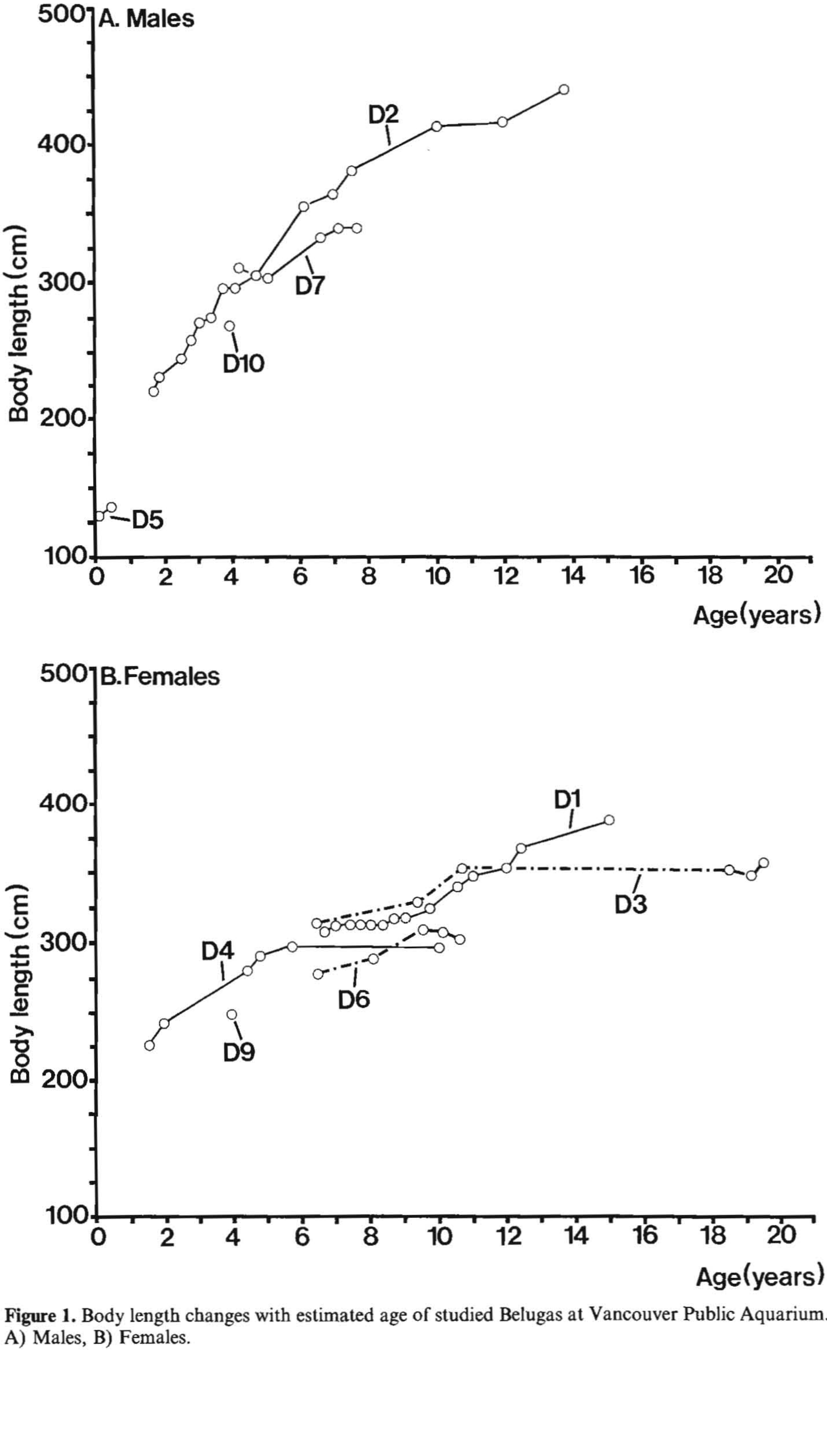

Figure 1. Body length changes with estimated age of studied Belugas at Vancouver Public Aquarium. A) Males, B) Females.

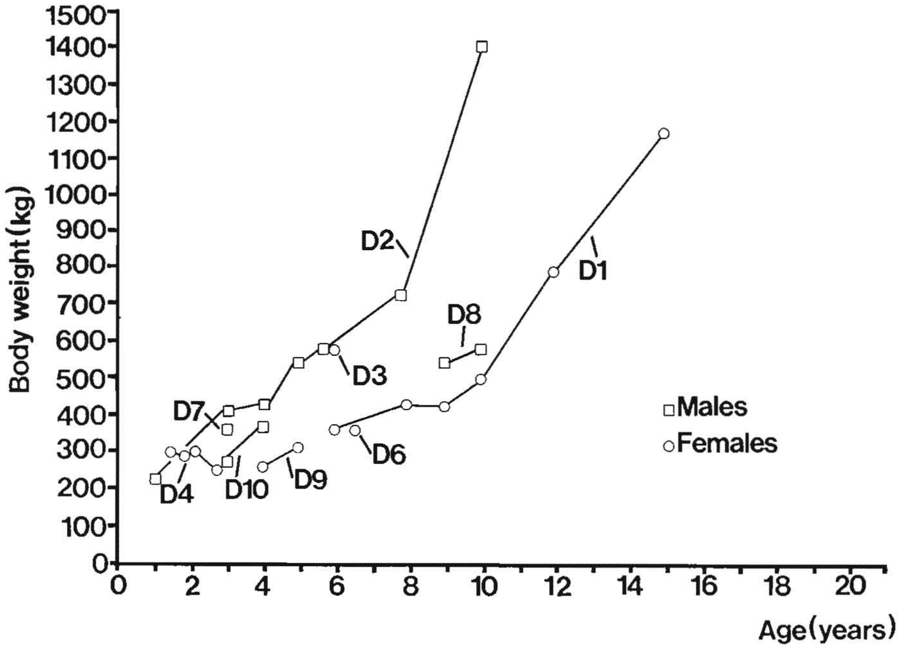

Figure 2. Body weight changes with estimated age of studied Belugas of both sexes at Vancouver Public Aquarium.

Food intake during lactation

Female D3 arrived at Vancouver Aquarium 12 months before she delivered her calf. As the gestation period in Belugas is 14.5 months (Brodie, 1971; Sergeant, 1973), she must have conceived in the wild. Her food intake before and after the birth was probably lower than it would have been in the wild due to her adaptation to a new environment, a new diet and feeding schedule (St. Aubin & Geraci, 1990). Her food consumption increased during the last 3 months of gestation to on average 12 kg/day during the last month (Fig. 7). The first month after the birth her food intake increased dramatically to 25 kg/day on average. Thereafter it decreased. Unfortunately calf D5 died of nocardium infection (*Nocardia farcinica*) at the age of 3.5 months (Drinnan & Sadleir, 1981). The following month D3's food intake decreased to a normal level.

Passage time of food through gastrointestinal tract

The passage times of carmine red dye are shown in Table 2. The average passage time was 4.5 hrs.

Discussion and Conclusions

Growth

The birth length of calf D5 was similar to that of wild calves in Canadian waters (Sergeant & Brodie, 1969; Doidge, 1990a). In general, the body lengths and body weight to body length ratios of the animals in the present study were similar to those found in Belugas of the same sex and age classes in various regions in the wild (Doidge, 1990a; Sergeant & Brodie, 1969b). Two of the animals (D1 and D2) in the present study were probably overfed for some time in 1976 (e.g. D2 when 8 to 9 years old, and D1 when 13 to 14 years old; Figs 2 & 3), since in that year the body weight to body length ratio was much higher than observed in general in wild conspecifics (Doidge, 1990a). The trainers tried to fatten the animals by being more patient when feeding. Belugas may become obese easily because:

a) They have a tendency to store fat, which is perhaps used during spring and autumn migration (Brodie, 1982), or in winter; and

b) Of wild Belugas part of the diet consists of small prey items of low energetic value, and feeding probably takes up a large proportion of their time. When hand-fed fish with a high energy content in oceanaria, the animals might store larger fat reserves than they could in the wild.

The length to age relationship in the animals in the present study is in close agreement of that of wild Belugas from Cumberland Sound, as noticed for the same male D2 by Brodie (1982). The males in the present study were larger than the females of the same age classes. This sexual dimorphism has also been noted in wild Belugas (Sergeant & Brodie,

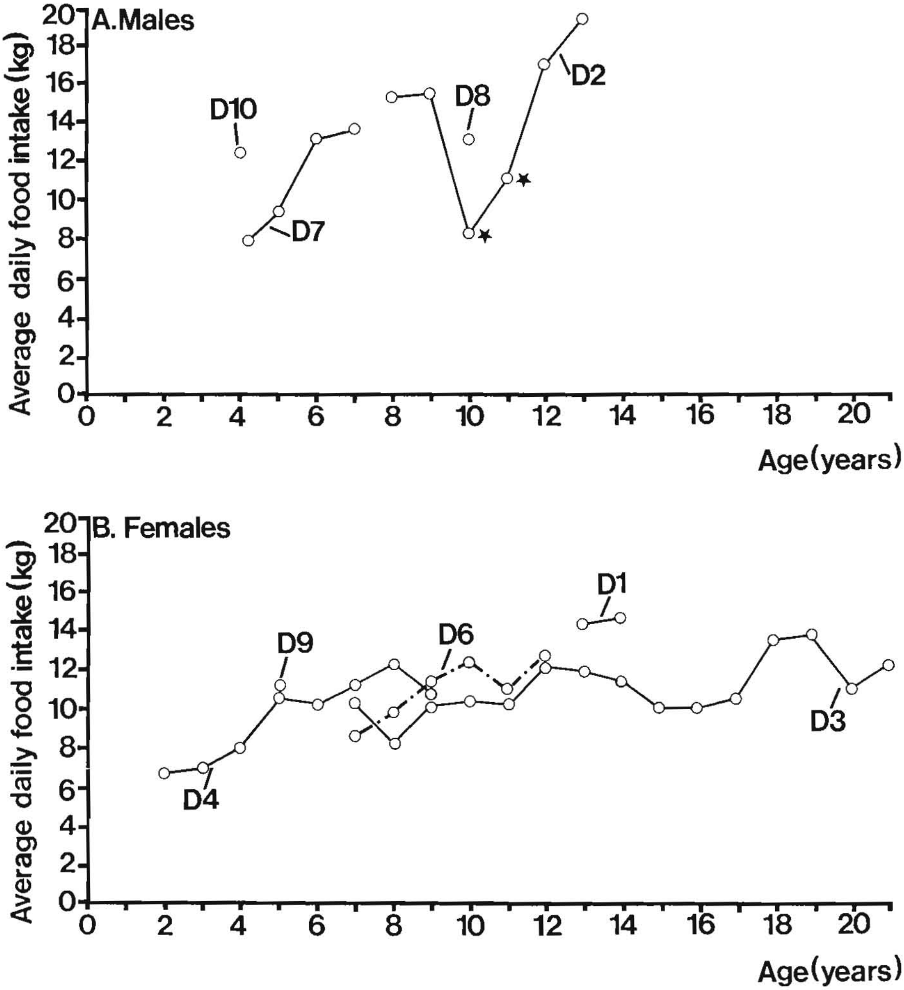

Figure 3. The average daily food consumption per year of Belugas at the Vancouver Aquarium relative to age. A) Males, B) Females. An * indicates low food intake corresponding with temporary changes in the composition of the group and location next to the Killer whale pool during part of the year.

1969b; Doidge, 1990a). Between the age of 8 and 10 years, male D2 increased his body weight quickly. This could be a maturation effect. In the wild, depending on the population, males show an increase in testis weight after they reach a body length of about 300 cm. They attain sexual maturity at 7–9 years of age (Brodie, 1971; Sergeant, 1973). The males in the present study reached a body length of 300 cm when they were 5 years old. Testosterone probably plays a role in the growth spurt during the period in which males become sexually mature. The maximum age in Belugas has been estimated to be between 25 and 30 years (Brodie, 1971; Sergeant, 1973), and in some cases even up to 35 years, assuming 2 dental growth layers per annum (Sergeant, 1986).

The 2 animals from Alaska (male D2 and female D1) were larger at the same age as the animals from the Hudson Bay (male D10 and female D3). This extremely small sample is in agreement with the suggested genotype difference in body size found in the wild between animals from Alaska and from Hudson's bay (Sergeant, 1973).

Annual food consumption

It is possible to extrapolate the food intake curve of male D7 in Fig. 3 towards the food intake level of male D2 at the age of 12 years. Beluga males

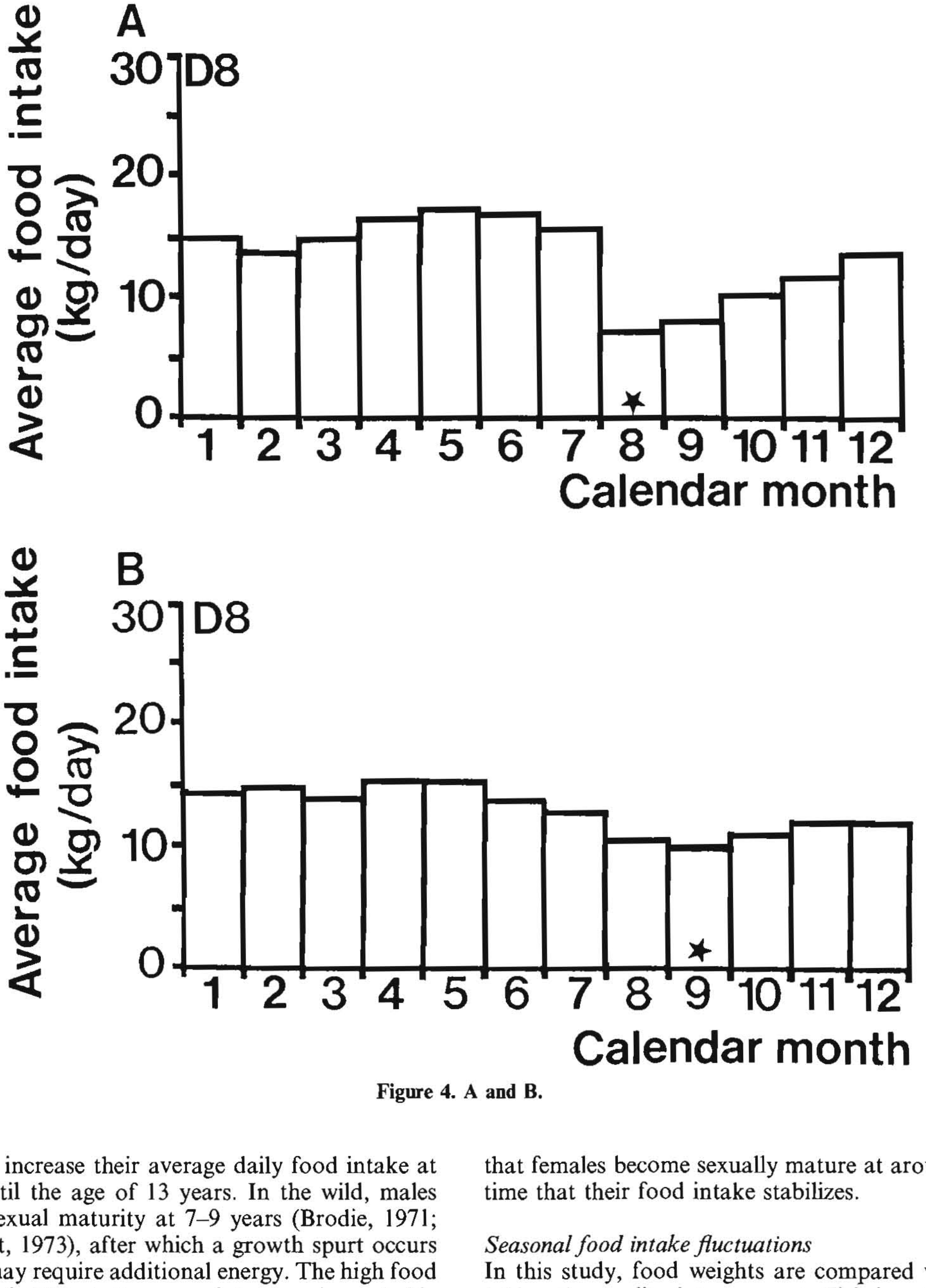

Figure 4. A and B.

seem to increase their average daily food intake at least until the age of 13 years. In the wild, males attain sexual maturity at 7–9 years (Brodie, 1971; Sergeant, 1973), after which a growth spurt occurs which may require additional energy. The high food intake of D10 at the age of 4 years is probably recovery from a low food intake after his transfer from the wild to the aquarium. Transport can cause hematologic and metabolic changes in Belugas (St. Aubin & Geraci, 1989).

The food intake of the females in the present study stabilized when they were around 5 years old. In the wild, females attain sexual maturity at 4–7 years (Brodie, 1971; Sergeant, 1973). This suggests that females become sexually mature at around the time that their food intake stabilizes.

Seasonal food intake fluctuations

In this study, food weights are compared without taking the quality into account. Fish has different caloric values, depending on species, season and origin. The diet of the animals in this study consisted of 75% Herring, a fish species with a high caloric value. The Herring fed at Vancouver Aquarium is caught once a year in December or January, and is stored until needed. The fat content of the Herring is generally more than 10%, and its caloric value, based on one test, is 1780 Kcal/kg.

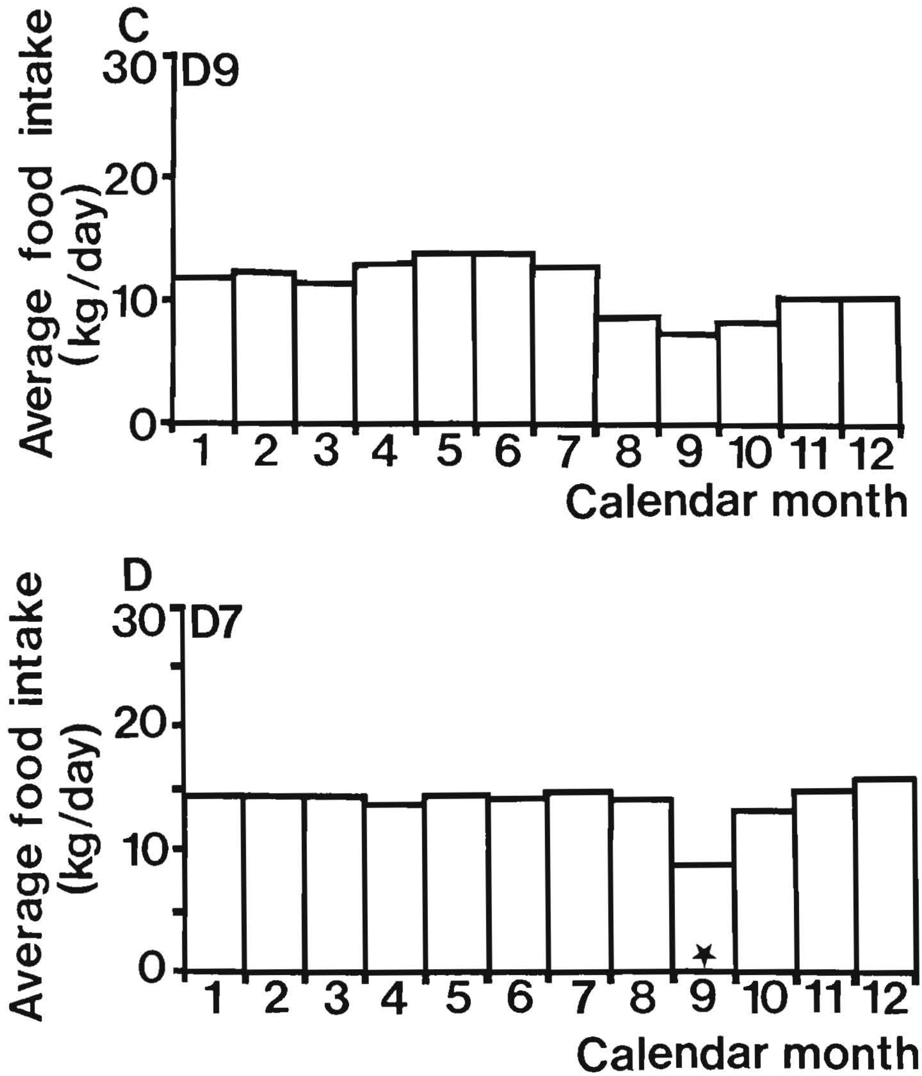

Figure 4. C and D.

Because of the long storage period, seasonal fluctuations in food intake cannot be caused by differences in energetic content of the food.

D8 displayed sexual behaviour at the age of 10 years. This was the year after he arrived at the park, and he may have been sexually active before that age in the wild. Male D7 showed sexual behaviour for the first time when he was 7 years of age. This corresponds with wild male Belugas, which attain sexual maturity at 7–9 years of age, although the age of sexual maturity depends on the location (Brodie, 1971; Sergeant, 1973). The males in the present study showed sexual behaviour in August and September, and ate relatively little during that period. This reduction in food consumption corresponds with the months in which wild Belugas probably reduce their food intake. In the wild, migration occurs in mid-August and September (Sergeant, 1973). Stomachs of Belugas caught on migration are usually empty, suggesting that they eat little during this period (Seaman *et al.*, 1982). However, this information may be biased because animals often vomit when shot. Little is known about Belugas' winter activities, and about what they eat during the winter.

During July and early August, female Belugas and their calves gather in relatively shallow, warm estuaries soon after giving birth (Sergeant & Brodie,

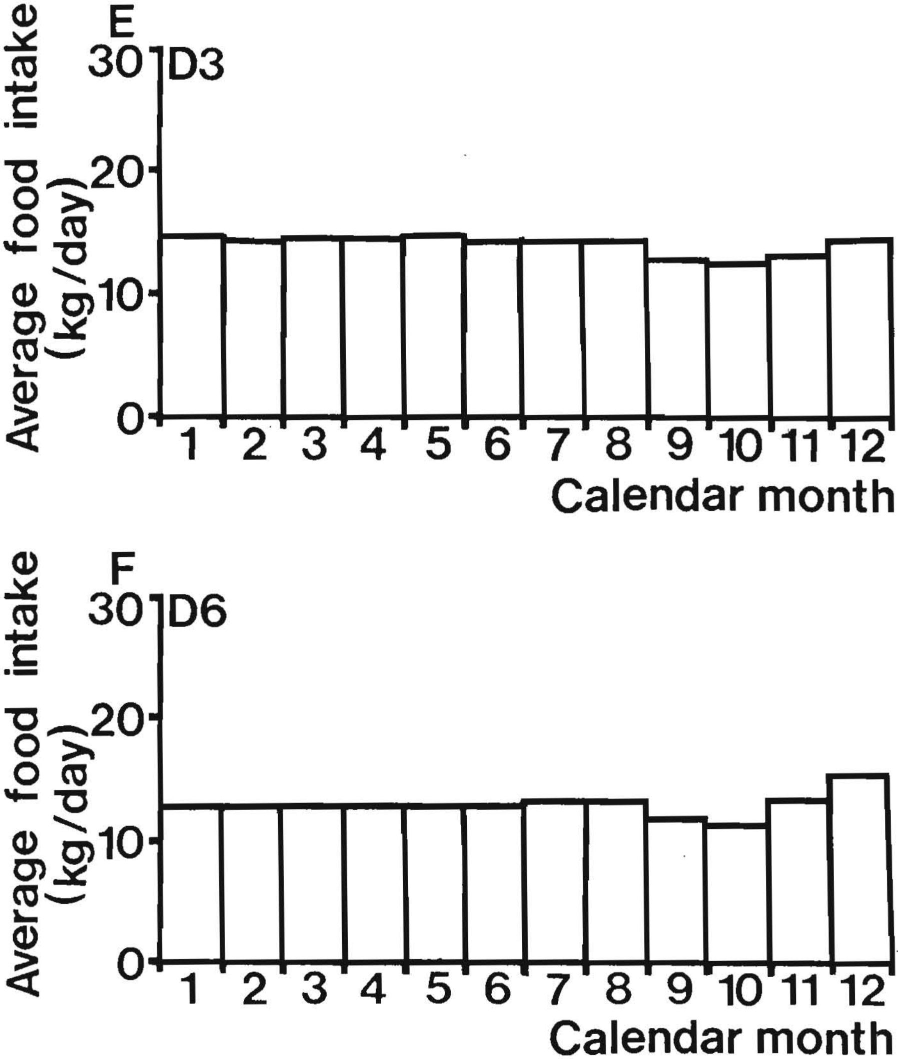

Figure 4. E and F.

Figure 4. The average daily food intake during the 10th year (A) and 11th year (B) of Beluga male D8, and of 5-year-old female D9 during the same year (C). The average daily food intake during the 7th year of male D7 (D), and of 19-year old female D3 and 10-year-old female D6 during the same year (E & F). The * indicates the month in which male sexual activity was observed.

1969b; Smith *et al.*, 1992). Whether females eat during this period is unknown. It is believed that Belugas lay down 2 dental layers each year, each layer consisting of one opaque and one translucent zone of dentine. The translucent material is thought to be laid down during periods of reduced feeding, which may occur either during autumn and spring migration or winter deprivation (Sergeant, 1973). As the females in the present study reduced their food intake between August and October, it seems likely that wild females eat during the July calving period. However, it is not known whether non-pregnant and non-lactating females also reside in the warmer estuaries in this period. At Duisburg Zoo, 2 female Belugas reduced their food intake by about 50% during August and September (Bartmann, 1974). The reduction in food intake of captive female Belugas in the same period in which wild Belugas reduce their food intake due to migration suggests that internal factors reduce the appetite of Belugas during this period.

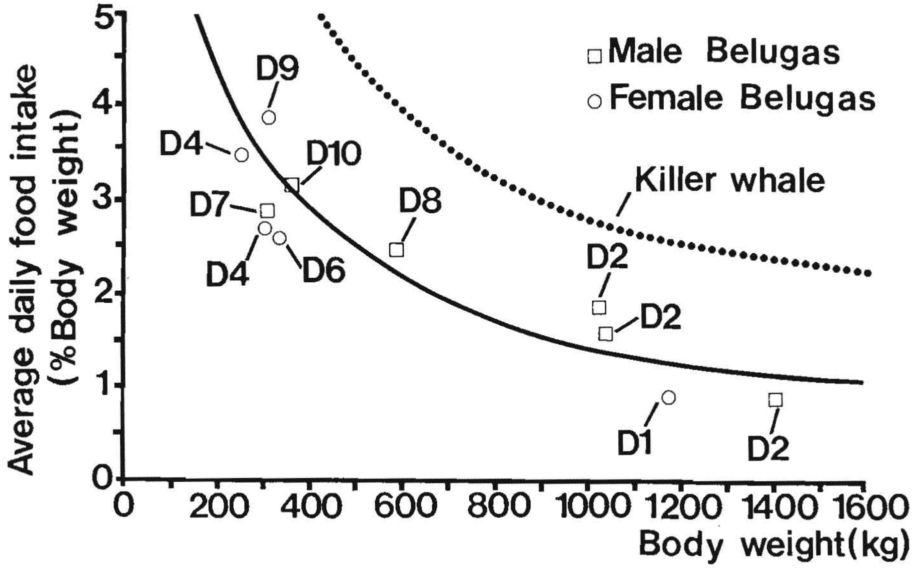

Figure 5. Average daily food intake in proportion to body weight of Belugas of different body weights at Vancouver Public Aquarium. The line is hand-drawn. The dotted line represents data from a growing female Killer whale housed at an average water temperature of 17°C (from Kastelein & Vaughan, 1989).

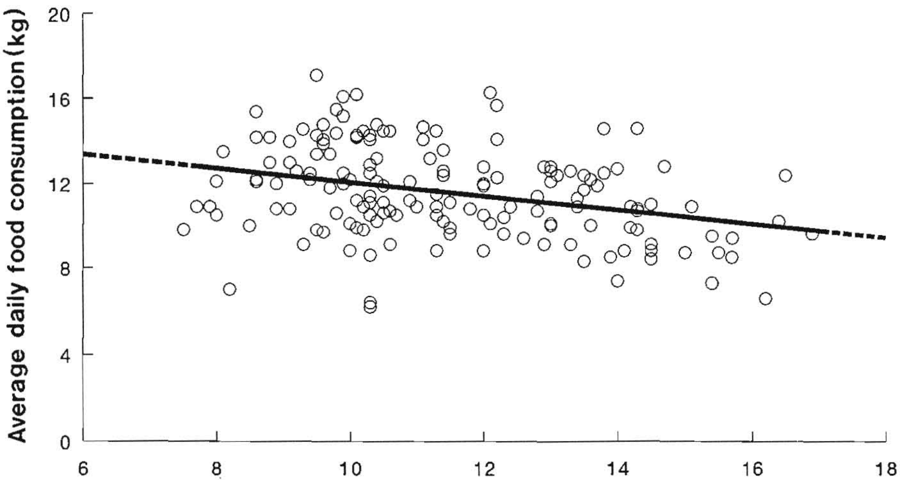

Figure 6. Relationship between the average monthly water temperature and average daily food intake per month for female D3 when her body weight varied between 600 and 700 kg (N=158, regression line: y=-0.33 × +15.4).

Food consumption relative to body weight
Small cetaceans typically eat much more in relation to their body weight than large cetaceans. For instance studies in captivity revealed that adult Harbour porpoises (*Phocoena phocoena*) weighing about 35 kg eat around 8% of their body weight per day in water of around 18°C (Andersen, 1965; Kastelein *et al.*, 1990), and adult Commerson's dolphins (*Cephalorhynchus commersonii*) of about 40 kg eat 10% of their body weight per day in water of between 14 and 18°C (Kastelein *et al.*, 1993b). The Beluga's lower proportional intake of food of similar caloric content, and its capacity to store large amounts of fat, probably mean that this animal can fast for long periods. Reduced feeding may occur during migration, when Belugas spend

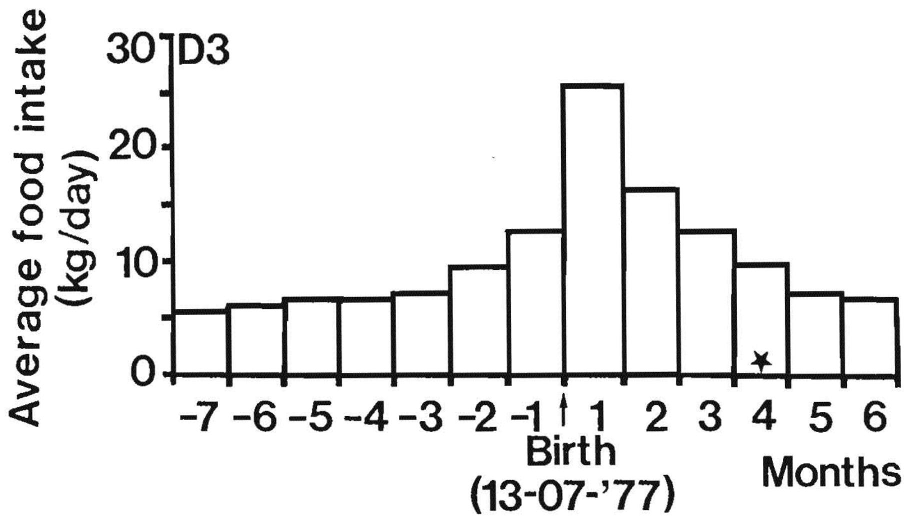

Figure 7. The average daily food intake of Beluga female D3, 7 months prior to and 6 months after the delivery of a calf. She gave birth 12 months after she arrived at the Vancouver Public Aquarium. The * indicates the month in which the calf died.

Table 2. Passage times of 6 g of carmine red dye in 3 Belugas at Vancouver Public Aquarium

Animal	Sex	Age (yr)	Est. weight (kg)	Time of day dye fed	Passage time (min)
D8	M	11	650	11.00	247
D8	M	11	650	11.00	305
D6	F	13	600	11.10	250
D6	F	13	600	11.05	230
D6	F	14	600	09.39	315
D6	F	14	600	09.38	259
D6	F	14	600	11.00	380
D10	M	7	650	09.35	287
D10	M	7	650	09.57	223
D10	M	7	650	09.30	238
					Average: 273 (SD 46 min)

their time travelling instead of foraging, and/or may have to swim through areas with low food availability.

The present study shows that adult Belugas of both sexes eat about 1% of their body weight per day when kept in water of around 11°C. Compared to a Killer whale (*Orcinus orca*) housed in a pool with a higher average water temperature of 17°C (Kastelein & Vaughan, 1989), Belugas of the same weight class (between 400 and 1400 kg) in the present study ate between 1.5 and 1.9% less in proportion to body weight (Fig. 5). If the Killer whale had been kept in water with the same temperature as the Vancouver Aquarium pool, the difference would probably have been larger (assuming that the Killer whale was kept at the relatively horizontal part of the U-shaped water temperature versus metabolic rate curve). The difference in food intake is probably due to a difference in the basal metabolic rate of the 2 species, that of the Killer whale being higher than that of Belugas of the same weight classes.

The difference in metabolic rate could have one or several of the following speculative causes:

1) The body composition of Belugas is probably different from that of Killer whales. Sergeant & Brodie (1969b) showed that 43.4% of a Beluga's body weight was composed of blubber and flippers,

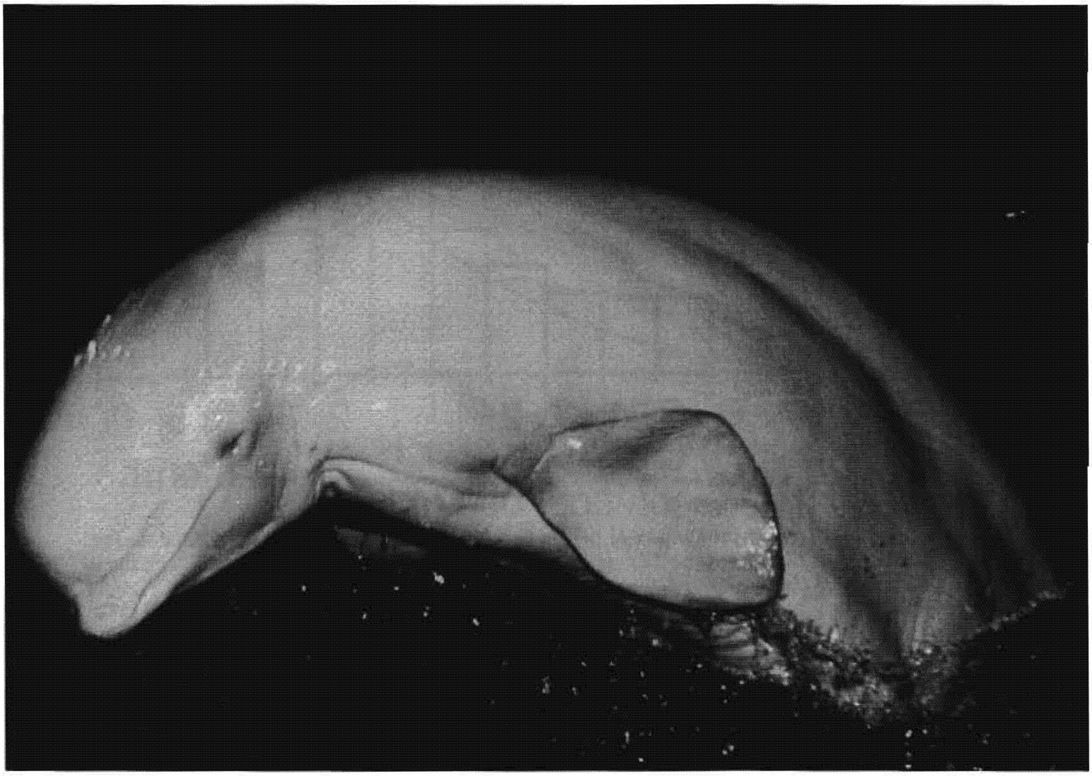

Figure 8. A young Beluga. Note the absence of a dorsal fin, a feature which allows Belugas to break through ice without injuries (Photo: Sea World of California photo department).

and 15.9% of muscles, whereas a Pilot whale (*Globicephala melaena*) of the same body length consisted of 29.1% blubber and flippers and 34.0% muscle. Such information is not available for Killer whales, but the body composition of the Pilot whale is probably more similar to that of the Killer whale than to that of the Beluga. A higher percentage of muscle probably requires a larger food intake, as muscle is energetically more demanding than adipose tissue.
2) The relatively small proportion of muscle makes Belugas, which are specialized in eating slow prey, swim slower than Killer whales which have to hunt for faster prey. Slow swimming requires less energy than fast swimming.
3) A Beluga's fat layer is relatively thicker than a Killer whale's, causing the Beluga's thermal neutral zone to be in a lower temperature range than a Killer whale's. This difference could be a species property.
4) In addition to genetic differences in fat layer thickness, the Belugas at the Vancouver Aquarium may have had to maintain a thicker insulating fat layer than the Killer whale at the Harderwijk Marine Animal Park, because they were kept in colder water (for this phenomenon in Bottlenose dolphins (*Tursiops truncatus*), see Williams *et al.*, 1992).
5) A Beluga's body shape is different to a Killer whale's. Possibly the body volume to surface ratio is larger in Belugas than in Killer whales of the same weight, so that they lose less energy to the environment by thermal conduction. Belugas have no dorsal fin (Fig. 8), whereas especially adult male Killer whales have large dorsal fins. Belugas can survive without a dorsal fin because they are slow swimmers, and thus need no stabilizer. Also, because they create less body heat and live in cold water, they may have a reduced cooling capacity. Unfortunately, Kasting *et al.* (1989) were not able to compare individual Belugas and Killer whales of similar body weights, but their study indicates that the contribution of the surface area of the appendages to the total body surface area is higher in Killer whales than in Belugas. When hunting, Killer whales with their proportionally larger muscle mass may have a greater need to lose excess heat through their appendages than the slower, relatively fat-rich Belugas.

Figure 9. An adult female Beluga with her calf. Note the birth folds in the skin of the calf (Photo: Sea World of California photo department).

6) The insulating qualities of the blubber layer vary among odontocetes (Worthy, 1991). The thermal conductance of the skin and blubber layer of the Beluga is lower than that of the Killer whale (Doidge, 1990b; Kasting *et al.*, 1989).
7) The blubber distribution may be different between the 2 species (for the distribution in Belugas, see Doidge, 1990b).
8) The skin of the Beluga is thicker, and thus probably a better insulator, than that of the Killer whale. On arrival in the warm fresh water of estuaries in mid-July to mid-August, Belugas moult, probably as a thermoregulatory adaptation to the environment (St. Aubin *et al.*, 1990; Smith *et al.*, 1992).

Changes in food consumption due to birth and lactation

Animal D3's increased food intake during the 2 months prior to birth could have at least 2 causes:
1) She ate more to meet the energy requirements of the foetus for its final growth; Commerson's dolphins eat less during the 11.5 month gestation period than during similar periods when they are neither pregnant nor lactating (Kastelein *et al.*, 1993b). Spotte & Babus (1980) found that the food intake of a pregnant Bottlenose dolphin, kept in water of 27°C, showed large fluctuations, but that the average food intake did not increase although her body mass increased by 37%. However, based on a larger sample, Ridgway *et al.*, 1991, found that captive Bottlenose dolphins consumed slightly more calories during the final stage of gestation.
(2) The female may have deposited fat reserves for utilization during the suckling period.

After birth, the calf was observed to suckle successfully, and up to the age of 95 days possibly to satiation (Drinnan & Sadleir, 1981). In addition to the energetic requirements of rapid growth and the establishment of a thick blubber layer by the calf, the female's large increase in food intake after birth was probably also due to the strong increase in total combined body surface area of the mother and calf at birth (Fig. 9). The mother not only has to supply energy for the calf's growth and locomotion, but also has to compensate for the increased heat loss to the environment.

In the wild, birth occurs between June and August at sea after which the females and their calves move in relatively warm estuaries (Smith *et al.*, 1992). In the St. Lawrence estuary, females with young calves remain in the south-central part where the temperature of the mixed water layer in July is above 9°C. There they mainly feed on benthic fish and invertebrates (Sergeant, 1973). Adult males live in the north-east marginal sector where the summer surface temperature at spring tides can be as low as 3°C, and where Capelin is abundant (Sergeant, 1986). Neonates have thick skins, but thin blubber layers compared to adults. The thick skin may serve as a thermal buffer at birth (Doidge, 1990b). The first period of suckling may well occur in relatively warm water to reduce heat loss by calves until they have ingested enough milk to increase body weight and synthesize an insulating blubber layer. Sergeant (1980) reported on an approximately 7-month-old toothless calf with a body length of 188 cm and a body weight of 116 kg. The blubber was exceptionally thick (around 10 cm) and blubber plus pectoral fins weighed about 50% of the body weight (Sergeant, pers. comm.). Perhaps in order to enable the mother to take in enough food during the energy demanding suckling period, the beginning of the calving season coincides with the beginning of the summer, the period in which food is probably abundant. This may not be relevant if the mother uses stored fat as a major energy source during suckling.

The decrease in the mother's food intake after the first month following birth is probably due to the calf's growth and the increase in its insulating blubber layer. The decrease seen in the present study may have occurred too early, and the calf may not have suckled enough after the age of 3 months. This could be due either to the nocardium infection itself (Drinnan & Sadleir, 1981), or to an unknown cause which may have made the calf more susceptible to the nocardium infection. In the wild, lactation lasts about 20 months (Brodie, 1971; Sergeant, 1973), so female D3's food consumption for about 3 months post partum cannot be used as a reference for what may occur in lactating females in the wild.

Maximum food intake per feed

Although the same food components are found in stomachs of young and old Belugas of both sexes, the smaller the animal, the smaller the prey size (Seaman *et al.*, 1982; Vladykov, 1946; Kleinenberg *et al.*, 1964). Because Belugas swallow the prey whole, prey size is limited by the size of the Beluga's mouth and esophagus (Fay, 1979).

Based on Cephalopod beaks found in Beluga stomachs, Seaman *et al.* (1982) calculated that Belugas from Point Hope ate encephalopods with an average weight of 205 g. This means that an adult female which eats 12 kg of fish a day would have to eat 58 encephalopods a day. However, this is a very conservative estimate because the caloric value of the fish fed in the present study is higher than that of encephalopods. The largest fish Vladykov (1946) found in a Beluga's stomach was 75 cm long and weighed 4.5 kg. An adult female Beluga would need to eat only 2.5 of such fishes each day to fulfil her energy requirements.

Vladykov (1946) found a forestomach volume of 19 l for a 345 cm long (approximately 600 kg) Beluga. This suggests that Belugas can ingest their annual average daily food requirement in one meal if necessary. The large stomach size may be an adaptation to a larger daily food intake during periods in which food is abundant, so that periods of lesser abundancy can be bridged.

Passage time of food through gastrointestinal tract

The passage time may vary according to the time of day. However, in the present study the carmine red dye was given between 09.30 and 11.10 hrs, so the differences in average passage times between individuals in the present study do not represent different activity levels of the digestive tract due to time of day. Future studies of food passage times should involve larger sample sizes of both sexes, animals of different ages, and the dyes should be given at different times of the day and night.

In spite of the small sample size, this study indicates a passage time in Belugas of about 270 min. For comparison, studies with carmine red dye in the food of Bottlenose dolphins showed an average food passage time of 235 min. (N=8, S.D.=25 min, Saskia Nieuwstraten, pers. comm), and in Commerson's dolphins 87–143 min (Kastelein *et al.*, 1993a). This indicates that wild Belugas may feed often. This may allow them to go through periods of heavy feeding and synthesize fat deposits, which are used during migration or winter when food is limited.

Ecological significance

As far as it is known, the Beluga is the only odontocete which deposits fat reserves in a non-cylindrical way. Most odontocetes simply become robust as they become heavier, whereas Belugas develop in addition fat rolls parallel to their body axis (Fig. 10). Very little is known about what Belugas do during the winter because the weather, drift ice, and darkness make studies very difficult during this season. The Beluga is one of the slowest odontocetes, so its swimming is probably not hindered by the absence of a dorsal fin and the presence of fat rolls. Fat rolls may create too much drag for fast swimming.

The thermal neutral zone or temperature range at which the metabolic rate is the lowest is unknown for Belugas. The relationship between water

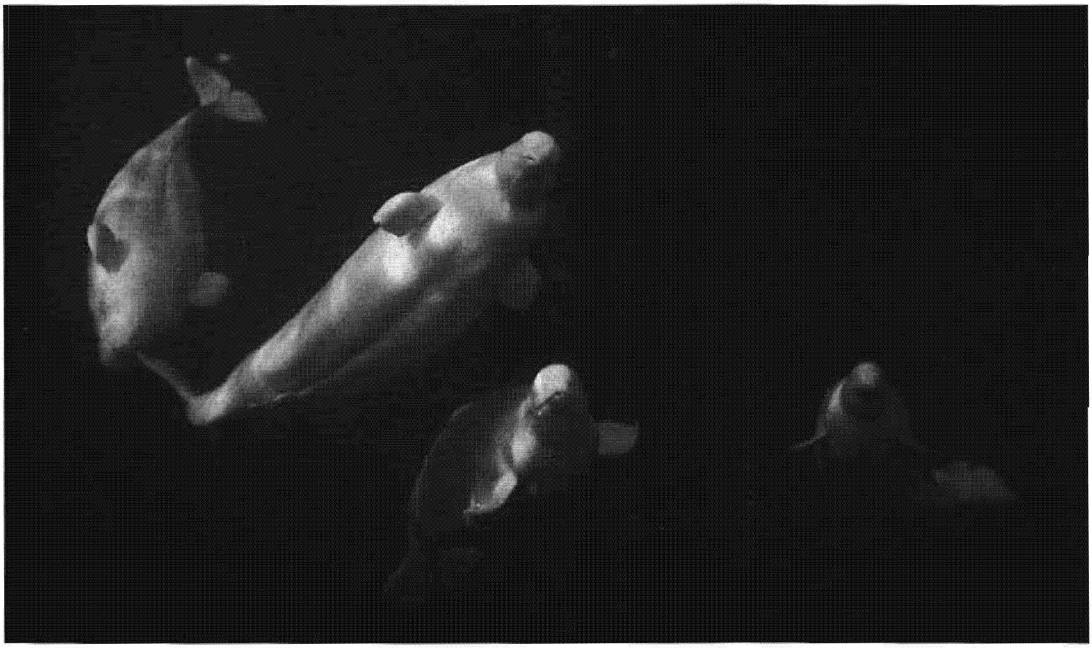

Figure 10. Belugas near Baffin island. Note the lateral rolls of fat, which may allow Belugas to go through periods of reduced food availability (Photo: John Ford).

temperature and food intake for one body size is shown in Fig. 6. It is likely that energy requirements would increase if the water temperature rose above a certain level, so that the animals had to dissipate heat actively to prevent heat stress. To do this, odontocetes circulate more blood through the superficial layers of their fins and flukes (Scholander & Schevill, 1955). If, at higher temperatures, food intake was to increase, the graph of Fig. 6 would be U-shaped (see Bartholomew, 1977). Belugas which were transported from Hawaii to San Diego ate more when kept in the warmer Hawaiian waters than when they were in California (Nachtigall, pers. comm.).

It is impossible to determine whether the food consumption of the animals at the Aquarium was equal to that of free living Belugas of the same sex and age classes. The study animals were in good physical condition during their stay at the Aquarium. They do not have to dive to forage for food like their wild conspecifics, but they do swim almost constantly at a speed comparable to wild Belugas, and exercise during training and performance.

In order to estimate the food intake of a wild Beluga, an estimate of the water temperature is needed. It is difficult to determine average monthly sea water temperatures because the Beluga has a wide circumpolar distribution. In addition the animals dive to deeper, colder, water for significant periods during foraging (Martin & Smith, 1992). Therefore the following estimate is very rough. Sea water temperatures are derived from Sergeant, (pers. comm.) Fraker *et al.* (1979), and KNMI (the Royal Dutch Meteorological Institute) and are shown in Table 3. Extrapolation of the regression line of Fig. 6 towards these temperatures which

Table 3. Typical surface water temperatures in Canadian waters where Belugas occur, and the estimated monthly and annual food intake of a 600–700 kg female Beluga, based on extrapolation of the line in Fig. 6

Month	Water temp. (°C)	Estimated monthly food intake (kg)
January	−1	487
February	−1	440
March	0	477
April	2	442
May	4	437
June	10	363
July	14	335
August	15	322
September	16	303
October	8	397
November	5	411
December	0	477

Annual food intake estimate: 4900 kg

Belugas may encounter in their distribution area produces an annual food consumption estimate for a 600–700 kg female Beluga in the wild of around 4900 kg for food with a caloric density of about 1662 Kcal/kg (Density based on a diet of 75% Herring (1780 Kcal/kg), 15% Mackerel (1587 Kcal/kg) and 10% squid (890 Kcal/kg)). This is around 8.144.000 Kcal/year.

Fig. 6 shows the linear relationship between water temperature and food intake for a 600–700 kg female Beluga in water between 7 and 17°C. For smaller Belugas, the line probably lies lower, and the slope is probably greater. For larger animals, the line probably lies higher, and is more horizontal. In addition to body size, body shape, which is somewhat age dependent according to Kasting *et al.* (1989), will influence food intake.

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References

Andersen, S. (1965) L'alimentation du Masouin (*Phocoena phocoena* L.) en captivité. *Vie et milieu* **16 A,** 799–810.

Bartholomew, G. A. (1977) Body temperature and metabolism. In: *Animal physiology: principles and adaptations* (ed. M. S. Gordon), pp. 364–449. Macmillan, New York.

Bartmann, W. (1974) Some remarks on the behaviour and handling of white whales (*Delphinapterus leucas*) in captivity. *Aquatic Mammals* **2**(1), 16–21.

Bonin, W. & Vladykov, V. D. (1940) La Peau du Marsouin Blanc ou Beluga. *Naturaliste canadien (Rev. Syst Ecologie)* **67,** 1–35.

Braham, H. W., Krogman, B. D. & Carroll, G. M. (1984) Bowhead and white whale migration, distribution and abundance in the Bering, Chukchi and Beaufort seas, 19775-78. NOAA Tech. Rept. NMFS SSRF-778, 39 pp. U.S. Dept. of Commerce, National Oceanic and Atmospheric Admin., National Marine Fisheries Service.

Braham, H. W. & Krogman B. D. (1977) Population biology of the bowhead (*Balaena mysticetus*) and beluga (*Delphinapterus leucas*) whale in the Bering, Chukchi and Beaufort Seas. Processed Report, U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northwest Alaska Fisheries Center, National Marine Mammal Laboratory, Seattle, Washington, 29 p.

Brodie, P. F. (1971) A reconsideration of aspects of growth, reproduction, and behavior of the white whale (*Delphinapterus leucas*), with reference to the Cumberland Sound, Baffin Island, population. *J. Fish. Res. Bd. Canada* **28,** 1309–1318.

Brodie, P. F. (1982) The Beluga (*Delphinapterus leucas*); growth at age based on a captive specimen and a discussion of factors affecting natural mortality estimates. *Rep. Int. Whal. Commn.* **32,** 445–447.

Dhindsa, D. S., Metcalfe, J., Hoversland, A. S. & Hartman, R. A. (1974) Comparative studies of the respiratory functions of mammalian blood X. Killer whale (*Orcinus orca Linnaeus*) and Beluga whale (*Delphinapterus leucas*) *Respiration Physiology* **26,** 93–103.

Doidge, D. W. (1990a) Age-length and length-weight comparisons in the beluga (*Delphinapterus leucas*), pp. 59–69. In *Advances in research on the beluga whale (Delphinapterus leucas)* (eds T. G. Smith, D. J. St. Aubin & J. R. Geraci) *Can. Bull. Fish. Aquat. Sci.* **224,** 59–68.

Doidge, D. W. (1990b) Integumentary heat loss and blubber distribution in the beluga (*Delphinapterus leucas*), with comparisons to the narwhal (*Monodon monoceros*), pp. 129–140. In *Advances in research on the beluga whale (Delphinapterus leucas)* (eds T. G. Smith, D. J. St. Aubin & J. R. Geraci) *Can. Bull. Fish. Aquat. Sci.* **224,** 129–140.

Drinnan, R. L. & Sadleir R. M. F. S. (1981) The suckling behavior of a captive Beluga (*Delphinapterus leucas*) calf. *Applied Animal Ethology* **7,** 179–185.

Fay, F. H. (1979) Belukha Whale. 'Whalewatcher'. *J. Amer. Cetacean Soc. Vol. 13,* **1,** 4–6.

Finley, K. J., Miller, G. W., Allard, M., Davis, R. A. & Evans, C. R. (1982) The belugas (*Delphinapterus leucas*) of northern Quebec: Distribution, Abundance, Stock identity, Catch history and Management. Can. Techn. Rept. of Fisheries and Quatic Scis., no. 1123, 57 pp.

Fraker, M. A., Gordon, C. D., McDonald, J. W., Ford, J. K. B. & Cambers, G. (1979) White whale (*Delphinapterus leucas*) distribution and abundance and the relationship to physical and chemical characteristics of the Mackenzie Estuary. Fish. and Mar. Serv. tech. rep. No. 863. 56 p.

Fraker, M. A. & Fraker, P. N. (1979) The 1979 whale monitoring program Mackenzie Estuary. For Esso Resources Canada Ltd. Edmonton, Alberta.

Fraker, M. A., Sergeant, D. E. & Hoek, W. (1978) Bowhead and white whales in the southern Beaufort Sea. Beaufort Sea Project Tech. Rep. No. 4, Department of Fisheries and the Environment, Victoria, B.C. 128 p.

Goren, A. D., Brodie, P. F., Spotte, S., Ray, G. C., Kaufman, H. W., Gwynnett, A. W., Sciubba, J. J. & Buck, J. D. (1987) Growth layer groups (GLG's) in the teeth of an adult beluka whale (*Delphinapterus leucas*) of known age. Evidence for two annual layers. *Mar. Mamm. Sci.* **3**(1), 14–21.

Hewlett, S. I. (1978) A New whale song: Pretty Baby. *Animal Kingdom* **81**(2), 1527.

Kastelein, R. A. & Vaughan N. (1989) Food consumption, body measurements and weight changes of a female Killer whale (*Orcinus orca*) *Aquatic Mammals* **15**(1), 18–21.

Kastelein, R. A., Bakker M. J. & Dokter, T. (1990) The medical treatment of 3 stranded Harbour porpoises (*Phocoena phocoena*) *Aquatic Mammals*, **15**(4), 181–202.

Kastelein, R. A., McBain, J., Neurohr, B., Mohri, M., Saijo, S., Wakabayashi, I. & Wiepkema, P. R. (1993b) The food consumption of Commerson's dolphins (*Cephalorhynchus commersonii*) *Aquatic Mammals* **19**(2), 99–121.

Kastelein, R. A., McBain, J. & Neurohr, B. (1993a) Information on the biology of Commerson's dolphins (*Cephalorhynchus commersonii*) *Aquatic Mammals* **19**(1), 13–19.

Kasting, N. W., Adderley, S. A. L., Safford, T. & Hewlett, K. G. (1989) Thermoregulation in Beluga (*Delphinapterus leucas*) and Killer (*Orcinus orca*) Whales. *Physiological biology* **62**(3), 687–701.

Kingsley, M. (1993) The programme to increase our knowledge of the St. Lawrence beluga. *Beluga* **4**(1), 1–2. Fisheries and Oceans Canada, Quebec Region, 901 Cap Diamant, P.O. Box 15500 Quebec, G1K 7Y7 Canada.

Kleinenberg, S. E., Yablokov, A. V., Bel'kovich V. M., and Tarasevich, M. N. (1964) Belukha (the white whale) Moscow. Publ. House Nauka. 456 p.

Martin, A. R. & Smith T. G. (1992) Deep diving in wild, free-ranging beluga whales, *Delphinapterus leucas. Can. J. Fish. Aquat. Sci.* **49**, 462–466.

Ridgway, S. H. (1972) Homeostasis in the aquatic environment. In *Mammals of the sea* (ed. S. Ridgway), Thomas publisher, Springfield, Illinois, 590–731.

Ridgway, S. H., Reddy, M., Kamolnick, T., Skaar, D. & Curry, C. (1991) Calorie consumption of growing, adult, pregnant, and lactating *Tursiops*. Presented at the IMATA conference in Vallejo, California.

Ridgway, S. H., Bowers, C. A., Miller, D., Schultz M. L., Jacobs, C. A. & Dooley, C. A. (1984) Diving and blood oxygen in the white whale. *Can. J. Zool.* **62**, 2349–2351.

Ross, W. G. (1974) Distribution, migration and depletion of bowhead whales in Hudson Bay, 1860 to 1915. *Arctic and Alpine Research* **6**(1), 85–98.

Scholander, P. F. & Schevill, W. E. (1955) Counter current heat exchange in the fins of whales. *J. Applied Physiol.* **8**, 279.

Seaman, G. A., Lowry, L. F. & Frost, K. J. (1982) Foods of Belukha Whales (*Delphinapterus leucas*) in Western Alaska. Cetology, 44 p.

Seaman, G. & Burns, J. J. (1981) The distribution, natural history, and utilization of belukha whales (*Delphinapterus leucas*) in Alaska. Unpublished.

Sergeant, D. E. (1969) Feeding rates of cetacea. *Fisk. Dir. Skr. Ser. HavUnders.*, **15**, 246–258.

Sergeant, D. E. (1973) Biology of white whales (*Delphinapterus leucas*) in western Hudson Bay. *J. Fish. Res. Board Can.* **30**, 1065–1090.

Sergeant, D. E. (1986) Present status of white whales (*Delphinapterus leucas*) in the St. Lawrence estuary. *Naturaliste can. (Rev. Ecol. Syst.)* **113**, 61–81.

Sergeant, D. E. (1980) Levels of mercury and organochlorine residues in tissues of sea mammals from the St. Lawrence estuary. Int. Council Explor. Sea CM 1980/E.55. MS 10 pp. Copenhagen.

Sergeant, D. E. (1988) An update of the status of white whales (*Delphinapterus leucas*) in the Saint Lawrence estuary, Canada. *Biological Conservation* **45**, 287–302.

Sergeant, D. E. & Hoek, W. (1974) Seasonal distribution of bowhead and white whales in the eastern Beaufort Sea. In *The Coast and Shelf of the Beaufort Sea* (eds J. C. Read & J. E. Sater), pp. 705–719. Arctic Inst. of N. America.

Sergeant, D. E. & Brodie, P. F. (1975) Identity, abundance and present status of populations of white whales (*Delphinapterus leucas*) in North America. *J. Fish. Res. Board Canada* **32**, 1047–1054.

Sergeant, D. E. (1991) Harp seals, Man and Ice. *Can. Special Publ. Fish. Aquatic Scis.* 114, 153 pp.

Sergeant, D. E. & Brodie, P. F. (1969a) Tagging white whales in the Canadian Arctic. *J. Fish. Res. Bd. Canada* **25**, 2201–2205.

Sergeant, D. E. & Brodie, P. F. (1969b) Body size in white whales (*Delphinapterus leucas*) *J. Fish. Res. Bd. Canada* **26**, 2561–2580.

Sergeant, D. E. & Hoek, W. (1973) Whale-watching. *Nature Canada (Ottawa)* **2**, 27–30.

Smith, T. G., St. Aubin, D. J. & Hammill, M. O. (1992) Rubbing behaviour of belugas, *Delphinapterus leucas*, in a high Arctic estuary. *Can. J. Zool.* **70**, 2405–2409.

Spotte, S. & Babus, B. (1980) Does a pregnant dolphin (*Tursiops truncatus*) eat more? *Cetology* **39**, 1–7.

St. Aubin, D. J. & Geraci, J. R. (1989) Adaptive changes in hematologic and plasma chemical constituents in captive Beluga whales, *Delphinapterus leucas. Ca. J. Fish. Aquat. Sci.* **46**, 796–803.

St. Aubin, D. J., Smith, T. G. & Geraci, J. R. (1990) Seasonal epidermal molt in beluga whales, *Delphinapterus leucas. Can. J. Zool.* **68**, 359–367.

Stewart, B. E. & Stewart, R. E. A. (1989) *Delphinapterus leucas. Mammalian Species* **336**, 1–8.

Vladykov, V. D. (1946) Etudes sur les mammifères aquatiques. IV.—Nourriture du Marsouin Blanc ou Béluga (*Delphinapterus leucas*) du fleuve Saint-Laurent. Dept. des pecheries, Québec, 17.

Williams, T. M., Haun, J. E., Friedl, W. A., Hall, R. W. & Bivens, L. W. (1992) Assessing the thermal limits of Bottlenose dolphins: a cooperative study by trainers, scientists, and animals. *IMATA Soundings*, Fall issue, 16–17.

Worthy, G. A. J. (1991) Thermoregulatory implications of the interspecific variations in blubber composition of odontocete cetaceans, 9th Biennial Conf. on the Biol. of Mar. Mammals, Chicago, pg 74.