

The food consumption of Commerson's dolphins (*Cephalorhynchus commersonii*)

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Summary

This study concerns the food consumption of Commerson's dolphins in 5 zoological parks. Adult animals of both sexes eat between 9 and 12% of their body weight per day. Food intake is influenced by many factors such as age, mating activity, lactation, time of year, reproductive status, diet, feeding pattern, water temperature and metabolic rate. Compared to calves of larger odontocetes, newborn Commerson's dolphin calves are large in proportion to adults. Calves approach adult body weight and adult food intake after approximately 2 years. Gestation mildly decreases female food consumption, but lactation causes a great increase in intake. Compared to larger odontocetes, Commerson's dolphins probably need to feed more frequently. Prey availability in the distribution area of this species should therefore be a key parameter in the design of a rational management plan. The annual food intake of an average adult Commerson's dolphin in the Strait of Magellan, South America, is estimated at around 1850 kg of Herring (37×10^5 kcal).

Key words: *Cephalorhynchus commersonii*, energetics, food consumption, reproduction, lactation, *Phocoena phocoena*.

Introduction

The Commerson's dolphin (*Cephalorhynchus commersonii*) is a small black and white dolphin indigenous to the waters around southern Chile, southern Argentina, the Falkland Islands and the Kerguelen Islands (Angot, 1954; Brownell, 1974;

Aguayo, 1975). What little is known about prey species taken by Commerson's dolphins, comes from descriptions of stomach contents (Harmer, 1922; Weber, 1929; Goodall *et al.*, 1988; Bastida *et al.*, 1988), and from Mermoz (1980) who drew conclusions from overlapping distribution of fish species and Commerson's dolphins. Stomach contents showed that Commerson's dolphins are opportunistic coastal feeders. They eat several fish species as well as a variety of invertebrates such as squid, mysid, shrimp, sessile tunicates, annelid worms and isopods. This diet indicates that these dolphins often feed on, or near, the sea floor. Commerson's dolphins have often been observed feeding in or just beyond the breakers, at a distance of 3-5 m from the shore, and in shallow harbours (Mermoz, 1980; Gewalt, 1985, 1990 & 1991; Goodall *et al.*, 1988). Gewalt (1990, 1991) describes feeding sessions near the coast lasting about one hour. He describes the dolphins swimming around in all direction, and herding 12-15 cm sardines (*Sprattus fuegensis*) towards the shore, chasing them up the beach. He observed Commerson's dolphins feeding in the morning, at midday and in the late afternoon, often in the same place.

Apart from anecdotal information on the daily food consumption (Gewalt, 1979; Spotte *et al.*, 1979; Shochi *et al.*, 1982; Joseph *et al.*, 1987; Cornell *et al.*, 1988), little is known about the energy requirements of Commerson's dolphins. This small cetacean's low body mass to surface ratio (see roughly comparable values for harbour porpoises in Andersen, 1981), and its active nature, suggests the likelihood of a high metabolic rate. When food deprived, marine mammals with high metabolic rates may rapidly lose weight and fitness,

due to the high heat conductivity of the water around them (Kanwisher and Sundnes, 1965). This may result in an increased susceptibility to disease. Weight loss in very small cetaceans, as indicated by the appearance of a depression over the cervical spine, may be apparent after as little as one day fasting (Fig. 1 in Boolootian, 1956; Spotte *et al.*, 1979; Gewalt, 1990; Figure 3 in Kastelein and van Battum, 1990).

The size of the Commerson's dolphin population in the Strait of Magellan has been estimated twice (Anonymous, 1987; Leatherwood *et al.*, 1988). Concern over this population was expressed by Goodall and Cameron (1980), because Commerson's dolphins were caught incidentally in *Robalo* (*Eleginops maclovinus*) and *Centolla* (*Lithodes antarctica*) nets and were harpooned for *Centolla* bait. Sightings and strandings suggest that the species has a disjointed distribution (Kastelein, 1984), which may make local populations more vulnerable.

In addition to data on the size of local dolphin populations and their sex ratio and age distribution, information on energy requirements is needed to set up an international conservation plan for Commerson's dolphins. Because energy requirement data are difficult to obtain in the field (Beddington *et al.*, 1985), the daily food consumption of Commerson's dolphins in 5 zoological parks is analysed in the present study. The objective is to assess food intake and the parameters which influence it. Details of growth and food consumption are useful for the management of this species in oceanaria, and perhaps for the conservation of this and other small odontocete species in the wild. For species which are not kept in zoological parks, data on food consumption is difficult to gather. We also provide a brief overview of the history of Commerson's dolphins in oceanaria up until January 1991.

Materials and methods

Sea World of California

Study animals

The age and sex of 14 Commerson's dolphins at Sea World of California, USA are shown in Table 1. The 6 original animals come from the Strait of Magellan, Chile, the others were born at Sea World. The study period was from December 1983 until January 1991.

Study area

The animals are housed in 2 pool systems. Pool system A is covered and consists of a main pool (13 m × 13 m; 3.9 m deep) and an adjacent holding pool (8.5 m × 4.5 m; 1.5 m deep). The dolphins

usually have free access to both pools, except during educational presentations when they are confined to the main pool. During the study period the water temperature varied from 12.8 to 24.4°C. Through an opening in the ceiling the animals are exposed to the natural light cycle. Artificial lights are additionally used during the day. Pool system B consists of an outdoor pool (12 m × 12 m; 3 m deep). By means of an adjoined examination pool (4 m × 8 m; 2.3 m deep) it is connected with pool system C (12 m × 12 m; 3 m deep). These systems are not used for educational presentations. During the study period the water temperature in pool systems B and C ranged from 13.3 to 21.7°C. In 1987 some animals were kept in another pool for 6 months, where the water temperature varied between 9.4 and 11.1°C. The salinity in all pools varied from 3.0 to 3.4% NaCl. Sea World of California is located at 117°14' west longitude and 32°46' north latitude. The average monthly air temperature between 1984 and 1990 varied between 13.9 and 22.4°C.

Pregnant females were housed in pool system B to ensure a calm environment. The males were housed in pool system C beginning about 5 weeks before parturition. Although physically separated, the sexes were able to maintain both visual and acoustic contact with each other.

Feeding

The animals were fed a thawed diet of 95% North Atlantic herring (*Clupea harengus*) and 5% Columbia river smelt (*Thaleichthys pacificus*), based on weight. The amounts fed at each feeding were recorded per animal with an accuracy of 0.1 kg. vitamins were added to this diet daily.

Feeding in pool system A (presentations to the public): Between June and September the animals were fed 10 times a day. Between October and May they were fed 4 times a day on week days and 7 times a day during the weekends. For each animal a daily food base was set. If an animal failed to eat its base amount, or showed a decreased appetite, the base was reduced. If the animal ate the base amount easily, it was increased. The animals were weighed regularly, but appetite was used as the primary indicator of their food requirements. The goal was to keep the animals healthy and looking robust at all times.

Feeding in pool system B (no presentations to the public): The animals were fed 3 to 4 times per day and were allowed all they could eat. At each feeding, fish were given to each dolphin until it started to drop fish. To monitor weight changes the animals were weighed regularly. No obesity was observed. The maximum amount of food ingested per feeding varied from 1.4 to 1.8 kg, depending on the individual.

Table 1. The Commerson's dolphins (*Cephalorhynchus commersonii*) in the present study

Location	Code M=male F=female	Birth date or est. year	Arrival date	Code sire	Code dam	Origin
Sea World	S1M	1978	13-12-83	wild	wild	Chile
Sea World	S2M	1978	13-12-83	wild	wild	Chile
Sea World	S6F	1978	13-12-83	wild	wild	Chile
Sea World	S7F	1978	13-12-83	wild	wild	Chile
Sea World	S3M	1978	13-12-83	wild	wild	Chile
Sea World	S8F	1978	13-12-83	wild	wild	Chile
Sea World	S4M	21-2-85	—	S2M	S8F	Sea World
Sea World	S10F	28-9-88	—	S1M	S6F	Sea World
Sea World	S11F	19-4-86	—	?	S6F	Sea World
Sea World	S5M	10-7-87	—	S1M	S8F	Sea World
Sea World	S9F	10-9-88	—	S1M	S7F	Sea World
Sea World	S12F	1-5-86	—	?	S7F	Sea World
Sea World	S13M	25-5-87	—	?	S7F	Sea World
Sea World	S14M	8-5-90	—	?	S8F	Sea World
Duisburg	D1M	<1974	18-12-78	wild	wild	Argentina
Duisburg	D2M	<1976	09-02-80	wild	wild	Argentina
Duisburg	D3M	<1976	09-02-80	wild	wild	Argentina
Duisburg	D4M	<1980	14-02-84	wild	wild	Chile
Sunshine Int.	U1M*	—	3-1987	wild	wild	Chile
Sunshine Int.	U2M*	—	3-1987	wild	wild	Chile
Sunshine Int.	U3M	—	3-1987	wild	wild	Chile
Sunshine Int.	U4F	—	3-1987	wild	wild	Chile
Sunshine Int.	U5F	—	3-1987	wild	wild	Chile
Matsushima	M3F	—	3-1987	wild	wild	Chile
Matsushima	M1M	—	3-1987	wild	wild	Chile
Matsushima	M4F	—	3-1987	wild	wild	Chile
Matsushima	M5F	—	3-1987	wild	wild	Chile
Matsushima	M2M	—	3-1987	wild	wild	Chile
Matsushima	M6F	1-7-89	—	?	M4F	Matsushima
Toba	T1M	—	3-1987	wild	wild	Chile
Toba	T2M	—	3-1987	wild	wild	Chile
Toba	T3F	—	3-1987	wild	wild	Chile

*Moved to Osaka Aquarium in June 1990.

Duisburg Zoo

Study animals

The sex and estimated age of 4 Commerson's dolphins at Duisburg Zoo are shown in Table 1. One animal came from the bay of San Jorge between Comodoro Rivadavia and Puerto Deseado Argentina, 2 from Bahía Grande, Argentina, and 1 from the Strait of Magellan, Chile. The study period was from January 1979 until January 1991.

Study area

The outdoor pool complex consists of a main pool (12 m × 15 m; 4.3 m deep) and 2 adjacent holding

pools (each 5.3 m × 3.0 m; 4.3 m deep). The animals usually have access to all 3 pools. Part of the pool complex is covered by a sheet of canvas as a roof. The Commerson's dolphins are housed with (1,1) Beluga whales (*Delphinapterus leucas*). During the study period the water temperature varied from 6 to 12°C (the pool has chilling facilities), the salinity varied from 2.5 to 3.0‰ NaCl. The air temperature varied from 14.9 to 37.2°C. Duisburg Zoo is located at 6°45' east longitude and 51°25' north latitude.

Feeding

The animals were fed 4 to 5 times per day. Once in the early morning, during 2 (November to

February) or 3 (March to October) midday presentations, and once during the late afternoon. The thawed diet consisted on average of 30% Squid (*Illex spp.*) or Whiting (*Merlangius merlangus*) and 70% Herring (*Clupea harengus*) and Sprat (*Sprattus sprattus*) or Mackerel (*Scomber scombrus*) and Sprat (*Sprattus sprattus*), according to the animal's preference. The percentages are based on weight, and rations per feeding per animal were weighed with an accuracy of 0.1 kg. Vitamins were added to this diet daily. The animals were always fed to saturation. The quantity of food offered was never influenced by the behaviour in the presentations. The dolphins did not seem to want more than 1 kg per meal, therefore the maximum per feeding was set to 0.8 kg. If the animals needed more food per day, an extra feeding was given.

Sunshine International Aquarium

Study animals

The arrival dates and sex of the 5 Commerson's dolphins at Sunshine International Aquarium, Tokyo, Japan are shown in Table 1. The animals were originally from the Strait of Magellan, Chile. The study period was from March 1987 until January 1991. Two animals (U1M and U2M) were sent to Osaka Aquarium in June 1990, where the average water temperature in the second half of 1990 was 14.6°C.

Study area

The animals are housed in an indoor pool system, consisting of a main pool and an adjacent hospital pool (total surface area 64.7 m²; 1.9 m deep; volume: 123 m³). They had access to both pools unless medical examination was taking place in the hospital pool. The animals were used for educational display only. During the study period the average monthly water temperature varied between 10.9 and 11.9°C, the salinity from 3.4 to 3.5‰ NaCl. The average monthly air temperature varied between 13.5 and 15.7°C. Through a window in the ceiling the animals were exposed to the outdoor light cycle. Sunshine International Aquarium is located at 139°43' east longitude and 36°44' north latitude.

Feeding

The dolphins were fed a thawed diet of 50% Mackerel (*Scomber japonicus*) and 50% Toothed Smelt (*Osmerus eperlanus mordax*), based on weight. Vitamins were added to this diet daily. The animals were fed three times a day until April 1990, after which a fourth daily feeding was introduced. This was initially done because the food intake of a pregnant dolphin was irregular, and later became

the norm. Each animal's daily food base was set at 10% of its body weight. If the animal ate its base amount easily or its weight decreased, the base was adjusted upwards.

Matsushima Aquarium

Study animals

The arrival dates and sex of 6 Commerson's dolphins at Matsushima Aquarium, Miyagi, Japan are shown in Table 1. The original 5 animals come from the Strait of Magellan, Chile, another was born at Matsushima Aquarium, so its age is known. The study period was from March 1987 until January 1991.

Study area

The animals are usually kept in a main indoor pool (octagonal; 9.6 m diameter; 3.7 m deep). A month before expected parturition (1989), the males were housed separately in a round indoor pool (diameter: 6 m; 3.7 m deep). During the study period the water temperature in the main pool was between 7.9 and 20.0°C, and the air temperature varied from 9.0 to 27.1°C. The salinity of the natural sea water was around 3‰. Through a window in the ceiling the animals were exposed to the outdoor light cycle. In addition artificial lights were used. Matsushima Aquarium is located at 141°49' east longitude and 38°21' north latitude.

Feeding

The animals were fed 3 times a day a thawed diet of North Pacific herring (*Clupea pallasii*) from March 1987 to 9 February 1988, and Chub mackerel (*Scomber japonicus*) after 9 February 1988. Vitamins were added to this diet daily. The animals were always allowed to eat as much as they wanted.

Toba Aquarium

Study animals

The arrival dates and sex of 3 Commerson's dolphins at Toba Aquarium, Mie, Japan are shown in Table 1. They originate from the Strait of Magellan, Chile. The study period was from March 1987 until January 1991.

Study area

The animals were kept in an indoor pool (9.0 m × 8.8 m; 5.4 m deep). During the study period the water temperature varied from 9.8 to 13.2°C. The air temperature was between 6.2 and 23.8°C. The pool contained natural sea water with a salinity of around 3‰. Daylight could enter the pool area indirectly through windows in the wall,

and artificial light was also used. Toba Aquarium is located at 136°50' east longitude and 34°29' north latitude.

Feeding

The animals were fed 3 times a day on a thawed diet of 100% White-tipped mackerel scad (*Decapterus maruadsi*) until June 1990, and 70% Yellowfin horse mackerel (*Trachurus japonicus*) and 30% White-tipped mackerel scad thereafter. Vitamins were added to this diet daily. The animals were always allowed to eat as much as they wanted.

Analysis units

The food intake data available in the present study was the amount of food per animal per day. From this information, monthly and annual food intake were calculated, which are the basic measures used for the analysis here.

Results

Although slightly different feeding schedules and feeding methods were used in the 5 parks, the animals were in general allowed to eat *ad libitum*, therefore it might be useful to compare the food intake between parks, and study the effects of several environmental and biological parameters on food intake.

Influences of age and sex on body weight and food consumption

The annual food consumption and body weights of Commerson's dolphins and the average annual pool water and air temperatures at Sea World of California are shown in Figure 1, at Duisburg Zoo in Figure 2, at Sunshine Aquarium in Figure 3, at Matsushima Aquarium in Figure 4, and at Toba Aquarium in Figure 5. Many of the animals (the males at Sea World, all animals at Matsushima and Toba Aquarium) increased their food intake during the first year(s) of captivity. The acclimation process may have contributed to the low initial food intake. In addition, some of the animals were still growing.

It is believed that catching a newborn cetacean to take body measurements may be lethal, so that body measurements are only available for 1 full-term Commerson's dolphin calf, which died shortly after birth at Sea World. It was 91 cm long, and weighed 8.8 kg. At Sea World, where the ages of the animals are best known, both sexes grew fast, reaching almost adult weights after about 2 years (Fig. 6). There was no clear difference in body weights of adult males (range 36–43 kg) and non-pregnant adult females (range 37–41 kg). Female body weight increased during pregnancy. The gestation period of Commerson's dolphins

based on 8 cases is 345 ± 20 days (Asper *et al.*, 1992). Six months after successful copulation, females weighed an average of 10.8 kg (S.D. = 1.9 kg, $N=4$) more than during non-pregnant periods. For health reasons, females in the present study were usually not weighed during the second part of the gestation period, except for female (S7F) which was weighed 4 months prior to delivery; she then weighed about 15 kg more than she had prior to pregnancy.

During their first full calendar year, the solid food intake of Sea World dolphin calves averaged between 6 and 10% of their body weight per day. The range is due in part to the different birth dates and to variations in the length of the suckling period. Thereafter the proportional food intake increased to around 11% at the age of 5 years. Males and non-pregnant, non-lactating females over 5 years of age consumed between 9 and 13% of their body weight per day.

The animals from the other 4 parks were all, except one, of unknown age. No sexual dimorphism in body weight could be detected when animals from all 4 parks were pooled. Male body weight was between 29 and 54 kg, while the non-pregnant female weight varied between 32 and 53 kg. Males ate between 8.1% to 13.5% of their body mass per day, and non-pregnant non-lactating females between 7.5 to 13.1%.

Perinatal changes

The food intake pattern prior to birth, during the lactation period and after weaning could be studied in 6 cases (Fig. 7). Pregnant females showed a progressive increase in weight (Fig. 1F, G, H), associated with increasing girth (Fig. 8). In all 6 cases, the total food intake during the 12 month gestation period was not higher than during non-pregnant, non-lactation 12 months periods (Table 2). In fact, they ate a little less when pregnant than when not pregnant. All 4 pregnant females maintained normal food intake until 1 or 2 days before parturition, when it decreased slightly. On the day of birth their appetites were poor.

During its first 4 days, calf S4M suckled about every 40 minutes with an average of 8 attachments, each lasting on average 5.5 seconds. The time that the calves were fully dependent on milk varied from 73 to 236 days (Kastelein *et al.*, 1993). The increase in solid food intake was gradual in all cases; they continued to suckle several times per day for some months. During the suckling period, when the calf was fully dependent on milk, the mothers' daily food consumption was on average about 30% higher than in the same periods of other years, when they were not pregnant or non-lactating (Table 3).

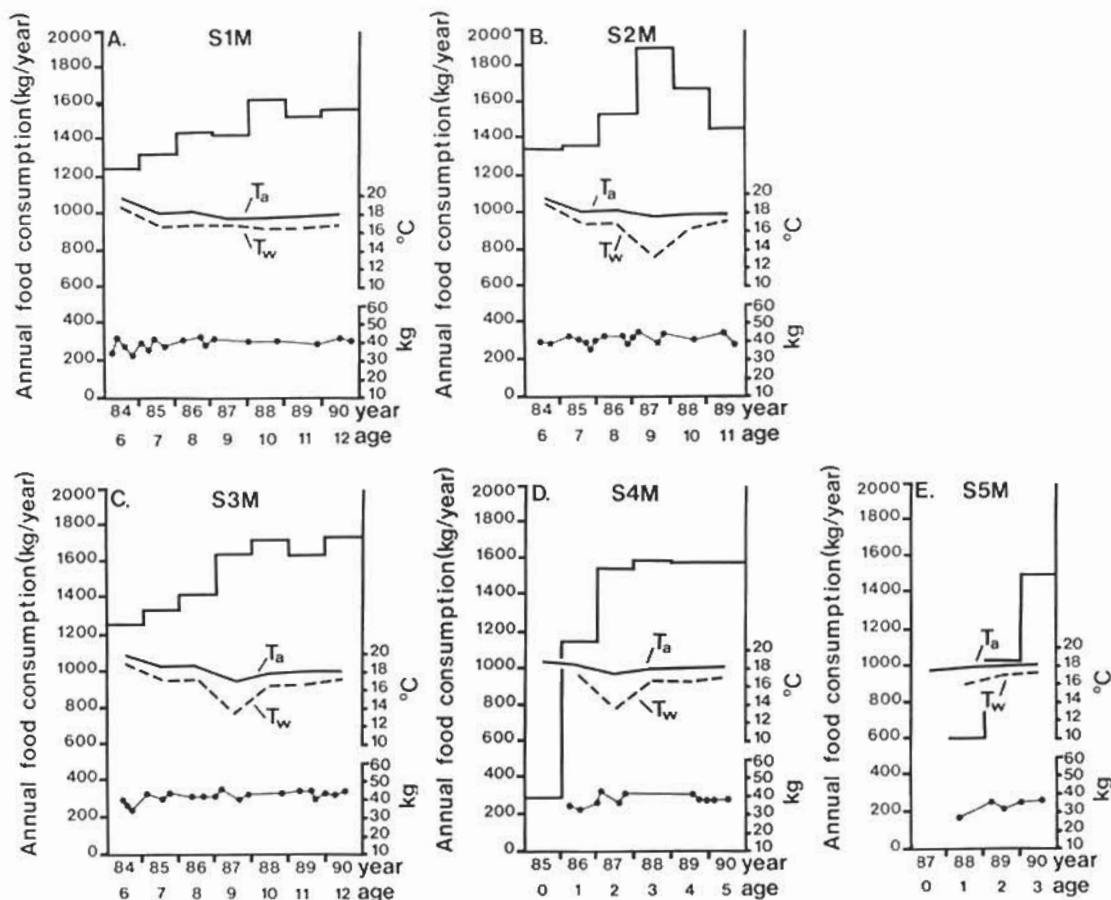


Figure 1. A-E.

Post partum, the monthly food intake of most females increased, peaking approximately 2 months after birth. Then, the food intake slowly decreased to a minimum at around the time the calves started to eat fish in addition to suckling (Fig. 7A, B, C, E, & F). After this, food consumption increased a little until it stabilized. An exception was female S8F, whose food intake increased dramatically (Fig. 7D) or remained high (Fig. 7E) after her calf started to eat fish.

Seasonal changes

Seasonal food intake changes can result from, among other things, reproductive cycles and variations in water temperature. In the present study, air and water temperatures fluctuated simultaneously, except in facilities which cooled the water. The air temperature is assumed to be of less significance than the water temperature because water conducts heat 25 times better than air (Kanwisher and Sundnes, 1965) and the animals

are below the surface most of the time. Only the dominant effect of the water temperature on food intake will be described here.

In parks with seasonal peaks in pool water temperatures (Duisburg Zoo, Sea World and Matsushima Aquarium; Fig. 9A, B and D), adult dolphins ate less in the warmer months. In parks with fairly constant water temperatures (Sunshine Aquarium and Toba Aquarium, Fig. 9C and E), individual animals showed seasonal variations, but these were not consistent between years.

Fish of the same species can have different nutritional or caloric values depending on the season and geographical area in which they were caught. The fish fed in each of the parks in the present study were caught in different seasons, quantities, areas, and sometimes stored for several months. It is probable, that seasonal or regional differences in fish caloric value of the fish cancelled each other out over the years, and did not

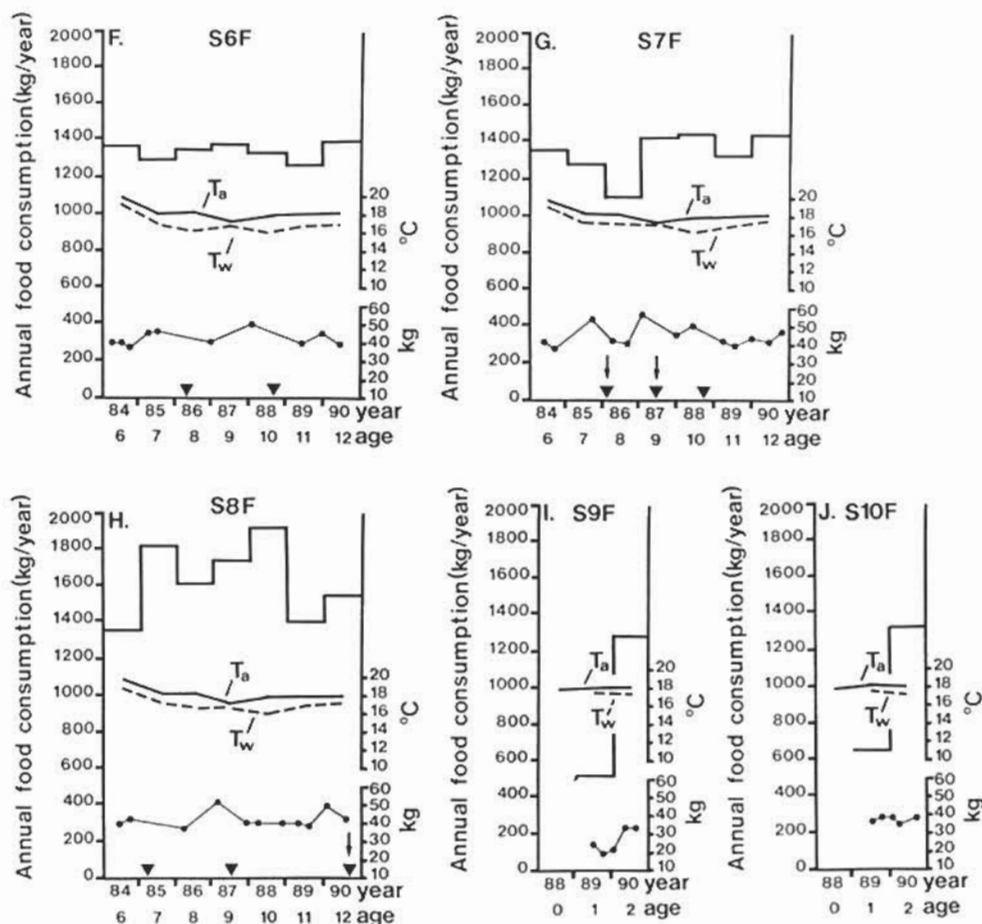


Figure 1. F-J.

Figure 1. A-J. The annual food intake and body weight of Commerson's dolphins and the average annual water (T_w) and air (T_a) temperature at Sea World of California. A triangle indicates a year in which a birth took place. An arrow above a triangle means that the calf did not suckle. Age 1 represents the first calendar year after the year of birth. The low average water temperature in 1987, was due to the temporary transport of S2M, S3M and S4M to another pool with a low water temperature.

lead to an artificial annual fluctuation in food consumption.

When the annual proportional food consumption data of all animals and the average annual water temperature per park are pooled, no correlation between proportional food consumption and average water temperature can be seen (Table 4). The absence of such an overall connection is surprising, but may simply result from combining divergent data over too long a period. The same relationship was calculated for a more homogenous group of animals that were followed over many years consistently. The animals involved are the four males from Sea World (S1M, S2M, S3M and S4M). Average water temperature

per month and total food intake for that month and per animal have been plotted in Figure 10. The data show a significant negative correlation (Pearson correl. coeff.: $R = -0.334$, $P < 0.0001$, $N = 295$), indicating the effect of ambient water temperature on food intake.

On days of great sexual activity, the males at Sea World ate less than normal, or nothing at all. However, they compensated for this reduction in food intake during the other days of the month, so that no changes could be detected in their total monthly food consumption data. About 11.5 months prior to delivering a calf, each female copulated repeatedly on 1 day. Food intake was 20 to 50% less than on days around the copulation

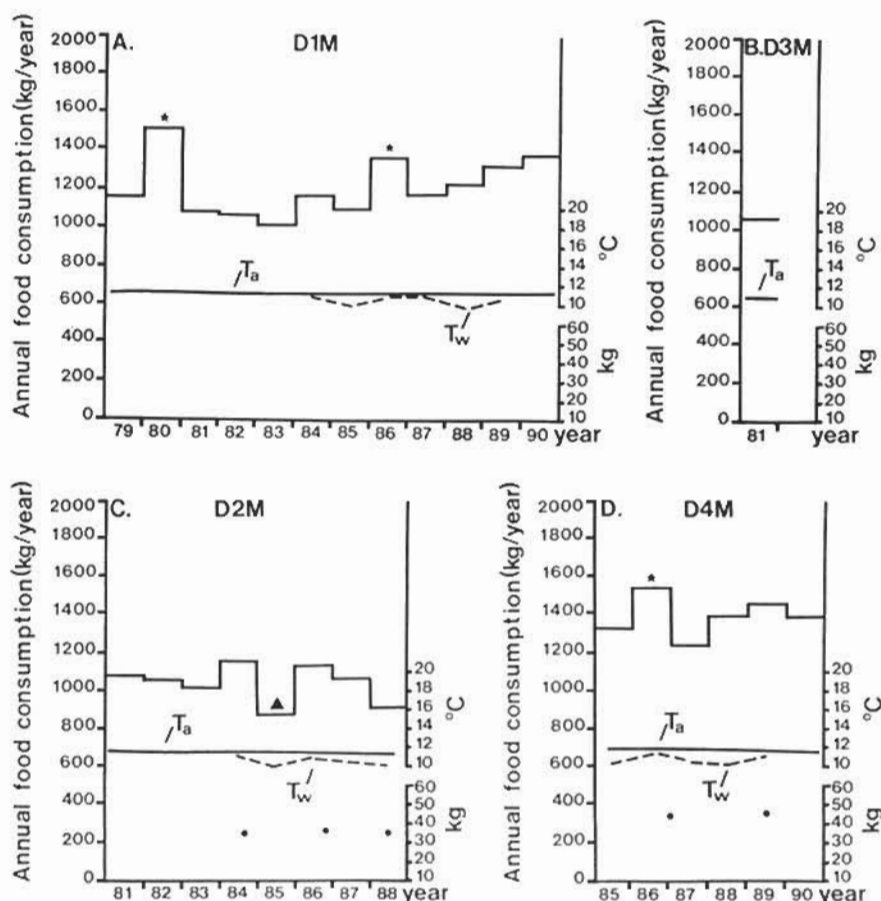


Figure 2. A–D. The annual food intake and only a few body weights of Commerson's dolphins and the average annual water (T_w) and air (T_a) temperatures at Duisburg Zoo. T_w is only available for years after 1983. An asterisk indicates high food intake due to large % of squid in the diet. A triangle indicates low food intake due to pneumonia.

day. Whether this reduction in food intake was the result of a hormone-influenced reduction in appetite due to oestrus, or simple business, is not clear.

Discussion and Conclusions

Before making an estimate of the annual amount of food a Commerson's dolphin needs in the wild, it is important to determine the parameters which influence food intake.

Factors influencing food intake

1. Gender

Based on the small sample size of the present study, it seems that there is no significant sexual dimorphism in Commerson's dolphin body weight. This is also reflected in the food consumption; adult

males eat on average as much as non-pregnant, non-lactating adult females. However, Lockyer *et al.* (1988) found in a larger sample that female Commerson's dolphins are on average 4 cm longer than males. In another small cetacean, the Harbour porpoise (*Phocoena phocoena*), females are also larger than males of the same age class (van Utrecht, 1978; Gaskin *et al.*, 1984), but the difference is more pronounced than in Commerson's dolphins.

2. Mating

Seasonal food consumption changes in marine mammals such as pinnipeds are usually related to reproduction and moulting (Kastelein *et al.*, 1990 a, b, & c; Kastelein *et al.*, 1991), which is often correlated with annual cycles of food availability. If food intake is influenced by reproduction,

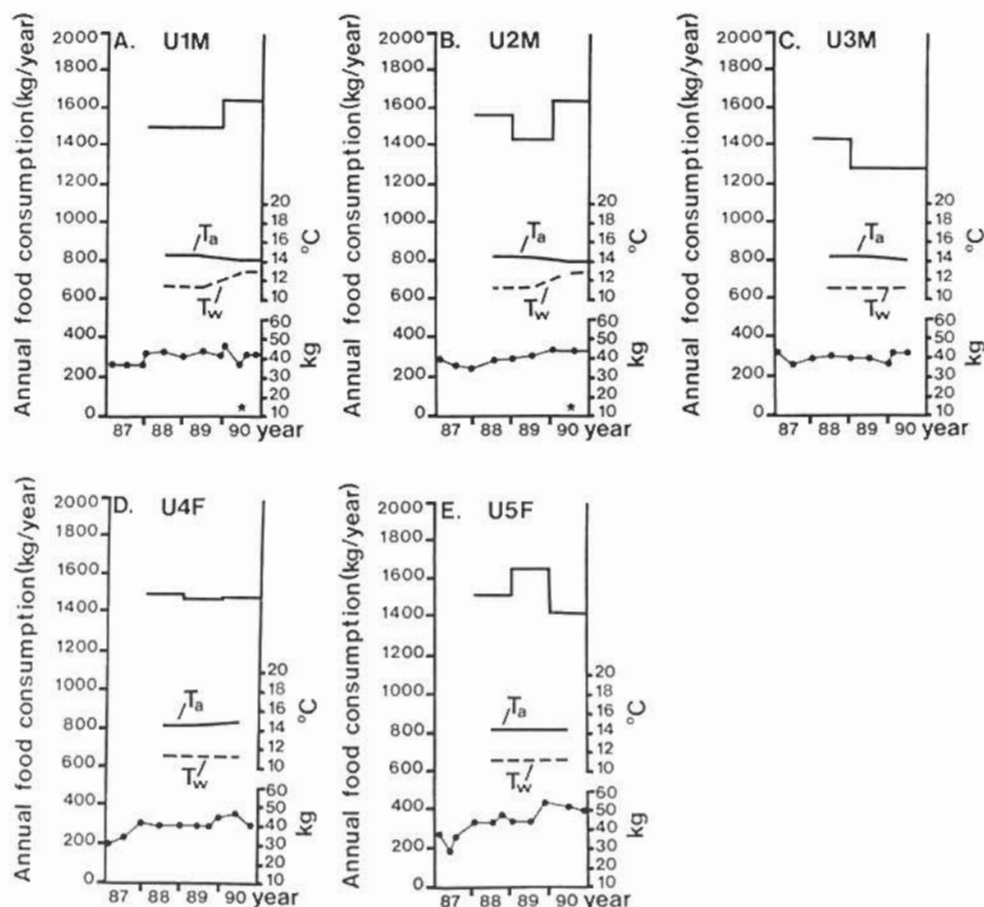


Figure 3. A-E. The annual food intake and body weight of Commerson's dolphins and the average annual water (T_w) and air (T_a) temperatures at Sunshine International Aquarium. An asterisk indicates the year in which the animal was transported to Osaka Aquarium in July.

fluctuations usually only occur after an animal reaches sexual maturity when sex hormones are produced in annual cycles. Strong reproduction-linked annual cycles in food consumption were not found in the present study, except in females during lactation. Only a one day oestrus-linked reduction in food intake was detected in the females. The males ate little or nothing for only a few days during the mating season.

3. Gestation and lactation

The females' food consumption did not increase during pregnancy. This could be explained by the fact that although a dam needs extra energy for foetal growth, her body weight increases because of the growth of the foetus, placenta and amnion fluid, thus increasing her body mass to surface ratio. The increase in body size, especially girth, is clearly shown in Figure 8. The pregnant female

therefore loses less heat by conduction and radiation through her skin. Energy expenditure for foetus growth and energy savings by decreased heat loss may be in balance. Maybe the blubber layer also thickens during gestation, providing extra insulation, and an energy source for use during lactation.

Immediately after giving birth, the dams' food consumption increased dramatically because of lactation costs (Fig. 11). After birth, the female has to provide 2 bodies with energy, and the heat conducting surface area is greatly increased (Fig. 12). Calves have a very unfavourable body weight to surface ratio at birth (body weight is about 22% of an adult animal, and the body surface around 50%). The last figure comes from a study on Harbour porpoises by Andersen (1981). The gradual decrease in a dam's food consumption after the second month post partum may be related to

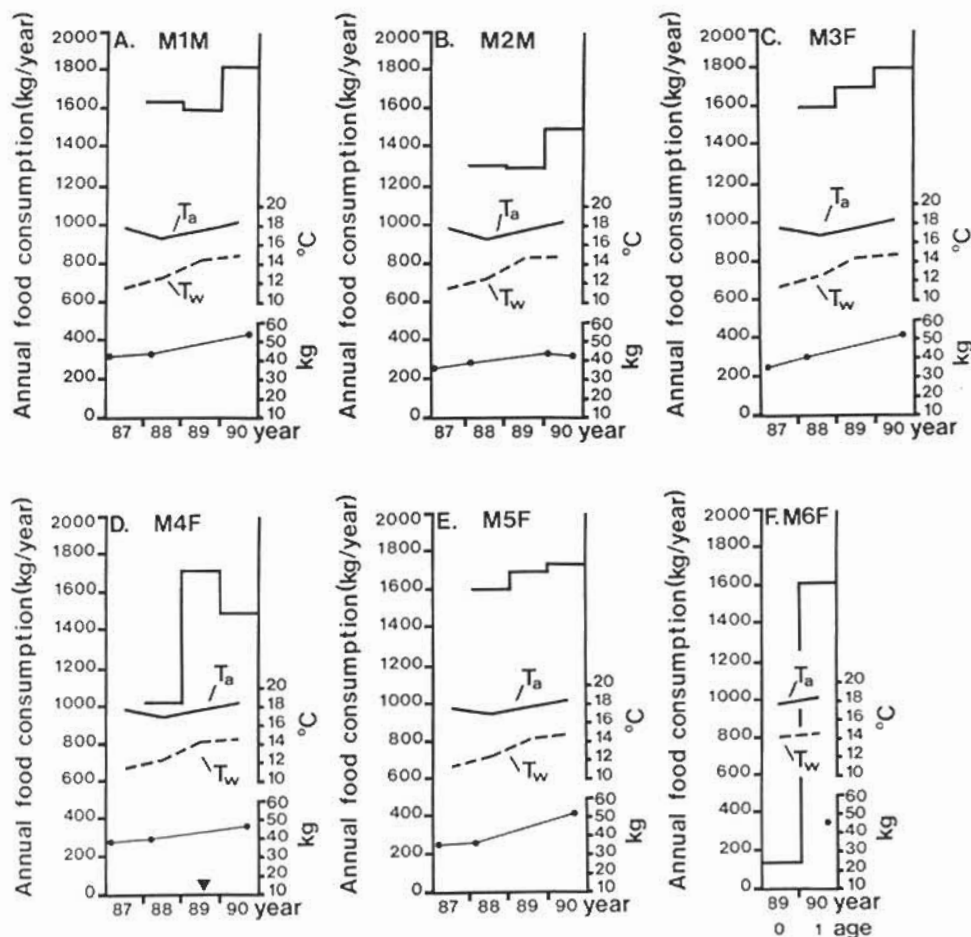


Figure 4. A–F. The annual food intake and body weight of Commerson's dolphins and the average annual water (T_w) and air (T_a) temperatures at Matsushima Aquarium. A triangle indicates a year in which a birth took place.

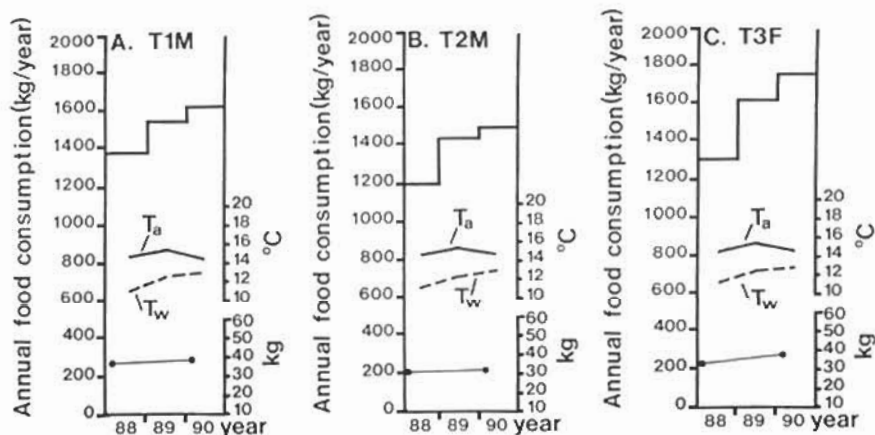


Figure 5. A–C. The annual food intake and body weight of Commerson's dolphins and the average annual water (T_w) and air (T_a) temperatures at Toba Aquarium.

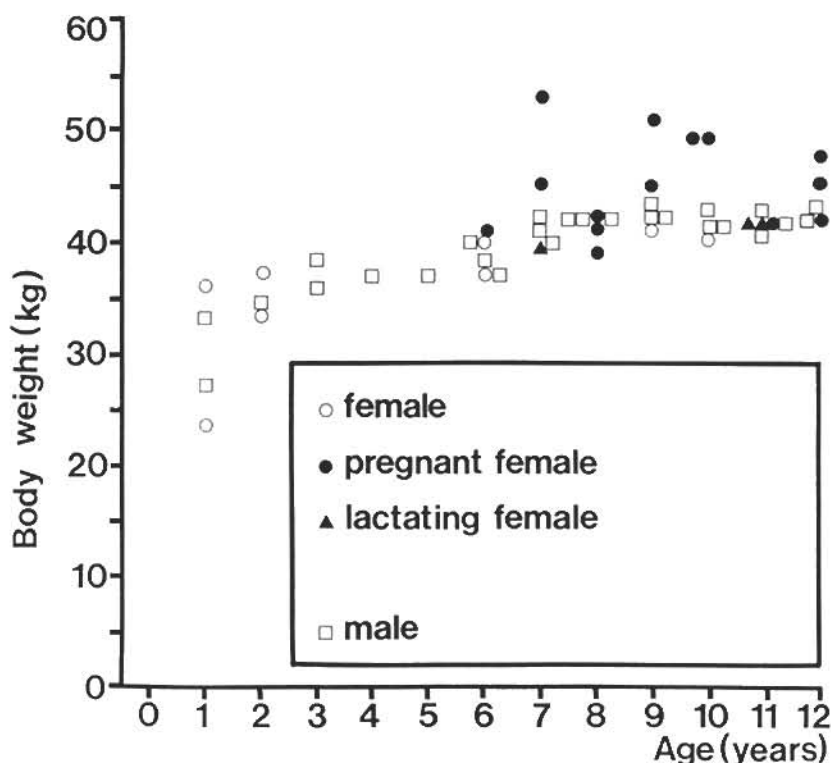


Figure 6. The body weight of Commerson's dolphin males and females (in different reproductive stages) at Sea World of California related to age. Age 1 represents the first calendar year after the year of birth.

reduced energy needs of the calf, which by then has reached a more favourable body weight to surface ratio. The body composition of the calf also changes over time; the insulating blubber layer becomes thicker, reducing heat conduction. The strong increase in the females' food consumption during the first stage of lactation may for a small part be due to increased energetic investment in swimming. During the first week after giving birth, female Commerson's dolphins usually swim a great deal and 'pull' their calves with them in a slip stream reducing the calves' energy expenditure on locomotion and allowing for a larger part of the milk to be used for growth. The stomach contents of Harbour porpoises in the wild showed that lactating females ingested more fish and had a significantly higher caloric intake than non-lactating females or mature males (Recchia and Read, 1989). As a comparison, for six months following parturition, lactating Bottlenose dolphin females (*Tursiops truncatus*) may consume 129 to 204% more energy than before they became pregnant (Ridgway *et al.*, 1991).

The mother's low food intake in the month the calves started to eat fish may be linked to a decrease in mammary gland activity due to a decrease in milk demand. Generally, dolphins lactate as long as the calf nurses. When the suckling frequency decreases, hormones probably reduce the mother's milk production. This may also affect the calf's and mother's feeding behaviour. The quality of the milk probably also changes during the lactation period, as is observed in killer whales, *Orcinus orca*. Whether the suckling behaviour of the calf influences the milk composition or vice versa is unknown. Although calves continue suckling after they have started to eat fish, the decrease in the mother's food consumption after this moment suggests that little or no milk is transferred during these suckling bouts and/or that the milk has a low caloric density. Maybe the calf performs this suckling behaviour mainly to maintain a bond with its mother.

Several parameters, such as water temperature, activity level, fitness and current body weight, could influence the dam's food consumption after

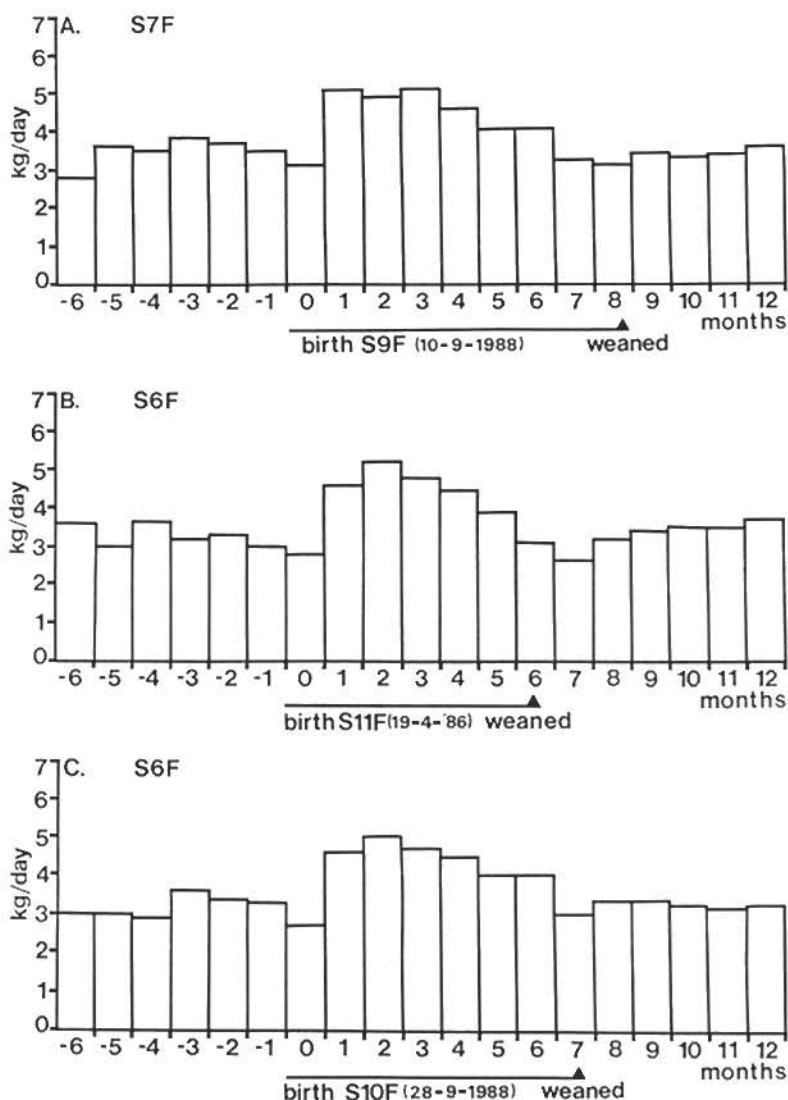


Figure 7. A, B and C.

weaning. Her intake during the suckling period could have been sufficient for milk production, so that no use was made of her fat reserves. After weaning, she would not need extra energy to compensate for weight loss (Fig. 7A, B & C). Alternatively, the dam's food consumption during the suckling period may not have been sufficient to produce enough milk, so that she had to use part of her energy reserves. After weaning she would need to replenish her fat (Fig. 7D, E & F). Female S8F did not increase her food intake much during S4M's suckling period in 1985. This might explain

why her food intake increased drastically after weaning (Figs. 1H & 7D).

4. Diet

The diet can influence food intake in at least 3 ways: palatability, caloric density, and bio-availability.

(a) *Palatability.* Food offered can be more or less attractive to the animals. An increase in food consumption at Matsushima Aquarium in October 1987 coincided with a new supply of smaller,

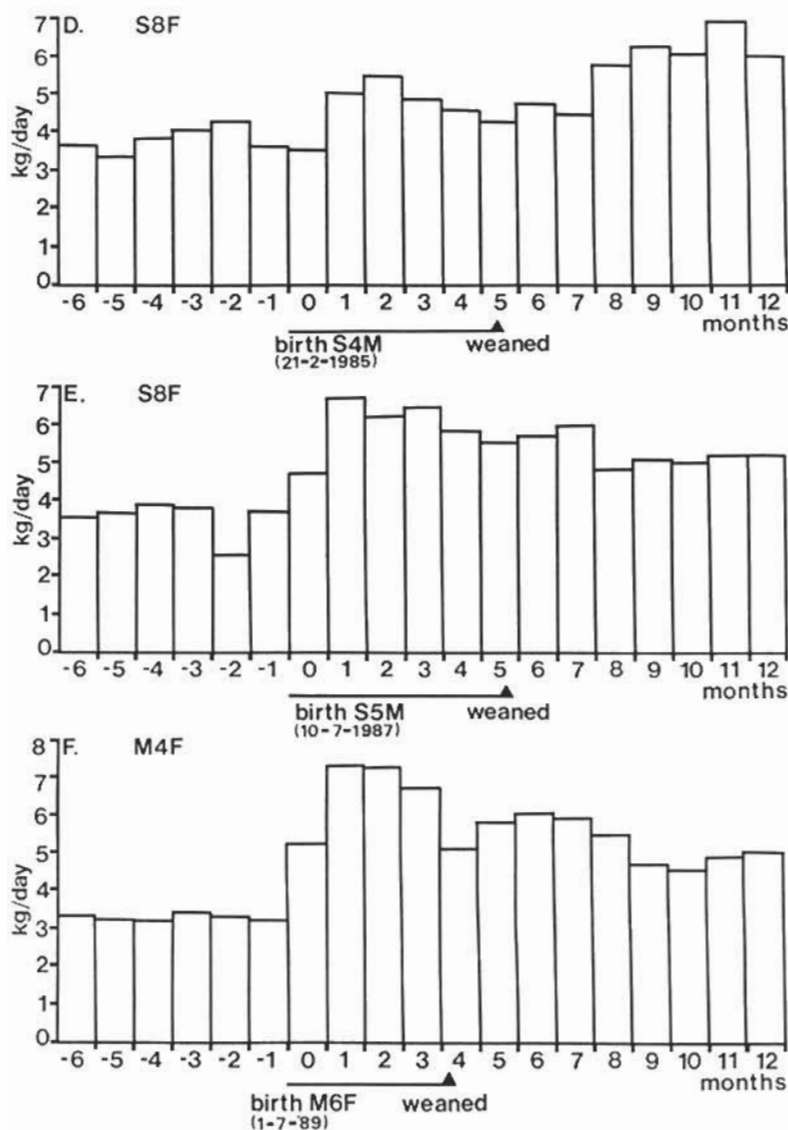


Figure 7. D, E, and F.

Figure 7. A-F The monthly food consumption of females S6F, S7F and S8F at Sea World of California, and of female M4F at Matsushima 6 months prior to and 12 months after the delivery of their calves. 0 indicates the month of birth. Weaning here means the moment when the calves started to eat fish, however, they continued to suckle for some months.

fresher fish. A decrease in food consumption in February 1988 at Matsushima Aquarium coincided with a change from Herring to Chub mackerel. Changes in food intake due to the preference for a particular fish species are probably short-term. When animals such as dolphins and pinnipeds

become hungry after some days to a week, they start to eat normal quantities.

(b) *Caloric density* The diet can contain more or less energy per unit weight. Table 4 shows that the relatively small animals at Duisburg Zoo ate

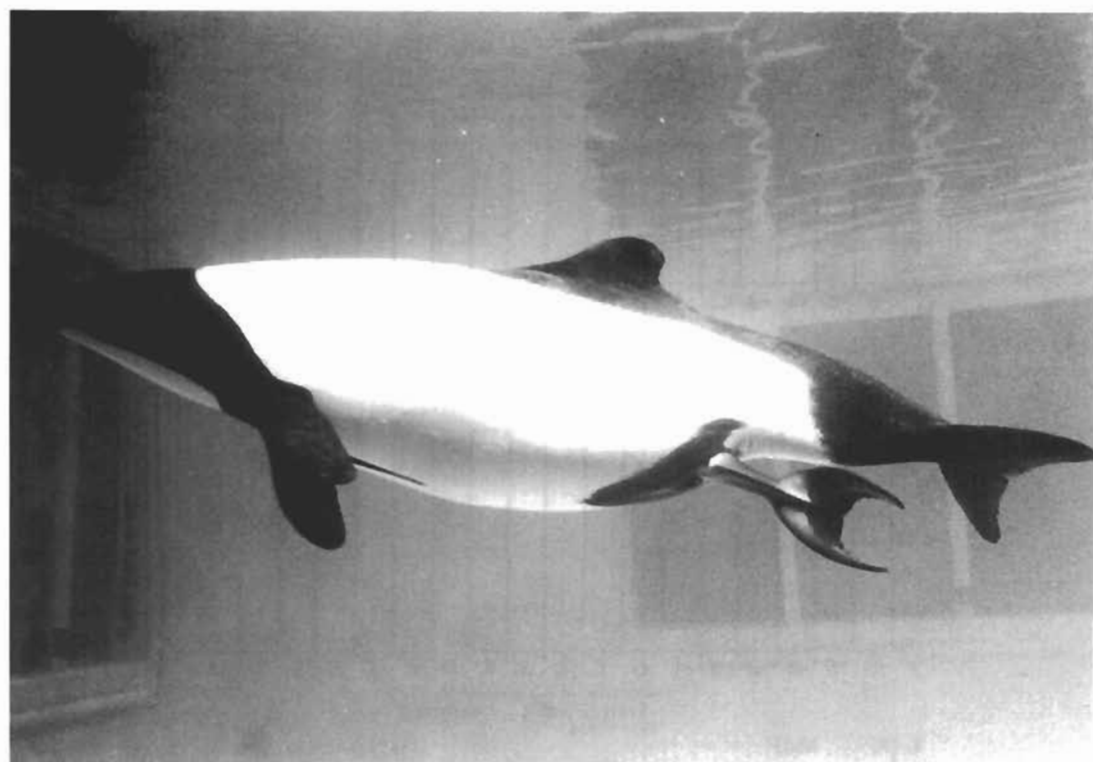


Figure 8. Birth of a Commerson's dolphin. Consider the large combined body sizes of mother and calf (Photo: Sea World of California photo department).

Table 2. The total food consumption in 12 months prior to delivery for 8 cases, compared to the food consumption during non-pregnant, non lactating 12 month periods of the same animals.

Animal	Birth date calf	Food intake during 12 months prior to birth (kg)	Food intake during non-pregnant, non-lactating 12 months periods (kg)
M4F	1/7/89	1246	1469 (July 87-July 88), 1499 (1990)
S6F	19/4/86	1192	139 (1987), 1299 (1989), 1404 (1990)
S6F	28/9/88	1312	
S8F	21/2/85	1448	1626 (1986), 1922 (1988), 1409 (1989), 1559 (1990)
S8F	10/7/87	1349	
S7F	5/12/85	1304	1376 (1984), 1442 (1988), 1327 (1989), 1426 (1990)
S7F	25/5/87	1241	
S7F	10/9/88	1452	

relatively little compared to their body weight while living in quite cold water. This may partly be explained by the high caloric density of the diet. A large part of their diet consists of Sprat, which on average has 15% more calories per weight unit than Herring (de Groot *et al.*, 1988). The caloric value of a specimen of a fish species may vary and depends on its age, sex, origin and the season. In 1980 and

1986 a larger proportion of squid was fed to D1M and D4M. This resulted in an increased food intake (Figs. 2A & D). D2M's food intake did not increase in those years because he generally did not accept squid. This may also explain his relatively low intake, as it consisted mainly of Herring and Sprat (Fig. 2C). The high food intake of the animals at Toba Aquarium may be partly explained by the

Table 3. The food intake in the mother during the period that the calf was fully dependent on milk, and during periods of the same length in the same season in non-pregnant, non-lactating years (Baseline).

Mother	Calf	Period only dependent on milk (days)	Food intake when calf was fully dependent a milk (kg/day)	Food intake during baseline period (kg/day)
S8F	S4M	133	5.5	4.9 (1986), 4.3 (1989)
S8F	S5M	163	6.0	4.8 (1988), 4.4 (1990)
S7F	S9F	236	4.4	4.3 (1984), 3.6 (1990)
S6F	S11F	73	4.6	3.9 (1984), 3.1 (1987), 3.8 (1990)
S6F	S10F	198	4.4	4.3 (1984), 3.2 (1989)
M4F	M6F	112	6.6	3.9 (1987), 4.0 (1990)

small size of the animals, and partly by the relatively low caloric value of the fish. Per unit weight, Mackerel has about 20% less energy than Herring, and 25% less than Columbia river smelt (Table 3; Ridgway *et al.*, 1991). However, the caloric content of Herring particularly is extremely variable depending on the season of catch.

(c) *Bio-availability.* The diet can be digested more or less efficiently. The enzymes of the digestive tract have to adapt to a new diet. Some of the fish species fed in the present study may not have been digested efficiently when the animals had recently arrived in human care. Changes in food intake due to digestibility changes are probably short-term, because the digestive tract will soon adapt to the new diet.

5. Metabolic rate

The metabolic rate influences the food intake, and depends on several factors.

a. Basal metabolism

Individual animals may have different basal metabolic rates, which influence the food intake. Cetaceans have large thyroid glands compared to terrestrial mammals of similar weights, and the thyroid hormones regulate the metabolism. However, there seems to be no simple correlation between thyroid hormone plasma levels and the activity level of a cetacean species (Ridgway and Patton, 1971). The basal metabolic rate of Commerson's dolphins has not yet been determined. Too few thyroid hormone measurements have been carried out on Commerson's dolphins to be of any value, as T3 and T4 levels have only been measured on 2 animals (D1M & D4M) at Duisburg Zoo (Kastelein *et al.*, 1993). T4 levels can fluctuate rapidly, so studies based on small sample sizes may lead to erroneous conclusions. A direct correlation between T4 levels and metabolic rate can therefore not be made.

b. Body weight

Body weight seems to play an important role in food intake, because the comparatively small animals at Toba Aquarium ate more per unit of body weight than the bigger animals from Sea World and Matsushima Aquarium (where the water temperature was higher), and Sunshine Aquarium (where the water temperature was similar, Table 4). The comparison between the food intake of animals of Sea World and Toba Aquarium, in regards of effect of water temperature, may not be valid, because both parks fed different diets to their animals.

Sergeant (1969) describes the feeding rates of eight odontocete species living in oceanaria and research facilities. In some cases he mentions the diet, but he unfortunately never mentions water temperatures. He concludes that the smaller the dolphin, the higher the feeding rate as a percentage of body weight, although the activity level and body composition of the species are of influence as well. The data of the present study agree with this; all else being equal, the smaller the animals, the higher the metabolic cost per unit of body weight ($\text{kg}^{0.75}$). This is true for virtually all mammals.

As a comparison, Kastelein and Vaughan (1989) describe the food consumption of a female killer whale (*Orcinus orca*). When she weighed 1900 kg, she ate 2.3% of her body weight per day. She was kept in a pool with a water temperature of between 15 and 22°C and on a diet of 35% Herring (*Clupea harengus*), 36% Mackerel (*Scomber scombrus*), 6% Whiting (*Merlangius merlangus*), 12% Sprat (*Sprattus sprattus*) and 11% Squid (*Illex spp.*) based on weight.

c. Growth

In general, growing young animals eat more than adults relative to their body weight. Kastelein *et al.* (1990) described the food consumption of Harbour porpoises. In a pool with water temperatures between 17 and 20°C, 2 adult males, which were

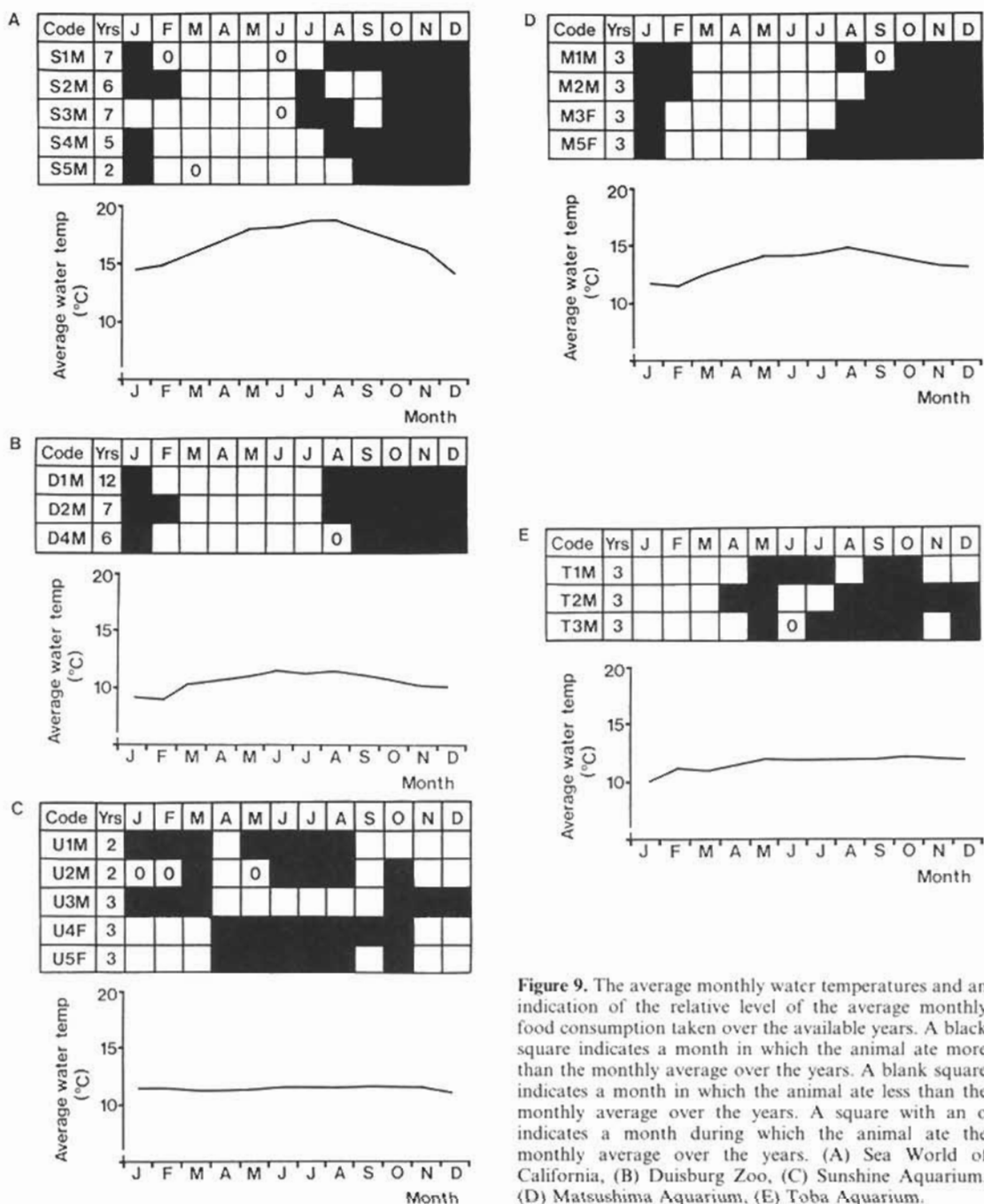


Figure 9. The average monthly water temperatures and an indication of the relative level of the average monthly food consumption taken over the available years. A black square indicates a month in which the animal ate more than the monthly average over the years. A blank square indicates a month in which the animal ate less than the monthly average over the years. A square with an o indicates a month during which the animal ate the monthly average over the years. (A) Sea World of California, (B) Duisburg Zoo, (C) Sunshine Aquarium, (D) Matsushima Aquarium, (E) Toba Aquarium.

stable at 38 and 32 kg, ate around 8% of their body weight per day, while a growing (16 to 24 kg) female ate 10.4% of her body weight per day. All animals were fed Herring. Meyers *et al.* (1978) described a growing female Harbour porpoise

which ate 10.8% of her body weight (Herring, Mackerel and Capelin, proportions not mentioned). This animal was kept in a pool at 19°C, and the data agree well with the above-mentioned growing female. Andersen (1965) described the

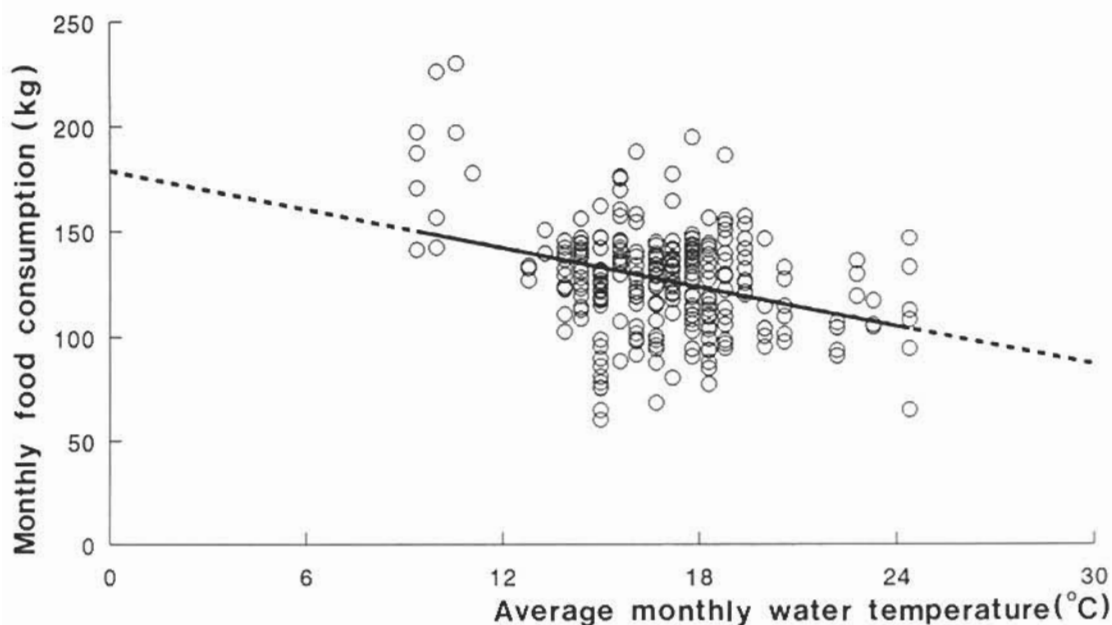


Figure 10. Relationship between average water temperature per month and total food intake per individual per month. Measurements ($N=295$) of 4 individual males from Sea World of California (S1M, S2M, S3M, S4M). Regression line: $y=179-3.1x$.

Table 4. The average annual water and air temperatures at the 5 parks, the average relative food consumption (% of total body weight), average body weight and main fish species in the diet of the adult Commerson's dolphins (males and non-pregnant, non-lactating females)

Park	Average water temp. (°C)	Average air temp. (°C)	Average body weight (kg)	Main fish species	Average daily food consumption of adult animals			
					(% of body weight)	N	SD	Range
Sea World	16.9	18.2	40.2	Herring	10.1	3	0.3	9.8–10.4
Matsushima Aquarium	13.4	17.7	42.5	Mackerel	10.6	4	0.5	10.0–11.0
Toba Aquarium	11.8	14.9	34.0	Mackerel	11.8	3	0.1	11.7–11.9
Sunshine Aquarium	11.3	14.6	41.4	Mackerel/Smelt	10.2	5	0.6	9.6–10.9
Duisburg Zoo	10.7	11.3	37.7	Sprat/squid	8.8	3	0.4	8.4–9.1

food consumption of 8 Harbour porpoises that were kept in an indoor pool (temperatures were not reported) and fed mainly Herring. He found that the adult animals weighing approximately 40 kg consumed on average around 8% of their body weight per day, whereas growing animals ate around 13% of their body weight each day.

Commerson's dolphins reach mature sizes early, and those in the present study eat as much as adult animals during their third year. At Matsushima, calf M6F even ate as much as an adult during her second year (Fig. 4F), 1 year in advance of the calves at Sea World. Table 1 shows that this calf was not born especially early in her first calendar year. During their growth period Commerson's

dolphins in the present study were not found to eat more than adults in proportion to their body weight. This may be explained by the fact that adult Commerson's dolphins retain a high activity level.

d. Activity level

The metabolic rate depends not only on the basal metabolism, but also on an animal's activity level. The adult Commerson's dolphins in the present study ate slightly more than adult Harbour porpoises under similar circumstances (Kastelein *et al.*, 1990), which, other than by a difference in body composition, could be explained by the difference in swimming behaviour between the two species. Harbour porpoises swim fast for a few

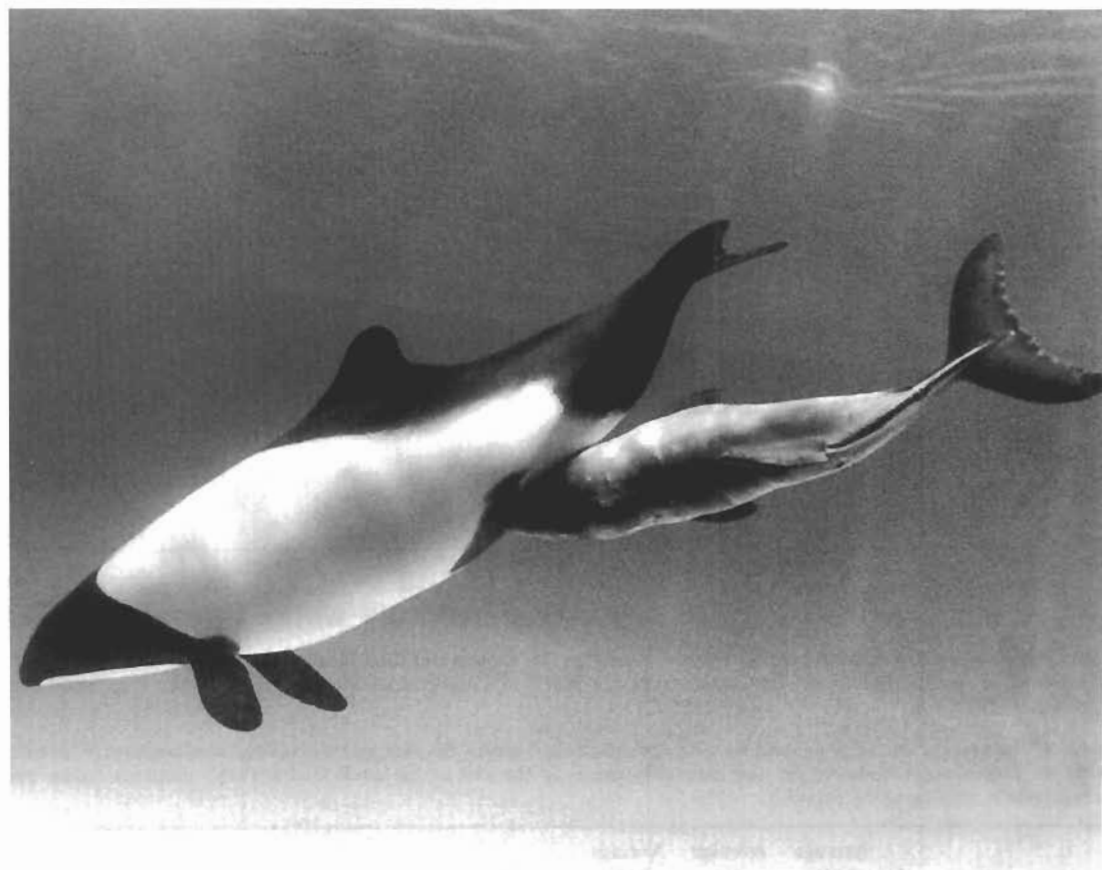


Figure 11. A newborn Commerson's dolphin calf suckling from its mother. This energy drain increases the mother's food intake (Photo: Sea World of California photo department).

minutes, then float at the surface. Commerson's dolphins usually swim much faster, and are very erratic.

When U1M and U2M were moved to the Osaka Aquarium in 1990, the animals lost weight at first, even though pool temperature and their food intake were higher than before (Fig. 3A+B). Adaptation to a new environment probably increases the metabolic rate because the animals are usually restless and temporarily swim faster. In addition, in warmer water, odontocetes often lose weight because their blubber layer becomes thinner (Williams *et al.*, 1992).

Although the animals in the present study were kept in pools, their activity level is not necessarily lower than that of conspecifics in the wild. The animals in the present study swam most of the day. Even in the wild the animals are not active all the time. In a group which followed and surrounded a 15 m fishing boat in the Strait of Magellan,

some animals were resting whereas others were swimming very fast around the bow of the boat.

e. Ambient water temperature

Ambient temperature has an effect on the metabolic rate in mammals (Innes *et al.*, 1987), and changes in temperature should affect the feeding rate. At Sea World, when in 1987 the average annual temperature of a male Commerson's (S2M) dolphin's pool dropped from 17 to 13°C, his annual food consumption increased from 1550 to 1900 kg, while his body weight remained fairly constant at around 45 kg (Fig. 1B). When the same happened to S3M, his annual food consumption increased from 1420 to 1640 kg, while his body weight remained fairly constant at around 42 kg (Fig. 1C). In 1989, U5F increased her food consumption while the water temperature remained constant, which resulted in an increase in body weight (Fig. 3E).



Figure 12. A new-born Commerson's dolphin calf with its mother. Note the oval genital patch, already indicating at this early age that it is a male, and the umbilical rostral of it. The calf has a large tail fluke relative to its body length. Also note the unfavourable body surface to body volume ratio of the calf relative to its mother. Even the adult is small in comparison to most odontocetes (Photo: Sea World of California photo department).

A comparison of the average proportional food consumption of males and non-pregnant, non-lactating females in the 5 institutions, yielded no significant correlation between proportional food consumption per year and water temperature. However, the data of Figure 9 do suggest that the animals eat less during the warmer months, and this is substantiated by the relationship between ambient water temperature and food intake expressed in Figure 10. Assuming a linear relationship between average monthly water temperature (x) and total monthly food intake (y) and assuming that the 4 males of Figure 10 are representative for Commerson's dolphins, it is possible to calculate how much one animal needs to eat per month ($y=179-3.1x$).

The thermal neutral zone (temperature range in which the metabolic rate is the lowest) of the Commerson's dolphin is unknown. The relation-

ship between water temperature and energy requirement is shown in fig 10. It is likely that the energy requirement also increases when the water temperature rises above a certain level, and the animals have to actively dissipate heat to prevent heat stress. To do so, dolphins circulate more blood through the superficial layers of their fins and flukes (Scholander and Schevill, 1955). It would be interesting to study whether redistribution of blood uses more or less energy than sweating or panting in terrestrial mammals. If at higher temperatures food intake increases, the graph of figure 10 would become U-shaped (see Bartholomew, 1977).

Only one other published report of Commerson's dolphin food consumption exists (Spotte *et al.*, 1979). Two animals were mainly fed Atlantic Herring (*Clupea harengus*). Average water temperature was 17°C. The average food consumption of 2 animals, which had an average weight of 35 kg, was

3.6 kg of Herring per day. This is 10.3% of their body weight, which is within the general range found in the present study, except at the Toba Aquarium and Duisburg Zoo (Table 4).

Possibly the radiation of the sun also has a small influence the metabolism of a Commerson's dolphin. When surface bobbing, the black dorsal fin and back are above the water. At Duisburg Zoo, the animals are very active swimmers most of the day, but when they float in the morning they do it in the sun, and later in the day they prefer to float in the shade.

f. Health status

Food intake usually decreased during the rare occurrences of illness experienced by the animals in the present study. In 1985, D2M suffered from pneumonia for 3 periods which totalled 6 months. This caused an annual food intake reduction of 20% (Fig. 2C). However, in most cases during illness the animals were force-fed for some days to keep their digestive tract active, so that the influence of illness was not always visible because the smallest analysis unit was the average food consumption per month. After recovery the animals usually compensated for the period of reduced food intake by eating more afterwards.

Ecological significance

The present study shows that Commerson's dolphin energy requirements depend on reproduction, lactation, diet, metabolic rate, body weight, growth, activity level, ambient temperature and health status. The relative importance of each parameter is difficult to determine when comparing data from different parks, due to the small sample size and the variation in parameters among the parks. Therefore it is difficult to isolate changes due to a single parameter.

Whether dolphins living in pools eat more or less than their conspecifics in the wild can only be speculated (Innes *et al.* 1987). However, food intake changes due to age, reproduction, water temperature and season are probably similar to those in the wild. The present study shows that lactating animals need a relatively large food supply, which should be available in the oceans at the time of year when lactation occurs. In the wild, births occur at the beginning of the austral summer (Gewalt, 1979 & 1981; Mermoz, 1980; Goddall *et al.*, 1988) when the water is relatively warm, and food becomes relatively abundant. The present study suggests that females which lose excessive weight before or during the lactation period, require relatively more food after weaning. These females might compete with their calves if the

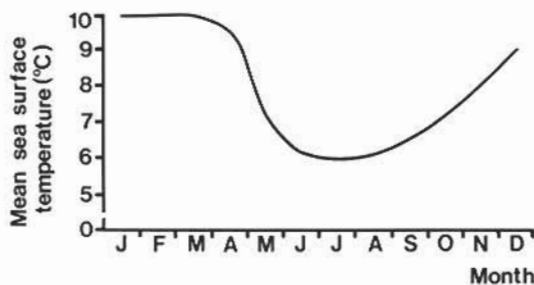


Figure 13. Annual fluctuations in the mean water surface temperature of the Strait of Magellan and surrounding waters.

Commerson's dolphin numbers are in balance with the amount of available prey in different seasons. The diets of young and adult animals may differ as it does in Harbour porpoises in Washington state waters (Gearin and Johnson, 1991). Different hunting skills due to age differences may serve to reduce competition among conspecifics.

How much food does an adult Commerson's dolphin require in the Straits of Magellan? The average monthly surface water temperature in the Straits of Magellan varies over the year between 6 and 10°C (Fig. 13). This means that most parks keep their Commerson's dolphins in warmer water than that experienced by their wild conspecifics (Table 4). However, using the extrapolated data from Figure 10 (and assuming that the animals were kept at temperatures below their thermal neutral zone), it is possible to make a rough food intake estimate for an average adult Commerson's dolphin in the Strait of Magellan. The data show that an adult Commerson's dolphin requires about 1850 kg of Herring (37×10^5 kcal) per year (Table 5). The fact that S2M ate more in 1987 with an average water temperature of 13°C (Fig. 1B) could be due to the fact that in that year the animal was moved to a new and colder pool twice, for a combined period of 5 months. Adaptations to a new environment probably made the animal more active than usual, causing him to require more energy, and when moved from a warmer pool to a colder pool, the animal needed some time to put on a thicker insulating layer. During that time the animal probably had to eat more to stay warm.

Estimating the number of Commerson's dolphins in a given area and measuring monthly water temperature enables a rough estimate to be made of the amount of food needed per month or per year by the Commerson's dolphin population involved. The fluctuation in the annual food intake can be related to the on and offshore fish migrations. It is possible that a shortage of fish in one particular season due to natural causes or activities of the fishing industry might cause a population decline in

Table 5. Average monthly surface water temperature in the Strait of Magellan, South America, and the estimated food intake per month per adult Commerson's dolphin, based on a diet of mainly Herring and the extrapolated line in Figure 10.

Month	Temp. (°C)	Food intake (kg)
January	10	148
February	10	148
March	10	148
April	10	148
May	7	157.3
June	6	160.4
July	6	160.4
August	6	160.4
September	7	157.3
October	7	157.3
November	8	154.2
December	9	151.1
Annual food intake		1850

dolphins, as has been suggested to occur for Northern fur seals, *Callorhinus ursinus* (Trites, 1992).

Unlike most larger cetaceans, but in common with Harbour porpoises, Commerson's dolphins have a very unfavourable (i.e. low) body weight to surface ratio (Andersen, 1981). This is disadvantageous to both species because they live in relatively cold water (Kanwisher and Sundnes, 1965). This unfavourable body weight to surface ratio is partly compensated for by a thick insulating blubber layer relative to larger odontocetes. Commerson's dolphins probably cannot go several consecutive days without food. They may forage almost continuously, as shown by the energetic part of the present study, and (except for days on which breeding activities occur) they need several feedings per day as shown by the short passage time of food (at least the dyes) through the gastro-intestinal tract (Kastelein *et al.*, 1993). Whether Commerson's dolphins in the wild feed at night is not known. This means that Commerson's dolphins cannot readily migrate long distances in areas without suitable prey, and this could explain the fact that this species inhabits coastal waters. If not fed sufficiently, the animals visibly lose weight within days, become more susceptible to the effects of parasites and infectious diseases. In extreme cases they may become hypothermic and die. These events may also occur the other way around: the dolphins may be rendered incapable of catching sufficient fish due to a disease. Therefore it is important to consider the size and dynamics of the prey fish stocks in the design of rational

management plans for small odontocetes in certain geographical areas.

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References

- Aguayo, L. A. (1975) Progress report on small cetacean research in Chile. *J. Fish. Res. Board Can.* **32**, 1123-1143.
- Andersen, S. (1965) L'alimentation du Marsouin (*Phocoena phocoena*), L. en captivité. *Vie et milieu*, **16A**, 799-810.
- Andersen, S. H. (1981) Body surface area of juvenile Harbour porpoise, *Phocoena phocoena*. *Aquatic Mammals*, **8**(3), 94-95.
- Angot, M. (1954) Observations sur les mammifères marins de l'archipel de Kerguelen, avec une étude détaillée de l'Elephant de mer *Mirounga leonina* (L.). *Mammalia*, **18**, 1-111.
- Anonymous (1987) Estimacion de densidad de Toninas overas (*Cephalorhynchus commersonii*, Lacépède, 1804) en el sector oriental del Estribo de Magallanes. Universidad de Magallanes, Instituto de la Patagonia. *Inf. Inst. Pat.* 42.
- Bartholomew, G. A. (1977) Body temperature and metabolism. In *Animal physiology: principles and adaptations* (ed. M. S. Gordon), pp. 364-449, Macmillan, New York.
- Bastida, R., Lichtschein, V. & Goodall, R. N. P. (1988) Food habits of *Cephalorhynchus commersonii* of Tierra del Fuego (SC/36/SM24). In *Biology of the Genus Cephalorhynchus* (eds R. L. Brownell Jr & G. P. Donovan) Rep. of the I.W.C. Special Issue 9, pp. 143-160.
- Beddington, J. R., Beverton, R. J. H. & Lavigne, D. M. (1985) Problems in estimating food consumption. In *Marine mammals and fisheries* (eds J. R. Beddington,

- R. J. H. Beverton & D. M. Lavigne). George Allen & Unwin, London, pp. 273-275.
- Booolootian, R. A. (1956) Notes on a specimen of the Harbour porpoise. *J. Mammalogy*, **38**(2), 265-266.
- Brownell, R. L. (1974) Small odontocetes of the Antarctic. In Antarctic mammals, Antarctic Map Folio series, *Am. Geogr. Soc.* New York, **18**, 13-19.
- Cornell, L. H., Antrim, J. E., Asper, E. D. & Pincheira, B. J. (1988) Commerson's dolphins (*Cephalorhynchus commersonii*) live-captured from the Strait of Magellan, Chile (SC/36/SM5) In *Biology of the Genus Cephalorhynchus* (eds R. L. Brownell, Jr & G. P. Donovan) Rep. of the I.W.C. Special Issue 9, pp. 183-196.
- Gaskin, D. E., Smit, G. J. D., Watson, A. P., Yasui, W. Y. & Yurick, D. B. (1984) Reproduction in the Porpoises (Phocoenidae): Implications for management. In *Reproduction in whales, dolphins and porpoises* (eds W. F. Perrin, R. L. Brownell Jr & D. P. DeMaster). Rep. Int. Whal. Comm. Cambridge. Special Issue 6, pp. 135-148.
- Gearin, P. J. & Johnson, M. A. (1991) Harbour porpoise food habits in Washington state. Abstract: a 9th biennial conference on the biology of marine mammals, Chicago.
- Gewalt, W. (1979) The Commerson's dolphin (*Cephalorhynchus commersonii*) capture and first experiences. *Aquatic Mammals* **7**(2), 37-40.
- Gewalt, W. (1981) Ein 'neues' Zootier, Der Jacobita oder Commerson's dolphin (*Cephalorhynchus commersonii*) La Cépède 1804, in *Walarium des Zoo Duisburg*. Zoologische Beiträge. Neue Folge. **27**, 199-204.
- Gewalt, W. (1985) Commerson's dolphin (*Cephalorhynchus commersonii*). *Aquatic Mammals* **11**(2), 41.
- Gewalt, W. (1990) The Jacobita, or Commerson's dolphin (*Cephalorhynchus commersonii*). *Aquatic Mammals* **16**(2), 53-64.
- Gewalt, W. (1991) Unsere Jacobita (*Cephalorhynchus commersonii* Lacépède 1804) Expeditionen 1978, 1980 und 1984 (in German). *Zool. Garten N.F.* **61** (5/6), 289-359.
- Goodall, R. N. P. & Cameron, I. S. (1980) Exploitation of small cetaceans off southern South America. *Rep. Int. Whal. Comm.* **30**, 445-450.
- Goodall, R. N. P., Galeazzi, A. R., Leatherwood, S., Miller, K. W., Cameron, I. S., Kastelein, R. A. & Sobral, A. P. (1988) Studies of Commerson's dolphins, *Cephalorhynchus commersonii*, of Tierra del Fuego, 1976-1984, with a review of information on the species in the South Atlantic (SC/36/SM8). In *Biology of the Genus Cephalorhynchus* (eds R. L. Brownell Jr & G. P. Donovan) Rep. of the I.W.C. Special Issue 9, pp. 3-70.
- De Groot, B., Dijkema, R. & Redant, F. (1988) Vis, schelp- en schaaldieren (in Dutch). SpectrumGids. Trendboek B. V. Maarssenbroek. 26-28.
- Harmer, S. F. (1922) On Commerson's dolphin and other species of *Cephalorhynchus*. *Proc. Zool. Soc. London*, 627-638+3 plates.
- Innes, S., Lavigne, D. M., Earle, W. M. & Kovacs, K. M. (1987) Feeding rates of seals and whales. *J. of Anim. Ecol.* **56**, 115-130.
- Joseph, B. E., Antrim, J. E. & Cornell, L. H. (1987) Commerson's dolphin (*Cephalorhynchus commersonii*): a discussion of the first live birth within a marine zoological park. *Zoo Biol.* **6**, 69-77.
- Kanwisher, J. & Sundnes, G. (1965) Physiology of a small cetacean. *Hvalradets Skrift*. **48**, 45-53.
- Kastelein, R. A. (1984) Commerson's dolphin, *Cephalorhynchus commersonii* (Lacépède, 1804). Review of published information and report on field research in the Strait of Magellan, Chile, January-February 1984. MSc. Thesis, Agricultural University Wageningen, NL.
- 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. & van Battum, R. (1990) The relationship between body weight and morphological measurements in Harbour porpoises (*Phocoena phocoena*) from the North Sea. *Aquatic Mammals* **16**(2), 48-52.
- Kastelein, R. A., Vaughan, N. & Wiepkema, P. R. (1990a) The food consumption of Steller sea lions (*Eumetopias jubatus*). *Aquatic mammals* **15**(4), 137-144.
- Kastelein, R. A., Verhoeven, I. & Wiepkema, P. R. (1990b) The food consumption of South African fur seals (*Arctocephalus pusillus*) at the Harderwijk Marine Mammal Park. *Int. Zoo. Yearbook*, **29**, 175-179.
- Kastelein, R. A., Wiepkema, P. R. & Vaughan, N. (1990c) The food consumption of Grey seals (*Halichoerus grypus*) in human care. *Aquatic Mammals*, **15**(4), 171-180.
- Kastelein, R. A., Kershaw, J. & Wiepkema, P. R. (1991) The food consumption of Southern elephant seals (*Mirounga leonina*). *Aquatic Mammals*, **17**(2), 76-87.
- Kastelein, R. A., McBain, J. & Neurohr, B. (1993) Information on the biology of Commerson's dolphins (*Cephalorhynchus commersonii*). *Aquatic Mammals*, **19**(1).
- Leatherwood, S., Kastelein, R. A. & Miller, K. W. (1988) Estimate of numbers of Commerson's dolphins in a portion of the northeastern Strait of Magellan, January-February 1984. (SC/36/SM7). In *Biology of the Genus Cephalorhynchus* (eds R. L. Brownell Jr & G. P. Donovan) Rep. of the I.W.C. Special Issue 9, pp. 93-102.
- Lockyer, C., Goodall, R. N. P. & Galeazzi, A. R. (1988) Age and Body-length characteristics of *Cephalorhynchus commersonii* from incidentally-caught specimens off Tierra del Fuego (SC/36/SM4). In *Biology of the Genus Cephalorhynchus* (eds R. L. Brownell Jr & G. P. Donovan) Rep. of the I.W.C. Special Issue 9, pp. 103-118.
- Mermoz, J. F. (1980) A brief report on the behaviour of Commerson's dolphin, *Cephalorhynchus commersonii*, in Patagonian shores. *Sci. Rep. Whales res. Inst.*, **32**, 149-153.
- Meyers, W. A., Horton, H. C., Heard, F. A., Jones, A., Winsett, G. & McCulloch, S. A. (1978) The role of recorded data in acclimatizing a harbour porpoise (*Phocoena phocoena*). *Aquatic Mammals*, **6**(2), 54-64.

- Recchia, Ch. A. & Read, A. J. (1989) Stomach contents of harbour porpoises, *Phocoena phocoena* (L.), from the bay of Fundy. *Can. J. Zool.* **67**, 2140–2146.
- Ridgway, S. H. & Patton, G. S. (1971) Dolphin thyroid: some anatomical and physiological findings. *Z. vergl. Physiologie*, **71**, 129–141.
- Ridgway, S., Reddy, M., Kamolnick, T., Skaar, D. & Curry, C. (1991) Calorie consumption of growing, adult, pregnant, and lactating *Tursiops*. IAAAM Abstract.
- Scholander, P. F. & Schevill, W. E. (1955) Counter current heat exchange in the fins of whales. *J. Applied Physiol.* **8**, 279.
- Sergeant, D. E. (1969) Feeding rates of Cetacea. *Fisk. Dir. Skr. Ser. Hav. Unders.*, **15**, 246–258.
- Shochi, Y., Zbinden, K., Kraus, C., Gihl, M. & Pilleri, G. (1982) Characteristics and directional properties of the sonar signals emitted by the captive Commerson's dolphin, *Cephalorhynchus commersonii* (Gray, 1846). In *Investigations on Cetacea* (ed. G. Pilleri) Vol. 13, Institute of Brain Anatomy, Berne, pp. 177–204.
- Spotte, S., Radcliffe, C. W. & Dunn, J. L. (1979) Notes on Commerson's dolphin (*Cephalorhynchus commersonii*) in captivity. *Cetology* **35**, 1–9.
- Trites, A. W. (1992) Northern fur seals: why have they declined? *Aquatic Mammals*, **18**(1), 3–18.
- Utrecht, W. L. van (1978) Age and growth in *Phocoena phocoena* Linnaeus, 1758 (Cetacea, Odontoceti) from the North sea. *Bijdr. tot de Dierk.* **48**(1), 16–28.
- Weber, H. (1929) *Als Pelzjäger im Feuerland* (in German). August Scherl G.m.b.H., Berlin.
- 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.

