Food consumption, food passage time, and body measurements of captive Atlantic bottlenose dolphins (*Tursiops truncatus*)

R. A. Kastelein[1]*, C. Staal[1] and P. R. Wiepkema[2]

[1]*Harderwijk Marine Mammal Park, Strandboulevard Oost 1, 3841 AB Harderwijk, The Netherlands (part of Grévin et Compagnie, France).*
[2]*Wageningen Agricultural University, Stationsweg 1, 6861 EA Oosterbeek, The Netherlands*

Abstract

The food consumption (recorded as kg of individual fish species), body length, and body mass of 19 (four males and 15 females) Atlantic bottlenose dolphins (*Tursiops truncatus*) kept at Harderwijk Marine Mammal Park, the Netherlands, between 1965 and 1995 are reported. This broad-scale, longitudinal study is based on data originally archived for short-term husbandry purposes. The chemical composition and caloric value of the diet were not measured. Because caloric content of fish varies seasonally and annually, and depends on the geographical region where it was caught, the food intake variations seen in this study may reflect the caloric content of the diet. However, because the effects of age, gender, and reproductive state are consistent in various animals, and all animals entered the study at different times, the effects are believed to be independent of variation in caloric content of the diet. After weaning, the average annual food consumption of males and non-pregnant, non-lactating females increased rapidly until the estimated age of 3–5 years, thereafter it averaged around 1900 kg (estimated at 133×10^5 kJ) per year. After the age of 20 years, food consumption of several dolphins decreased slightly. Two females reproduced and nursed their calves successfully. Twelve months before parturition, consumption by both ceased almost entirely for one week, probably indicating estrus. Food intake did not increase during pregnancy. After they gave birth, the food consumption of the two mothers showed a comparable pattern; the food intake remained at a consistent level during the month of birth, but increased rapidly in the following month. Food consumption dropped during the third month of lactation in one case and during the fourth month in the other case. During the lactation period, the mothers consumed 2600 kg (48%) and 3300 kg (72%) more than during similar periods in non-reproductive years. The two calves began to eat fish, in addition to suckling, at the ages of 6 and 19 months respectively. Average standard body length at birth was 116 ± 6 cm for males (n=15) and 114 ± 10 cm for females (n=6). It increased rapidly until around the age of 5 years, after which growth rate declined. Body length reached an asymptote (between 260 and 280 cm) between the ages of 15 and 20 years. Average body mass at birth was 18.0 ± 3.8 kg for males (n=15) and 15.6 ± 4.9 kg for females (n=5). Weight gain was rapid until around the age of 3 years, after which it decreased. The relationship between body mass and standard body length was:

Body mass (kg) $= 12.904e^{0.017(\text{body length (cm)} - 100)}$.

There was a negative relationship between body mass and average daily food consumption expressed as a percentage of body mass. The average initial passage time of food through the digestive tract of five animals (with an average body mass of 185 kg) was 235 min.

Key words: bottlenose dolphin, carmine red, energetics, feeding, initial passage time, nutrition, odontocetes, reproduction, weaning, growth, body mass, body length, *Tursiops*.

Introduction

Although the bottlenose dolphin (*Tursiops* spp.) has a wide distribution and is the most widely-kept toothed whale in the world (Wells & Scott, 1999), relatively little is known about its food requirements (McBride & Kritzler, 1951; Essapian, 1953; Tavolga, 1966; Sergeant, 1969; White, 1970; Shapunov, 1971; Van de Hurk, 1972; Van Dyke & Ridgway, 1977; Prescott, 1977; Hinga, 1979; Geraci & St. Aubin, 1980; Spotte & Babus, 1980; Geraci, 1981; Cates & Schroeder, 1986; Cockcroft & Ross,

*Present address: Julianalaan 46, 3843 CC Harderwijk, The Netherlands.

Table 1. Characteristics of the Atlantic bottlenose dolphins used in this study.

Animal code	Sex	Estimated birth date (year)	Birth location	Study period
TtZH005	M	1958	Wild	1965–1995
TtZH006	F	1962	Wild	1969–1995
TtZH007	F	1962	Wild	1968–1995
TtZH008	F	1963	Wild	1968–1995
TtZH009	M	1982	Wild	1982–1991
TtZH010	F	1983	Wild	1985–1995
TtZH013	F	1982	Wild	1985–1995
TtZH014	F	1982	Wild	1985–1995
TtZH015	F	1960	Wild	1965–1982
TtZH016	M	1950	Wild	1970–1981
TtZH017	F	1960	Wild	1971–1982
TtZH018	F	4/August/1974	Harderwijk	1974–1976
TtZH019	F	12/August/1975	Harderwijk	1975–1977
TtZH022	F	1961	Wild	1969–1979
TtZH023	F	1955	Wild	1970–1979
TtZH025	F	1960	Wild	1971–1987
TtZH027	F	1946	Wild	1965–1977
TtZH034	F	1962	Wild	1968–1977
TtZH078	M	1960	Wild	1965–1975

1990*a*; Peddemors *et al.*, 1992; Reddy *et al.*, 1994; Kastelein *et al.*, 2002). The food consumption, body measurements, and weight change of toothed whales may provide a reference for veterinary and husbandry purposes to zoological parks keeping odontocetes. Food consumption data from captive odontocetes can also be used to estimate the impact of wild conspecifics on fish populations, and to determine the carrying capacity of a certain area. In this paper, the food consumption, body weight, and morphological measurements of bottlenose dolphins at the Harderwijk Marine Mammal Park between 1965 and 1995 are described.

Materials and Methods

Study animals
Seventeen of the 19 Atlantic bottlenose dolphins (*Tursiops truncatus*) used in this study originated from the eastern Gulf of Mexico. Two of the animals were born at Harderwijk. The sex, estimated birth date, origin, and study period of each dolphin are shown in Table 1. Age estimates were based on the body length-age relationship in the Gulf of Mexico bottlenose dolphin population near Sarasota, Florida (Read *et al.*, 1993). These estimates are likely (considering the variance in lengths per age in Read *et al.*, 1993) to be accurate to within one year for animals that arrived at the park at between 1 and 10 years of age. The age estimates for animals that arrived after they were 10

years old are less accurate, because the growth curve provided by Read *et al.* (1993) flattens after this age. Body measurements were taken infrequently and opportunistically in various months of the year, for instance before transport or during pool maintenance. Body masses and standard body lengths of full-term neonatal calves that died during or shortly after birth were recorded, although both measurements were not made for all calves. These calves may have been premature, so the data derived from them may be underestimates of mass and length at birth. Standard body length is defined as the length of a straight line between the tip of the rostrum and the notch in the tail fluke.

Estimating the duration of lactation in cetaceans is problematic, because it is difficult to observe the last suckling session (Whitehead & Mann, 2000). Since the actual suckling events were not recorded in the present study, the duration of the suckling period could only be assessed indirectly. In the present study, the end of the weaning process of calf 019 therefore is defined as the time at which the monthly food consumption of the mother returned to a level similar to that in non-reproductive years.

Because the dolphins arrived at the Harderwijk Park at different ages and times, and were born and died in different years, the number of years for which food intake data are available are variable among individuals. The animals were in good health throughout their study periods. The animals
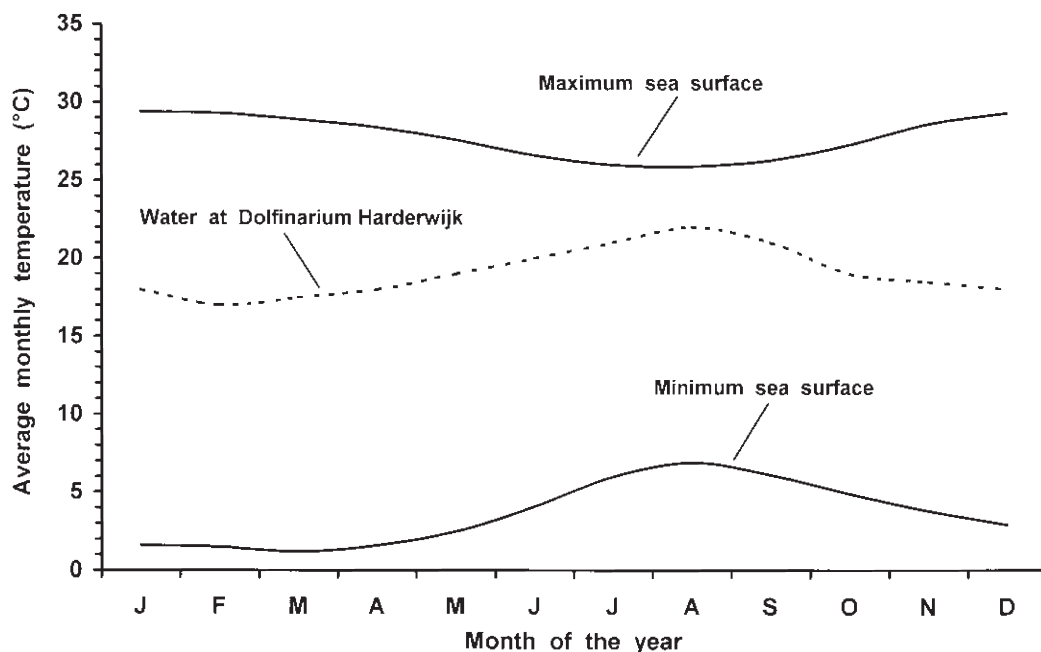
Figure 1. Average monthly water temperatures at the Harderwijk Marine Mammal Park and the minimum and maximum sea surface temperatures (of the Southern Hemisphere) in the distribution area of wild bottlenose dolphins. Based on the distribution area reported by Wells & Scott (1999) and the average monthly sea surface temperatures (Bottomley *et al.*, 1990).

participated in shows and training programs all year.

Study area

The study dolphins were kept indoors at the Harderwijk Marine Mammal Park in a main pool (30 m × 15 m, 4 m deep) with two adjacent holding pools (9-m diameter, depths: 2.9 m and 4 m). These pools were connected by a canal to another complex consisting of a main pool (21 m × 7.5 m, 3 m deep) and 4 holding pools (Dudok van Heel, 1970). A group of up to 14 bottlenose dolphins was kept with a female killer whale (*Orcinus orca*) between 1976 and 1987, and with 3 false killer whales (*Pseudorca crassidens*) between 1987 and 1993. Water temperatures were measured daily. The average monthly water temperatures varied between 17°C in February and 22°C in August (Fig. 1). Between 1987 and 1993, the average annual water temperature (based on 365 measurements per year) increased from 18 to 20°C. Air temperature varied between approximately 0°C and 30°C, and salinity between 2.0 and 2.5% NaCl. Salinity changes were unrelated to season. Windows in the roof allowed the animals to be exposed to the natural daily light cycle at 5°37′E and 52°20′N.

Food

Historical daily food records, originally collected for short-term husbandry purposes, form the basis of the present study. The animals were fed 3–5 times per day on an average diet of 25% herring (*Clupea harengus*; approx. 8880 kJ/kg wet weight) and 75% mackerel (*Scomber scombrus*; approx. 9550 kJ/kg wet weight) by weight, until 1980, and 30% herring, 30% mackerel, 15% whiting (*Merlangius merlangus*; approx. 4750 kJ/kg wet weight), 20% sprat (*Sprattus sprattus*; approx. 10 400 kJ/kg wet weight), and 5% squid (*Illex* spp.; approx. 1000 kJ/kg wet weight) between 1980 and 1995. Ratios of the fish species given varied with availability. The composition and caloric content of the fish and squid species were not measured, but probably varied by year class of fish, seasonally, and depending on the location where the fish was caught (Cates & Schroeder, 1986). Records were kept of the amount and type of food consumed during each feed, although total daily food intake forms the basic unit in the present study. To estimate the energy consumed by the dolphins, the food intake was calculated in kJ using average values (shown above) for the fish species (van der Heijden *et al.*, 1998). This yielded an average caloric value for
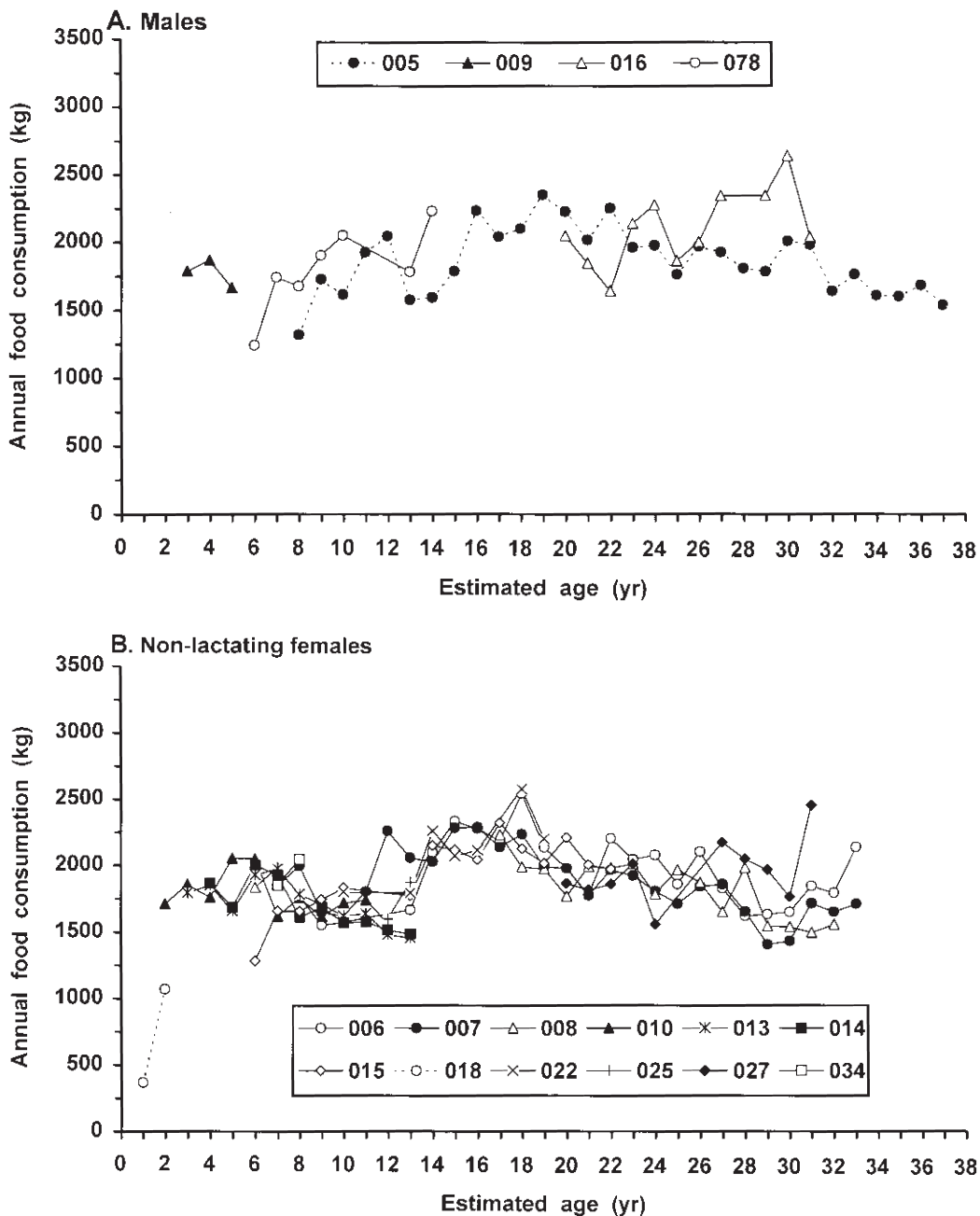
Figure 2. A and B.

this diet of *ca.* 7000 kJ/kg. Vitamins (Seavit®, 1 tablet per 2.5 kg of food) were added to the fish, after it had been defrosted in running tap water. The frozen fish was stored for a maximum of 4 months. The animals were allowed to eat *ad lib.* (until the fish was not eaten immediately, or was played with) during the last meal of the day. Records of animals in poor health and from incomplete calendar years are excluded from this analysis.
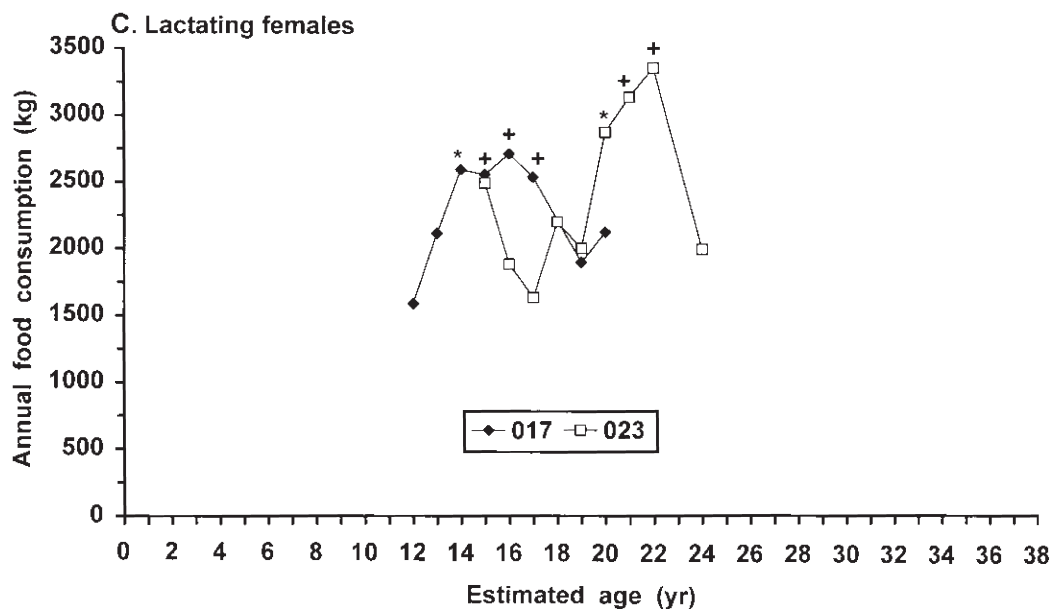
Figure 2. C.

Figure 2. Annual food consumption of 4 males (A), 12 non-lactating females (B), and 2 lactating females (C) bottlenose dolphins at Harderwijk Marine Mammal Park. Age 1 represents the first calendar year after birth. *A year during which a female was pregnant, delivered a calf and nursed it. +A year during which a calf was nursed.

Passage time of food through the digestive tract
Between 13 May and 16 July 1993, the passage time of food through the gastrointestinal tract was measured in 5 dolphins (weight range: 160–221 kg; average: 186 kg; see Table 2 for other characteristics). Three gelatin capsules, each containing 100 mg carmine red dye, were fed to the dolphins in a herring or mackerel (each meal consisted of a mix of both fish). The capsules were offered between 0800 and 1700h and the time taken for the dye to first appear in the feces was recorded (initial passage time).

Results

Annual food consumption
After weaning, the average annual food consumption of males (Fig. 2) and non-pregnant, non-lactating females (Fig. 2) increased rapidly until around the estimated ages of 3–5 years. Thereafter, it averaged around 1900 kg (estimated at 133×10^5 kJ) per year (SD=270 kg, n=201 years). After the estimated age of 20 years, food consumption of several animals decreased slightly.

Influence of reproduction on food intake in females
Although most calves died during or shortly after birth, two female calves were successfully nursed and raised by their mothers. Twelve months before parturition, consumption by both females ceased almost entirely for one week, probably indicating estrus. Food consumption was not noticeably higher during pregnancy than during previous seasons, in which the females were not pregnant (Fig. 2). The food consumption of the two mothers remained consistent during the month of delivery, increased during the following month, and dropped during the third month in one case and in the fourth month in the other case (Figs 3 and 4). The monthly food intake of female 017, whose calf (018) began to eat fish at the age of 6 months, remained above the monthly average for most of the nursing period. Weaning occurred abruptly at 34 months of age when the calf was moved to another park. During the lactation period, the mother consumed 2600 kg (48%) more than during similar periods in non-reproductive years (Figs 2 and 3). Between 6 and 34 months of age, the calf consumed a total of 2500 kg of fish in addition to suckling. The monthly food intake of female 023, whose calf (019) began to eat fish at the age of 19 months, remained above average for the entire nursing period (Fig. 4). During the 26-months nursing period, the mother consumed 3300 kg (72%) more than during similar periods in non-reproductive years (Figs 2 and 4). Between 19 and 26 months of
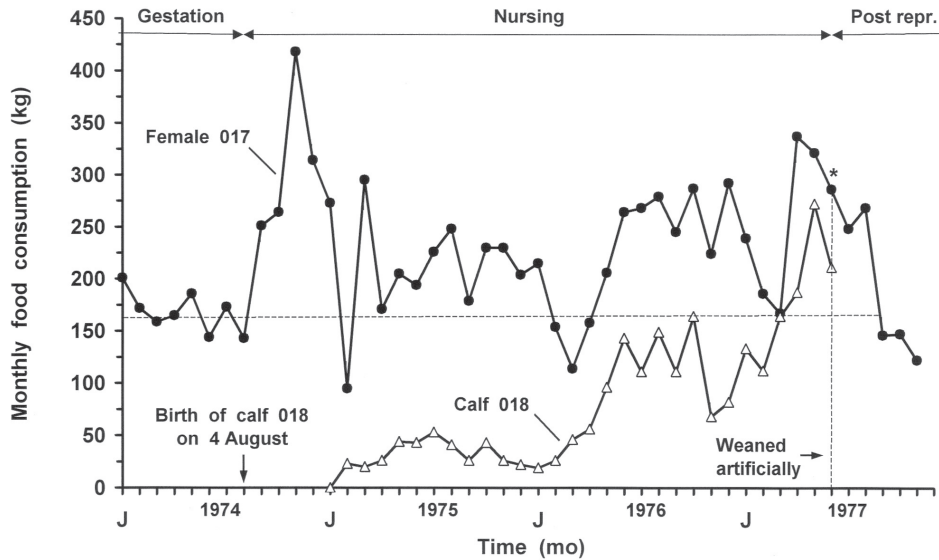
Figure 3. Impact of reproduction on the monthly food intake of a bottlenose dolphin female (017) and the transition from milk to solid food in her calf (018). J signifies January. The horizontal dashed line indicates the average monthly food consumption of the female during recent non-reproductive periods. *Calf moved to another park without its mother, resulting in acute weaning (vertical dashed line).

age, the calf consumed a total of 570 kg of fish in addition to suckling.

Body measurements
The mean standard body length of neonates was 116 ± 6 cm for males ($n=15$) and 114 ± 10 cm for females ($n=6$). Some of these animals may have been premature. Body length increased rapidly until around the age of 5 years, after which the growth rate declined (Fig. 5). The body length reached an asymptote (between 260 and 280 cm) between the ages of 15 and 20 years.

The average body mass at birth was 18.0 ± 3.8 kg for males ($n=15$) and 15.6 ± 4.9 kg for females ($n=5$). Weight gain was rapid until around the age of 3 years, after which it increased more slowly (Fig. 5). Due to the small number of weight measurements nothing can be said about potential seasonal body mass changes.

There was a positive relationship between standard body length (cm) and body mass (kg) which, using only one randomly-selected measurement per animal (Fig. 6), can be expressed as:

$$\text{Body mass} = 12.904e^{0.017(\text{body length} - 100)}$$

Food consumption as a percentage of body mass
Based on one randomly-selected measurement per animal there was a negative relationship between body mass and average daily food consumption as a percentage of body mass taken over the calendar month in which the body mass was measured (Fig. 7).

Passage time of food through the digestive tract
The average initial passage time of carmine red dye in a mixed diet of herring and mackerel through the digestive tract of five bottlenose dolphins was 235 ± 49 min ($n=8$, Table 2).

Discussion

Annual food consumption
The annual food consumption of adult male and non-reproducing female bottlenose dolphins in the present study was around 1900 kg, slightly lower than the intake of Atlantic bottlenose dolphins at Windsor Safari Park, which were housed outdoors (Kastelein *et al.*, 2002). Annual food consumption by individuals of similar age however, varied by up to 1000 kg, presumably owing to differences in body mass, activity level, and degree of participation in shows. Food intake changes among years of adult males and adult non-lactating females could have been caused by changes in social structure or the level of participation in shows.

No obvious difference was apparent between annual food consumption of male and non-pregnant, non-lactating females in the present
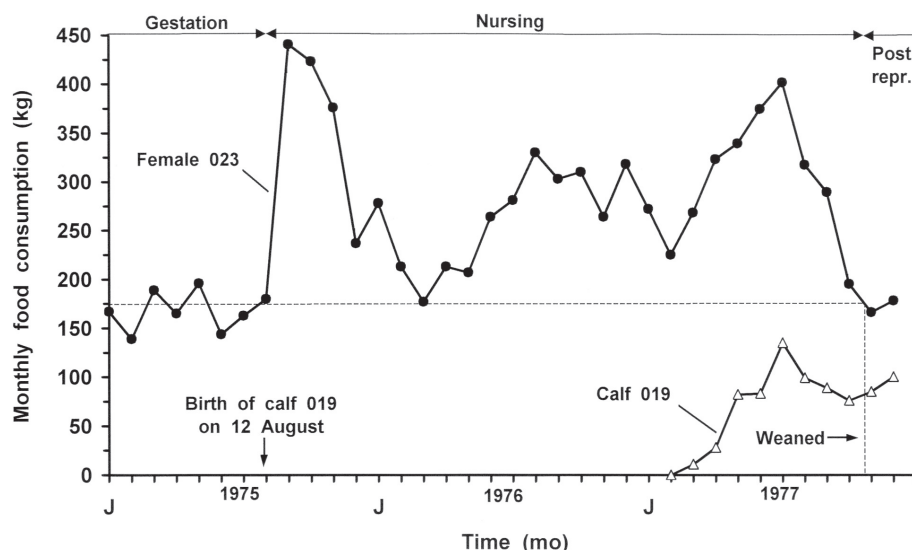
Figure 4. Impact of reproduction on the monthly food intake of bottlenose dolphin female 023 and the transition from milk to solid food in her calf (019). J signifies January. The horizontal dashed line indicates the average monthly food consumption of the female during recent non-reproductive periods. The vertical dashed line indicates the suggested moment the calf was fully weaned.

Table 2. Initial passage times of carmine red dye through the digestive tract of five Atlantic bottlenose dolphins at Harderwijk Marine Mammal Park.

Animal	Sex	Estimated age (yr)	Body mass (kg)	Date (d/mo/yr)	Time of day dye fed (h)	Meal size (kg)	Passage time (min)
TtZH006	F	31	189	13/05/1993	08.19	4	271
TtZH006	F	31	189	04/06/1993	10.53	3.5	231
TtZH006	F	31	189	10/06/1993	11.02	6	203
TtZH010	F	10	182	19/05/1993	10.34	4	255
TtZH007	F	31	177	18/05/1993	08.19	6.5	265
TtZH007	F	31	177	02/06/1993	16.43	5.5	213
TtWS005	M	19	221	25/05/1993	10.31	5.5	212
TtWS007	M	8	160	16/07/1993	10.36	5	235

study. This is in agreement with a study of bottlenose dolphins at Windsor Safari Park, U.K. (Kastelein *et al.*, 2002). After the age of 20 years, the annual food consumption of animals in the present study decreased slightly. This could indicate the end of the growth period.

Impact of reproduction on the food intake in females
The calves in the present study were both born in August. Female bottlenose dolphins are polyoestrous, and have 2 to 7 ovulations per year (Schroeder, 1990; Schroeder & Keller, 1990). They are spontaneous ovulators, ovulating even in the absence of males (Ozharovskaya, 1990). Pregnancy

lasts for 11.5 to 12 months (Cornell *et al.*, 1987; Schroeder, 1990) with a calving interval of 2–3 years (Kasuya, 1985; Cornell *et al.*, 1987).

Pregnancy in female bottlenose dolphins cannot generally be detected by a change in food intake. Food consumption by female odontocetes, as demonstrated in studies on bottlenose dolphins, Commerson's dolphins (*Cephalorhynchus commersonii*), and killer whales (*Orcinus orca*) does not appear to increase during pregnancy (Kastelein *et al.*, 1993b; 2002; 2003), although Reddy *et al.* (1994) suggested that food consumption by bottlenose dolphins shows a slight increase shortly before delivery. Nonetheless, a 244-cm female fed *ad lib.* increased in body mass by 37% (from 150 to 205 kg) in the last trimester of pregnancy (Spotte & Babus,
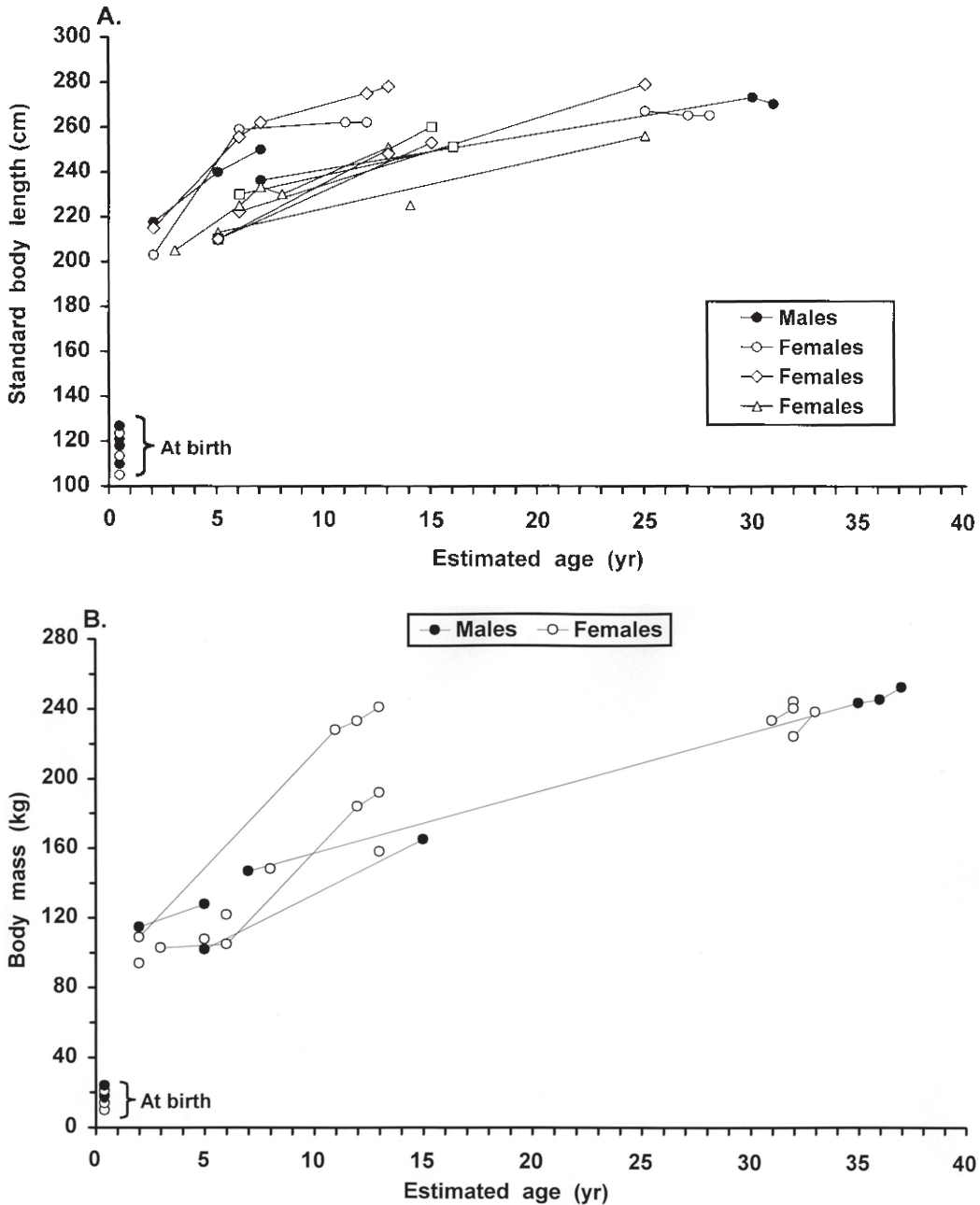
Figure 5. Estimated age versus standard body length (A) and body mass (B) for 7 male and 13 non-pregnant, non-lactating female bottlenose dolphins at Harderwijk Marine Mammal Park. The measurements of neonates were very similar and there is some overlap, so the sample appears lower than mentioned in the section 'Body Measurements'. Data points of the same animal are connected with lines which do not indicate the animal's body weight or length in the intervening period.

1980). The unchanged food intake of female odontocetes during pregnancy, despite the requirement of the growing fetus, could be explained to some degree by increased body size during pregnancy (McBride & Kritzler, 1951; Tavolga & Essapian, 1957). The consequently lower surface area to
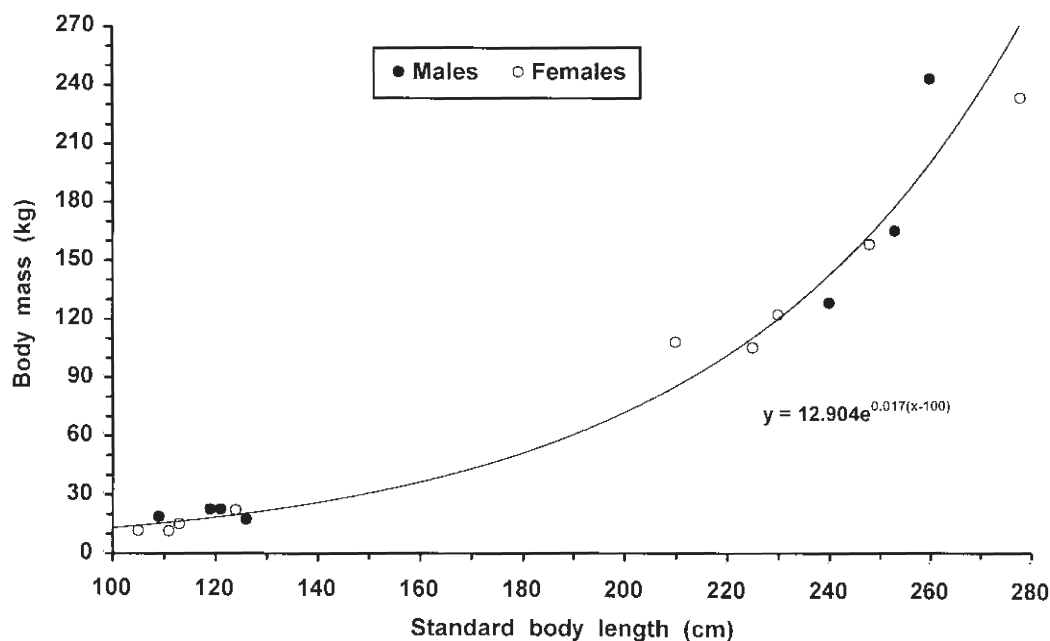
Figure 6. Standard body length versus body mass for 7 male and 9 non-pregnant, non-lactating female bottlenose dolphins at Harderwijk Marine Mammal Park (one data point per animal). The data points up to 130 cm are from calves that died during birth or shortly after birth. The lack of data points between standard body lengths of 130–200 cm is because calves suckle during this period, and are usually not removed from their mothers in fear of causing acute weaning.

volume ratio is expected to reduce conductive heat loss. Energy for future milk production, stored as blubber during gestation (which may be hormonally regulated), could increase the thermal insulation, thus further reducing energy loss to the environment.

In the present study, the food consumption by females did not increase in the first 2–3 weeks after parturition, despite the energy requirement of lactation. Much energy expenditure is believed to be in milk, which has a fat content of 6 to 27%, depending on sample timing (Ridgway *et al.*, 1995). This suggests that during the first 2–3 weeks after delivery, fat reserves were relied on to provide the calves with energy for growth, locomotion, and thermoregulation, allowing the mother to focus most of her attention on her new-born calf. During the second month after birth, food consumption increased rapidly, suggesting that female fat reserves were reduced. By the third and fifth months, food consumption by the mothers decreased. The suckling time per day of a bottle-nose dolphin calf decreases rapidly after the age of 4 months (Cockcroft & Ross, 1990b). This could be due to lower energy loss in the calf, resulting from a smaller surface area to volume ratio and a thicker blubber layer. Food consumption by female

Commerson's dolphins remains high for about 6 months after parturition (Joseph *et al.*, 1987; Kastelein *et al.*, 1993b). This is longer than in bottlenose dolphins, and could be related to the much smaller body size of Commerson's dolphins.

The extra energy bottlenose dolphin mothers in the present study required during the entire nursing period probably depended, among other factors, on the length of the suckling period, and the age at which the calf began to consume fish in addition to suckling (see also Kastelein *et al.*, 2002). The annual food intake of lactating females has been demonstrated to be 1700 to 1800 kg higher than during non-lactating years, representing a food intake increase from 5 to 8% of body mass per day. Daily food consumption in the first 6 months of lactation is 2 to 3 times higher than before delivery (Cockcroft & Ross, 1990b; Reddy *et al.*, 1994; Kastelein *et al.*, 2002). Female killer whales, also increase their food intake during the nursing period (Kastelein *et al.*, 2003).

Transition from milk to solid food
The two calves in the present study began to eat some solid food at the ages of 6 and 19 months respectively. Previous observations varied from 7 to 18 months (Peddemors *et al.*, 1992; Reddy *et al.*,
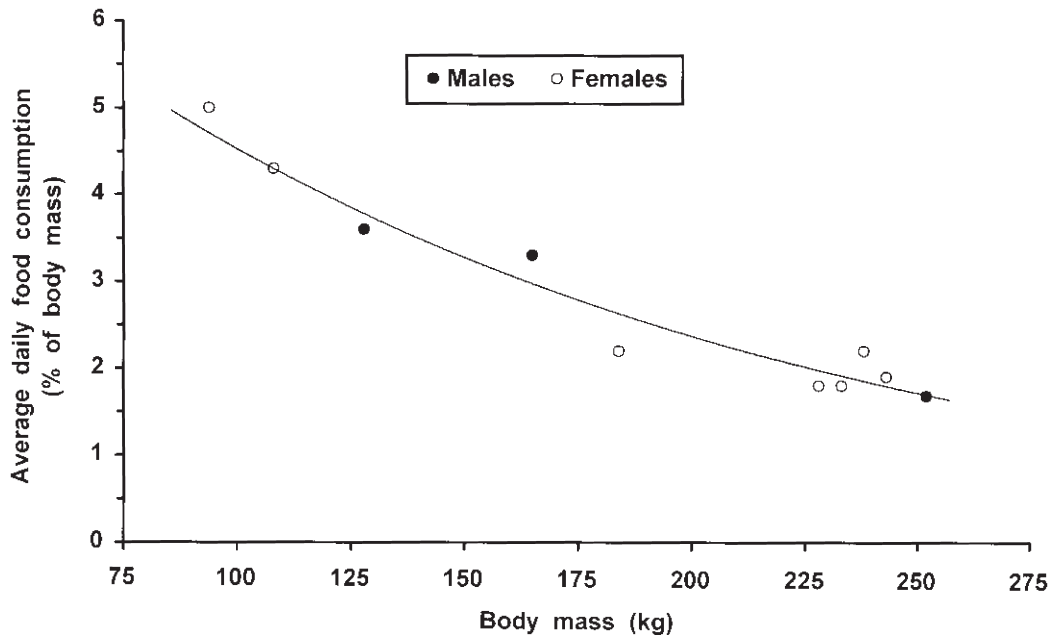
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Figure 7. Body mass versus the daily food consumption as a percentage of body mass for three male and seven non-pregnant, non-lactating female bottlenose dolphins (one data point per animal).

1994; Kastelein *et al.*, 2002). In the present study, suckling continued until the ages of 26 and 34 (forced weaning) months, whereas in previous studies, the suckling time per day decreased strongly after the age of 4 months, and calves were usually completely weaned by 18 months of age (McBride & Kritzler, 1951; Essapian, 1953; Prescott, 1977; Peddemors *et al.*, 1992). In the wild, calves sometimes suckle for considerably longer (Connor *et al.*, 2000). However, in the above-mentioned studies, the moment of weaning is defined as the last time suckling was observed, whereas in the present study it was defined (energetically) as the time at which the food intake of the mother D23 returned to the pre-reproduction level. Kastelein *et al.* (2002), using the same definition for weaning as in the present study, found that lactation periods in captive bottlenose dolphins varied between 14 and 37 months (n=6 calves).

Body measurements
At birth, the average body length of 116 cm for males and 114 cm for females, and body masses of 18.0 kg for males and 15.6 kg for females, fall within the range of observations for neonatal bottlenose dolphins from the north-west Atlantic Ocean, which averaged 117 cm and 21.2 kg (Mead & Potter, 1990). In the present study, no body measurements of dolphins between birth and wean-

ing were available, because handling could have interfered with lactation. Consequently, there are no records of lengths between 120 and 200 cm or body masses between 20 and 90 kg. However, using photographs of live animals against a background grid, Cockcroft & Ross (1990*b*) showed body length to increase from 109 to 215 cm between birth and the age of 2.5 years.

In the present study, the sample size is too small to detect sexual dimorphism in standard body length. In addition, the age estimates are too inaccurate to investigate differences between animals of similar age of different sexes. Sexual dimorphism in body length exists in wild bottlenose dolphins; generally males are larger than females (Tolley *et al.*, 1995; Connor *et al.*, 2000). The body length of both sexes in the present study appeared to reach an asymptote between 260 and 280 cm. This is within the range of body lengths reported for wild bottlenose dolphin populations. Asymptotic body lengths (230–290 cm) vary geographically and depend on the age and sex composition of the samples the studies are based on (Sergeant *et al.*, 1973; Solangi & Dukes, 1983; Kasuya *et al.*, 1986; Ross, 1977; 1984; Mead & Potter, 1990; Read *et al.*, 1993).

A spurt in weight gain in male bottlenose dolphins was found at sexual maturity (Ridgway & Fenner, 1982; Read *et al.*, 1993). This apparent

growth spurt could be the result of an increase in testosterone levels during puberty. Sexual maturity in males is reached between 8 and 13 years, and in females at 7 to 10 years of age (Schroeder, 1990; Whitehead & Mann, 2000). The animals in the present study were weighed and measured too infrequently to detect a growth spurt at puberty.

The relationship between body length and body mass in the present study is similar to that found by Mead & Potter (1990) in dead wild bottlenose dolphins stranded off the central Atlantic coast of the USA and reported by Ridgway & Fenner (1982) and Kastelein *et al*. (2002) for individuals in captivity.

Food consumption as a percentage of body mass
A negative relationship was apparent between body mass and average daily food intake, expressed as a percentage of body mass. Food intake per kg body mass in non-pregnant, non-lactating bottlenose dolphins also has been shown to decrease with age (i.e. body mass; Reddy *et al*., 1994; Kastelein *et al*., 2002). Previous studies on bottlenose dolphins reported average food consumptions of between 3 and 6.5% of body mass per day (Sergeant, 1969; Shapunov, 1971; Spotte & Babus, 1980; Barros & Odell, 1990; Peddemors *et al*., 1992). Differences between the present study and the above-mentioned studies could be due to differences in basal metabolic rate, water temperature, activity levels, caloric value of the diets, growth stage, or reproductive status (lactating or non-lactating).

Passage time of food through the digestive tract
Although the sample size is small, the passage times of carmine red through the digestive tract of Atlantic bottlenose dolphins in the present study agree with the body mass to passage time relationship of seven other odontocete species (Kastelein *et al*., 1993a, 1994, 1997, 1999, 2000a,b). The mean initial passage time in the seven species ranged from 140 to 250 min.

Ecological significance
A positive relationship exists between dolphin body mass and mean prey length and between body mass and stomach volume (Cockcroft & Ross, 1990a). This suggests that larger dolphins take larger prey. The average daily food consumption of animals in the present study was compared with the stomach volumes of animals of similar body mass reported by Cockcroft & Ross (1990a). This showed that 60-kg animals must fill their stomachs three times a day to obtain their daily energy requirement; 100-kg animals twice a day. Animals weighing

≥ 140 kg can obtain their daily requirement in one meal. In conjunction with previously discussed estimates from stomach content analysis (Barros & Odell, 1990), this suggests that only large individuals will need to feed less frequently than once a day.

Differences between food intake reported in the present study and that of wild animals of similar size, gender, and reproductive state, are likely to be caused mainly by differences in water temperature, digestibility, and caloric content of food (Reddy *et al*., 1994), and the activity levels of the dolphins.

The thermoneutral zone (i.e., the water temperature range in which metabolic rate is lowest) of the bottlenose dolphin varies with the thickness of blubber (Williams & Friedl, 1990; Williams *et al*., 1992b). Because the bottlenose dolphin is found worldwide, in tropical and temperate waters, it is subjected to a wide range of water temperatures (Mead & Potter, 1989) with average monthly sea surface temperatures varying from 1.2 to 29.5°C (Fig. 1). The water temperatures in which the animals in the present study were kept lay within the range that conspecifics may experience in the wild (Fig. 1). The study animals therefore, were probably maintained within their natural thermoneutral zone, and probably required similar amounts of energy for thermoregulation as most wild conspecifics.

The bottlenose dolphin has one of the widest distributions of all odontocetes (Martin, 1990), and its diet varies greatly with geographical area, seasonally, and annually (Barros & Odell, 1990; Cockcroft & Ross, 1990a; Corkeron *et al*., 1990; Mead & Potter, 1990). It is therefore difficult to compare the diet of the animals in the present study with that of conspecifics in the wild. Nonetheless, the diet in the present study consisted of fish with a high caloric energy content, so wild conspecifics probably have a diet of similar or lower caloric value.

The animals in the present study swam almost constantly, exercised in play, and were active during training programs and performances. It is impossible to determine differences in energy use for locomotion between the study animals and wild conspecifics. However, wild bottlenose dolphins need to forage for food. Only very little information is available about the energetic requirements of locomotion in bottlenose dolphins (Williams *et al*., 1992a). The difference in energy expenditure between surface swimming and diving is not yet well understood (Williams *et al*., 1996).

On the basis of differences in diet and activity between animals in the present study and wild conspecifics, wild bottlenose dolphins probably consume more than the animals in the present study. The food intake data reported here (in kg)

therefore, can be used only to calculate a conservative estimate of the amount of fish consumed by Atlantic bottlenose dolphin populations in the wild.

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