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Food consumption and body measurements of Amazon river dolphins (*Inia geoffrensis*)

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Abstract

This report is on the food consumption of 3 male Amazon river dolphins which were housed in water of between 27 and 29°C at Duisburg Zoo, Germany. The food consumption of 2 animals was recorded for 17 successive complete calendar years, that of the third animal for 3 complete successive years. In male 002 the total annual food intake increased to 1280 kg at the age of 10 years, after which it decreased slightly and stabilised at around 1170 kg/year. Male 001 was adult on arrival at the zoo. His annual food intake fluctuated at around 1200 kg. Male 003 consumed around 930 kg/year during his third and fourth year. The food intake fluctuated during the year and was often low in February. Between the ages of 26 and 31 years, adult male 001 had a body length of 232 cm, an estimated weight of 145 kg, and consumed on average around 2.5% of his body weight daily. At the age of 12 years, male 002 was 200 cm long and weighed an estimated 95 kg. That year he ate on average 3.4% of his body weight daily. When he was 17 years old he was 212 cm long, weighed an estimated 105 kg and ate on average 3.1% of his body weight daily. The initial passage time of carmine red dye through the gastrointestinal tract of the 2 adult animals was on average 250 min. The 2 adult males breathed on average 6.7 and 7.3 times per 5 min.

Introduction

The Amazon river dolphin or boto (*Inia geoffrensis*) is found in the Amazon and Orinoco river basins. It inhabits slow and fast flowing rivers, side channels, lakes, and flooded forests and grasslands. The principal limits to its distribution seem to be impassable rapids and cold waters in small tributaries at the headwaters of the Amazon basin in the Andes (Best and da Silva, 1989). Although the Amazon river dolphin is the most widespread freshwater dolphin in the world, its distribution is limited compared to that of most marine odontocetes and it is therefore very likely to become a threatened species. For the management of Amazon river dolphins in the wild, information is needed about the population size, age composition and sex ratio, seasonal distribution, diet, energy requirements relative to seasonal prey distribution and density, and about competition with other animals and with fisheries. This information could facilitate prey management to allow for a certain number of Amazon river dolphins in their distribution area.

The Amazon river dolphin is a generalist feeder whose diet is known to include over 50 fish species. Fish types taken by Amazon river dolphins (mainly sciaenids, cichlids and characins in order of importance) and their proportions in the diet have been described by Best and da Silva (1989; 1993).

Very little is known about the energetic requirements of individual odontocetes of various ages and sizes, as it is, at present, impossible to measure their energetic requirements in the wild. Such information should therefore come from captive animals. The present study describes the food consumption of Amazon river dolphins kept at Duisburg Zoo, Germany.

Materials and methods

Study animals

The study was done on 3 male Amazon river dolphins housed at Duisburg Zoo. The animals are from the Venezuelan Amazon and arrived at the zoo in 1975. On arrival, male 001 was judged to be 15 years old, male 002 one year old, and male 003 two years old. Age estimates were based on the length of the animals and the fact that male 002 was still fully dependent on mother's milk, but soon after arrival started to eat fish. Morphological

measurements of animals 001 and 002 were taken on 31 October 1986 and on 10 July 1991.

Study area
The indoor pool complex consisted of a main pool (6.8 m × 5.5 m; 1.7 m deep) and an adjacent holding pool (2.7 m × 1.9 m; 1.7 m deep). The animals usually had access to both pools. The non-chlorinated fresh water was cleaned by means of a biological filter and U.V. light irradiation. During the study period the water was heated to 28°C (+or − 1°C). The air temperature varied between 26 and 36°C. Natural light came through several skylights, and the pool was artificially lit between 0730 and 1900h. U.V. irradiation continued 24 h a day in order to prevent algae growth. Duisburg Zoo is located at 6°45′E and 51°25′N.

Feeding
The animals were individually fed 2 or 3 times a day, usually with live fish or freshly killed fish. Based on weight, the diet consisted on average of 60% trout (*Salmo trutta*), 35% carp (*Cyprinus carpio*) and 5% tench (*Tinca tinca*). Marine mammal multi-vitamins were added to this diet daily, and the animals were always fed to satiation; i.e. until they started to play with the fish instead of swallowing it. They were in public view, but no trained animal presentations were given. All available food consumption records between 1975 and 1992 were analysed.

Passage time of food through the gastrointestinal tract
To measure the passage time of food through the gastrointestinal tract, gelatine capsules containing carmine red dye were fed to the dolphins in trout and carp. The capsules were offered at various times of the day, but never at night. After the dye was given, the animals were watched constantly, and the time when it appeared in the excreted faeces was recorded (initial passage time). Tests were conducted on males 001 and 002 between February and May 1993.

Respiration rate
In March and April 1993 the respiration rates of males 001 and 002 were recorded, each during 36 five minute periods.

Statistics
The seasonal fluctuations in food intake between years were tested with the Kendall's coefficient of concordance test. The average daily food intake of each month of a year was given a rank number from 1 to 12.

Results

Annual food consumption
Male 002's total annual food intake increased gradually to 1280 kg at the age of 10 years, after which it decreased slightly and stabilized at around 1170 kg/year (Fig. 1a). His food intake was elevated at the age of 15 years (1989). In this year the animal was given anabolic steroids and antibiotics for 4 weeks, because it was very lean due to pneumonia. The treatment was successful and the animal gained weight.

Male 001 was adult on arrival at the zoo. His annual food intake fluctuated at around 1200 kg (Fig. 1b). His low food intake in 1978 (at age 18) coincided with the death of pool mate 003 from pneumonia and with his own pneumonia. The high food intake in his 24th, 25th and 29th year coincided with 4-week treatments of pneumonia with anabolic steroids in combination with antibiotics. Both treatments were successful and the animal gained weight.

Male 003 only lived for 4 years at the zoo. In his 3rd and 4th year he consumed about 930 kg/year (Fig. 1c). This was about 170 kg more per year than male 002 ate at the same age.

Seasonal food intake fluctuations
When determining seasonal food intake fluctuations for male 001, food intake data from incomplete years in which he was sick or during which pool maintenance was carried out, were not considered (ages 18, 24, 25, 28 and 29 years). The food intake fluctuated during the year in a systematic seasonal pattern (Kendall's coefficient of concordance test: $\chi^2_r=21.78$, $P<0.05$). The food intake was often below average in February when an increase in sexual activity was observed (Fig. 2). In the following 6 months (March–August), he usually ate more than the monthly average. In September and November the animal usually ate less than the annual monthly average.

Between the age of 2 and 9 years (the period of growth), the food intake of animal 002 fluctuated systematically throughout the year (Kendall's coefficient of concordance test: $\chi^2_r=21.56$, $P<0.025$, Fig. 3a). When calculating the average seasonal food intake fluctuations for male 002 when he was adult (between the ages of 10–18 years), food intake data from incomplete years and years in which he was sick were not considered (ages 15 and 16 years). The food intake fluctuated during the year in a systematic seasonal pattern (Kendall's coefficient of concordance test: $\chi^2_r=31.57$, $P<0.001$). The food intake was often lowest in February when an increase in sexual activity was observed (Fig. 3b). In the following 8 months (March–October), he usually ate more than the monthly average. Between

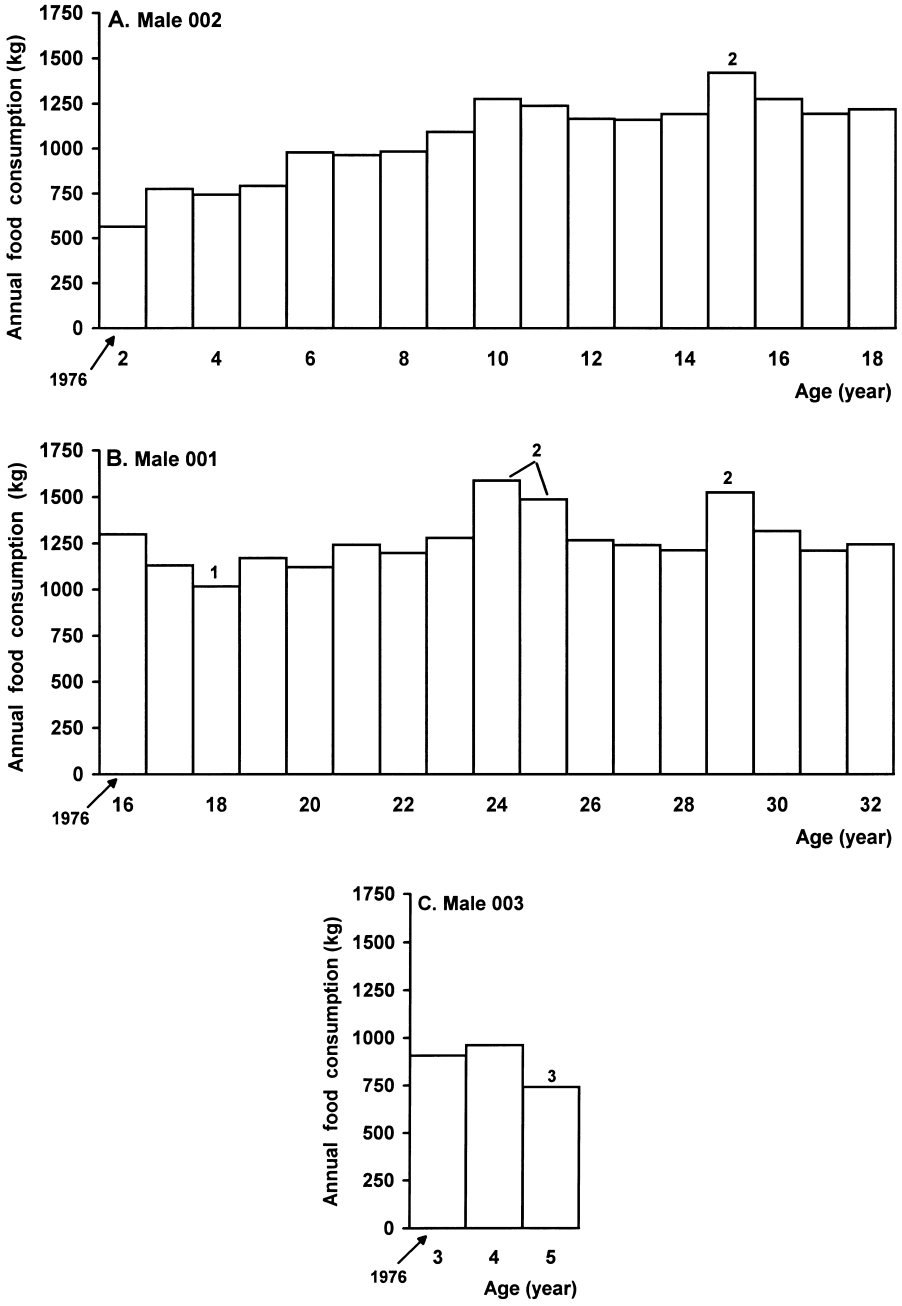

Figure 1. The annual food consumption of 3 Amazon river dolphins at Duisburg Zoo relative to age. (a) Male 002, (b) Male 001 and (c) Male 003. (1) A year in which the animal had pneumonia, (2) a year in which an anabolic steroid was administered to induce weight gain after pneumonia, and (3) A year during which the animal was ill (the animal died the day after this calendar year). Age 1 represents the first calendar year after birth.

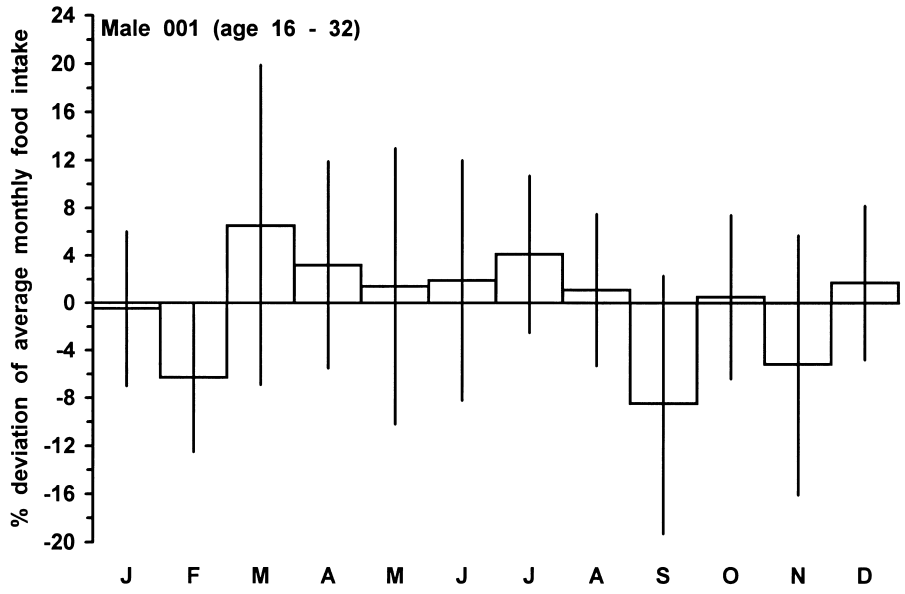

Figure 2. The average proportional deviation of the average monthly food intake of male 001 between the age of 16 and 32 years (years with illness or pool maintenance are not included; $n=11$). The bars indicate the standard deviations.

November and February the animal usually ate less than the annual monthly average.

Body measurements
The body shapes of animals 001 and 002 are shown in Fig. 4. Measurements show that between 31 October 1986 and 10 July 1991 male 002 was growing, while male 001's standard body length remained constant (Table 1).

Food consumption relative to estimated body weight
Adult males 001 and 002 were similar in body length to adult male Amazon river dolphins in the wild (Best and da Silva, 1989). Although the animals in the present study were never weighed, their body weight can be estimated by comparing their body lengths with healthy animals weighed and measured by Best and da Silva (1989). Between 31 October 1986 (age 26 yrs) and 10 July 1991 (age 31 yrs) adult male 001 had a body length of 232 cm, and weighed an estimated 145 kg. During that period he consumed on average around 2.5% of his body weight daily.

On 31 October 1986, 12-year-old male 002 had a body length of 200 cm and weighed an estimated 95 kg. That year he ate on average around 3.4% of his body weight daily. On 10 July 1991 he was 17 years old, 212 cm long, and weighed an estimated 105 kg. That year he ate on average around 3.1% of his body weight daily.

Maximum food intake per day
When adult, male 001's maximum daily food intake was 6.9 kg, that of male 002 was 5.5 kg.

Passage time of food through the gastrointestinal tract
The initial passage times of carmine red dye in animals 001 and 002 are shown in Table 2. The mean initial passage time was 250 min in the small sample number. No systematic variation in initial passage time could be detected in the 7 h of the day during which the animals received the dye.

Respiration rate
On average male 001 breathed 6.7 times per 5 min (SD: 2.1, $n=36$), and had an average respiration interval of 45 s. Male 002 breathed on average 7.3 times per 5 min (SD: 2.9, $n=36$), with an average respiration interval of 41 s.

Discussion and conclusions

Annual food consumption
The subadult male Amazon river dolphin 002 increased its average daily food intake until the age

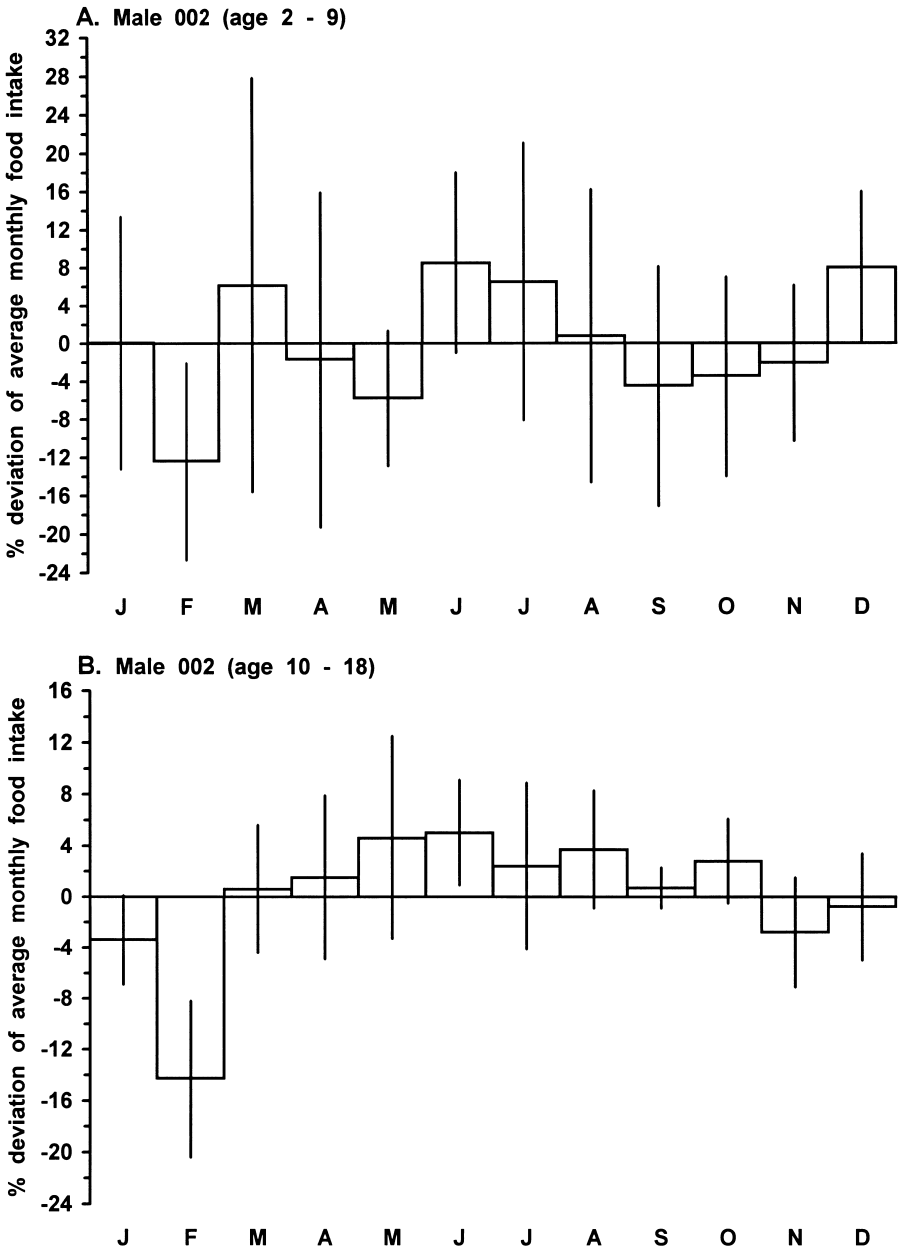

Figure 3. The average proportional deviation of the average monthly food intake of male 002. (a) While growing between the age of 2 and 9 years ($n=8$) and (b) between the age of 10 and 18 years ($n=7$). Years with illness are not included. The bars indicate the standard deviations.

of 10 years. Klocek (1981) describes a relatively constant weight gain of 4.8 kg/yr before sexual maturity in an Amazon river dolphin in human care. In the wild, males reach sexual maturity between the age of 10 and 12 years, at a body length of about 198 cm, when testicular weight is in excess of 0.4% of body weight (Best and da Silva, 1989). This suggests that testosterone plays a role in the growth spurt during the period that the males become sexually mature. On 31 October 1986, with a body length of 200 cm and at the age of 12 years, male 002 was probably just mature. Two years

Figure 4. Adult males 001 and 002 at Duisburg Zoo. Note the relatively large pectoral fins, and the low and broad dorsal fins (Photo: Bernhard Neurohr).

before this he ate a great deal, perhaps to power a growth spurt. Unfortunately the animal was not weighed or measured during that period. A sudden body mass increase of 21.9 kg/yr has been recorded in an Amazon river dolphin in human care (Herald, 1967). After male 002 reached maturity, his food intake stabilised.

Seasonal food intake fluctuations

In the present study, fish weights are compared without reference to the composition or caloric content of the fish. Fish species have different calorific values, and even in different regions or seasons a species may vary in composition and caloric content. Since their arrival, the Amazon river dolphins at Duisburg Zoo have eaten live and freshly killed fish from a fish farm. This origin probably reduced seasonal differences in the fish's composition and energetic value to some extent relative to that of wild fish.

Wild Amazon river dolphins move seasonally, following fish migrations and the annual flood cycle. In the dry season they are restricted to deep channels, while during the wet season (December to June) they are found along the edges of flooded meadows and forests, and often at the confluence of tributaries (Best and da Silva, 1989). The reduced food intake of the adult Duisburg dolphins in November coincides with April in the southern hemisphere; the middle of the wet season. Maybe in this period fish density in the river basins is low because the rivers are in spate. Although this is highly speculative, seasonal changes in hormone levels may reduce appetite in periods of low food availability.

In the wild, Amazon river dolphins are born between May and July. This coincides with peak river levels at the start of the dry season and is just before the time of highest food availability, as fish are driven from inundated forests by falling water levels (Best and da Silva, 1984). Gestation lasts 10–11 months (Caldwell *et al.*, 1966; da Silva, 1994), so that mating occurs from June to September. Assuming a 6 month shift in activity due to the 6 month shift in light cycle between the southern and northern hemispheres, mating should occur between December and March at Duisburg. The reduced food intake of the males at Duisburg in February may be due to changes in reproductive hormones. In Commerson's dolphins (*Cephalorhynchus commersonii*), an odontocete which only lives in waters on the southern hemisphere, a 6 month shift in breeding season was seen after transport to the northern hemisphere (Kastelein *et al.*, 1993*a*).

Body measurements

Compared to the bottlenose dolphin (*Tursiops truncatus*), the Amazon river dolphin has a dorsal fin which is short (measurement 18 in Table 1), but broad at the base, relatively large pectoral fins (measurements 16 and 17 in Table 1) and a long rostrum (measurements 10 and 11 in Table 1). The short dorsal fin prevents the Amazon river dolphin from becoming stuck in terrestrial vegetation which

Table 1. Body measurements (cm) of 2 male Amazon river dolphins at Duisburg Zoo

Animal	002	002	001	001
Estimated age (year)	12	17	26	31
Date of measurement	31-10-86	10-7-91	31-10-86	10-7-91
1. Tip upper jaw to deepest part of fluke notch	200	212	232	232
2. Tip of upper jaw to centre of anus	105	—	106	—
3. Tip of upper jaw to centre of genital slit	97	—	98	—
4. Tip of upper jaw to centre of umbilicus	93	—	94	—
5. Tip of upper jaw to top of dorsal fin	135	—	145	—
6. Tip of upper jaw to anterior insertion of right flipper	59	—	61	—
7. Tip of upper jaw to centre of blowhole	23	—	33	—
8. Tip of upper jaw to right external auditory meatus	40	—	45	—
9. Tip of upper jaw to centre of right eye	38	—	30	—
10. Tip of upper jaw to angle of gape	31	—	28	—
11. Tip of upper jaw to apex of melon	—	21	—	—
12. Length of right eye	0.8	—	0.8	—
13. Centre of eye to right external auditory meatus	14	—	16	—
14. Blowhole width	3.5	—	4	—
15. Right flipper width	22	22	24	25
16. Right flipper length: tip to anterior insertion	45	48	44	50
17. Right flipper length: tip to axilla	36	39	36	38
18. Dorsal fin height	9	—	13	—
19. Fluke span	46	48	51	56
20. Notch of fluke to centre of anus	—	70	—	91
21. Notch of fluke to nearest point on leading edge of flukes	16	20	19	22
22. Girth at anus	67	76	71	64
23. Girth at axilla	87	—	90	—
24. Girth immediately in front of dorsal fin	107	111	117	114

Table 2. Initial passage times of carmine red dye through the digestive tract in 2 adult male Amazon river dolphins at Duisburg Zoo in 1993

Animal	Date	Time of day dye fed (h)	Initial passage time (min)
001	01 March	15.00	242
001	16 April	10.25	230
002	26 February	08.25	268
002	28 February	08.23	247
002	14 April	10.20	275
002	17 April	15.17	239

is flooded, and the large pectoral fins allow it to manoeuvre in small spaces (Fig. 4). Only a few body measurements of Amazon river dolphins have been published, some of which are from sub-adult animals (Layne, 1958; Pilleri and Gihr, 1969; Tobayama and Kamiya, 1988; Boede *et al*., 1998).

Food consumption relative to estimated body weight

When kept in water of 28°C, adult male 002 ate on average about 3.1% of his estimated body weight per day, while male 001 ate on average about 2.5% of his estimated body weight. This difference may be due to a lower body weight of male 002 compared to that of male 001, and thus a smaller volume to surface area ratio, and/or to differences in individual metabolic rate.

Tobayama and Kamiya (1988) describe an adult male Amazon river dolphin which was in human care for over 16 years. He ate on average 2.5% of his body weight in mackerel (*Scomber scombrus*) daily, while kept in water of around 24°C. Best and da Silva (1989) describe a daily food consumption of 2.2–4.0% of the species body weight. However, they do not mention the ages and sex of the animals, or the temperature of the water in which the animals were kept. They conclude that Amazon river dolphins have a low metabolic rate due to the low thermal demand of their environment.

Figure 5. Male 001 at Duisburg Zoo with 2 fish in its mouth. Note the long rostrum (Photo: Bernhard Neurohr).

The Amazon river dolphin's food intake as a proportion of body weight is difficult to compare with that of other odontocete species, because the river dolphins are generally kept in warmer water than other species. Comparison must therefore be approached with caution, although as a general rule, smaller species would be expected to have higher proportional food intakes than larger species. For instance, adult harbour porpoises (*Phocoena phocoena*) weighing about 35 kg eat around 8% of their body weight per day in water of 17–20°C (Andersen, 1965; Kastelein *et al*., 1990; 1997*a*), whereas adult Commerson's dolphins weighing about 40 kg eat 10% of their body weight per day in water of 11–16°C (Kastelein *et al*., 1993*b*). Belugas (*Delphinapterus leucas*) of 200 kg ate 4.5% of their body weight per day and those of 1400 kg 1.2% while in 11°C water (Kastelein *et al.*, 1994), and a 1900 kg killer whale (*Orcinus orca*) ate 2% of her body weight while kept in water of 15–22°C (Kastelein and Vaughan, 1989).

Maximum food intake per day

Adult male 001 required on average 3.3 kg of fish a day, but he sometimes ate 6.9 kg per day. When adult, male 002 required on average 3.2 kg of fish a day, while he sometimes ate 5.5 kg/day. This indicates that the Amazon river dolphin is adapted to exploit unevenly distributed food sources by eating enough food during one day to provide energy for about 2 days. It can also use its large stomach to profit from large seasonal fluctuations in food availability by eating an excess of energetic needs when food is available. Fat can be stored and used during periods of low food availability.

Amazon river dolphins catch fish with their anterior teeth, then transfer them to the stronger posterior teeth to crush them and swallow the head first (Fig. 5). Larger fish are torn to pieces, the head being shaken off before ingestion (da Silva, 1983). This means that Amazon river dolphins are not restricted to fish that can pass whole through the oesophagus. This is a limitation for many other odontocetes. The long rostrum, the flexible neck and the molar-like rear mastication teeth of Amazon river dolphins appear to be adaptations to their feeding technique. The large forestomach of the Amazon river dolphin may also be an adaptation for taking large prey.

Passage time of food through the gastrointestinal tract

Although the sample size is small, the present study indicates a relatively slow passage of food in Amazon river dolphins in relation to body weight, compared to in other odontocetes which were tested with the same dye (Kastelein *et al.*, 1993*a* and *b*, 1994, 1997*b*, 1999, 2000 *a*, *b* and *c*).

Intestinal length of Amazon river dolphins can be calculated with the formula: intestinal length

(m) = 4.598 + 15.299 × body length (m) (da Silva, 1983). This results in intestinal lengths of 40.1 m for male 001 and 37 m for male 002. The total digestive tract length (mouth to anus) can be estimated by adding 1.1 m (distance from the base of the tongue to the small intestine) to these numbers, making 41.2 m for 001 and 38.1 m for 002. The average passage speed of carmine red through the entire digestive tract is therefore 0.29 cm/s for male 001 (mean passage time: 236 min) and 0.25 cm/s for 002 (mean passage time: 257 min). However, this calculation may not be valid, as the digesta velocity usually varies per compartment of the digestive tract (Warner, 1981). Compared to terrestrial carnivores the digestive tract of the Amazon river dolphin is very long, especially considering that it consumes easily digestible fish.

Respiration rate

Similar to the animals in the present study, a male Amazon river dolphin in an oceanarium in Japan had an average respiration interval of about 42 s, while a female breathed at intervals of just over 30 s (Tobayama and Kamiya, 1988). Other respiration interval records for Amazon river dolphins in human care are 60–90 s for adults and 20 s for neonates (Layne, 1958; Layne and Caldwell, 1964; Caldwell and Caldwell, 1972; Trebbau, 1975). Wild Amazon river dolphins have been recorded to breathe at an average interval of 78 s (SD = 66.5 s, range: 8–210 s, $n = 38$) when hunting (Best and da Silva, 1989). Thus, the mean respiration intervals of the animals in the present study (41 and 45 s) are similar to those of other conspecifics in human care, and the mean respiration rate is within the range of rates measured for wild conspecifics.

Ecological significance

Whether the food consumption of wild adult male Amazon river dolphins can be estimated by using the results of the present study depends on the Amazon river dolphin's thermoneutral zone and the water temperatures it encounters in the wild. In addition its activity level in the wild is of importance.

The thermoneutral zone (temperature range at which the metabolic rate is lowest) is unknown for Amazon river dolphins. In the species' distribution area, water temperature varies between 23 and 30°C (Best and da Silva, 1989), and if the species is optimally adapted this may be its thermoneutral zone. The animals at Duisburg Zoo were probably kept within their natural thermoneutral zone, so the thickness of their fat layer may have been similar to that of wild conspecifics.

Because temperatures between 23 and 30°C are higher than those experienced by most other odontocetes, it would be of interest to know how Amazon river dolphins can dissipate enough heat to prevent heat stress during strenuous activity. To do this, most dolphins circulate more blood through the superficial layers of their fins and flukes (Scholander and Schevill, 1955). The Amazon river dolphin's pectoral fins are very large compared to those of most other odontocetes, and may play an important role in thermoregulation. In addition, the blubber layer in Amazon river dolphins is relatively thin (Bernhard Neurohr, pers. obs.).

The animals in the present study did not have to forage for food like their wild conspecifics, but they did have to catch live fish. They swam almost constantly, and exercised by playing with each other or with toys (Gewalt, 1989). In the wild this species usually swims at speeds of about 1.5–3.2 km/h and only makes shallow dives (Cabrera and Yepes, 1940; Layne, 1958; Klima *et al.*, 1980). These speeds are similar to those observed at other oceanaria (Defran and Pryor, 1980) and at Duisburg Zoo. However, the study animals' diving was limited by the depth of the pool.

Wild Amazon river dolphins feed both diurnally and nocturnally, but forage most actively between 0600 and 0900h and between 1500 and 1600h (da Silva, 1983). At Duisburg Zoo the animals were fed between 0800 and 1630h, which is, to some degree, comparable to their natural feeding schedule.

The similarities in parameters which may influence food intake in the wild and at Duisburg Zoo suggest that the food intake of the male Amazon river dolphins in the present study may be comparable to that of their wild conspecifics. The information provided is not only of value for husbandry purposes, but also for conservation. Because this species is sexually dimorphic (adult males reach a length of 2.55 m, and weigh up to 160 kg, whereas females only reach 1.96 m and 96.5 kg (Best and da Silva, 1984)), the present study (based on the food consumption of males) cannot be used to estimate the food requirements of the females.

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