

Seasonal changes in food consumption, respiration rate and body condition of a male harbor porpoise (*Phocoena phocoena*)

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December 2016



Body weight/body measurements relationship
in harbour porpoises



Report:

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Seasonal changes in food consumption, respiration rate and body condition of a male harbor porpoise (*Phocoena phocoena*)

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Summary

Seasonal changes in food consumption, respiration rate and body condition in a healthy male harbor porpoise (*Phocoena phocoena*) from the North Sea were recorded, along with water and air temperature. The animal had previously stranded and had been rehabilitated. He was kept in a large pool at water and air temperatures similar to those experienced by wild conspecifics in the nearby North Sea. At the age of approximately 3 years and 10 months, the porpoise's body length stabilized at around 148 cm. Body mass was considered the best indicator of body condition. Between the ages of 2 years and 5.5 years the study animal's body mass increased to around 40 kg, after which fluctuated by 5-10 kg. His food consumption varied between ~1200 g/day and ~4400 g/day, but was generally ~2400 g/day. His energy intake varied between ~9000 kJ/day and ~26000 kJ/day, but was generally ~18000 kJ/day. He consumed ~7% of his body mass in food daily. Once his body length had stabilized, the mean daily respiration rate of porpoise 02 was between ~17 and 26 respirations/5 min. Correlation analysis revealed that both when he was growing rapidly and after his body length stabilized, the porpoise's food consumption decreased as his body mass increased. His respiration rate and body mass declined with increasing water temperature, and his respiration rate increased with increasing food consumption. When he was stable in body length, his food consumption also decreased as the water temperature increased. Male harbor porpoises need different amounts of food depending on whether they are growing or adult, and depending on the season. Food consumption is highest in the winter. Seasonality in energy requirements should be taken into account in energetics studies on harbor porpoises. Depending on the food availability at sea (which probably fluctuates as well), harbor porpoises may be more or less vulnerable to disturbances that decrease their foraging efficiency at various times of the year. Based on food intake information derived from another small odontocete species living in temperate waters, the Commerson's dolphin (*Cephalorhynchus commersonii*), female harbor porpoises are expected to require 30% more energy when they are lactating (~July-March). With the information from this study, experts will be better informed when a new expert elicitation is conducted for the Interim Population Consequences of Disturbance (iPCoD) model.

Key words: Energetics, Food intake, Foraging ecology, Fisheries, Growth, Marine mammals, Metabolism, Nutrition.

Introduction

Anthropogenic activities at sea often cause underwater sound that may affect marine fauna. Sound may affect their hearing, causing temporary hearing threshold shift (TTS) or permanent hearing threshold shift (PTS), mask ecologically relevant sounds, or change the behavior of animals in such a way that their foraging efficiency decreases. Regulators need to assess whether or not such disturbances affect the population dynamics of a species. Models, such as the Population Consequences of Acoustic Disturbance model (PCAD, National Research Council, 2005), the Interim Population Consequences of Disturbance model (iPCoD; Harwood et al., 2014; King et al., 2015) and the Disturbance Effects of Noise on the Harbour Porpoise Population in the North Sea model (DEPONS; Nabe-Nielsen et al., 2014), are being developed to estimate population dynamics effects. Important input parameters for these models are the energetic needs of a species, the relevant food availability, and other parameters affecting the vital rates (birth rate and death rate). So far, most of the information needed is lacking for most marine mammal species, though estimates have been made by an expert elicitation method (Donovan et al., 2016).

The harbor porpoise (*Phocoena phocoena*) is especially susceptible to disturbance by underwater sound. It has been shown to react to pile driving sound (Carstensen et al., 2006; Brandt et al., 2011; Dähne et al., 2013) and sounds from seismic surveys (Thompson et al., 2013; van Beest et al., in prep). It inhabits the cold waters of the northern hemisphere (Kanwisher and Sundnes, 1965; Gaskin, 1992) and is a relatively small odontocete. Though harbor porpoises have relatively small appendages and dorsal fins (Ryg *et al.*, 1993), compared to larger odontocetes they have large body surface area to volume ratios due to their small size, so they lose a great deal of energy through radiation and conduction to the surrounding water (Feldman and McMahon, 1983). In order to maintain a stable internal body temperature, they need to consume sufficient food. The harbor porpoise has a higher metabolism than terrestrial mammals of similar size (Kanwisher and Sundnes, 1965 and 1966; Kanwisher, 1971; Reed et al., 2000). The initial food passage time is short: ~1.5 hrs (Kastelein et al., 1997e). To ingest sufficient energy, harbor porpoises need to feed often; wild harbor porpoises consume up to 550 small prey items per hour (Wisniewska et al., 2016). The high prey number and low energetic content per prey item suggest that these high feeding rates are necessary for survival, and even a small decrease in foraging efficiency due to an anthropogenic disturbance may have large fitness consequences. Harbor porpoises represent one end of a continuum of odontocete life histories that spans a wide diversity of strategies. In comparison with other, larger, odontocetes, harbor porpoises mature at an earlier age, reproduce more frequently, and live for shorter periods (Read and Hohn, 1995).

In order to predict the effect of a disturbance on the fitness of harbor porpoises, information is needed about the energetic requirements of this species. The food consumption of harbor porpoises in captivity has been described by Dudok van Heel (1962), Andersen (1965), Myers *et al.* (1978), Koga (1991), and Kastelein *et al.* (1990; 1997), but only a few animals have been kept in sea water with a naturally fluctuating water temperature (Lockyer et al., 2003; this study spanned only three years). More information is needed from more individuals, and over longer periods of time.

At the SEAMARCO Research Institute in the Netherlands, a male harbor porpoise was kept for 8.5 years (a record period), in natural sea water, at naturally fluctuating water and air temperatures, and was fed on a diet similar to that of some conspecifics in the wild, so his body mass and food intake fluctuations are likely to resemble those of wild conspecifics. The aim of this study was to quantify growth and seasonal fluctuations in food consumption, respiration rate and body condition in this captive harbor porpoise, and to investigate

correlations between body condition parameters and seasonally varying temperature. The results of this study will form the basis for future experimental energetics studies on harbor porpoises.

Materials and methods

Study animal and study area

The male harbor porpoise (identified as no. 02) had been found stranded on the North Sea coast. His age was estimated based on his length (van Utrecht, 1978; Gaskin *et al.*, 1984) and the marginal papillae on his tongue indicated that he was young (Kastelein and Dubbeldam, 1990). Porpoise 02 was ~1.5 years old when he stranded. He was rehabilitated at SOS Dolfijn, at Dolfinarium Harderwijk, the Netherlands, after which he was housed for several months in an exhibit. He was then transported to the SEAMARCO Research Institute to participate in research, including this study.

The harbor porpoise was trained to allow weekly body measurements. At the time of the study, the animal was healthy, in good physical condition, and growing (rapidly at first, then much more slowly). Porpoise 02 was healthy during the entire study period, and data were available for a period of 7 years and 8 months, from the age of 2 years.

The porpoise was kept at the SEAMARCO Research Institute, the Netherlands (latitude 51°32'11.24"N, longitude 3°55'30.58"E; this latitude is within the geographical range of harbor porpoises, and 200 m away harbor porpoises are frequently observed in coastal waters), in a pool complex consisting of an outdoor pool (12 x 8 m; 2 m deep) connected via a channel (4 x 3 m; 1.4 m deep) to an indoor pool (8 x 7 m; 2 m deep). The bottom was covered with a 20 cm thick layer of sloping sand on which aquatic vegetation grew and invertebrates lived. Skimmers kept the water level constant. Seawater was pumped directly from the Oosterschelde, a lagoon of the North Sea, into the water circulation system; partial recirculation through biological and sand filters ensured year-round water clarity. The environmental conditions experienced by the captive study animal were similar to those experienced by wild conspecifics living in the Oosterschelde and in the North Sea.

Food consumption

The harbor porpoise was fed 4-5 times a day on a diet of thawed sprat (*Sprattus sprattus*), herring (*Clupea harengus*) and capelin (*Mallotus villosus*). Vitamins (Aquavit 100, Arie Blok, Animal Nutrition) were added to the thawed fish. Fish were fed at a temperature of ~4 °C. The fish were weighed digitally (2 g accuracy), and the mass of fish of each species eaten during each meal was recorded. The energy content of the fish species was quantified for each fish delivery by Parlevliet & van der Plas Inc., and in the present study food consumption was expressed both in kg and in kJoules per day. The daily food intake as a percentage of the body mass was calculated.

The animal received a basic food ration each day, which was adjusted at the end of each week when the animal was weighed, based on the animal's body mass and performance during psychophysical research projects during the previous week and the expected change in water and air temperatures in the following week. This kept the motivation to feed stable during the year.

Respiration rate and body condition parameters

Four times per day, the number of times the porpoise respired was counted during a period of 5 minutes. The daily mean respiration rate was used for the analysis.

Once a week at 0830 h, before the first meal of the day, the porpoise was asked to swim onto a ramp and was lifted and placed on a foam rubber mattress on a weighing platform. The following measurements were taken:

- 1) Body mass. The animal was weighed digitally (50 g accuracy).
- 2) Standard body length (straight line between tip of the upper jaw and notch of the tail fluke).
- 3) Girth at axilla.
- 4) Blubber thickness. For the purposes of this paper, blubber is defined as the epidermis, dermis, and hypodermal tissues (Parry 1949): the integument of terrestrial mammals. The blubber thickness of the study animals was measured ultrasonically with a Renco Lean-Meater®, which produced a 2.2 MHz, 3 or 4 cycle, dampened sinusoid with a pulse repetition rate of 200 Hz. The apparatus measured the distance between the skin surface and the underlying muscle layer with ± 1 mm accuracy. Blubber thickness was measured 10 cm ventral of base and at the onset of the dorsal fin (on the left side of the body).

Water and air temperature

The water temperature was measured once per day. The water temperature and salinity (~3.4‰) were similar to those of the nearby sea from which the water was pumped continuously during most of the day (**Fig. 1**). The minimum and maximum air temperatures over each 24 hr period were also recorded daily starting in May 2008 (**Fig. 1**).

Multicollinearity and association among the temperature variables were assessed by means of Pearson correlations. Over the period of the study, the water temperature was highly significantly correlated with the minimum, maximum and mid-range value for air temperature (Pearson correlations; $P < 0.000$ for all combinations). Since the water temperature was an excellent predictor of air temperature, and because the porpoises were mostly in the water, only water temperature was used in the analysis.

Data visualization and analysis

Food consumption, respiration rate, body condition parameters, and the water temperatures experienced by the study animal are described and plotted. The study period was divided into a period of relatively rapid increase in body length (rapid growth) and a period of relatively stable body length (stability or much slower growth). Separately for the periods of growth and stability, multicollinearity (which exists when two or more of the predictors in a model are moderately or highly correlated) and association among the 4 body condition variables were assessed by means of Pearson correlations. Relationships between the most appropriate body condition variables and food consumption, respiration rate and water temperature were also investigated by correlation analyses. The Bonferroni method was used to adjust for multiple correlations where appropriate (Altman, 1991); the significance level is 0.05 throughout. Statistical analyses were carried out on Minitab release 17 (Ryan and Joiner, 1994).

Results

Total body length and body mass

Porpoise 02 grew rapidly in total body length between his arrival at SEAMARCO at the age of 2 years and the age of 3 years and 10 months, after which the growth rate decreased and his body length stabilized at around 148 cm (**Fig. 1a**). Between the ages of 2 years and 5.5 years his body mass generally increased to around 40 kg, but it fluctuated by 5-10 kg (**Fig. 1b**).

Girth at axilla and blubber thickness

Porpoise 02's girth at axilla varied between 63 and 79 mm and was generally greatest between December and March, decreased from April to July, was lowest in August and increased from September to November (**Fig. 1c**). His blubber thickness varied between 15 and 32 mm (**Fig. 1d**).

Food consumption

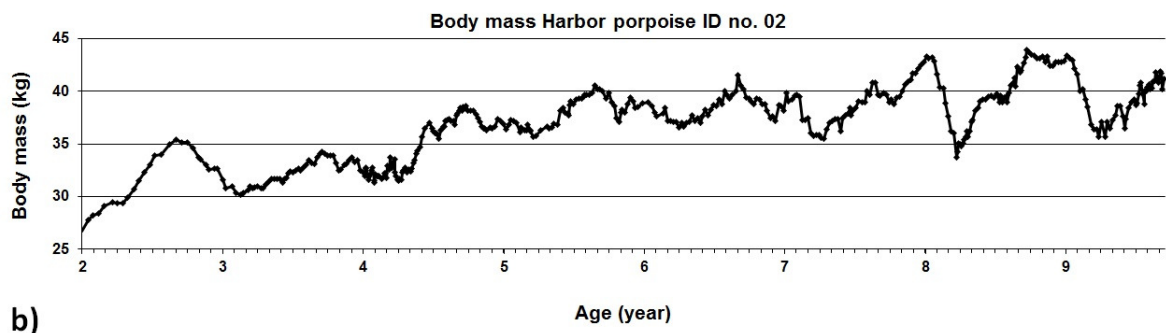
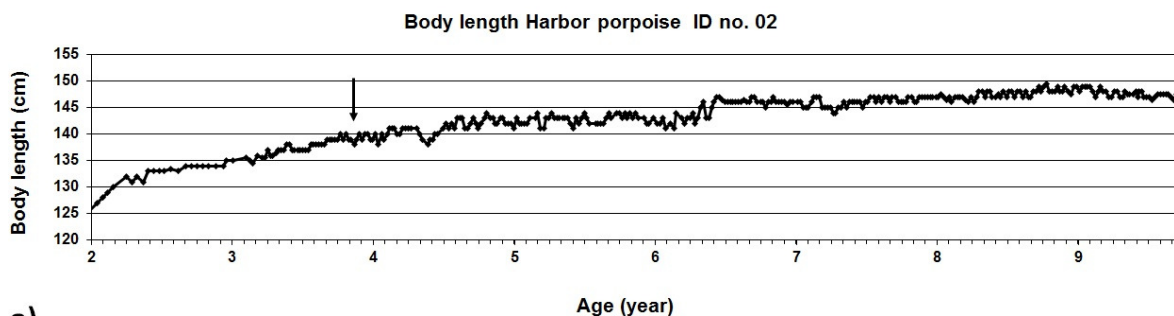
The food consumption of porpoise 02 (with the diet fed at SEAMARCO) varied between ~1200 g/day and ~4400 g/day, but was generally ~2400 g/day (**Fig. 1e**). His energy intake varied between ~9000 kJ/day and ~26000 kJ/day, but was generally ~18000 kJ/day (**Fig. 1f**). He consumed generally ~7% of his body mass in food daily (**Fig. 1g**).

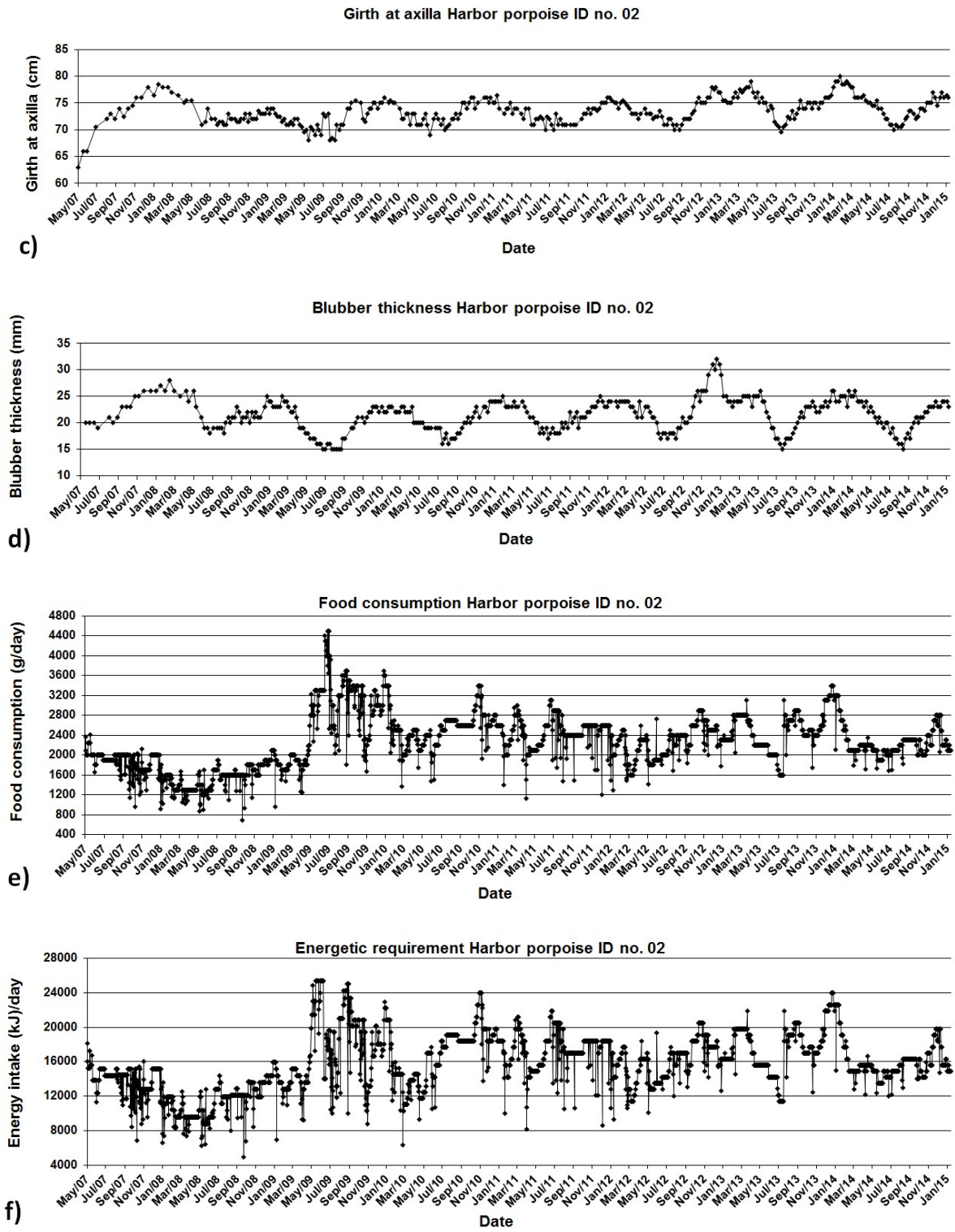
Respiration rate

The mean daily respiration rate of porpoise 02 was relatively high (around 25/5 min) during the second year of his period of body length growth, compared to during his period of stability in body length, and fluctuated during the following years between ~17 and 26 respirations/5 min (**Fig. 1h**).

Water and air temperatures

The water (**Fig. 1i**) and air (**Fig. 1j**) temperatures experienced by porpoise 02 showed seasonal fluctuations which varied slightly from year to year.





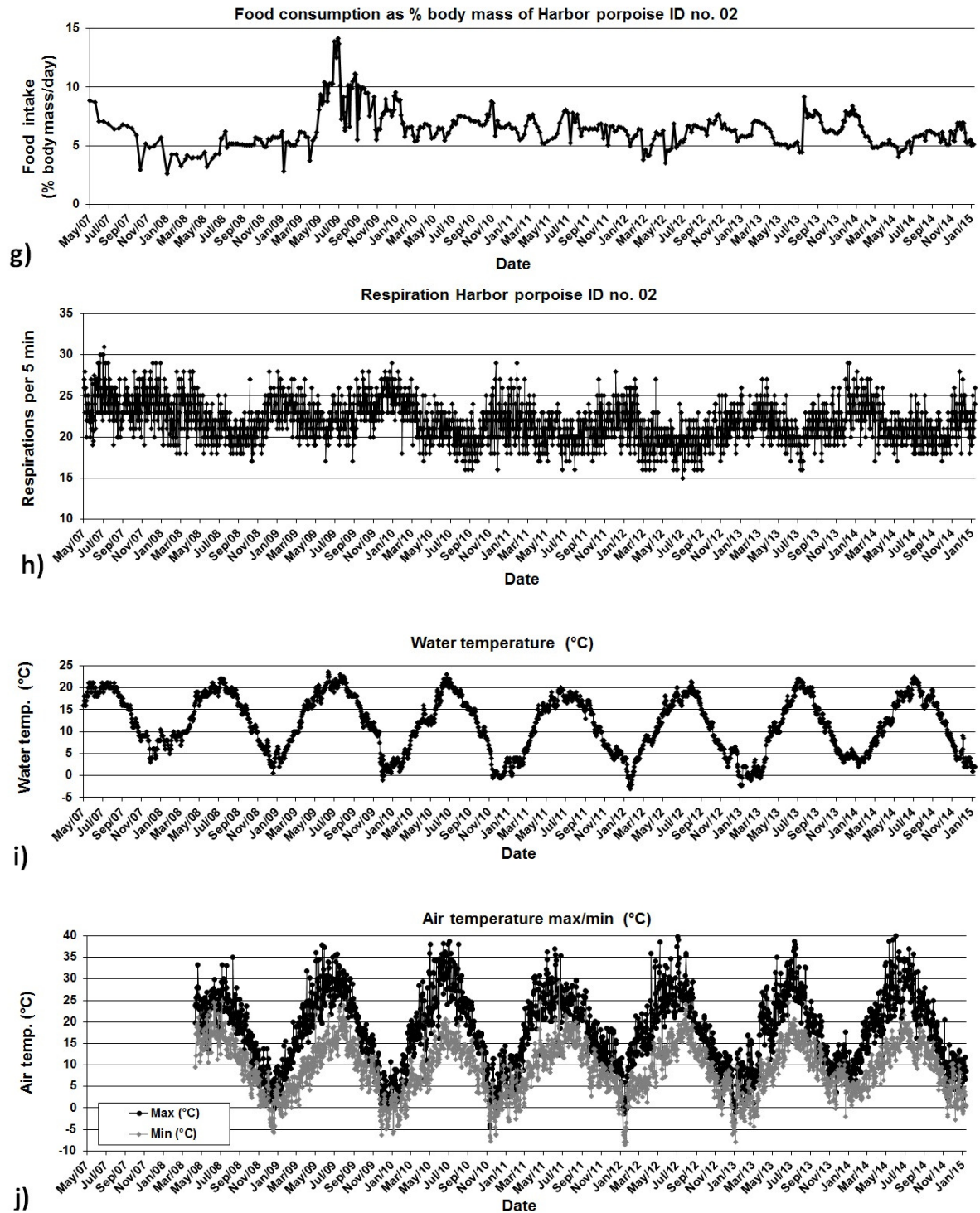


Figure 1. Body condition parameters, food consumption and respiration rate of male harbor porpoise 02 and the temperatures at which he was kept: a) body length, b) body mass, c) girth at axilla, d) blubber thickness (mm), e) food consumption (expressed in g/day), f) food intake (expressed in kJ/day), g) food intake (expressed as % of body mass/day), h) daily mean ($n = 4$) number of respirations per 5 min., i) daily water temperature in the pool, and j) daily minimum and maximum air temperature near the pool. Jan/10 means January 2010, etc. All figures are lined up so that the x-axis of age and date are synchronous. The arrow in a) indicates the end of the period of rapid growth in body length and the start of the period of relative stability in body length.

Correlations during the period of rapid growth

Correlation analysis to show associations between the body condition variables during the period of rapid growth in body length showed that body mass was a good predictor of girth at axilla and blubber thickness, but body length was not correlated with girth or blubber thickness (**Fig. 2**). Since body mass and body length were correlated (Pearson correlation coefficient: 0.591, $P < 0.000$, $n = 63$), further analysis was conducted on body mass only, as the best indicator of body condition.

Correlation analysis (**Table 1**) revealed that, when he was growing rapidly, porpoise 02's food consumption decreased as his body mass increased, and that both his respiration rate and body mass declined with increasing water temperature. Respiration rate increased with increasing food consumption.

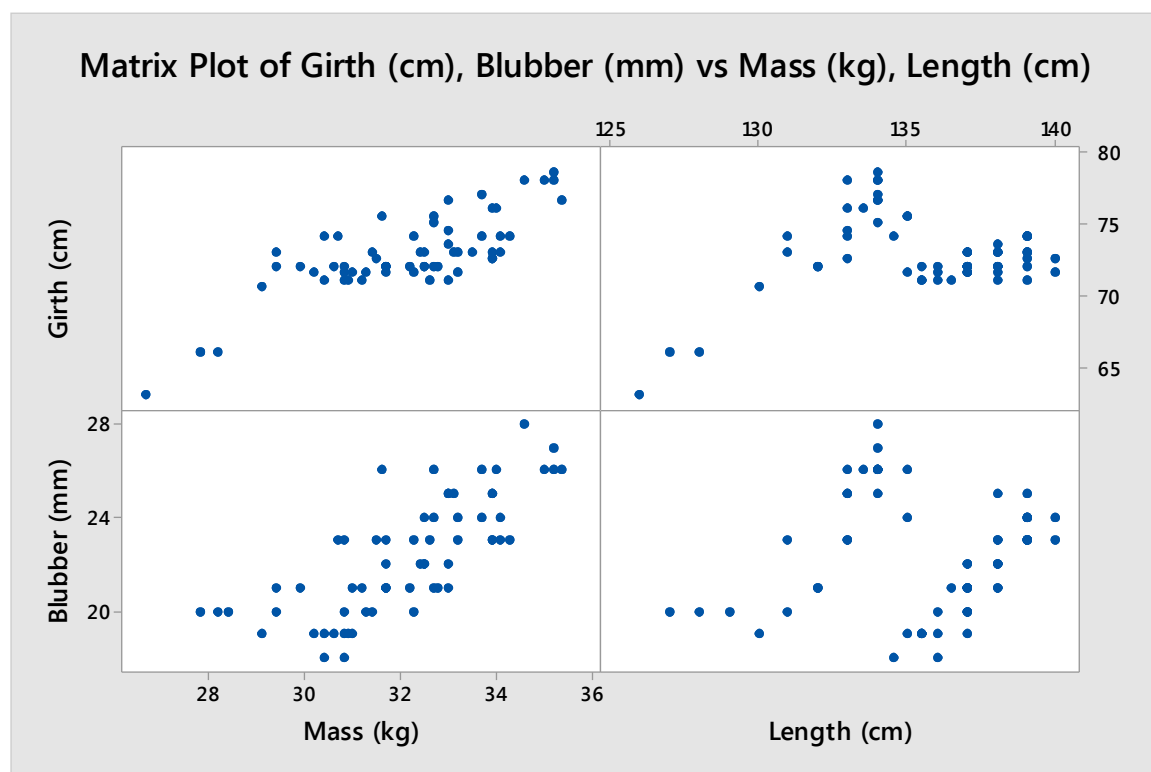


Figure 2. Matrix plot of body mass and body length vs girth at axilla and blubber thickness in male harbor porpoise 02 during his period of rapid growth in body length; $n = 61-63$.

Table 1. Results of Pearson correlation analysis between: food consumption (kJoules per day), respiration rate (over 5 mins, average per day), body mass (an indicator of body condition) and water temperature. Each cell shows the correlation coefficient, followed by the Bonferroni-adjusted P value (adjusted by multiplication by 6, as 6 related correlations were examined) or NS if the test was not significant after adjustment, followed by the sample size for the correlation. The data are divided into a period of rapid growth in body length and a period of stability, characterized by little increase in body length, as defined in the text.

Comparison	Rapid growth	Stability
Body mass vs. food consumption	-0.339, 0.024, n = 71	-0.150, 0.024, n = 368
Body mass vs. respiration rate	0.021, NS; n = 71	0.097, NS, n = 368
Food consumption vs. water temperature	-0.074, NS; n = 682	-0.129, 0.000, n = 2132
Respiration rate vs. water temperature	-0.139, 0.000; n = 682	-0.358, 0.000, n = 2130
Body mass vs. water temperature	-0.827, 0.000; n = 71	-0.618, 0.000, n = 368
Respiration rate vs. food consumption	0.285, 0.000; n = 682	0.191, 0.000, n = 2130

Correlations during the period of relative stability in body length

Correlation analysis to show associations between the body condition variables once growth had slowed down showed relationships similar to that during the period of rapid body length growth. Body mass was a good predictor of girth at axilla and blubber thickness (**Fig. 3**). Body mass and body length were correlated (Pearson correlation coefficient: 0.694, $P < 0.000$, $n = 283$). Further analysis was conducted on body mass only, as the best indicator of body condition.

Correlation analysis revealed that, while the porpoise was relatively stable in body length, food consumption decreased as his body mass increased. His food consumption, respiration rate and body mass all tended to decrease as the water temperature increased. His respiration rate increased with food consumption (**Table 1**).

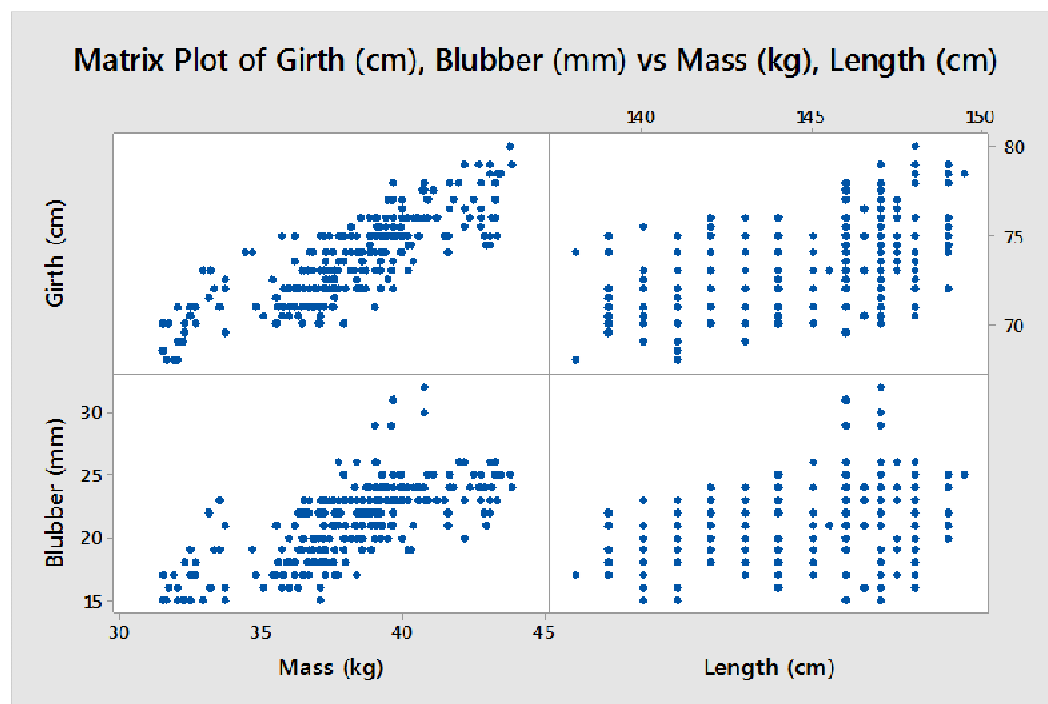


Figure 3. Matrix plot of body mass and body length vs girth at axilla and blubber thickness in male harbor porpoise 02 during his period of relative stability in body length; $n = 279 - 290$.

Discussion and conclusions

Validation

Diet

The diet of the study animal consisted of sprat, herring and capelin: species with a high energy content that are sometimes eaten by wild harbor porpoises. The natural diet of harbor porpoises consists mainly of smooth-rayed fish, especially gadoids and clupeoids of 10 - 25 cm in length. The diet varies geographically and seasonally, and differences in diet between sexes or age classes exist (Scott, 1903; Stephen, 1926; Orr, 1937; Wilke and Kenyon, 1952; Svårdson, 1955; Sergeant and Fisher, 1957; Fink, 1959; Lindroth, 1962; Rae, 1965 and 1973; Smith and Gaskin, 1974; Andersen, 1965; Tomilin, 1967; Smith and Gaskin, 1974; Recchia and Read, 1989; Silber and Smultea, 1990; Gearin *et al.*, 1994 Aarefjord *et al.*, 1995; Brodie, 1995; Teilmann and Lowry, 1996; Rogan and Berrow, 1996; Gannon *et al.*, 1998; Börjesson *et al.*, 2003; Víkingsson *et al.*, 2003; Santos *et al.*, 2004; Leopold, 2015). Shrimp (*Meganyctiphanes norvegica*) have been found in the stomachs of calves (Smith and Read, 1992). The diet provided to the study animal was within the range of the natural diet of harbor porpoises, so the conclusions from this study can be generalized.

Body length

At birth, the body length of harbor porpoises in the North Sea is 65-90 cm (Fisher and Harrison, 1970; Lockyer, 1995; Learmonth *et al.*, 2014). Weaning occurs at a body length of around 100-104 cm (Smith and Gaskin, 1973). Males reach their maximum length of approximately 146 cm at around the age of 10 years; females reach their maximum length of approximately 170 cm at around the age of 14 years. Sexual maturation occurs at 5-6 years of age when males are around 133 cm and females around 145 cm (Fisher and Harrison, 1970; van Utrecht, 1978; Gaskin *et al.*, 1984; Learmonth *et al.*, 2014).

Slijper (1958) presented the lengths and weights of 28 harbor porpoises from the North Sea. For porpoises of between 80 and 140 cm long, the body length-mass relationships of the animal in the present study and of those described by Slijper are similar. However, animals of more than 140 cm in length described by Slijper were heavier than the animal in the present study when he was the same length. Lockyer *et al.* (2003) report on captive porpoises of which the male's body length reached asymptote at around 139 cm, and the female's at 150 cm. The male in the present study seemed to reach asymptote at around 148 cm. Male porpoises from Icelandic waters grow to the asymptotic length of 150 cm (Ólafsdóttir 2002). For porpoises in the Bay of Fundy, asymptotic values for body length were 156 cm for females and 143 cm for males.

Thus, the body length of study animal was typical of a young male harbor porpoise. His period of rapid growth was similar to that of porpoises in the wild in the Bay of Fundy (Read and Tolley, 1997). He was hardly growing at the end of the study period.

Blubber thickness and girth at axilla

Blubber has several functions; it serves as an energy store and insulator, makes the body hydrodynamic, and contributes to buoyancy (Kipps *et al.*, 2002).

To compensate for their small size to some extent, harbor porpoises have evolved a relatively thick blubber layer (Parry, 1949; Read, 1990; Koopman, 1994; Lockyer, 1995; Kastelein *et al.*, 1997 b). Blubber can make up 45% of the body mass of porpoises from Danish waters (Slijper, 1958) and 31% in porpoises from near New Brunswick (Yasui, 1980). The blubber of harbor porpoises has a relatively high lipid content and therefore a relatively low thermal conductance compared to that of other cetaceans (Worthy and Edwards, 1990).

Conductivity values for harbor porpoises are the lowest measured in any cetacean species. As a harbor porpoise loses weight, it loses more thermal energy to the environment because the insulating blubber layer decreases in thickness and its body surface to volume ratio increases.

In the wild, differences in blubber thickness have been observed between ages, sexes, locations on the body, and seasons. Read (1990) found differences in blubber content between lactating and non-lactating females, between sexes and between age classes in bycaught harbor porpoises in the Gulf of Main. Blubber is generally thickest anterior of the dorsal fin in a band around the body (Parry, 1949; Lockyer, 1995, Kastelein et al., 1997b). Koopman (1996) found stratification in the blubber fatty acids of harbor porpoises; fatty acids with chain lengths shorter than 18 carbon atoms were present in outer blubber layer, while the longer-chain unsaturated fatty acids were more prevalent in the inner layer. The thicker the blubber layer, the higher the lipid content (Lockyer, 1995). Koopman (1998) measured the blubber thickness at 48 sites on the bodies of 68 male, and 46 female harbor porpoises accidentally bycaught in the Bay of Fundy. Blubber anterior to the anus ranged from 15 to 25 mm. Blubber thickness of calves was thicker than that of older animals, and blubber was thinnest in lactating females - this was also observed by Lockyer 1995 in lactating female porpoises from British waters. Blubber thickness was correlated negatively with body length, which was also observed in live porpoises (Kastelein et al., 1997b); as animal grow older and longer, the annual mean blubber thickness decreases.

In common with the present study, Locker et al. (2003) found seasonally fluctuating blubber thickness, and correlated mid-body girth in 2 captive harbor porpoises kept in natural sea water with seasonally fluctuating water temperature; mid-dorsal blubber thickness varied between 18 mm (in summer) and 42 mm (in winter). Porpoise 02's blubber thickness varied between 15 in summer and 32 mm in winter; this appears to be typical for harbor porpoises. His girth at axilla varied between 63 and 79 mm and also varied seasonally, as expected.

Apart from seasonal changes, blubber thickness can also change quickly due to changes in the energy requirements of an animal. Kastelein et al. (1997b) report on a harbor porpoise which was moved from a small pool to a floating pen. Due to an increase in activity level, her blubber thickness decreased at a rate of 6 mm per week. After feeding her *ad lib*, her blubber thickness increased at a rate of 7 mm/week.

A few researchers have tried to estimate the body mass of harbor porpoises from their body length, some using different equations for males and females (Møhl-Hansen, 1954; van Utrecht, 1978). The present study and some studies mentioned above indicate that such a formula is limited by the fact that body mass changes during the year. A body mass estimate can be improved by taking body condition into account by including girth measurements in the equations, and this method only requires one equation for both sexes; Lockyer (1995) used one girth measurement and Kastelein and van Battum (1990) used two girth measurements. Like Kastelein et al. (1997c) the present study showed that body mass was highly predictive of girth at axilla and blubber thickness, and body mass was used as the indicator of body condition to calculate the correlations with the other measured body and environmental parameters.

Body mass

Birth mass of harbor porpoises in the North Sea is between 3 and 9 kg (Lockyer, 1995). The body length-mass relationships of the animal in the present study, of those described by van Utrecht (1978), Andersen (1965 and 1981), Spotte et al. (1987), Kastelein and van Battum (1990), Lockyer (1995), and Learmonth et al. (2014), and of the rehabilitated animals described by Kastelein *et al.* (1990; 1997c), are similar, suggesting that the study animal was representative of a male harbor porpoise. The animals in all these studies probably came from

the North Sea. Male harbor porpoises of the same length from the Baltic Sea are on average ~5 kg heavier (Møhl-Hansen, 1954; Gaskin *et al.*, 1984), perhaps because the Baltic Sea is generally colder than the North Sea. Harbour porpoises of similar length from Japanese waters are also generally heavier than the animal in the present study (Gaskin *et al.*, 1993). Even in one geographical area, body mass may change due to changing circumstances over longer time periods (years); porpoises in West Greenland responded to warmer waters and increased availability of Atlantic cod (*Gadus morhua*) by staying there longer, which resulted in improved body condition than in colder periods when cod were available in smaller numbers and were smaller (Heide-Jørgensen *et al.* 2011).

Seasonal changes in food consumption, respiration rate and body condition

Food consumption

Both when he was growing rapidly and after his body length stabilized, the study animal's food consumption decreased as his body mass (an indicator of body condition) increased. His respiration rate increased with increasing food consumption, perhaps indicating the positive correlation between metabolism and food consumption. When he was stable in body length, his food consumption decreased as the water temperature increased.

Some information on mean food intake of captive porpoises has been published, though no time series were investigated, and the animals were often kept in water with fairly stable temperatures, so no seasonality in food intake could be detected. Anderson (1965) reports on 8 captive harbor porpoises (mean body mass 40 kg) that ate on average 4.3 kg of fish (3.9 kg herring, 0.3 kg whiting, 0.1 kg other fish species) per day. This is a mean of 10.8% of body mass/day (range: 5-14%). The water temperature of the pool and enclosure in the sea was low (1- 4 °C). Myers (1978) reports on a 41.4 kg harbor porpoise in captivity that consumed 4.5 kg of herring, mackerel and capelin daily (10.8% of body mass) when kept in 19°C pool water. Koga (1991) estimated that immature porpoises required a daily ration of 7-8% of their body mass to maintain a stable body mass. Kastelein *et al.* (1990) described the food intake of 3 stranded harbor porpoises; after they had been rehabilitated, they consumed between 8 and 12% of their body mass per day (herring and sprat) when kept in water of 17-20 °C. Kastelein *et al.* (1997c) found that, on average, harbor porpoises of various body sizes kept in water between 18 and 21°C consumed 750-3250 g of fish (herring and sprat) per day (between 4 and 9.5% of their body mass), which is between 8000 and 25000 kJ per day. The food intake as a percentage of body mass is much higher in harbor porpoises than in larger odontocetes (Kastelein *et al.*, 1989, 1994, 2000 a,b,c,d, 2002, 2003a,b) that have lower higher metabolic rates (Kanwisher and Sundnes, 1965, 1966). The study animal's food consumption varied between ~1200 g/day and ~4400 g/day, but was generally ~2400 g/day. His energy intake varied between ~9000 kJ/day and ~26000 kJ/day, but was generally ~18000 kJ/day. He consumed ~7% of his body mass in food daily. Overall, he appears to be typical in terms of his food consumption.

Seasonality in harbor porpoise food intake was only reported previously by a few authors. Anderson and Dziedzic (1964) and Dudok van Heel (1962) found that their harbor porpoises which were kept in sea pens needed more food in winter than in summer. Lockyer *et al.* (2003) described seasonal changes in food consumption in 2 captive harbor porpoises living in natural sea water over a period of 3 years, mainly during the period of rapid body length growth. These porpoises ate more in the summer than in winter, but this was probably due to changes in the husbandry procedures, and the fact that the animals were in the rapid growth period.

The reported food consumption data of captive harbor porpoises are difficult to compare, as the food consumption of an animal depends on parameters such as:

- 1) The blubber thickness (an indicator of body condition).
- 2) The insulative quality (chemical composition) of the blubber layer. This may change depending on age, body mass or environmental conditions (Worthy and Edwards, 1990).
- 3) The growth stage. The blubber thickness decreases as healthy harbor porpoises increase in body length (Ryg *et al.*, 1993; Koopman, 1994; Kastelein *et al.*, 1997 b). So, the effect of increasing body volume on food consumption appears to be counteracted to some extent by the effect of the decreasing thermal insulation of the blubber layer.
- 4) The basal metabolic rate of the individual.
- 5) The activity level (see Kastelein *et al.*, 1997b).
- 6) The diet (energy content of the prey species).
- 7) The digestibility of the food. The ingested gross energy of the fish fed in the present study does not represent the metabolized energy. To determine metabolized energy, the fecal and urinary energy have to be subtracted from the gross energy ingested. Information on fecal and urinary energy is difficult to obtain for odontocetes, as they urinate and defecate under water and their feces disperse quickly.
- 8) The season.
- 9) The reproductive state (Recchia and Read, 1989; Kastelein *et al.*, 1993a).
- 10) The water and air temperature.

Respiration rate

Harbor porpoises may increase their metabolism in order to increase heat production (Parry, 1949). Kooyman and Sinnett (1979) measured the lung properties of the harbor porpoise and concluded that in comparison to terrestrial mammals, the lung volume to body mass in harbor porpoises is relatively large (also reported by Kanwischer and Sundness, 1965; Schmidt-Nielsen, 1997; Reed *et al.*, 2000). The lungs are able to empty up to < 17% of total lung capacity, flow rates are relatively high compared to those of terrestrial mammals, and the lung emptying time is short (<0.2 s). Cartilaginous airway reinforcement in the porpoise's lungs is responsible for their unusual flow-volume properties. The tidal volume of a non-moving animal was between 0.2 and 1.1 l (Kastelein *et al.*, 1997f; Reed *et al.*, 2000).

Porpoises thus have the ability to exchange a large percentage of their lung gas very rapidly during their brief pass through the air-water interface. The heart mass to body mass ratio of harbor porpoises is relatively high compared to that of larger odontocetes (Slijper, 1958), allowing the porpoise to pump the oxygenated blood quickly throughout the body. Porpoises also have a very high heart rate (Andersen, 1969) and show respiratory arrhythmia (Kastelein and Meijler, 1989), so the oxygen from the lungs is quickly distributed throughout the porpoise's body.

Watson and Gaskin (1983) recorded the respiration rates of harbor porpoises in the wild. Two respiration patterns were recognized: while travelling with short submergence periods (mean 24 s), and while feeding with longer submergence periods (mean 1.44 min) followed by multiple breaths. The mean number of breaths per minute was the similar for both respiration patterns (around 2.4 breaths/min = 12/5 min). The authors conclude that the energetic requirements for travelling and feeding are similar. Myers (1978) found a respiration rate of about 4 times per min (20/5 min) for a 41.4 kg female harbor porpoise in a pool. Parker (1932) also measured the respiration rate of a harbor porpoise in a pool; it varied depending on the activity of the animal, but the mean was 4 times per min (20 times/5 min). Kastelein *et al.* (1989) reported the respiration rate of 3 porpoises in a small pool to vary between 20 and 25 times per 5 minute. Once his body length had stabilized, the mean daily

respiration rate of porpoise 02 was between ~17 and 26 respirations/5 min, which is typical. The present study confirms what Parry (1949) postulated: when harbor porpoises increase their food intake, they also increase their metabolism, thus requiring more oxygen to digest their food, and so they respire more often. The study animal's respiration rate declined with increasing water temperature and increased with increasing food consumption; both these relationships demonstrate the positive correlation between metabolism and respiration.

Body condition

Body mass was considered the best indicator of body condition. Between the ages of 2 years and 5.5 years the study animal's body mass increased to around 40 kg, after which fluctuated by 5-10 kg. Both when he was growing rapidly and after his body length stabilized, the porpoise's food consumption decreased as his body mass increased. His respiration rate and body mass declined with increasing water temperature, and his respiration rate increased with increasing food consumption.

Only a few authors have studied body mass changes over time in porpoises living in natural sea water of which the temperature fluctuated seasonally, like in the present study (Locker et al., 2003; Kastelein et al., 1997c). Lockyer et al. (2003) reported the body mass of 2 porpoises (a ~40 kg male and a ~50 kg female) kept in sea water which fluctuated between 3 and 18 °C; they weighed 4-5 kg less in the summer than in the winter. Daily food consumption was 7-9% of body mass.

Apart from seasonal changes, body mass can change quickly due to the physical condition of an animal. Kastelein et al. (1990) described 2 stranded male harbor porpoises that increased in body mass during the recovery period. Their mass increase was associated with an increase in their blubber layer thickness but not in their length; both animals were mature. A substantial mass change in adult harbor porpoises was also observed by Spotte et al. (1978): a stranded adult harbor porpoise increased in mass from 27 kg to 42 kg without changing in length (148 cm). Wild-caught adult animals from the Baltic of the same length may differ in mass by up to 25 kg (Møhl-Hansen, 1954), and mass changes over short time periods are mainly caused by changes in the blubber layer thickness (Kastelein et al., 1997 b).

Application

Ecological significance

Small odontocetes living in relatively cold water need to eat frequently. Harbor porpoises need such a large amount of food per day relative to their body mass that they cannot survive by filling their stomachs completely only a few times per day, even though their forestomachs can expand and act as food reservoirs (Kastelein and Lavaleije, 1992; Kastelein et al., 1997 a, c). This means that harbor porpoises require a relatively dependable, though not necessarily abundant, food supply to survive, and must eat often (Wisniewska et al., 2016).

Mammals use energy to warm up food that is below 37 °C when ingested. Perhaps harbor porpoises eat so much relative to their body mass partly because their prey is much colder than 37°C. They need to use a large proportion of the energy of ingested food to heat it up (this probably mainly occurs in the forestomach, where the flesh is also separated from the bones). In most studies on harbor porpoise food consumption, the temperature of the fish fed to the animals was not recorded. The fish in the present study was fed at ~4 °C. How this compares to the temperature of the fish eaten by wild harbor porpoises is not known, but it is safe to assume that the temperature varies depending on the season and the depth at which the fish is ingested. The sea surface temperature in the harbor porpoise's distribution area is between 4 and 16 °C (Gaskin, 1992), but harbor porpoises find most of their prey in deeper

water (Westgate *et al.* 1995; Leopold, 2015), where the temperature is lower and more stable (possibly often close to the temperature at which the fish in the present study were fed).

So far, the effect of air temperature on the energy budget of the harbor porpoise has not been evaluated. However, the harbor porpoise has a large lung volume to body mass ratio (Kanwischer and Sundness, 1965; Kooyman and Sinnett, 1979; Schmidt-Nielsen, 1997), and after inhaling cold air in winter, it keeps the air (about 1 l) in its lungs for tens of seconds. As well as oxygen exchange, heat exchange occurs (as it does in all mammals). This certainly affects the energy needs of the porpoise; it has to use some energy from its food to heat the inhaled air. In the distribution area of the harbor porpoise, the air is always below 37°C. In winter, when the water and air temperatures are low, harbor porpoises have two strategies to keep their internal body temperature stable (around 36°C; Kastelein *et al.*, 1990): they can increase insulation by producing a thicker blubber layer, and they can increase their metabolism. The present study shows that the harbor porpoise uses both techniques, as both respiration rate and body mass (~blubber thickness) increased with declining water temperature.

Data from the present study, combined with data from captive porpoises reported by Kastelein (1997c) and Lockyer *et al.* (2003), based on the food records of animals of different ages and body sizes kept in sea water which fluctuated naturally in temperature, show that non-lactating harbor porpoises require between 4 and 9.5% of their body mass in fish each day, depending on the energetic content and temperature of the fish, and on the age, body mass, exercise level, reproductive stage, and individual basal metabolic rate of the porpoise.

Wild harbor porpoises dive deeper than captive animals (Linnenschmidt *et al.*, 2013). Based on respiration rates of wild porpoises, Watson and Gaskin (1983) concluded that travelling and deep diving have similar energetic costs. This suggests that despite its shallow dives, the study animal may have had a similar energy requirement as wild conspecifics.

Using the food consumption of the study animal, it is possible to estimate how much food wild male harbor porpoises eat in a particular month of the year. The following information of the animal in the wild and the environmental conditions it encounters need to be compared to those of the animal in the present study:

- 1) Body length of the animal.
- 2) The local and momentary diet (based on fish distributions and stomach contents of porpoises).
- 3) The energetic content of the diet.
- 4) Water temperature.

For female harbor porpoises, other food consumption data are needed, as their energetic requirements are not only influenced by the environmental temperature and diet, but also by their reproductive state (gestation, and probably more severely, lactation, which are seasonal). Female harbor porpoises probably have a relatively high food intake during their period of rapid growth and when they are reproducing. What little is known about the energetics of reproduction in small cetaceans is derived from Commerson's dolphins (*Cephalorhynchus commersonii*; Kastelein *et al.*, 1993 a and b). Commerson's dolphins and harbor porpoises are similar in body size and appear to have roughly similar habitat requirements. Commerson's dolphins live in the temperate waters of the Southern hemisphere. Captive Commerson's dolphins kept in water of between 10 and 17 °C and consume around 10% of their body mass per day (herring and mackerel; Kastelein *et al.*, 1993 a). Their energetic requirements are similar to those of harbor porpoises, although Commerson's dolphins of similar weight, gender and reproductive state, appear eat slightly more than harbor porpoises, probably because they spend more energy on locomotion; they generally swim faster and more erratically than harbor porpoises (Kastelein *et al.*, 1993 a).

Surprisingly female Commerson's dolphins eat similar amounts of food during gestation as when they are not reproducing (probably because during gestation their body surface to body volume ratio decreases and their blubber thickness increases, so they lose less energy to the environment). However, their food intake increases markedly during lactation (by 30% compared to similar non-reproductive periods). If the same is true for harbor porpoises, reproducing females would require more food between June and ~March (lactation lasts for about 9 months; Sørensen and Kinze, 1994). Small calves with solid food in their stomach were mainly found between February and May (Learmonth et al., 2014). This is probably the transition period between suckling and eating solid food (weaning).

Future energetics studies

The present study shows that male harbor porpoises need different amounts of food depending on their growth stage and on the season. Seasonal changes in food consumption are related to the diet, the water temperature and, probably to a lesser degree, to the air temperature of their environment. Thus, any follow-up energetics studies with harbor porpoises should take this seasonality in energetic requirements into account. The food consumption of male harbor porpoises is highest in the winter. Depending on the food availability at sea (which is probably seasonal, unless harbor porpoises are able to follow their main prey fish species as suggested by Sveegaard et al., 2012a,b), harbor porpoises may be more vulnerable to disturbances that decrease their foraging efficiency in some periods of the year than in others (MacLeod et al., 2007). We cannot say with certainty in which period of the year female porpoises have the highest food requirements (thus studies on this topic are needed), but in reproducing females the highest food intake is probably during the lactation period, as was observed in the Commerson's dolphin (Kastelein et al., 1993 a).

Estimating the effect of disturbance on population dynamics

This study does not provide all answers needed to estimate the effect of disturbing an individual animal on the dynamics of a harbor porpoise population. However, it is an important step towards understanding this effect. This study is part of a harbor porpoise research program consisting of a series of studies in which the effect of sound on foraging efficiency will be evaluated, as well as the effect of variation in diet on body condition, the digestive efficiency of various fish prey species, the effect of fasting on body condition, the maximum food intake after fasting, the effect of swimming speed on food consumption, and the energetic cost of reproduction. Once it is completed, this research program will allow more accurate assessment of the effects of human offshore activities on harbor porpoise population dynamics. When, in the future, a new expert elicitation for the iPCoD model is conducted, the experts will be better informed before giving their advice.

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