Aquatic Mammals 2018, *44*(1), 76-91, DOI 10.1578/AM.44.1.2018.76

Seasonal Changes in Food Consumption, Respiration Rate, and Body Condition of a Male Harbor Porpoise (*Phocoena phocoena*)

Ron A. Kastelein,[1] Lean Helder-Hoek,[1] and Nancy Jennings[2]

[1]*Sea Mammal Research Company (SEAMARCO), Julianalaan 46, 3843 CC Harderwijk, The Netherlands*
E-mail: researchteam@zonnet.nl
[2]*Dotmoth, 1 Mendip Villas, Crabtree Lane, Dundry, Bristol BS41 8LN, UK*

Abstract

Seasonal changes in food consumption, respiration rate, and body condition in a healthy captive male harbor porpoise (*Phocoena phocoena*) from the North Sea were recorded over 8 y. He was kept at water and air temperatures similar to those experienced by wild conspecifics. At the age of 3 y and 10 mo, the porpoise's body length stabilized at 148 cm. Body mass, an indicator of body condition, increased to ~40 kg between the ages of 2 and 5.5 y, after which it fluctuated seasonally by 5 to 10 kg. The porpoise's food consumption was ~1,200 to ~4,400 g/d but was generally ~2,400 g/d (nearly 7% of body mass). Based on the caloric content of the fish diet, his energy intake was 9,000 to 26,000 kJ/d; the average was ~18,000 kJ/d. Once his body length had stabilized, the porpoise's daily mean respiration rate was 17 to 26 breaths per 5 min (3 to 5 breaths/min). Correlation analysis revealed that respiration rate and body mass declined with increasing water temperature and that respiration rate increased with increasing food consumption. When the porpoise's body length was stable, his food consumption also decreased as the water temperature increased. If the data from the present study are representative of other male harbor porpoises, these results indicate that male harbor porpoises may need different amounts of food depending on the season and on whether they are growing or adult. Food consumption peaks in winter; thus, seasonality should be taken into account in energetics studies. Depending on food availability at sea, harbor porpoises may be more or less vulnerable to disturbances that decrease their foraging efficiency. With information from this longitudinal study, experts will be better informed on typical body condition patterns when considering the Interim Population Consequences of Disturbance (iPCoD) model. In addition, hypotheses about the effects of climate change on cetaceans' susceptibility to disturbance, in relation to seasons and life history, can be generated.

Key Words: energetics, food intake, foraging ecology, growth, marine mammals, metabolism, nutrition, odontocete

Introduction

Anthropogenic activities at sea often cause underwater sound that may affect marine mammals. Sound may affect their hearing, mask ecologically relevant sounds, or change their behavior 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 (PCAD) model (National Research Council, 2005), the Interim Population Consequences of Disturbance (iPCoD) model (King et al., 2015), and the Disturbance Effects of Noise on the Harbour Porpoise Population in the North Sea (DEPONS) model (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 and death rates). Most of the information needed is lacking for most marine mammal species, though estimates of the effect of disturbance on vital rates in the iPCoD model have been made via 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; Haelters et al., 2014) and to sounds from seismic surveys (Thompson et al., 2013). It inhabits the temperate coastal waters of the northern hemisphere (Bjorge & Tolley, 2008) where human offshore activities occur relatively often. Though harbor porpoises have small appendages and dorsal fins (Ryg et al., 1993) compared to larger odontocetes, they have a 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 & McMahon, 1983). To maintain a stable internal body temperature, they need to consume sufficient food. The harbor porpoise has a higher metabolism than most odontocetes (Kanwisher & Sundnes, 1965, 1966; Kanwisher, 1971; Reed et al., 2000). The initial food passage time is short: ~2.5 h (Kastelein et al., 1997b). To ingest sufficient energy, harbor porpoises need to feed often. In some areas and seasons, wild harbor porpoises have been observed to chase up to 550 small prey items per hour and achieve a high catch rate (Wisniewska et al., 2016). The high prey number and low energetic content per prey item suggest that these high feeding rates are sometimes necessary for survival, and that even a small decrease in foraging efficiency due to anthropogenic disturbance may have large consequences for physical fitness. 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 & Hohn, 1995).

To predict the effect of an environmental disturbance on the physical 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, 1997d), but only a few animals have been kept in sea water with a naturally fluctuating water temperature (Lockyer et al., 2003—a study spanning 3 y). 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 y in natural sea water at naturally fluctuating water and air temperatures. It was fed on a diet similar to that of some conspecifics in the wild. The study animal was confined to a pool, and his energetic requirement for activity may have differed from that of some wild conspecifics, but his energetic requirement for thermoregulation was probably similar. His seasonal body mass and food intake fluctuations, therefore, 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 ultimate goal of this longitudinal study is to provide information on harbor porpoise energetics for the next expert elicitation that will be conducted for the iPCoD model. This study is thus applied research.

Methods

Study Animal

The study is based on detailed husbandry data from a male harbor porpoise, identified as Porpoise 02, that was found stranded on the North Sea coast. His age when he stranded, estimated from his length (van Utrecht, 1978; Gaskin et al., 1984) and from the marginal papillae on his tongue (Kastelein & Dubbeldam, 1990), was approximately 1.5 y. He was rehabilitated 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. He was not on public display.

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

On most days, between 0800 and 1700 h, the study animal participated in behavioral audiometric assessments and an acoustic behavioral response study. He also engaged in an animal husbandry training session. Between 1700 and 0800 h, the animal spent most of his time playing with floating toys that were offered as behavioral therapy. Apart from during a few short periods of rest (~5 min each), the animal swam. He was kept with a young male conspecific during the first year and the last 2 y of the study. The animal extended his penis more during the second part of the study period than during the first part of the study period, but he was not kept with females, and, therefore, no actual sexual behavior was observed.

Study Area

The harbor 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; 200 m away, wild harbor porpoises can be observed in coastal waters), in a pool complex consisting of an outdoor pool (12 × 8 m; 2 m deep) connected via a channel (4 × 3 m; 1.4 m deep) to an indoor pool (8 × 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. Sea water 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. Temperature-wise, the environmental conditions experienced by the captive study animal were similar to those experienced by wild conspecifics living in the nearby Oosterschelde and in the North Sea.

Food Consumption
The harbor porpoise was fed four to five times per day on a diet of thawed sprat (*Sprattus sprattus*), herring (*Clupea harengus*), mackerel (*Scomber scombrus*), and capelin (*Mallotus villosus*). Vitamins (Akwavit, Arie Blok Animal Nutrition) were added to the thawed fish to replace the vitamins lost due to freezing and storage of the 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 by an ISO 17025 accredited laboratory (Silliker Netherlands BV trading as Merieux NutriSciences, Ede, The Netherlands) for each fish delivery by Parlevliet & van der Plas, Inc. In the present study, food consumption was expressed both in kg and in kJ per day (mean energetic content of sprat: 7.9 kJ/g; herring: 6.5 kJ/g; mackerel: 7.7 kJ/g; and capelin: 6.1 kJ/g). The daily food intake as a percentage of the body mass was also calculated.

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

Respiration Rate and Body Condition Parameters
The number of times the harbor porpoise respired was counted four times per day during a period of 5 min. This was done for husbandry purposes to detect potential signs of pneumonia as early as possible (although no pneumonia was ever detected in the study animal), but it also provided a way to quantify metabolism. The daily mean respiration rate per 5 min was used for the analysis.

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

- *Body mass* – The animal was weighed digitally (50 g accuracy).
- *Standard body length* – Straight line between tip of the upper jaw and notch of the tail fluke (0.5 cm accuracy).
- *Girth at axilla* (0.5 cm accuracy)
- *Blubber thickness* – Blubber was defined as the epidermis, dermis, and hypodermal tissues (Parry 1949): the integument of terrestrial mammals. The blubber thickness of the study animal was measured ultrasonically with a Renco Lean-Meater®. The apparatus measured the distance between the skin surface and the underlying muscle layer (1 mm accuracy). Blubber thickness was measured 10 cm ventrally of the base of the dorsal fin (on the left side of the body; Location No. 4 in Kastelein et al., 1997e).

Water and Air Temperature
The water temperature was measured once per day. The water temperature and salinity (~3.4%) were similar to those in the Oosterschelde from which the water was pumped continuously during most of the day (Figure 1). The minimum and maximum air temperatures over each 24-h period were also recorded daily, starting in May 2008 (Figure 1).

Multicollinearity (which exists when two or more of the predictors in a model are moderately or highly correlated) 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 harbor porpoise was 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 were described and plotted. The study period was divided into a period in which the harbor porpoise experienced a 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 and association among the four body condition variables were assessed by means of Pearson correlations.

Correlation analysis, used to determine 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; however, body length was not correlated with girth or blubber thickness. Since body mass and body length were correlated (Pearson correlation coefficient: 0.591, $n = 63$, $p < 0.000$), further analysis was conducted on body mass only as the best indicator of body condition.

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

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 (α) was 0.05 throughout. Statistical analyses were carried out on *Minitab*, Release 17 (Ryan & 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 y and the age of 3 y and 10 mo, after which the growth rate decreased and his body length stabilized at ~148 cm (Figure 1a). The age of 3 y and 10 mo is therefore defined as the end of the period of rapid growth and the onset of the period of relative stability. Between the ages of 2 and 5.5 y, the harbor porpoise's body mass generally increased to around 40 kg; thereafter, it fluctuated seasonally by 5 to 10 kg. Seasonal fluctuation in body mass increased as the animal became older (Figure 1b).

Girth at Axilla and Blubber Thickness

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

Food Consumption

The food consumption of Porpoise 02 (with the diet fed at SEAMARCO) varied between ~1,200 g/d and ~4,400 g/d but was generally ~2,400 g/d (Figure 1e). His energy intake varied between ~9,000 kJ/d and ~26,000 kJ/d, averaging ~18,000 kJ/d (Figure 1f). He consumed ~7% of his body mass in food daily (Figure 1g).

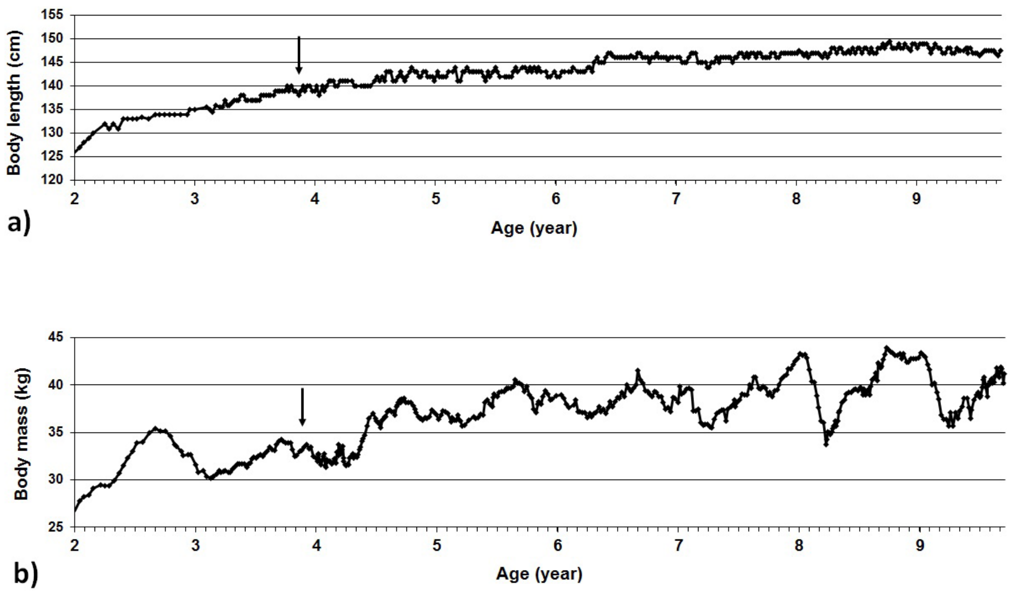

Figure 1a-b. Body condition parameters, food consumption, and respiration rate of a male harbor porpoise (*Phocoena phocoena*), Porpoise 02, and the temperatures at which he was kept: (a) body length and (b) body mass. All figures are lined up so that the x-axis of age and date are synchronous. The arrows in (a) and (b) indicate the end of the period of rapid growth in body length and the start of the period of relative slow growth and stability in body length.

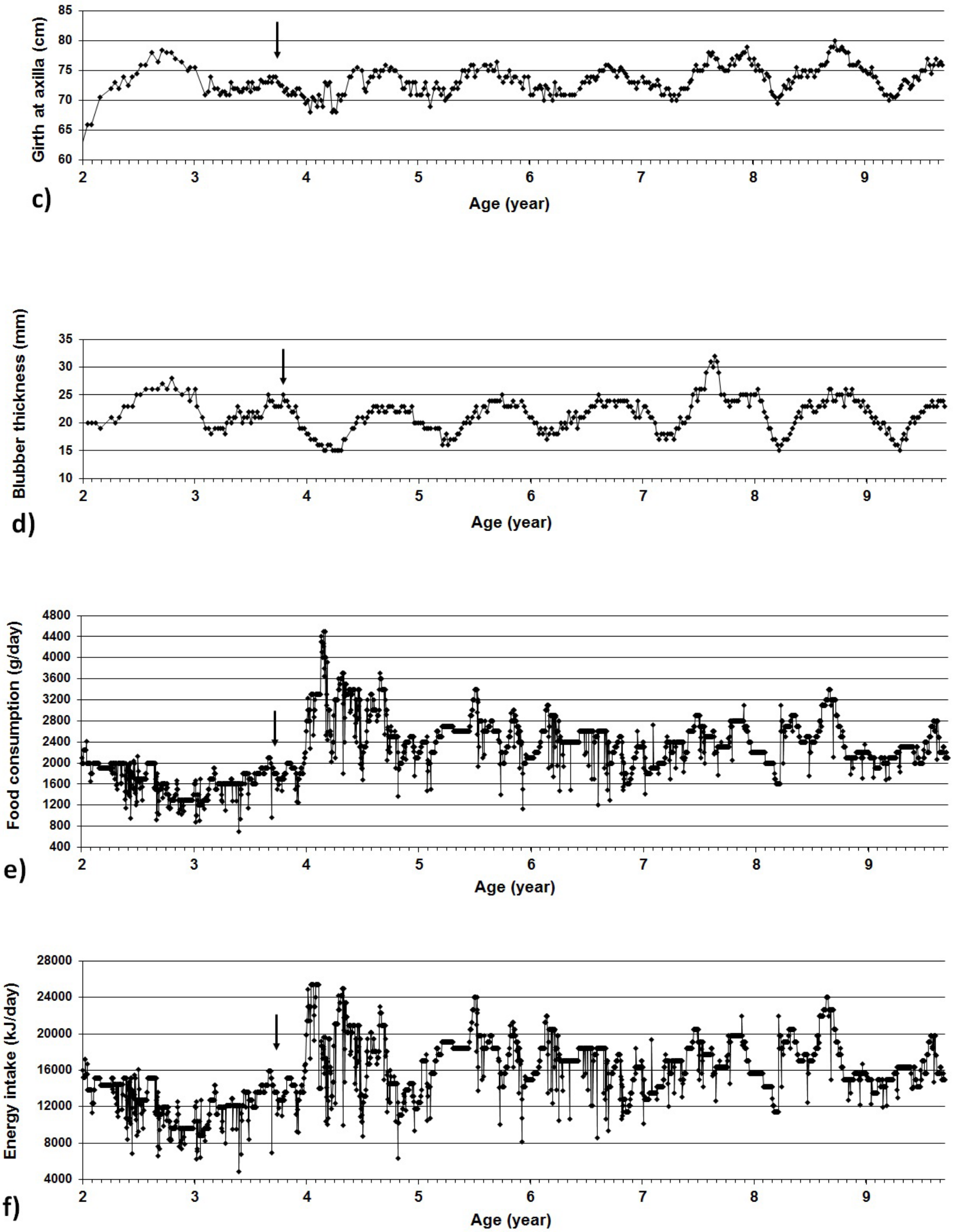

Figure 1c-f. Body condition parameters, food consumption, and respiration rate of Porpoise 02 and the temperatures at which he was kept: (c) girth at axilla, (d) blubber thickness, (e) food consumption, and (f) energy intake. All figures are lined up so that the x-axis of age and date are synchronous. The arrows in (c) through (f) indicate the end of the period of rapid growth in body length and the start of the period of relative slow growth and stability in body length.

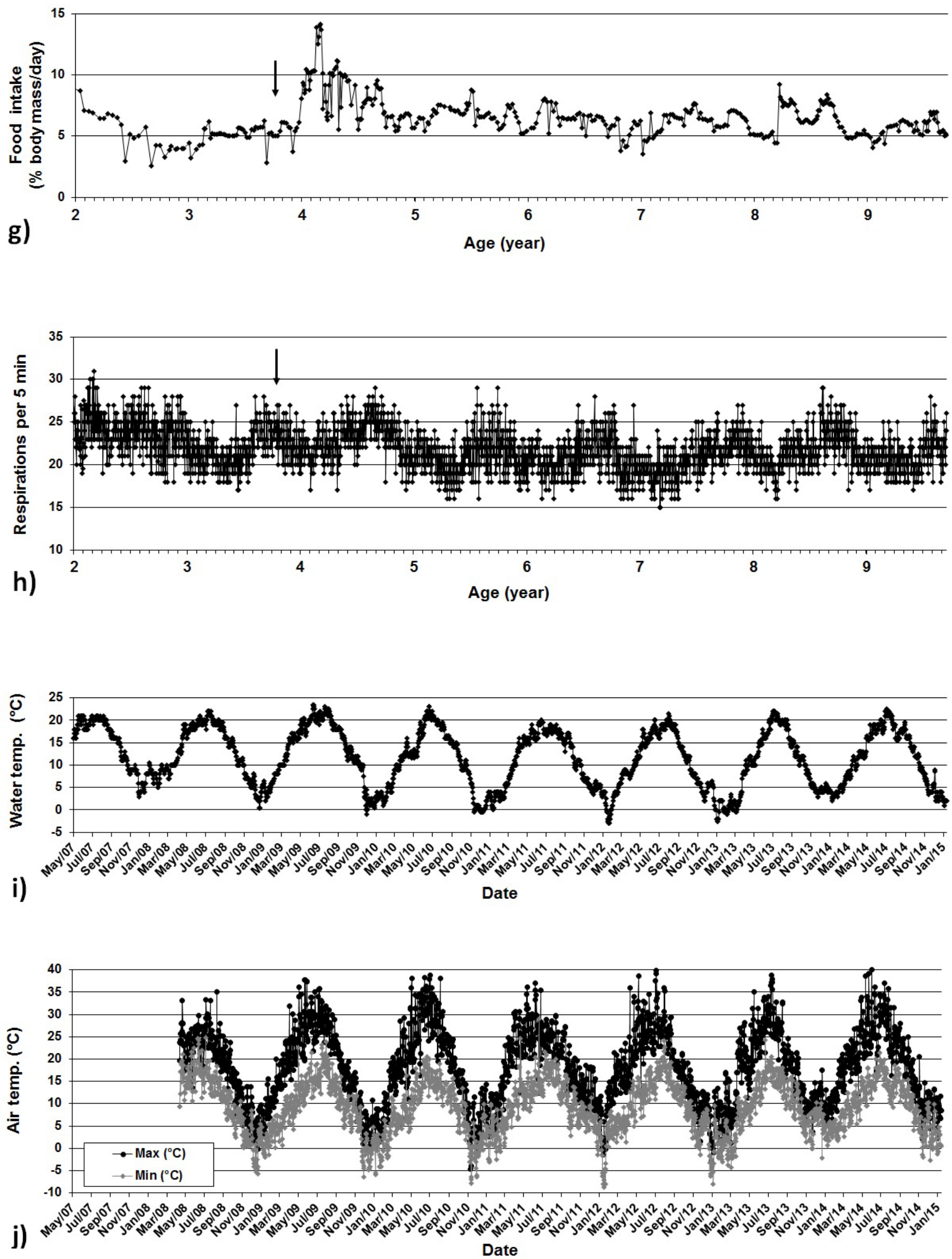

Figure 1g-j. Body condition parameters, food consumption, and respiration rate of Porpoise 02 and the temperatures at which he was kept: (g) daily food intake as % of body mass, (h) daily mean ($n = 4$) number of respirations/5 min, (i) daily water temperature in the pool, and (j) daily minimum and maximum air temperature near the pool. May/07 means May 2007, etc. All figures are lined up so that the x-axis of age and date are synchronous. The arrows in (g) and (h) indicate the end of the period of rapid growth in body length and the start of the period of relative slow growth and stability in body length.

Respiration Rate
The mean daily respiration rate of Porpoise 02 was relatively high (around 25 breaths/5 min or 5 breaths/min) during the second year of his period of rapid body length growth compared to during his period of stability in body length. It fluctuated during the following years between ~17 and 26 respirations/5 min (3 to 5 times/min; Figure 1h).

Water and Air Temperatures
The water (Figure 1i) and air (Figure 1j) temperatures experienced by Porpoise 02 showed seasonal fluctuations which varied slightly from year to year.

Correlations During the Periods of Rapid Growth and Stability
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.

Correlation analysis also revealed that while Porpoise 02 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).

Discussion

Comparison with Wild Harbor Porpoises
Diet—The natural diet of harbor porpoises generally consists mainly of smooth-rayed fish, especially gadoids (cod) and clupeids (herring and sprat) of 10 to 25 cm in length, and sometimes of very small fish such as gobies (Gobiidae). However, the diet varies geographically and seasonally, and between sexes and age classes (Fink, 1959; Lindroth, 1962; Rae, 1965, 1973; Smith & Gaskin, 1974; Recchia & Read, 1989; Aarefjord et al., 1995; Rogan & Berrow, 1996; Gannon et al., 1998; Börjesson et al., 2003; Lockyer & Kinze, 2003; Víkingsson et al., 2003; Santos et al., 2004; Jansen et al., 2013; Leopold, 2015; Andreasen et al., 2017). The diet of the study animal consisted of sprat, herring, mackerel, and capelin. These are species with a high energy content that are also consumed by wild harbor porpoises; therefore, the diet provided to the study animal was within the range of the natural diet of harbor porpoises.

Body Length—At birth, the body length of harbor porpoises in the North Sea is 65 to 90 cm (Fisher & Harrison, 1970; Lockyer, 1995; Lockyer & Kinze, 2003, Learmonth et al., 2014). Weaning occurs at a body length of around 100 to 104 cm (Smith & Gaskin, 1974). Males reach their maximum length of approximately 146 cm at around the age of 10 y; females reach their maximum length of approximately 170 cm at around 14 y. Sexual maturation occurs at 3 to 6 y of age when males are ~133 cm and females are ~145 cm (Fisher & Harrison, 1970; van Utrecht, 1978; Gaskin et al., 1984; Read, 1990b; 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. In a report by Lockyer et al. (2003) on captive porpoises, a male's body length reached asymptote at ~139 cm and a female's at 150 cm. The male in the present study seemed to reach asymptote at ~148 cm. Male porpoises from Icelandic waters grow to the asymptotic length of 150 cm (Ólafsdóttir et al., 2002). For porpoises in the Bay of Fundy, asymptotic values for body length were 143 cm for males

Table 1. Results of Pearson correlation analysis between food consumption (kJ/d), respiration rate (over 5 min average/d), body mass (as 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, $n = 2{,}132$
Respiration rate vs water temperature	-0.139, 0.000; $n = 682$	-0.358, 0.000, $n = 2{,}130$
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, $n = 2{,}130$

and 156 cm for females. The age–body length relationship of the animal in the present study was similar to the age–length relationship found in harbor porpoises in eastern Newfoundland, Canada (Richardson et al., 2003). The period of rapid growth of the study animal was similar to that of porpoises in the wild in the Bay of Fundy (Read & Tolley, 1997), and he was hardly growing at the end of the study period, suggesting that he was an adult by that time. Thus, the body length–age relationship of the study animal was typical of a male harbor porpoise.

Body Mass—Birth mass of harbor porpoises in the North Sea is between 3 and 9 kg (Lockyer, 1995; Lockyer & Kinze, 2003). The body length–mass relationships of the animal in the present study; of those from the North Sea described by van Utrecht (1978), Andersen (1965, 1981), Spotte et al. (1978), Kastelein & van Battum (1990), Lockyer (1995), and Learmonth et al. (2014); and of the rehabilitated animals described by Kastelein et al. (1990, 1997d) are similar, suggesting that in terms of body mass–length relationship, the study animal was representative of a male harbor porpoise from the North Sea.

Male harbor porpoises of the same length from the Baltic Sea weigh on average ~5 kg more (Møhl-Hansen, 1954; Gaskin et al., 1984), perhaps because the Baltic Sea is generally colder than the North Sea. Harbor porpoises of similar length from Japanese waters are also generally heavier than the animal in the present study (Gaskin et al., 1993). However, mean body mass, even in one geographical area, may change due to changing circumstances over longer time periods (years; Heide-Jørgensen et al., 2011).

Apart from seasonal changes, body mass can change quickly with the physical condition of an animal. Kastelein et al. (1990) described two stranded male harbor porpoises that increased in body mass during their 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 emaciated adult harbor porpoise increased in mass from 27 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., 1997c).

Food Consumption—The study animal was not fed *ad libitum*. It is unlikely that wild porpoises can eat *ad libitum*, and the study animal had to work for each fish it received, just like wild conspecifics. The type of work was different. The study animal had to participate in behavioral audiometric assessments and husbandry training, whereas wild conspecifics have to search for, chase, and catch prey items. When wild animals have full stomachs, their motivation to forage declines. If the study animal showed a drop in motivation (which was evaluated on a weekly basis), his daily food ration was slightly reduced.

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

Food consumption data from captive harbor porpoises are difficult to compare, as the amount of food eaten depends on various parameters. These include the blubber thickness (an indicator of body condition) and the insulative quality (chemical composition) of the blubber, which may depend on age, body mass, or environmental conditions (Worthy & Edwards, 1990). Food consumption also depends on the activity level, the basal metabolic rate, the reproductive state (Yasui & Gaskin, 1987; Recchia & Read, 1989; Kastelein et al., 1993a), and the growth stage of the individual. The blubber thickness decreases as healthy harbor porpoises increase in body length (Ryg et al., 1993; Kastelein et al., 1997c; Koopman, 1998). 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. The season (perhaps via changes in air and water temperature) also affects food consumption, as does the energy content of the diet and the digestibility of the food. The gross energy of the fish ingested does not represent the metabolized energy. To determine the 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 where their feces and urine disperse quickly.

Some (mostly anecdotal) information on mean food intake of captive harbor porpoises has been published, though no time series were investigated, and the animals were often kept in water with fairly stable temperatures so seasonality in food intake could not be detected. Andersen (1965) reports on eight captive harbor porpoises (mean body mass 40 kg) that ate on average 4.3 kg of fish (mostly herring) per day—a mean of 10.8% of body mass/d (range: 5 to 14%). The water temperature of the pool and enclosure in the sea was low (1 to 4°C).

Myers et al. (1978) report on a 41.4 kg harbor porpoise that consumed 4.5 kg of herring, mackerel, and capelin daily (10.8% of body mass) when kept in a pool at 19°C. Koga (1991) estimated that immature porpoises required 7 to 8% of their body mass daily. Kastelein et al. (1990) described the food intake of three stranded harbor porpoises. After they had been rehabilitated, they consumed 8 to 12% of their body mass per day (herring and sprat) when kept in water of 17 to 20°C. Lockyer et al. (2003) reported the body mass of two porpoises (a ~40 kg male and a ~50 kg female) kept in sea water which fluctuated between 3 and 18°C. Daily food consumption was 7 to 9% of body mass. Kastelein et al. (1997d) found that, on average, harbor porpoises kept in water of 18 to 21°C consumed 750 to 3,250 g or 8,000 to 25,000 kJ of fish (herring and sprat) per day (4 to 9.5% of their body mass). In general, the animal in the present study, consuming ~2,400 g, ~18,000 kJ, or ~7% of his body mass daily, appears to be typical of harbor porpoises in terms of his food consumption.

The food intake as a percentage of body mass is much higher in harbor porpoises than in larger odontocetes (Figure 2; Kastelein & Vaughan, 1989; Kastelein et al., 1994, 2000a, 2000b, 2000c, 2000d, 2002, 2003a, 2003b) that have lower metabolic rates (Kanwisher & Sundnes, 1965, 1966). Yasui & Gaskin (1986) developed an energetic model for the harbor porpoise and predicted a daily food intake of only 3.8% of total body mass. They realized that this estimate did not match the observed food intake of captive animals published at the time and attributed this to the model's imperfection and the lack of good input data for the model.

Respiration Rate—Watson & Gaskin (1983) recorded the respiration rates of harbor porpoises in the wild and found that two patterns were used: one while traveling with short submergence periods (mean 24 s), and one while feeding with longer submergence periods (mean 1.44 min) followed by multiple breaths. The mean number of breaths/min was similar for both respiration patterns (around 2.4 breaths/

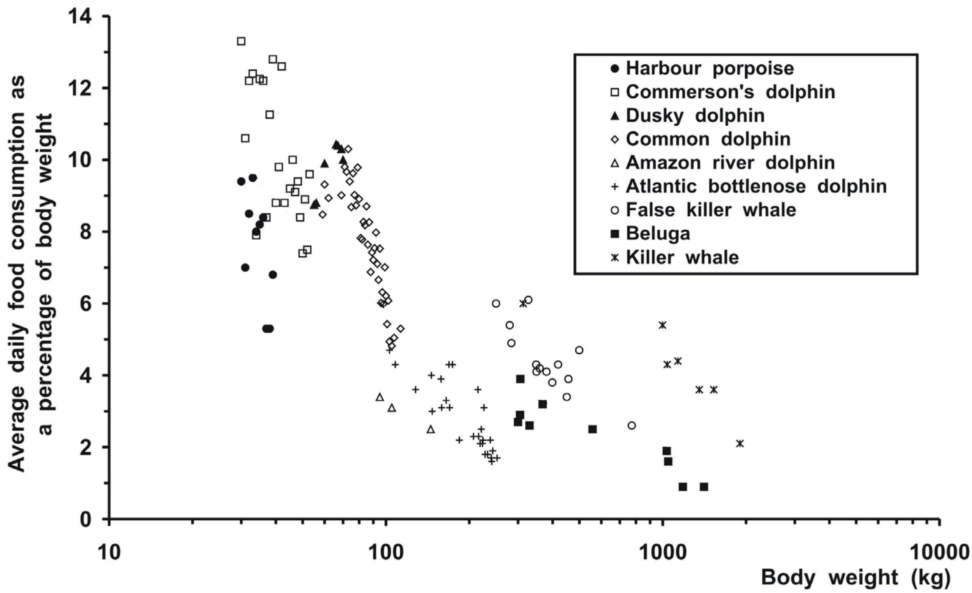

Figure 2. The relationship between body weight and average daily food consumption as a percentage of body weight in nine captive odontocete species (reproducing females are excluded). The species are, in order of increasing adult body weight, the harbor porpoise (Kastelein et al., 1990, 1997a, 1997b, 1997c, 1997d; the porpoise in the present study is not included [his intake was ~7% of body weight—body weight ~40 kg; see Figure 1]), the Commerson's dolphin (*Cephalorhynchus commersonii*; Kastelein et al., 1993a, 1993b), the dusky dolphin (*Lagenorhynchus obscurus*; Kastelein et al., 2000c), the common dolphin (*Delphinus delphis*; Kastelein et al., 2000c), the Amazon river dolphin (*Inia geoffrensis*; Kastelein et al., 1999), the Atlantic bottlenose dolphin (*Tursiops truncatus*; Kastelein et al., 2002, 2003a), the false killer whale (*Pseudorca crassidens*; Kastelein et al., 2000b), the beluga (*Delphinapterus leucas*; Kastelein et al., 1994), and the killer whale (*Orcinus orca*; Kastelein & Vaughan, 1989; Kastelein et al., 2000d, 2003b). Note that the energetic content of the diets and the water temperature in which they were kept differed per odontocete species.

min = 12 times/5 min), so the authors conclude that the energetic requirements for traveling and feeding are similar. Myers et al. (1978) found a respiration rate of about 4 times/min (20 times/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/min (20 times/5 min). Kastelein & Meijler (1989) reported the respiration rates of three porpoises in a small pool to vary between 20 and 25 breaths/5 min. Once his body length had stabilized, the mean daily respiration rate of the porpoise in the present study varied between ~17 and 26 respirations/5 min, which is typical.

Seasonal Changes

Seasonal Changes in Body Mass, Blubber Thickness, and Girth at Axilla—Only a few authors have studied body mass changes over time in harbor porpoises living in natural sea water with seasonally fluctuating temperature as in the present study (Kastelein et al., 1997d; Lockyer et al., 2003). Lockyer et al. (2003) reported the body mass of two harbor porpoises (a ~40 kg male and a ~50 kg female) kept in sea water which fluctuated between 3 and 18°C; they weighed 4 to 5 kg less in the summer than in the winter.

To compensate for their small size to some extent, harbor porpoises have evolved a relatively thick blubber layer (Parry, 1949; Read, 1990a; Lockyer, 1995; Koopman et al., 1996; Kastelein et al., 1997c; Koopman, 1998). Blubber can make up 45% of the body mass of harbor porpoises from Danish waters (Slijper, 1958) and 31% of that of harbor porpoises from near New Brunswick (Yasui, 1980). The blubber of harbor porpoises has a high lipid content and, therefore, a low thermal conductance compared to that of other cetaceans (Worthy & 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 because its body surface to volume ratio increases. As well as having a thermoregulatory function, blubber also serves as an energy store, makes the body hydrodynamic, and contributes to buoyancy (Kipps et al., 2002).

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

A few researchers have tried to estimate the body mass of harbor porpoises from their body length, with 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 including girth measurements, and this method only requires one equation for both sexes. Lockyer (1995) used one girth measurement, and Kastelein & van Battum (1990) used two girth measurements. Like Kastelein et al. (1997d), the present study showed that body mass was highly predictive of girth at axilla and blubber thickness, so body mass was used as the indicator of body condition to calculate the correlations with environmental parameters.

Seasonal Changes in Food Consumption—Seasonality in food intake by harbor porpoises was only reported previously by a few authors who kept porpoises at naturally fluctuating water temperatures for a sufficient amount of time to detect the differences in food intake between seasons. Dudok van Heel (1962) and Andersen & Dziedzic (1964) found that harbor porpoises kept in sea pens needed more food in winter than in summer. Lockyer et al. (2003) described seasonal changes in food consumption in two captive harbor porpoises living in natural sea water over a period of 3 y, mainly during the period of rapid body length growth. These porpoises ate more in summer than in winter, but the pattern of food intake may have been influenced by changes in the husbandry procedures (it was the first time porpoises had been kept at this facility) and by the fact that the animals were growing rapidly.

Seasonal Changes in Respiration Rate—Harbor porpoises may increase their metabolism to increase heat production (Parry, 1949). 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 causing them to 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 rate.

Ecological Significance

Small odontocetes living in relatively cold water need to eat frequently. Harbor porpoises need a large amount of food per day relative to their body mass. To survive, they probably need to fill their stomachs more than once each day (Kastelein & Lavaleije, 1992; Kastelein et al., 1997a, 1997b). This means that harbor porpoises require a dependable food supply to survive and, thus, must occur in waters with a sufficient food supply (MacLeod et al., 2007; Sveegaard, 2012a, 2012b), spend a lot of time foraging, and eat often, as has recently been confirmed in a field study (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 from their food to heat it up (this probably mainly occurs in the forestomach, where the flesh is also separated from the bones). 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 unknown, but it is safe to assume that this temperature varies depending on the season and the water depth at which the fish is ingested as fish are generally the same temperature as the surrounding water. 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 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 (Kanwisher & Sundnes, 1965; Kooyman & Sinnett, 1979; Schmidt-Nielsen, 1997); and after inhaling cold air in winter, it keeps the air (about one l) in its lungs for tens of seconds. As well as oxygen exchange, heat exchange occurs (as in all mammals). This must affect the energy needs of the porpoise. Some energy from the food is used to heat the inhaled air. In the distribution area of the harbor porpoise, the air is generally well below 37°C. In winter, when the water and air temperatures are low, harbor porpoises can use two strategies to keep their internal body temperature stable (at around 36°C; Kastelein et al., 1990): (1) they can increase insulation by producing a thicker blubber layer, and (2) 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 other captive harbor porpoises of various ages and body sizes kept in sea water which fluctuated naturally in temperature (Kastelein et al., 1997d; Lockyer et al., 2003), show that male and non-lactating female harbor porpoises require between 4 and 9.5% of their body mass in fish each day, probably depending on factors such as 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 & Gaskin (1983) concluded that traveling and deep diving have similar energetic costs. This suggests that, despite its relatively shallow dives, the study animal's energy requirement for locomotion may have been similar to that of wild conspecifics.

It is possible to estimate how much food wild male harbor porpoises eat in a particular month of the year from the food consumption of the study animal as long as the following information about the wild animal and the environmental conditions it encounters can be compared to those of the study animal:

- Body length
- The local and momentary diet (based on fish distributions and stomach contents of porpoises)
- The energetic content of the diet
- Water temperature

In female harbor porpoises, food consumption may be different, as their energetic requirements are influenced not only by the environmental temperature and diet, but also by their reproductive state (gestation, and probably more severely, lactation, both of 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., 1993a, 1993b). Commerson's dolphins and harbor porpoises are similar in body size and appear to have similar habitat requirements. Whereas harbor porpoises live in the temperate waters of the Northern hemisphere, 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 consumed around 10% of their body mass per day (herring and mackerel; Kastelein et al., 1993a). Their energetic requirements are similar to those of harbor porpoises, although Commerson's dolphins of similar weight, gender, and reproductive state appear to eat slightly more than harbor porpoises, probably because they use more energy for locomotion: they generally swim faster and more erratically than harbor porpoises (Kastelein et al., 1993a).

Pregnant female Commerson's dolphins eat similar amounts of food as females that 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 during lactation is ~30% higher than during 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 mo; Sørensen & Kinze, 1994). Small calves with solid food in their stomachs were mainly found between February and May (Learmonth et al., 2014), so this is probably the transition period between suckling and eating solid food (weaning).

Future Energetics Studies and Effects of Disturbance on Population Dynamics

Seasonal fluctuations in food intake are likely to occur in all male harbor porpoises living in water for which the temperature varies seasonally. The total amount eaten per day also depends on the age of the animal, its sex, its metabolic rate, and its reproductive state. Therefore, more studies of food consumption with animals differing in age, sex, and reproductive state are needed to get a more complete picture of the food intake of harbor porpoises.

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 the amount of food consumed are related to the water temperature (and possibly other factors such as hormonal changes and food availability). Thus, future energetics studies on harbor porpoises should take this seasonality in energetic requirements into account.

The food consumption of male harbor porpoises is highest in the winter. In reproducing female harbor porpoises, the highest food intake is probably during lactation as observed in the Commerson's dolphin (Kastelein et al., 1993a). In harbor porpoises, the second half of the lactation period (~November to ~March) is probably the period of greatest need for food; at this time, the young are biggest and the water temperature is relatively low.

This study does not provide all the information needed to estimate the effect of disturbance of individual porpoises on the dynamics of a harbor porpoise population. However, it is an important step towards understanding this effect. This study is part of a research program consisting of a series of studies in which the effect of sound on foraging efficiency and energy consumption of harbor porpoises is being evaluated. Once the program is completed, it will be possible to assess the effects of human offshore activities on harbor porpoise population dynamics more accurately. When, in the future, a new expert elicitation for the iPCoD model is conducted, the experts will be better informed.

Acknowledgments

We thank assistants Tess van der Drift, Loek van der Drift, Krista Krijger, Saskia Roose, Kiki Ernst, Nele Steen, Léonie Huijser, Jessica Schop, Naomi Claeys, Fransien Moerland, Céline van Putten, Ruby van Kester, Jesse Dijkhuizen, Jennifer Covi, and a large number of volunteers and students for their help with feeding and weighing the harbor porpoise and for record keeping over the years. We thank Bert Meijering (Topsy Baits) for providing space for the SEAMARCO Research Institute. We thank Mieke Leuning (Parlevliet & van der Plas BV) for supplying the energetic content of the fish fed to the porpoise. We thank Terrie Williams (University of Santa Cruz, USA), Shirley Van de Voorde (SEAMARCO), Suzanne Lubbe (Rijkswaterstaat), and Cormac Booth (SMRU consulting) for their constructive comments on the manuscript. Funding was received from The Netherlands Ministry of Infrastructure and the Environment (Case Number 31118293). Supervisors for the commissioner were Inger van den Bosch and Aylin Erkman. The harbor porpoise for this study was made available by the ASPRO group.

Literature Cited

Aarefjord, H., Bjørge, A. J., Kinze, C. C., & Lindstedt, I. (1995). Diet of the harbour porpoise (*Phocoena phocoena*) in Scandinavian waters. *Reports of the International Whaling Commission*, Special Issue 16, 211-222.

Altman, D. G. (1991). *Practical statistics for medical research*. London: Chapman and Hall.

Andersen, S. (1965). L'alimentation du Marsouin (*Phocoena phocoena*, L.) en captivité [The feeding of the porpoise (*Phocoena phocoena*, L.) in captivity]. *Vie et Milieu*, *16A*, 799-810.

Andersen, S. H. (1981). Body surface area of juvenile harbour porpoise, *Phocoena phocoena*. *Aquatic Mammals*, *8*(3), 94-95.

Andersen, S., & Dziedzic, A. (1964). Behavioral patterns of captive harbor porpoise *Phocoena phocoena* L. *Bulletin de l'Institut Océanographique de Monaco*, *63*, 1-20.

Andreasen, H., Ross, S. D., Siebert, U., Andersen, N. G., Ronnenberg, K., & Gilles, A. (2017). Diet composition and food consumption rate of harbor porpoises (*Phocoena phocoena*) in the western Baltic Sea. *Marine Mammal Science*, *33*(4), 1053-1079. https://doi.org/10.1111/mms.12421

Bjorge, A., & Tolley, K. A. (2008). Harbor porpoise *Phocoena phocoena*. In W. F. Perrin, B. Würsig, & J. G. M. Thewissen (Eds.), *Encyclopedia of marine mammals* (2nd ed., pp. 530-532). London: Academic Press.

Börjesson, P., Berggren, P., & Ganning, B. (2003). Diet of harbor porpoises in the Kattegat and Skagerrak Seas: Accounting for individual variation and sample size. *Marine Mammal Science*, *19*, 38-58. https://doi.org/10.1111/j.1748-7692.2003.tb01091.x

Brandt, M. J., Diederichs, A., Betke, K., & Nehls, G. (2011). Responses of harbour porpoises to pile driving at the Horns Rev II offshore wind farm in the Danish North Sea. *Marine Ecology Progress Series*, *421*, 205-216. https://doi.org/10.3354/meps08888

Carstensen, J., Henriksen, O. D., & Teilmann, J. (2006). Impacts of offshore windfarm construction on harbour porpoises: Acoustic monitoring of echolocation activity using porpoise detectors (T-PODs). *Marine Ecology Progress Series*, *321*, 295-308. https://doi.org/10.3354/meps321295

Dähne, M., Gilles, A., Lucke, K., Peschko, V., Adler, S., Krügel, K., . . . Siebert, U. (2013). Effects of pile-driving on harbour porpoises (*Phocoena phocoena*) at the first offshore wind farm in Germany. *Environmental Research Letters*, *8*, 025002. https://doi.org/10.1088/1748-9326/8/2/025002

Donovan, C., Harwood, J., King, S., Booth, C., Caneco, B., & Walker, C. (2016). Expert elicitation methods in quantifying the consequences of acoustic disturbance from offshore renewable energy developments. In A. N. Popper & A. Hawkins (Eds.), *The effects of noise on aquatic life. II: Advances in experimental medicine and biology* (pp. 29-31). New York: Springer. https://doi.org/10.1007/978-1-4939-2981-8_27

Dudok van Heel, W. H. (1962). Experiments with *Phocoena phocoena* L. *Netherlands Journal of Sea Research*, *1*, 427-458.

Feldman, H. A., & McMahon, T. A. (1983). The 3/4 mass exponent in metabolism is not an artefact. *Respiration Physiology*, *52*, 149-163. https://doi.org/10.1016/0034-5687(83)90002-6

Fink, B. D. (1959). Observation of porpoise predation on a school of Pacific sardines. *California Fish and Game*, *45*, 216-217.

Fisher, H. D., & Harrison, R. J. (1970). Reproduction in the common porpoise (*Phocoena phocoena*) of the North Atlantic. *Journal of Zoology, London*, *161*, 471-486. https://doi.org/10.1111/j.1469-7998.1970.tb02050.x

Gannon, D. P., Craddock, J. E., & Read, A. J. (1998). Autumn food habits of harbor porpoises, *Phocoena phocoena*, in the Gulf of Maine. *Fisheries Bulletin*, *96*, 428-437.

Gaskin, D. E. (1992). Status of the harbour porpoise, *Phocoena phocoena*, in Canada. *Canadian Field-Naturalist*, *106*, 36-54.

Gaskin, D. E., Yamamoto, S., & Kawamura, A. (1993). Harbour porpoise, *Phocoena phocoena* (L.), in the coastal waters of northern Japan. *Fisheries Bulletin*, *91*, 440-454.

Gaskin, D. E., Smith, G. J. D., Watson, A. P., Yasui, W. Y., & Yurick, D. B. (1984). Reproduction in the porpoises (Phocoenidae): Implications for management. In W. F. Perrin, R. L. Brownell, Jr., & D. P. DeMaster (Eds.), Reproduction in whales, dolphins and porpoises. *Reports of the International Whaling Commission*, Special Issue 6, 135-148.

Haelters, J., Dulière, V., Vigin, L., & Degraer, S. (2014). Towards a numerical model to simulate the observed displacement of harbour porpoises *Phocoena phocoena* due to pile driving in Belgian waters. *Hydrobiologia*, *756*, 105-116. https://doi.org/10.1007/s10750-014-2138-4

Heide-Jørgensen, M. P., Iversen, M., Nielsen, N. H., Lockyer, C., Stern, H., & Ribergaard, M. H. (2011). Harbour porpoises respond to climate change. *Ecology and Evolution*, *1*, 579-585. https://doi.org/10.1002/ece3.51

Jansen, O. E., Michel, L., Lepoint, G., Das, K., Couperus, A. S., & Reijnders, P. J. H. (2013). Diet of harbor porpoises along the Dutch coast: A combined stable isotope and stomach contents approach. *Marine Mammal Science*, *29*, 295-311. https://doi.org/10.1111/j.1748-7692.2012.0062

Kanwisher, J. W. (1971). Temperature regulation in the sea. In V. G. Dethier et al. (Eds.), *Topics in the study of life manual: The bio source book, XIII* (pp. 209-214). New York: Harper & Row Publishers.

Kanwisher, J., & Sundnes, G. (1965). Physiology of a small cetacean. *Hvalradets Skrift*, *48*, 45-53.

Kanwisher, J., & Sundnes, G. (1966). Thermal regulation of cetaceans. In K. S. Norris (Ed.), *Whales, dolphins and porpoises* (pp. 397-407). Berkeley: University of California Press.

Kastelein, R. A., & Dubbeldam, J. L. (1990). Marginal papillae on the tongue of the harbour porpoise (*Phocoena phocoena*), bottlenose dolphin (*Tursiops truncatus*) and Commerson's dolphin (*Cephalorhynchus commersonii*). *Aquatic Mammals*, *15*(4), 158-170.

Kastelein, R. A., & Lavaleije, M. S. S. (1992). Foreign bodies in the stomach of a female harbour porpoise (*Phocoena phocoena*) from the North Sea. *Aquatic Mammals*, *18*(2), 40-46.

Kastelein, R. A., & Meijler, F. L. (1989). Respiratory arrhythmia in the hearts of harbour porpoises (*Phocoena phocoena*). *Aquatic Mammals*, *15*(2), 57-63.

Kastelein, R. A., & van Battum, R. (1990). The relationship between body weight and morphological measurements in harbour porpoises (*Phocoena phocoena*) from the North Sea. *Aquatic Mammals*, *16*(2), 48-52.

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

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

Kastelein, R. A., Hardeman, J., & Boer, H. (1997a). Food consumption and body weight of harbour porpoises (*Phocoena phocoena*). In A. J. Read, P. R. Wiepkema, & P. E. Nachtigall (Eds.), *The biology of the harbour porpoise* (pp. 217-233). Woerden, The Netherlands: De Spil Publishers.

Kastelein, R. A., Macdonald, G. J., & Wiepkema, P. R. (2000a). A note on food consumption and growth of common dolphins (*Delphinus delphis*). *Journal of Cetacean Research and Management*, *2*, 69-73.

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

Kastelein, R. A., Nieuwstraten, S. H., & Verstegen, M. W. A. (1997b). Passage time of carmine red dye through the digestive tract of harbour porpoises (*Phocoena phocoena*). In A. J. Read, P. R. Wiepkema, & P. E. Nachtigall (Eds.), *The biology of the harbour porpoise* (pp. 265-275). Woerden, The Netherlands: De Spil Publishers.

Kastelein, R. A., Staal, C., & Wiepkema, P. R. (2003a). Food consumption, food passage time, and body measurements of captive bottlenose dolphins (*Tursiops truncatus*). *Aquatic Mammals*, *29*(1), 53-66.

Kastelein, R. A., Kershaw, J., Berghout, E., & Wiepkema, P. R. (2003b). Food consumption and suckling of killer whales *Orcinus orca* at Marineland, Antibes. *International Zoo Yearbook*, *38*, 204-218. https://doi.org/10.1111/j.1748-1090.2003.tb02081.x

Kastelein, R. A., Koene, P., Nieuwstraten, S. H., & Labberté, S. (1997c). Skin surface temperature changes in a harbour porpoise. In A. J. Read, P. R. Wiepkema, & P. E. Nachtigall (Eds.), *The biology of the harbour porpoise* (pp. 255-264). Woerden, The Netherlands: De Spil Publishers.

Kastelein, R. A., Mosterd, J., Schooneman, N. M., & Wiepkema, P. R. (2000b). Food consumption, growth, body dimensions, and respiration rates of captive false killer whales (*Pseudorca crassidens*). *Aquatic Mammals*, *26*(1), 33-44.

Kastelein, R. A., Neurohr, B., Nieuwstraten, S. H., & Wiepkema, P. R. (1999). Food consumption and body measurements of Amazon river dolphins (*Inia geoffrensis*). *Aquatic Mammals*, *25*(3), 173-182.

Kastelein, R. A., Schooneman, N. M., Staal, C., & Boer, H. (1997d). A method for tube-feeding juvenile harbour porpoises (*Phocoena phocoena*). In A. J. Read, P. R. Wiepkema, & P. E. Nachtigall (Eds.), *The biology of the harbour porpoise* (pp. 63-83). Woerden, The Netherlands: De Spil Publishers.

Kastelein, R. A., van der Elst, C. A., Tennant, H. K., & Wiepkema, P. R. (2000c). Food consumption and growth of a female dusky dolphin (*Lagenorhynchus obscurus*). *Zoo Biology*, *19*, 131-142. https://doi.org/10.1002/1098-2361(2000)19:2<131::AID-ZOO4>3.0.CO;2-Y

Kastelein, R. A., van der Sijs, S. J., Staal, C., & Nieuwstraten, S. H. (1997e). Blubber thickness in harbour porpoises (*Phocoena phocoena*). In A. J. Read, P. R. Wiepkema, & P. E. Nachtigall (Eds.), *The biology of the harbour porpoise* (pp. 179-199). Woerden, The Netherlands: De Spil Publishers.

Kastelein, R. A., Vaughan, N., Walton, S., & Wiepkema, P. R. (2002). Food intake and body measurements of Atlantic bottlenose dolphins (*Tursiops truncatus*) in captivity. *Marine Environmental Research*, *53*, 199-218. https://doi.org/10.1016/S0141-1136(01)00123-4

Kastelein, R. A., Ford, J., Berghout, E., Wiepkema, P. R., & van Boxsel, M. (1994). Food consumption, growth and reproduction of belugas (*Delphinapterus leucas*) in human care. *Aquatic Mammals*, *20*(2), 81-97.

Kastelein, R. A., Walton, S., Odell, D., Nieuwstraten, H., & Wiepkema, P. R. (2000d). Food consumption of a captive female killer whale (*Orcinus orca*). *Aquatic Mammals*, *26*(2), 127-131.

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

King, S. L., Schick, R. S., Donovan, C., Booth, C. G., Burgman, M., Thomas, L., & Harwood, J. (2015). An interim framework for assessing the population consequences of disturbance (C. Kurle, Ed.). *Methods in Ecology and Evolution*, *6*, 1150-1158. https://doi.org/10.1111/2041-210X.12411

Kipps, E. K., McLellan, W. A., Rommel, S. A., & Pabst, D. A. (2002). Skin density and its influence on buoyancy in the manatee (*Trichechus manatus latirostris*), harbor porpoise (*Phocoena phocoena*), and bottlenose dolphin (*Tursiops truncatus*). *Marine Mammal Science*, *18*, 765-778. https://doi.org/10.1111/j.1748-7692.2002.tb01072.x

Koga, T. (1991). Relationship between food consumption and growth of harbour porpoises *Phocoena phocoena* in captivity. *International Marine Biology Research Institute Report*, *2*, 71-73.

Koopman, H. N. (1998). Topographical distribution of the blubber of harbor porpoises (*Phocoena phocoena*). *Journal of Mammalogy*, *79*, 260-270. https://doi.org/10.2307/1382862

Koopman, H. N., Iverson, S. J., & Gaskin, D. E. (1996). Stratification and age-related differences in blubber fatty acids of the male harbour porpoise (*Phocoena phocoena*). *Journal of Comparative Physiology B*, *165*, 628-639. https://doi.org/10.1007/BF00301131

Kooyman, G. L., & Sinnett, E. E. (1979). Mechanical properties of the harbor porpoise lung, *Phocoena phocoena*. *Respiratory Physiology*, *36*, 287-300. https://doi.org/10.1016/0034-5687(79)90042-2

Learmonth, J. A., Murphy, S., Luque, P. L., Reid, R. J., Patterson, I. P., Brownlow, A., . . . Pierce, G. J. (2014). Life history of harbor porpoises (*Phocoena phocoena*) in Scottish (UK) waters. *Marine Mammal Science*, *30*, 1427-1455. https://doi.org/10.1111/mms.12130

Leopold, M. F. (2015). *Eat or be eaten: Porpoise diet studies* (Ph.D. thesis). Wageningen University, Wageningen, The Netherlands. 239 pp.

Lindroth, A. (1962). Baltic salmon fluctuations 2: Porpoise and salmon. *Report of the Institute of Freshwater Research, Drottingholm*, *44*, 105-112.

Linnenschmidt, M., Teilmann, J., Akamatsu, T., Dietz, R., & Miller, L. A. (2013). Biosonar, dive, and foraging activity of satellite tracked harbor porpoises (*Phocoena pho-*

coena). *Marine Mammal Science*, *29*, E77-E97. https://doi.org/10.1111/j.1748-7692.2012.00592.x

Lockyer, C. (1995). Aspects of the morphology, body fat condition and biology of the harbour porpoise, *Phocoena phocoena*, in British waters. In A. Bjørge & G. P. Donovan (Eds.), The biology of the Phocoenids. *Report of the International Whaling Commission*, Special Issue 16, 199-209.

Lockyer, C., & Kinze, C. (2003). Status, ecology and life history of harbour porpoise (*Phocoena phocoena*), in Danish waters. In T. Haug, G. Desportes, G. A. Víkingsson, & L. Witting (Eds.), *Harbour porpoises in the North Atlantic* (pp. 143-175). Tromsø, Norway: The North Atlantic Marine Mammal Commission.

Lockyer, C. H., Desportes, G., Hansen, K., Labberté, S., & Siebert, U. (2003). Monitoring growth and energy utilisation of the harbour porpoise (*Phocoena phocoena*) in human care. *NAMMCO Scientific Publications*, *5*, 107-120. https://doi.org/10.7557/3.2743

MacLeod, C. D., Santos, M. B., Reid, R. J., Scott, B. E., & Pierce, G. J. (2007). Linking sandeel consumption and the likelihood of starvation in harbour porpoises in the Scottish North Sea: Could climate change mean more starving porpoises? *Biological Letters*, *3*, 185-188. https://doi.org/10.1098/rsbl.2006.0588

Møhl-Hansen, U. (1954). Investigations on reproduction and growth of the porpoise (*Phocoena phocoena* (L)) from the Baltic. *Videnskabelige Meddelelser Dansk Naturhistorisk Forening*, *166*, 369-396.

Myers, W. A., Horton, H. C., Heard, F. A., Jones, A., Winsett, G., & McCulloch, S. A. (1978). The role of recorded data in acclimatizing a harbour porpoise (*Phocoena phocoena*). *Aquatic Mammals*, *6*(2), 54-64.

Nabe-Nielsen, J., Sibly, R. M., Tougaard, J., Teilmann, J., & Sveegaard, S. (2014). Effects of noise and by-catch on a Danish harbour porpoise population. *Ecological Modelling*, *272*, 242-251. https://doi.org/10.1016/j.ecolmodel.2013.09.025

National Research Council. (2005). *Marine mammal populations and ocean noise: Determining when noise causes biologically significant effects*. Washington, DC: The National Academies Press. 126 pp.

Ólafsdóttir, D., Víkingsson, G. A., Halldórsson, S. D., & Sigurjónsson, J. (2002). Growth and reproduction in harbour porpoises (*Phocoena phocoena*) in Icelandic waters. *NAMMCO Scientific Publications*, *5*, 195-210. https://doi.org/10.7557/3.2747

Parker, G. H. (1932). The respiratory rate of the common porpoise. *Journal of Mammalogy*, *13*, 68-69. https://doi.org/10.2307/1374174

Parry, D. A. (1949). The structure of whale blubber, and a discussion of its thermal properties. *Journal of Microscopic Science*, *90*, 13-25.

Rae, B. B. (1965). The food of the common porpoise (*Phocaena phocaena*). *Journal of Zoology, London*, *146*, 114-122. https://doi.org/10.1111/j.1469-7998.1965.tb05204.x

Rae, B. B. (1973). Additional notes on the food of the common porpoise (*Phocoena phocoena*). *Journal of Zoology, London*, *169*, 127-131. https://doi.org/10.1111/j.1469-7998.1973.tb04657.x

Read, A. J. (1990a). Estimation of body condition in harbour porpoises, *Phocoena phocoena*. *Canadian Journal of Zoology*, *68*, 1962-1966. https://doi.org/10.1139/z90-276

Read, A. J. (1990b). Age at sexual maturity and pregnancy rates of harbour porpoises *Phocoena phocoena* from the Bay of Fundy. *Canadian Journal of Fisheries and Aquatic Science*, *47*, 561-565. https://doi.org/10.1139/f90-240

Read, A. J,. & Hohn, A. A. (1995). Life in the fast lane: The life history of harbour porpoises from the Gulf of Maine. *Marine Mammal Science*, *11*, 423-440. https://doi.org/10.1111/j.1748-7692.1995.tb00667.x

Read, A. J., & Tolley, K. A. (1997). Postnatal growth and allometry of harbour porpoises from the Bay of Fundy. *Canadian Journal of Zoology*, *75*, 122-130. https://doi.org/10.1139/z97-016

Recchia, C. A., & Read, A. J. (1989). Stomach contents of harbour porpoises, *Phocoena phocoena* (L.), from the Bay of Fundy. *Canadian Journal of Zoology*, *67*, 2140-2146. https://doi.org/10.1139/z89-304

Reed, J. Z., Chambers, C., Hunter, C. J., Lockyer, C., Kastelein, R. A., Fedak, M. A., & Boutilier, R. G. (2000). Gas exchange and heart rate in the harbour porpoise (*Phocoena phocoena*). *Journal of Comparative Physiology B*, *170*, 1-10. https://doi.org/10.1007/s003600050001

Richardson, S. F., Stenson, G. B., & Hood, C. (2003). Growth of the harbour porpoise (*Phocoena phocoena*) in eastern Newfoundland, Canada. *NAMMCO Scientific Publications*, *5*, 211-222. https://doi.org/10.7557/3.2748

Rogan, E., & Berrow, S. D. (1996). A review of harbour porpoises, *Phocoena phocoena*, in Irish waters. *Report of the International Whaling Commission*, *46*, 595-605.

Ryan, B. F., & Joiner, B. L. (1994). *Minitab handbook* (3rd ed.). Belmont, CA: Wadsworth Publishing Company.

Ryg, M., Lydersen, C., Knutsen, L. Ø., Bjørge, A., Smith, T. G., & Øritsland, N. A. (1993). Scaling of insulation in seals and whales. *Journal of Zoology, London*, *230*, 193-206. https://doi.org/10.1111/j.1469-7998.1993.tb02682.x

Santos, M. B., Pierce, G. J., Learmonth, J. A., Reid, R. J., Ross, H. M., Patterson, I. A. P., . . . Beare, D. (2004). Variability in the diet of harbor porpoises (*Phocoena phocoena*) in Scottish waters 1992-2003. *Marine Mammal Science*, *20*, 1-27. https://doi.org/10.1111/j.1748-7692.2004.tb01138.x

Schmidt-Nielsen, K. (1997). *Animal physiology: Adaptation & environment*. Cambridge, UK: Cambridge University Press.

Slijper, E. J. (1958). Organ weights & symmetry problems in porpoises and seals. *Archives Néerlandaises de Zoologie*, *13*, 97-113.

Smith, G. J. D., & Gaskin, D. E. (1974). The diet of harbour porpoises (*Phocoena phocoena*) (L.) in coastal waters of eastern Canada, with special reference to the Bay of Fundy. *Canadian Journal of Zoology*, *52*, 777-782. https://doi.org/10.1139/z74-102

Sørensen, T. B., & Kinze, C. C. (1994). Reproduction and reproductive seasonality in Danish harbor porpoises, *Phocoena phocoena*. *Ophelia*, *39*, 159-176. https://doi.org/10.1080/00785326.1994.10429541

Spotte, S., Dunn, J. L., Kezer, L. E., & Heard, F. M. (1978). Notes on the care of a beach-stranded harbour porpoise (*Phocoena phocoena*). *Cetology*, *32*, 1-5.

Sveegaard, S., Andreasen, H., Mouritsen, K. N., Jeppesen, J. P., Teilmann, J., & Kinze, C. C. (2012a). Correlation between the seasonal distribution of harbour porpoises and their prey in the Sound, Baltic Sea. *Marine Biology*, *159*, 1029-1037. https://doi.org/10.1007/s00227-012-1883-z

Sveegaard, S., Nabe-Nielsen, J., Stæhr, K-J., Jensen,T. F., Mouritsen, K. N., & Teilmann, J. (2012b). Spatial interactions between marine predators and their prey: Herring abundance as a driver for the distributions of mackerel and harbour porpoise. *Marine Ecology Progress Series*, *468*, 245-253. https://doi.org/10.3354/meps09959

Thompson, P. M., Brookes, K. L., Graham, I. M., Barton, T. R., Needham, K., Bradbury, G., & Merchant, N. D. (2013). Short-term disturbance by a commercial two-dimensional seismic survey does not lead to long-term displacement of harbour porpoises. *Proceedings of the Royal Society B: Biological Sciences*, *280*, 20132001. https://doi.org/10.1098/rspb.2013.2001

van Utrecht, W. L. (1978). Age and growth in *Phocoena phocoena* Linnaeus, 1758 (Cetacea, Odontoceti) from the North Sea. *Bijdragen tot de Dierkunde*, *48*, 16-28.

Víkingsson, G. A., Ólafsdóttir, D., & Sigurjónsson, J. (2003). Diet of harbour porpoises (*Phocoena phocoena*) in Icelandic coastal waters. *NAMMCO Scientific Publications*, *5*, 243-270. https://doi.org/10.7557/3.2829

Watson, A. P., & Gaskin, D. E. (1983). Observations on the ventilation cycle of the harbour porpoise *Phocoena phocoena* (Linnaeus, 1785) in coastal waters of the Bay of Fundy. *Canadian Journal of Zoology*, *61*, 126-132. https://doi.org/10.1139/z83-015

Westgate, A. J., Read, A. J., Berggren, P., Koopman, H. N., & Gaskin, D. E. (1995). Diving behaviour of harbour porpoises, *Phocoena phocoena*. *Canadian Journal of Fisheries and Aquatic Science*, *52*, 1064-1073. https://doi.org/10.1139/f95-104

Wisniewska, D. M., Johnson, M., Teilmann, J., Rojano-Donate, L., Shearer, J., Sveegaard, S., . . . Madsen, P. T. (2016). Ultra-high foraging rates of harbor porpoises make them vulnerable to anthropogenic disturbance. *Current Biology*, *26*, 1441-1446. https://doi.org/10.1016/j.cub.2016.03.069

Worthy, G. A. J., & Edwards, E. F. (1990). Morphometric and biochemical factors affecting heat loss in a small temperate cetacean (*Phocoena phocoena*) and a small tropical cetacean (*Stenella attenuata*). *Physiological Zoology*, *63*, 432-442. https://doi.org/10.1086/physzool.63.2.30158506

Yasui, W. Y. (1980). *Morphometrics, hydrodynamics and energetics of locomotion for a small cetacean,* Phocoena phocoena *(L.)* (Master's thesis). University of Guelph, Ontario, Canada. 86 pp.

Yasui, W. Y., & Gaskin, D. E. (1986). Energy budget of a small cetacean, the harbour porpoise, *Phocoena phocoena*. *Ophelia*, *25*, 183-197. https://doi.org/10.1080/00785326.1986.10429749