Aquatic Mammals 2019, *45*(1), 37-47, DOI 10.1578/AM.45.1.2019.37

Reduction in Body Mass and Blubber Thickness of Harbor Porpoises (*Phocoena phocoena*) Due to Near-Fasting for 24 Hours in Four Seasons

Ronald A. Kastelein,[1] Lean Helder-Hoek,[1] Nancy Jennings,[2]
Ruby van Kester,[1] and Rowanne Huisman[1]

[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

When wild harbor porpoises (*Phocoena phocoena*) are disturbed by (and perhaps flee from) anthropogenic sound, they probably do not forage, and thus they fast for a period of time. The rate of body mass loss during fasting is probably related to internal parameters such as initial body mass and blubber thickness, hormonal and reproductive state, and anxiety and activity levels, as well as to environmental parameters such as water and air temperature. Reduced blubber thickness causes reduced insulation which, in turn, increases heat loss to the environment. If blubber cannot be replenished by eating extra food, porpoises' fitness may decline, which may eventually result in hypothermia and pneumonia. To increase understanding of the effects of fasting, the body condition of two captive porpoises was quantified while they were kept under ambient temperature conditions similar to those experienced by wild conspecifics in the North Sea, and while they were near-fasting (i.e., almost fasting) for 24 hours (consuming 3 to 10% of the average daily food intake of their normal ration in each period). Replicated near-fasting periods took place during each of the four seasons of the year, and body mass (an indicator of body condition) declined in all 30 near-fasting periods (15 for each animal). For both porpoises in all seasons, body mass loss represented approximately 4% of initial body mass (of which ~0.7% was due to loss of food in the alimentary canal). Blubber thickness was difficult to quantify due to low measurement accuracy in relation to loss, but small decreases in blubber thickness (0 to 3 mm) occurred. A linear mixed-effects model showed that mass loss was greatest overall in autumn, lowest in summer, and intermediate in winter and spring. Harbor porpoises, therefore, appear to be most vulnerable to the effects of fasting due to disturbance in autumn, perhaps because their blubber layer has to increase in autumn to cope with the decreasing water temperature.

Key Words: body condition, anthropogenic sound, diet, iPCoD, DEPONS, nutrition, effect disturbance, energetics, odontocete

Introduction

Anthropogenic underwater sound may affect hearing, mask ecologically relevant sounds, or change the behavior of marine animals in such a way that their foraging efficiency decreases (Pirotta et al., 2014; Senigaglia et al., 2016). It is important for policymakers to understand whether and how acoustic disturbances affect the population dynamics of a species. The harbor porpoise (*Phocoena phocoena*) is known to flee from areas with loud anthropogenic sounds such as sounds from seismic surveys (Thompson et al., 2013) and pile driving (produced, for instance, during the construction of offshore wind parks; Carstensen et al., 2006; Brandt et al., 2011; Dähne et al., 2013; Haelters et al., 2014). The species is exposed to underwater sound to a great extent because it inhabits many of the temperate coastal waters of the northern hemisphere (Bjørge & Tolley, 2008) where many anthropogenic activities occur.

As a result of their relatively small body size, harbor porpoises have a larger body surface area to body volume ratio than most other odontocetes, so they have the potential to lose a great deal of energy through radiation and conduction to the surrounding water (Kanwisher & Sundnes, 1965; Feldman & McMahon, 1983; Gaskin, 1992). Alongside their small body size, harbor porpoises have evolved a relatively high metabolic rate compared to the larger odontocetes (Parry, 1949; Read, 1990; Lockyer, 1995; Kastelein et al., 1997d, 2018; Koopman, 1998). To maintain a stable internal body temperature, harbor porpoises need to consume sufficient food (Kanwisher & Sundnes, 1965; Yasui & Gaskin, 1986; Kastelein et al., 1997b; Koopman et al., 2002; Bjørge, 2003; Lockyer & Kinze, 2003). High feeding rates are necessary for the survival of harbor porpoises, and these porpoises are capable of extremely high feeding rates (Wisniewska et al., 2016; Hoekendijk et al., 2017). Depending on food availability, even a small decrease in the foraging efficiency of a harbor porpoise due to an anthropogenic acoustic disturbance, for example, may have large consequences for that animal's fitness. Porpoises obtain all of their water from prey ingestion, so fasting may also lead to the release of water from increased catabolism of blubber and lean tissue (Ortiz et al., 1978; Worthy et al., 1992).

Harbor porpoise blubber is relatively thick and has low thermal conductance compared to the blubber of other odontocetes (Worthy & Edwards, 1990). Despite this, as a harbor porpoise loses body mass, it loses more thermal energy to the environment through the loss of insulating blubber and the consequent increase in body surface to volume ratio. When kept in water at temperatures that change seasonally (as do the water temperatures throughout their natural geographic range), harbor porpoises show seasonal changes in body mass and blubber thickness (Kastelein et al., 1997d, 2018; Lockyer & Kinze, 2003). This may make harbor porpoises more vulnerable to disturbance in particular seasons. Policymakers devising environmental legislation to protect harbor porpoises from acoustic disturbance need to know in which seasons, if any, the porpoises are most vulnerable to disturbance. In the Dutch part of the North Sea, for instance, pile driving activities are currently regulated by setting a limit to the amount of impulsive sound generated. The limit is flexible and varies with season and location, based on seasonal and spatial variability in harbor porpoise abundance (Heinis et al., 2015). Seasonal variation in vulnerability to disturbance that may exist in harbor porpoises has not so far been taken into account in policies to protect the species.

Models such as the Population Consequences of Acoustic Disturbance model (PCAD; National Research Council, 2005), implemented to generate the Interim Population Consequences of Disturbance model (iPCoD; 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, 2018), provide an energetics-based approach to estimating population effects for marine mammals. However, much of the information required to develop and implement such models is lacking.

Disturbance is likely to result in reduced food intake. To quantify the effects of relatively short periods of fasting and investigate seasonal variation in harbor porpoises' vulnerability to severe reduction in food intake, the body mass and blubber thickness of two captive harbor porpoises that were kept in water and air temperatures similar to those experienced by wild conspecifics in the North Sea were measured before and during 24-h near-fasting periods in each of the four seasons.

Methods

Study Animals

The two harbor porpoises had been found stranded on the North Sea coast. They were rehabilitated but not released because they had been hand-reared on formula and, thus, had not learned to catch fish efficiently. The female, identified as Porpoise F05, was ~11 mo old when she stranded; and the male, identified as Porpoise M06, was ~7 mo old. After rehabilitation, the harbor porpoises were trained to allow weekly body measurements to be taken.

At the time of the study, both animals were healthy and in good physical condition. Porpoise F05 had reached her maximum body length (154 cm) and was 6 to 7 y old (girth at axilla: 80 to 85 cm; body mass: 40 to 45 kg); she was average size (Fisher & Harrison, 1970; van Utrecht, 1978; Gaskin et al., 1984; Read, 1990; Learmonth et al., 2014). Subadult Porpoise M06 was 3 to 4 y old and was still growing (body length: 128 to 130 cm; girth at axilla: 73 to 82 cm; body mass: 29 to 34 kg). His body length was ~10% below average for male porpoises of his age, but his body length–body weight ratio was normal (Kastelein et al., 1997b).

Study Area

The study was conducted at the SEAMARCO Research Institute, The Netherlands (latitude 51° 32' 11.24" N, longitude 3° 55' 30.58" E). The animals were kept 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 Eastern Scheldt, an inlet of the North Sea, into the water circulation system; partial recirculation through biological and sand filters ensured year-round water clarity.

The minimum and maximum air temperatures over each 24-h period were recorded (Figure 1a). The pool water temperature was measured once per day in the morning (Figure 1b). The air and water

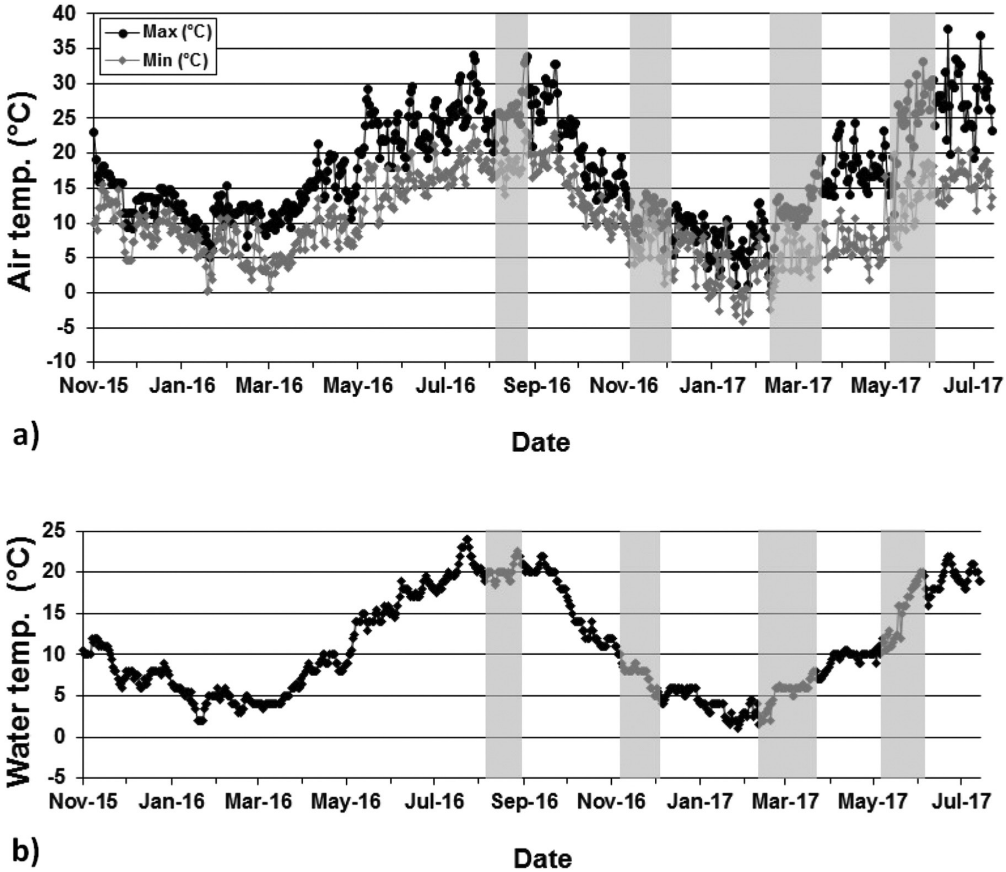

Figure 1. (a) The daily minimum and maximum air temperature and (b) daily pool water temperature before, during, and after the study, from November 2015 to July 2017 (Nov-15 = 1 November 2015). The four seasons (summer, autumn, winter, and spring) in which the effect of near-fasting in the two harbor porpoises was measured are indicated by the light grey bars.

temperatures and salinity (~3.4%) experienced by the captive study animals were similar to those experienced by wild conspecifics in the North Sea (wild porpoises occurred 200 m away on the other side of the dyke in the Eastern Scheldt).

Normal Food Consumption

When not fasting, the harbor porpoises were fed four to five times a day on a diet of 65% thawed sprat (*Sprattus sprattus*), 25% herring (*Clupea harengus*), and 10% mackerel (*Scomber scombrus*) (percentages based on mass; complete fish were given). The last feed of each day was at 1630 h, and the first feed of the next day was at 0830 h. The other two to three meals were given between 1030 and 1430 h, with at least 2 h between meals; initial food passage time in harbor porpoises is ~2.5 h (Kastelein et al., 1997c), so the forestomach is probably empty after ~2 h and can accommodate the next meal. Vitamins (Akwavit; Arie Blok Animal Nutrition, Woerden, The Netherlands) were added to the thawed fish, as some vitamins are reduced due to storage in the freezer and the thawing process which occurred in water. Fish were at a temperature of ~4°C when they were fed to the porpoises. The fish was weighed digitally (±1 g accuracy), and the mass of fish of each species eaten by each porpoise during each meal was recorded. The energy content of each fish species was quantified by an ISO 17025 accredited laboratory (Silliker Netherlands BV, trading as Merieux NutriSciences, Ede, The Netherlands) for each fish delivery so that food consumption could be expressed both in kg and in kJ per day (mean of 4 random samples: energetic content of sprat: 7.9 kJ/g wet weight, herring: 6.5 kJ/g, and mackerel: 7.7. kJ/g).

The animals received a basic food ration each day, which was adjusted at the end of each week when the animals were weighed, based on their 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 their motivation to feed stable during the year.

Measurement of Body Condition Parameters

The study animals participated in the measurements voluntarily under trainer control with positive reinforcement. The harbor porpoises were trained to swim individually onto the ramp of a lift when the trainer gave a hand signal. From the ramp, each porpoise was lifted by two people and placed on a foam rubber mattress on a digital weighing platform where it was weighed (±0.05 kg accuracy) and its blubber thickness was measured (±1 mm accuracy). Blubber was defined as the epidermis, dermis, and hypodermal tissues (Parry, 1949)—the integument of terrestrial mammals. The blubber thickness of each study animal was measured ultrasonically with a Renco Lean-Meater®. The apparatus measured the distance between the skin surface and the underlying muscle layer. Blubber thickness was measured on the lateral surface of the animal, 10 cm below the anterior insertion of the dorsal fin (on the left side of the body; location no. 4 in Kastelein et al., 1997d). Measurements made in this way at this location while a porpoise is on land are similar to those made while the porpoise is in the water, and they are similar to those made with a ruler on a recently deceased porpoise (Kastelein, pers. obs.). Body mass is highly correlated with blubber thickness measured in this way and with the girth at axilla; body mass is considered the best indicator of body condition (Kastelein et al., 2018). Each study animal was lifted back into the water about 2 min after swimming onto the ramp.

Fasting

Fasting for a period of 24 h was not expected to cause health problems for the captive harbor porpoises, as they were used to fasting for 16 h each 24-h period (from the last feed at 1630 h until the first feed of the next day at 0830 h), and because they were offered a double ration in the 24-h period after each fast.

When near-fasting, the harbor porpoises were weighed, measured, and fed just before 1500 h, and then they were only fed very small fish rewards until 1500 h the next day. During each 24-h near-fasting period, the degree and progression of body mass loss and blubber thickness decline was quantified. In the first of the four near-fasting periods (summer), the porpoises were weighed and measured every 2 h starting at 1500 h. As mass loss over 24 h was approximately linear, in subsequent near-fasting periods, the animals were not weighed and measured during the night to avoid disturbing them. Small amounts of food were offered as rewards in each measurement session: half a sprat (mean ± SD mass: 4.4 ± 1.2 g) was offered to separate the animals from each other (one animal went into the outdoor pool and one into the indoor pool), one sprat was used to reward each animal for swimming onto the lift, and half a spat was given after each animal had been returned to the water. The total amount of fish given as rewards to each animal during each 24-h near-fasting period varied between 56 and 240 g depending on the number of measurements in the 24-h fasting period (3 to 10% of the normal average daily food intake). Therefore, near-fasting (also referred to for simplicity as *fasting*) was defined in the present study as eating < 10% of the normal daily ration over a 24-h period.

Changes in the body mass and blubber thickness of the harbor porpoises during near-fasting periods were measured during each of the four seasons of the year: (1) summer (August 2016) when the animals are lean, (2) autumn (November-December 2016) when the animals are gaining weight, (3) winter (February-March 2017) when the animals are generally fattest (although this was not the case with Porpoise F05), and (4) spring (May-June 2017) when the animals are losing weight. A 24-h near-fasting period took place once a week for 4 wks in each season. The near-fasting periods were conducted 1 wk apart to allow compensatory body mass gain between them; gain was verified by bi-weekly weighing and blubber thickness measurements. Porpoise F05 was sick (the specific illness could not be determined; she exhibited lethargic behavior and slow food intake but had normal blood parameters) for 2 wks in March 2017. Staff were fully occupied with treating the sick animal, so only three instead of the planned four near-fasting periods were conducted for both animals in the winter period.

Data Analysis

Just before each near-fasting period at 1500 h, the harbor porpoises were weighed and measured, and then immediately given their last feed before the fast so that the mass of the food given in this feed was added to their body mass to provide the adjusted pre-fast body mass for analysis. The mass change (difference between the adjusted pre-fast body mass and the post-fast body mass) was submitted to a linear mixed effects model in which *season* was the fixed factor and *study animal* the random factor (Minitab 18 Statistical Software, 2017; www.minitab.com).

For blubber thickness, the changes over the 24-h near-fasting period were similar to the measurement accuracy (1 mm), so pre-fast and post-fast blubber thickness were reported but not submitted to statistical analysis.

Results

Both harbor porpoises lost body mass during each of their 15 near-fasting periods (range of change: -0.7 to -3.0 kg; measurement accuracy: ±0.05 kg). For blubber thickness, the accuracy of measurement was similar to the change over 24 h so that blubber thickness appeared to remain constant or decreased during the near-fasting periods (range of change in blubber thickness: 0 to -3 mm; measurement accuracy: ±1 mm; Table 1).

For Porpoise F05, mass change was negative in every season, and the mean mass change varied from -1.3 kg (-3.0%) in summer to -2.4 kg (-5.4%) in autumn (Table 1). The overall mean mass change for F05, expressed as a percentage of the adjusted pre-fast body mass, was -4.1% (±1.2%; range: -1.7 to -6.8%; n = 15). The pattern of change in body mass during the 24-h near-fasting periods was approximately linear (Figure 2).

For the subadult harbor porpoise, Porpoise M06, mass change was also negative in every season, and the mean mass change varied from

Table 1. The mean daily food intake, body mass, blubber thickness, and rate of body mass change (absolute values and, for body mass, as a percentage of the adjusted pre-fast body mass) for the female and male harbor porpoises during 24-h periods of near-fasting in each of the four seasons. The mean daily food intake is based on the period in which the near-fasting period occurred. The mean water temperature, based on two measurements per day, and the mean mass of fish rewards given during the near-fasting periods are also shown. Pre-fast body mass is adjusted to include the mass of the meal given just after the body mass was quantified. All means are shown ± SD, n = 4 data points except for winter when n = 3, and for water temperatures where n = 6 or 8 as indicated (the temperature measurements were from the morning before fasting started and from the morning during the near-fasting period). In all cases, the mean post-fast body mass was lower than the mean adjusted pre-fast body mass.

	Summer (Aug. 2016)	Autumn (Nov.-Dec. 2016)	Winter (Feb.-March 2017)	Spring (May-June 2017)
Mean water temperature on study days (°C)	19.9 ± 1.3 (n = 8)	8.1 ± 1.9 (n = 8)	4.7 ± 1.5 (n = 6)	14.3 ± 3.8 (n = 8)
Porpoise F05 (Female)				
Mean daily food intake (kg)	1.7	2.6	2.0	2.1
Mass of fish rewards given during fasting period (kg)	0.153 ± 0.036	0.102 ± 0.002	0.148 ± 0.047	0.065 ± 0.007
Mean adjusted pre-fast body mass (kg)	41.6 ± 0.9	44.5 ± 0.6	42.7 ± 0.4	43.2 ± 0.4
Mean body mass after fasting (kg)	40.3 ± 0.5	42.1 ± 0.7	41.3 ± 0.6	41.4 ± 0.6
Mean body mass change (kg/24 h)	-1.3 ± 0.4	-2.4 ± 0.5	-1.4 ± 0.2	-1.8 ± 0.2
Mean body mass change (% of adjusted pre-fast body mass)	-3.1% ± 0.9	-5.4% ± 1.0	-3.3% ± 0.5	-4.2% ± 0.6
Mean blubber thickness before fasting (mm)	18 ± 1	22 ± 1	24 ± 2	22 ± 1
Mean blubber thickness after 24 h fasting (mm)	17 ± 1	21 ± 1	22 ± 1	21 ± 1
Porpoise M06 (Male)				
Mean daily food intake (kg)	1.7	1.9	2.1	1.6
Mass of fish rewards given during fasting period (kg)	0.130 ± 0.048	0.107 ± 0.029	0.155 ± 0.075	0.095 ± 0.025
Mean adjusted pre-fast body mass (kg)	29.4 ± 0.6	32.1 ± 0.1	33.0 ± 0.8	29.3 ± 0.6
Mean body mass after fasting (kg)	28.2 ± 0.2	30.6 ± 0.1	31.5 ± 0.6	28.3 ± 0.7
Mean body mass change (kg/24 h)	-1.2 ± 0.3	-1.5 ± 0.1	-1.5 ± 0.3	-1.0 ± 0.2
Mean body mass change (% of adjusted pre-fast body mass)	-4.1% ± 1.0	-4.7% ± 0.2	-4.5% ± 0.7	-3.4% ± 0.8
Mean blubber thickness before fasting (mm)	16 ± 1	22 ± 1	25 ± 0	19 ± 1
Mean blubber thickness after 24 h fasting (mm)	15 ± 0	21 ± 1	25 ± 1	18 ± 1

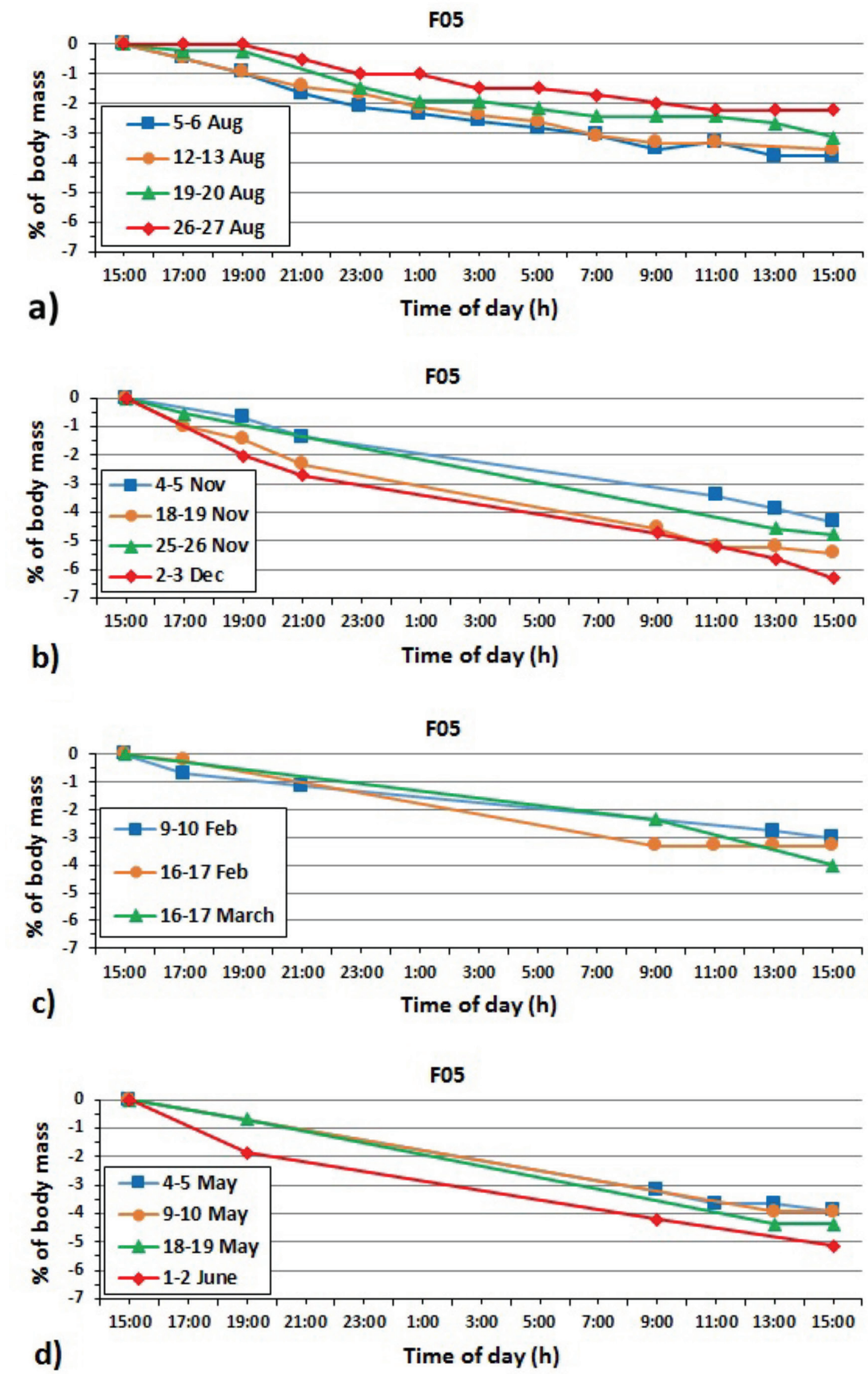

Figure 2. The percentage loss of the initial body mass of Porpoise F05 during 24-h near-fasting periods in (a) summer, (b) autumn, (c) winter, and (d) spring. The initial mass (at 1500 h, the start of the fast) is the adjusted pre-fast body mass. The mean adjusted pre-fast mass varied (41.6-44.5 kg) for each near-fasting period due to seasonal changes in body mass (see Table 1).

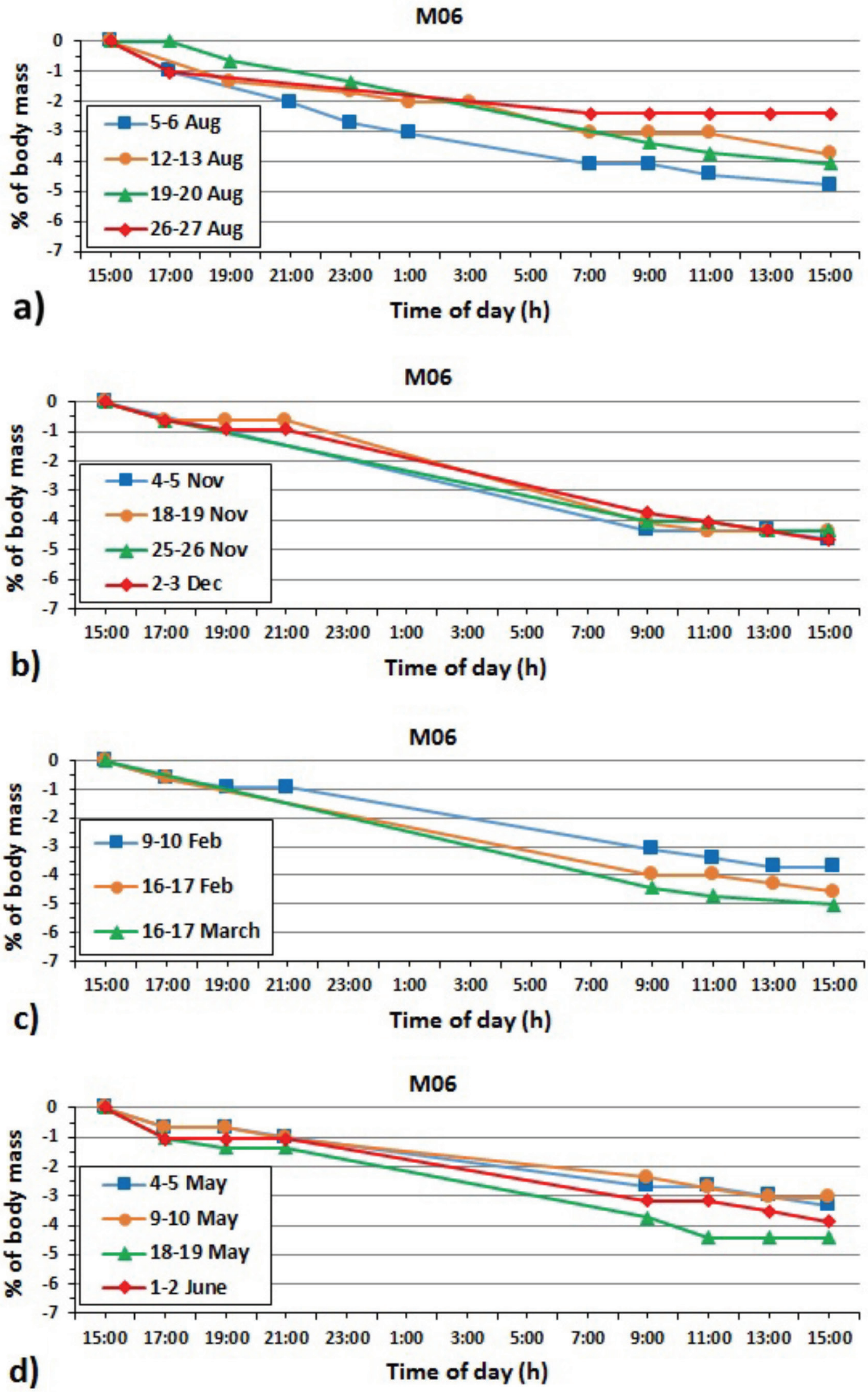

Figure 3. The percentage loss of the initial body mass of Porpoise M06 during 24-h near-fasting periods in (a) summer, (b) autumn, (c) winter, and (d) spring. The initial mass (at 1500 h, the start of the near-fast) is the adjusted pre-fast body mass. The mean adjusted pre-fast mass varied (29.3-33.0 kg) for each near-fasting period due to seasonal changes in body mass (see Table 1).

-1.0 kg (-3.5%) in spring to -1.5 kg (-4.5%) in autumn (Table 1). His overall mean mass change, expressed as a percentage of the adjusted pre-fast body mass, was -4.0 ± 0.8% (range: -2.4 to -5.0%; $n = 15$). His pattern of change in body mass during the 24-h near-fasting periods was approximately linear (Figure 3).

In the linear mixed effects model with both animals, the interaction term (season × study animal) was not significant ($p = 0.166$), so it was removed from the final model. In the final model, there was no significant effect of study animal on the mass change (adjusted pre-fast body mass minus post-fast body mass; $p = 0.254$), but there was a significant effect of season ($p = 0.003$). Tukey post-hoc pair-wise comparisons revealed two overlapping sets of statistically similar levels: mass change was statistically similar in summer, spring, and winter, and also in in autumn, spring, and winter. Autumn was the season of greatest mass loss for both porpoises, though it was not the coldest season (Table 1). Summer, the warmest season, was the season when mass changed the least due to near-fasting; mass change in winter and spring was intermediate.

Discussion

This was the first study on the effects of severe food restriction on body mass and blubber thickness in harbor porpoises. The study animals were given only small amounts of food during the near-fasting periods so that they were severely food-deprived. Only two animals were available for study, and effects of fasting may vary with sex, age, and other characteristics that we were unable to vary in this study. For instance, growing subadult harbor porpoises (represented by Porpoise M06 in the present study) generally need more food than adults, and adult females eat more during gestation and lactation than during non-reproductive periods (represented by Porpoise F05 in the present study).

Wild harbor porpoises probably do not forage-while swimming away from sounds such as those with anthropogenic origin (Pirotta et al., 2014). While fasting for an initial period of 24 h, they are likely to suffer approximately linear body mass loss over time, similar to that reported herein. During 24-h near-fasting periods, Porpoise F05, the larger study animal, lost more mass than the smaller study animal, Porpoise M06, but their mass loss as a percentage of initial body mass was similar (Table 1). Thus, a decrease in body mass in the range of 3 to 5% during the first 24 h of fasting is likely to occur in healthy harbor porpoises in the North Sea. Note that because the last meal of the porpoises was added to the initial body mass measurement, ~0.7% of the body mass loss was due to loss of food in the alimentary canal.

The mass losses described herein for harbor porpoises after a 24-h near-fasting period are in themselves unlikely to result in declines in fitness in an animal in good condition. After they were offered twice the normal amount of food for 2 d after each near-fasting period, the porpoises' body weight and blubber thickness had returned to the pre-fasting values. If food is abundant, wild harbor porpoises may eat more than this per day in the post-fast period and, thus, may recover even quicker. However, repeated disturbances may have negative effects on fitness, as predicted for the sperm whale (*Physeter macrocephalus*; Farmer et al., 2018). If fasting continues for longer than 24 h, if food is not abundant, or if disturbance and fasting occur frequently, effects on porpoises are likely to be severe and may be long lasting.

In this study, near-fasting periods were not extended beyond 24 h to avoid detrimental effects on the study animals. However, if a fasting period lasts longer than 24 h, mass loss is likely to continue, the blubber layer will become thinner, and heat loss will increase. Harbor porpoises have limited internal lipid stores, so the blubber provides most of their energy during fasting. Fasting may also lead to the release of water from increased catabolism of blubber and lean tissue (Ortiz et al., 1978; Worthy et al., 1992). The decrease in body mass may not continue to be approximately linear if fasting continues for longer than 24 h because as the blubber layer becomes thinner, the porpoise will lose more heat to the environment and, thus, it will have to catabolize more body fat to keep its internal body temperature at around 36°C. As suggested by Rosen et al. (2007), as well as affecting thermoregulation, consuming insufficient prey is likely to have feedback effects on foraging and digestive capacity. Meeting energy deficits through catabolism of blubber may affect buoyancy and gait, increasing the costs and decreasing the efficiency of foraging attempts. Increased thermoregulatory costs will decrease foraging ability through higher metabolic overheads. Insulation may be reduced to the point of increasing the energetic cost of thermoregulation; this may lead to reduced body condition and increased energy deficit until thermal balance cannot be maintained. Once this happens, animals become more susceptible to disease (Rosen et al., 2007).

If blubber loss cannot be reversed by eating extra food, it may eventually result in hypothermia and, in harbor porpoises, this often leads to pneumonia (Kastelein et al., 1997a). Declines in fitness may result in reduced fecundity and survival. The magnitude of the resulting effects on population dynamics cannot be quantified, but, based on the results from the present study, the detrimental effects of disturbance are likely to be greatest in autumn and lowest in summer. In autumn, porpoises should be gaining weight in order to be sufficiently insulated for the cold water in winter.

Effects of fasting due to a disturbance may be more severe in animals whose body condition is less than optimal due to health issues. During rehabilitation of stranded harbor porpoises, large body mass loss has been observed in animals that were already sick and emaciated (Kastelein, pers. comm.). In some cases, the animals' lives could only be saved by feeding them the maximum food quantity they could ingest every hour, and by keeping them in warm water (20 to 30°C; Kastelein et al., 1997a) to reduce energy loss to the environment so that the ingested food could be used to build up an insulating blubber layer instead of mainly being used for maintaining an appropriate core body temperature.

Information from the present study can be used to help inform models such as the iPCoD model (King et al., 2015) and the DEPONS model (Nabe-Nielsen et al., 2014, 2018), which were developed to estimate population effects of disturbance for marine mammals. Information on marine mammal energetics is needed to define parameters affecting the vital rates (birth and death rates). The data from the present study will increase the information on which the experts can base their judgements, thus aiding future expert elicitations on the effect of disturbance on harbor porpoise energetics and allowing the iPCoD model to be updated and improved.

Acknowledgments

We thank assistant Shirley Van de Voorde and students Fabian Hoekstra, Stephanie de Ruijter, Manon Horvers, Fransien Moerland, Lotte Dalmeijer, Céline van Putten, Susan Janssen, Iris Keurntjes, Simone de Winter, Stacey van der Linden, Daniek Kuipers, Tessa Kreeft, and Leonie Huijser for their help with weighing and measuring the blubber thickness of the harbor porpoises for this project. We thank Bert Meijering (Topsy Baits) for providing space for the SEAMARCO Research Institute; we thank Mieke Leuning (Parlevliet & van der Plas B.V) for supplying the energetic content of the fish fed to the porpoises. We thank Floor Heinis (Heinis Water Management & Ecology), Cormac Booth (SMRU Consulting), Mardik Leopold (Wageningen Marine Research), the editor David Rosen, and two anonymous reviewers for their constructive comments on the manuscript. Funding was received from The Netherlands Ministry of Infrastructure and Water Management (Zaaknummer 31118293). Supervisors for the commissioner were Aylin Erkman and Inger van den Bosch. The harbor porpoises for this study were made available by the ASPRO group.

Literature Cited

Bjørge, A. (2003). The harbour porpoises (*Phocoena phocoena*) in the North Atlantic: Variation in habitat use, trophic ecology and contaminant exposure. *NAMMCO Scientific Publications*, *5*, 223-228.

Bjørge, 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). San Diego, CA: Academic Press.

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*(2), 025002. https://doi.org/10.1088/1748-9326/8/2/025002

Farmer, N. A., Noren, D. P., Fougères, E. P., Machernis, A., & Baker, K. (2018). Resilience of the endangered sperm whale *Physeter macrocephalus* to foraging disturbance in the Gulf of Mexico, USA: A bioenergetic approach. *Marine Ecology Progress Series*, *589*, 241-261. https://doi.org/10.3354/meps12457

Feldman, H. A., & McMahon, T. A. (1983). The 3/4 mass exponent in metabolism is not an artefact. *Respiration Physiology*, *52*(2), 149-163. https://doi.org/10.1016/0034-5687(83)90002-6

Fisher, H. D., & Harrison, R. J. (1970). Reproduction in the common porpoise (*Phocoena phocoena*) of the North Atlantic. *Journal of Zoology, London*, *161*(2), 471-486. https://doi.org/10.1111/j.1469-7998.1970.tb02050.x

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

Gaskin, D. E., Smit, G. J. D., Watson, A. P., Yasui, W. Y., & Yurick, D. B. (1984). Reproduction in the porpoises (Phocoenidae): Implications for management. In 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*(1), 105-116. https://doi.org/10.1007/s10750-014-2138-4

Heinis, F., de Jong, C. A. F., & Rijkswaterstaat Underwater Sound Working Group. (2015). *Cumulative effects of impulsive underwater sound on marine mammals* (Report TNO 2015 R10335-ENG). 86 pp.

Hoekendijk, J. P. A., Spitz, J., Read, A. J., Leopold, M. F., & Fontaine, M. C. (2017). Resilience of harbor porpoises to anthropogenic disturbance: Must they really feed continuously? *Marine Mammal Science*, *34*(1), 258-264. https://doi.org/10.1111/mms.12446

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

Kastelein, R. A., Bakker, M. J., & Staal, C. (1997a). The rehabilitation and release of stranded harbour porpoises (*Phocoena phocoena*). In A. J. Read, P. R. Wiepkema, & P. E. Nachtigall (Eds.), *The biology of the harbour porpoise* (pp. 9-61). Woerden, The Netherlands: De Spil Publishers.

Kastelein, R. A., Hardeman, J., & Boer, H. (1997b). 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., Helder-Hoek, L., & Jennings, N. (2018). Seasonal changes in food consumption, respiration rate, and body condition of a male harbor porpoise (*Phocoena phocoena*). *Aquatic Mammals*, *44*(1), 76-91. https://doi.org/10.1578/AM.44.1.2018.76

Kastelein, R. A., Nieuwstraten, S. H., & Verstegen, M. W. A. (1997c). 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., van der Sijs, S. J., Staal, C., & Nieuwstraten, S. H. (1997d). 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.

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. *Methods in Ecology and Evolution*, *6*(10), 1150-1158. https://doi.org/10.1111/2041-210X.12411

Koopman, H. N. (1998). Topographical distribution of the blubber of harbor porpoises (*Phocoena phocoena*). *Journal of Mammalogy*, *79*(1), 260-270. https://doi.org/10.2307/1382862

Koopman, H. N., Pabst, D. A., McLellan, W. A., Dillaman, R. M., & Read, A. J. (2002). Changes in blubber distribution and morphology associated with starvation in the harbor porpoise (*Phocoena phocoena*): Evidence for regional differences in blubber structure and function. *Physiological and Biochemical Zoology*, *75*, 498-512.

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*(4), 1427-1455. https://doi.org/10.1111/mms.12130

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. Reports of the International Whaling Commission*, *16*, 199-209.

Lockyer, C., & Kinze, C. (2003). Status, ecology and life history of harbour porpoise (*Phocoena phocoena*), in Danish waters. In T. Hung, D. Desportes, G. A. Víkingsson, & L. Witting (Eds.), *Harbour porpoises in the North Atlantic* (pp. 143-175). Tromsø, Norway: The North Atlantic Marine Mammal Commission. https://doi.org/10.7557/3.2745

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

Nabe-Nielsen, J., van Beest, F. M., Grimm, V., Sibly, R. M., Teilmann, J., & Thompson, P. M. (2018). Predicting the impacts of anthropogenic disturbances on marine populations. *Conservation Letters*, e12563. https://doi.org/10.1111/conl.12563

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.

Ortiz, C. L., Costa, D., & Le Boeuf, B. J. (1978). Water and energy flux in elephant seal pups fasting under natural conditions. *Physiological Zoology*, *51*(2), 166-178. https://doi.org/10.1086/physzool.51.2.30157864

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

Pirotta, E., Brookes, K. L., Graham, I. M., & Thompson, P. M. (2014). Variation in harbour porpoise activity in response to seismic survey noise. *Biological Letters*, *10*(5), 20131090. https://doi.org/10.1098/rsbl.2013.1090

Read, A. J. (1990). 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*(3), 561-565. https://doi.org/10.1139/f90-064

Rosen, D. A. S., Winship, A. J., & Hoopes, L. A. (2007). Thermal and digestive constraints to foraging behaviour in marine mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1487), 2151-2168. https://doi.org/10.1098/rstb.2007.2108

Senigaglia, V., Christiansen, F., Bejder, L., Gendron, D., Lundquist, D., Noren, D. P., . . . Lusseau, D. (2016). Meta-analyses of whale-watching impact studies: Comparisons of cetacean responses to disturbance. *Marine Ecology Progress Series*, *542*, 251-263. https://doi.org/10.3354/meps11497

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*(1771), 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.

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*(11), 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*(2), 432-442. https://doi.org/10.1086/physzool.63.2.30158506

Worthy, G. A. J., Morris, P. A., Costa, D. P., & Le Boeuf, B. J. (1992). Moult energetics of the northern elephant seal (*Mirounga angustirostris*) on land. *Journal of Zoology*, *227*, 257-265. https://doi.org/10.1111/j.1469-7998.1992.tb04821.x

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