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SEAMARCO final report 2018-01  
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## **Reduction in body mass and blubber thickness of harbor porpoises (*Phocoena phocoena*) due to near-fasting for 24 hours in four seasons**

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### **Abstract**

When wild harbor porpoises are disturbed by (and perhaps flee from) anthropogenic sound, they probably do not forage, and thus 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, anxiety and activity level, as well as to environmental parameters such as water and air temperature. Reduced blubber thickness causes reduced insulation, and thus 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. In order 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 almost fasting for 24 h (consuming 3 - 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 (0-3 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:** anthropogenic sound, body condition, diet, DEPONS, effect disturbance energetics, iPCoD, nutrition, 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 (Pirodda et al., 2014; Senigaglia et al., 2016). It is important for policy-makers 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 the temperate coastal waters of the northern hemisphere (Bjorge & 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.*, 1997b; Koopman, 1998; Kastelein *et al.*, 2018). In order to maintain a stable internal body temperature, harbor porpoises need to consume sufficient food and eat often (Kanwisher & Sundnes 1965; Yasui & Gaskin 1986; Kastelein *et al.* 1997; Koopman *et al.*, 2002; Bjørge, 2003; Lockyer *et al.* 2003). High feeding rates are necessary for the survival of harbor porpoises, and 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, for example due to an anthropogenic acoustic disturbance, 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 and 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.*, 1997b; Lockyer *et al.*, 2003, Kastelein *et al.*, 2018). This may make harbor porpoises more vulnerable to disturbance in particular seasons. Policy-makers 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. In order 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.

## Materials and 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 had not learned to catch fish efficiently. The female, identified as harbor porpoise F05, was ~11 months old when she stranded, and the male, identified as harbor porpoise M06, was ~7 months 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 6-7 years old (girth at axilla: 80-85 cm; body mass: 40-45 kg); she was average size (Fisher & Harrison, 1970; van Utrecht, 1978; Gaskin et al., 1984; Read, 1990b; Learmonth et al., 2014). Subadult porpoise M06 was 3-4 years old and was still growing (body length 128-130 cm; girth at axilla: 73-82 cm; body mass: 29-34 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., 1997c).

### *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 x 8 m; 2 m deep) connected via a channel (4 x 3 m; 1.4 m deep) to an indoor pool (8 x 7 m; 2 m deep). The bottom was covered with a 20 cm thick layer of sloping sand on which aquatic vegetation grew and invertebrates lived. Skimmers kept the water level constant. Seawater was pumped directly from the 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 (**Fig. 1a**). The pool water temperature was measured once per day, in the morning (**Fig. 1b**). The air and water 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).

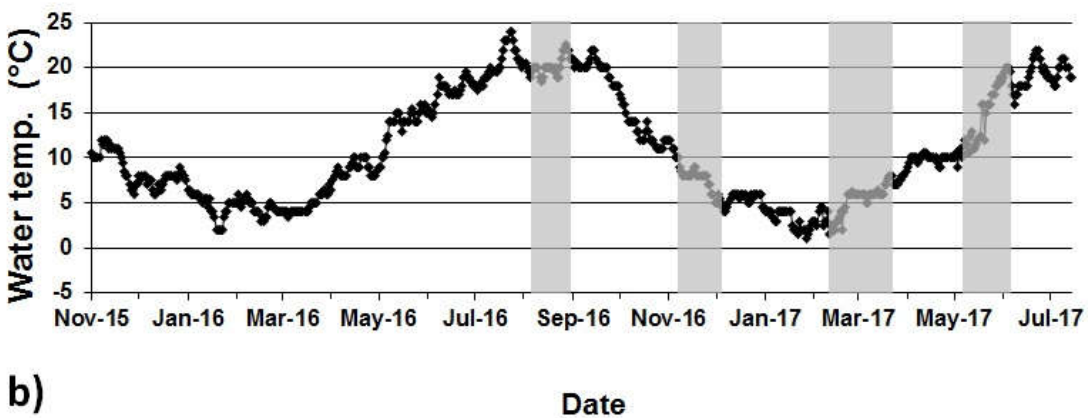
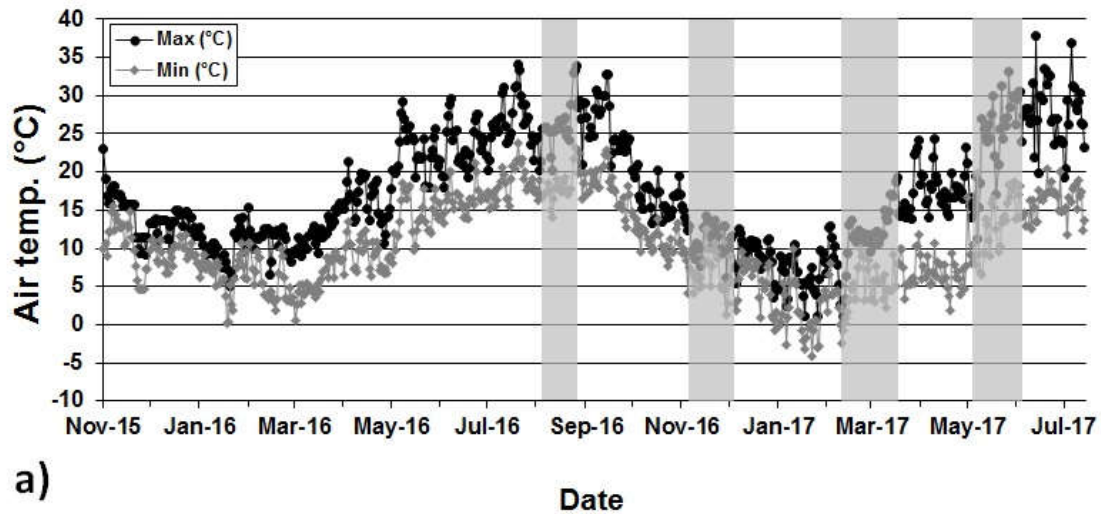


Figure 1. The daily maximum and minimum air temperature (a) and daily pool water temperature (b) before, during and after the study, from November 2015 to July 2017 (Nov-15 = 1 November 2015). The four seasons (summer, autumn, winter and spring) in which the effect of near-fasting was measured are indicated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

#### *Normal food consumption*

When not fasting, the harbor porpoises were fed 4-5 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 2-3 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. 1997d), so the forestomach is empty after ~2 h, and can accommodate the next meal. Vitamins (Akwavit, Arie Blok Animal Nutrition) 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 ( $\pm 1$  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, 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 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 ( $\pm 0.05$  kg accuracy) and its blubber thickness was measured ( $\pm 1$  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.*, 1997b). 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 similar to those made with a ruler on recently a 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 two minutes 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 porpoises were weighed, measured and fed just before 1500 h, 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 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, in order to avoid disturbing them. Small amounts of food were offered as rewards in each measurement session: half a sprat (mean  $\pm$  SD mass:  $4.4 \pm 1.2$  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 sprat 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 (3 - 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: summer (August 2016), when the animals are lean, autumn (November-December 2016), when the animals are gaining weight, winter (February-March 2017), when the animals are generally fattest (although this was not the case with porpoise F05), and spring (May-June 2017), when the animals are losing weight. A 24 h near-fasting period took place once a week for four weeks in each season. The near-fasting periods were conducted one week apart to allow compensatory body mass gain between them; gain was verified by bi-weekly weighing and blubber thickness measurements. Animal F05 was sick (the specific illness could not be determined; lethargic behavior, slow food intake, normal blood parameters) for two weeks 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 porpoises were weighed and measured, and then immediately given their last feed before the fast, so 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 porpoises lost body mass during each of their 15 near-fasting periods (range of change: -0.7 to -3.0 kg; measurement accuracy:  $\pm 0.05$  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:  $\pm 1$  mm, **Table 1**).

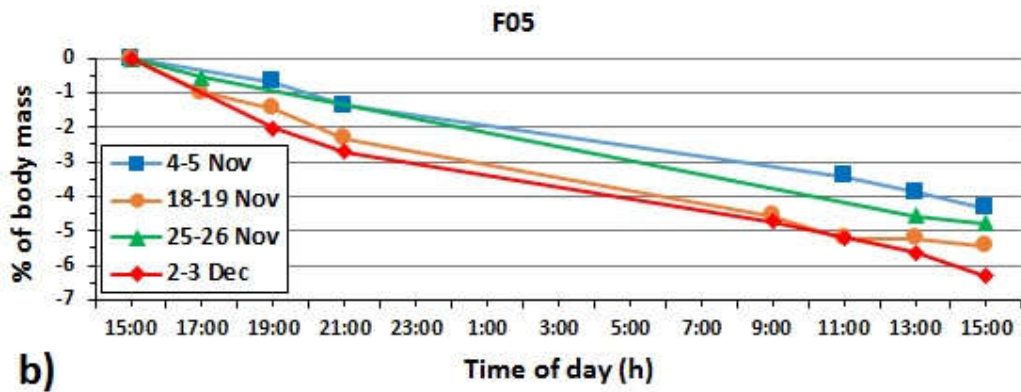
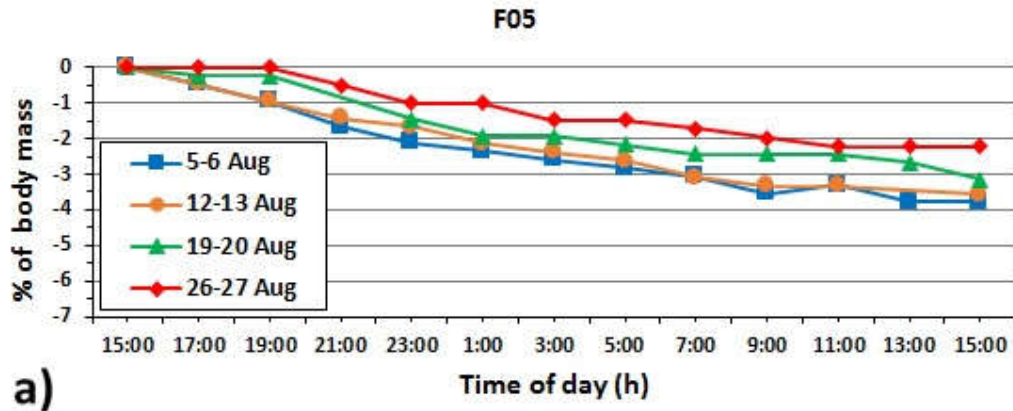
For porpoise F05, mass change was negative in every season, and the mean mass change varied from -1.3 kg (-3.0%) in summer to -2.4 kg (-5.4%) in autumn (**Table 1**). The overall mean mass change for F05, expressed as a percentage of the adjusted pre-fast body mass, was -4.1% ( $\pm 1.2\%$ , range: -1.7%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

For the subadult harbor porpoise M06, mass change was also negative in every season, and the mean mass change varied from -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%  $\pm 0.8\%$ ; 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 (**Fig 3**).

In the linear mixed effects model with both animals, the interaction term (season x 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 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.



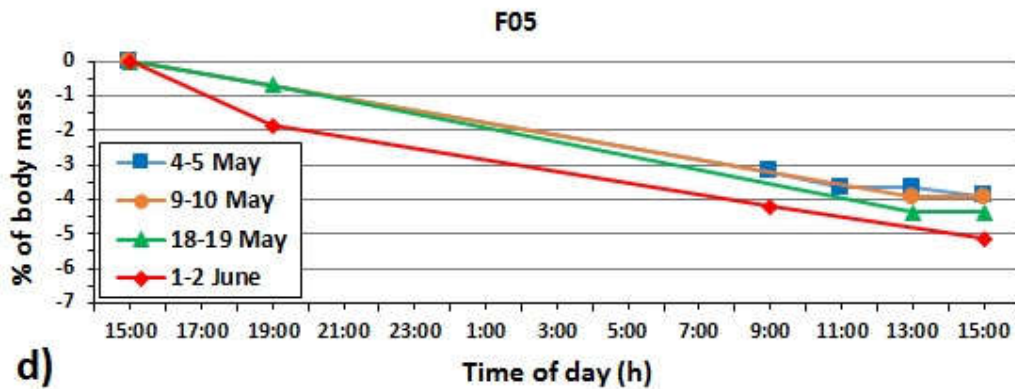
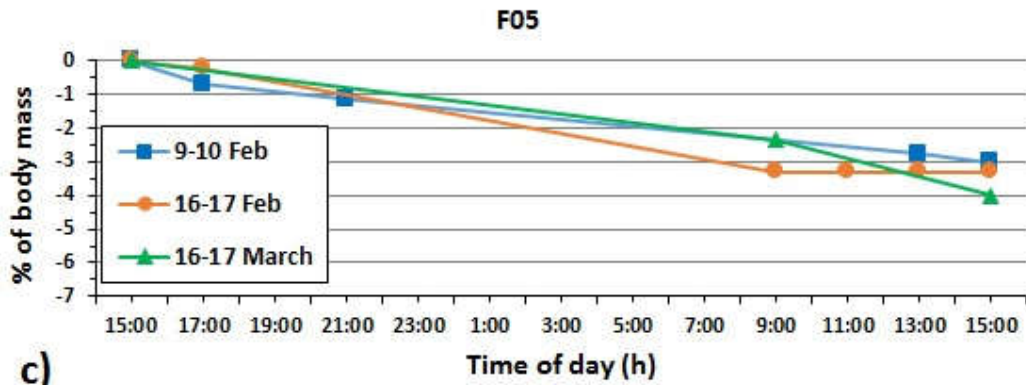
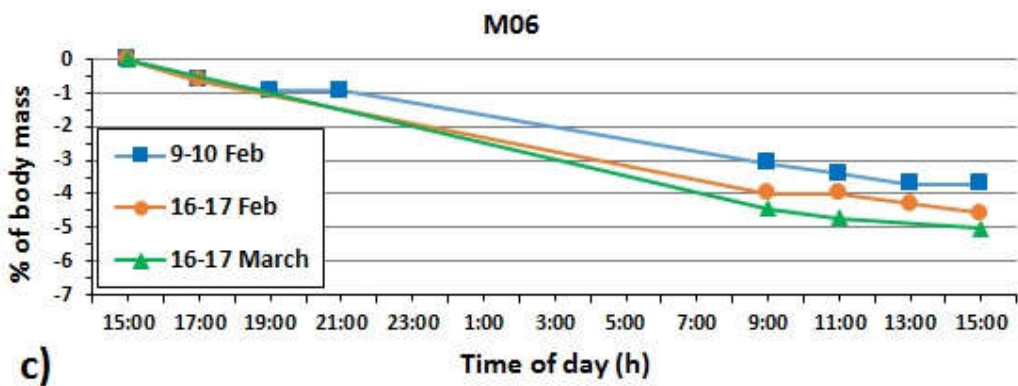
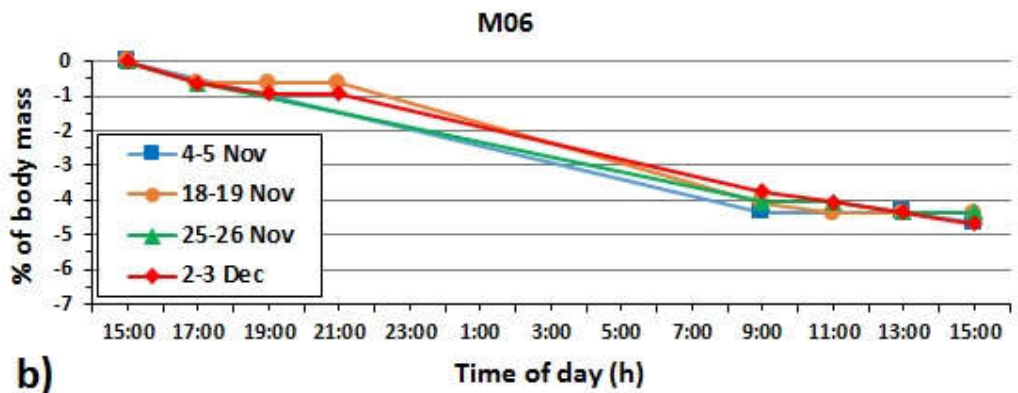
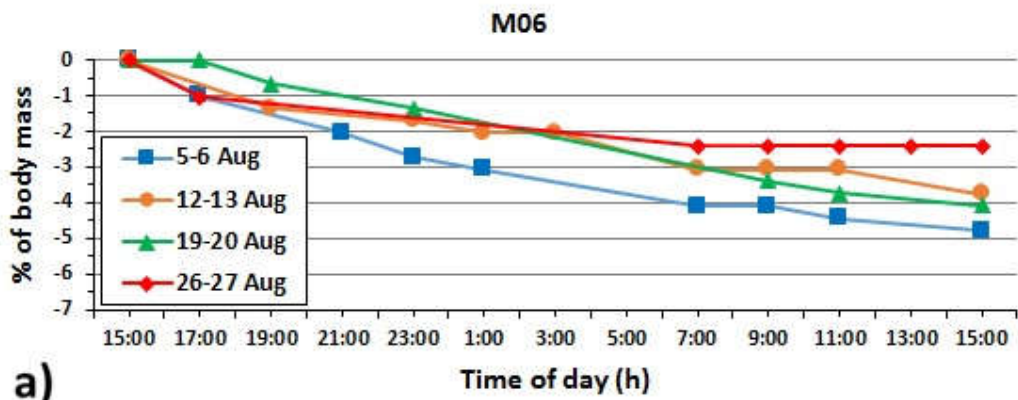


Fig. 2. The percentage loss of the initial body mass of harbor porpoise F05 during 24 h near-fasting periods in summer (a), autumn (b), winter (c) and spring (d). The initial mass (at 1500 h, the start of the fast) is the adjusted pre-fast body mass. The adjusted pre-fast mass varied (40-45 kg) for each near-fasting period due to seasonal changes in body mass (**Table 1**).



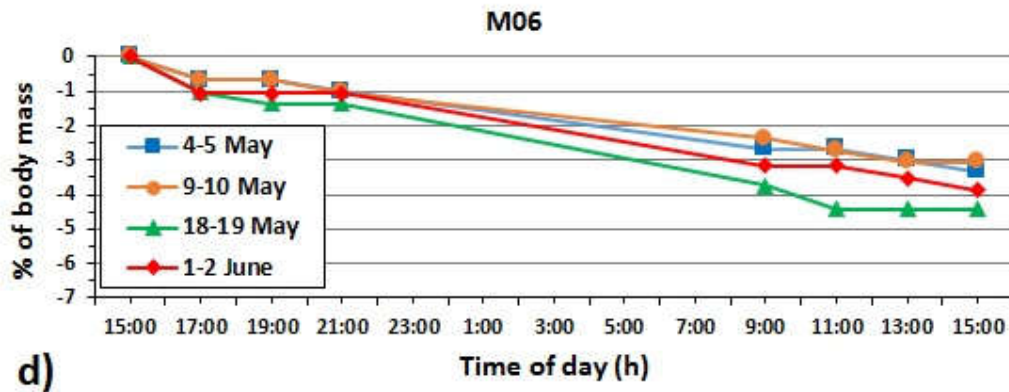


Fig. 3. The percentage loss of the initial body mass of harbor porpoise M06 during 24 h near-fasting periods in summer (a), autumn (b), winter (c) and spring (d). The initial mass (at 1500 h, the start of the near-fast) is the adjusted pre-fast body mass. The adjusted pre-fast mass varied (29-34 kg) for each near-fasting period due to seasonal changes in body mass (**Table 1**).

Table 1. The mean 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 meal given just after the mass was quantified. All means are shown  $\pm$  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.

	<b>Summer (Aug. 2016)</b>	<b>Autumn (Nov. 2016)</b>	<b>Winter (Feb.-March 2017)</b>	<b>Spring (May 2017)</b>
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)
<b>Female Harbor porpoise F05</b>				
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
<b>Male Harbor porpoise M06</b>				
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

## 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 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 F05 in the present study).

While swimming away from sounds, such as those with anthropogenic origin, wild harbor porpoises probably do not forage (Pirotta et al., 2014). While fasting, they are likely to suffer approximately linear body mass loss over time, similar to that reported here. During 24 h near-fasting periods, harbor porpoise F05, the larger study animal, lost more mass than the smaller 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 3-5% 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 alimentary canal.

The mass losses described here 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 two days after each near-fasting period, the porpoises' body weight and blubber thickness was back to the pre-fasting values. If food is abundant, wild harbor porpoises may eat more than this in the post-fast period, and may thus recover even quicker. However, repeated disturbances may have negative effects on fitness, as predicted for the sperm whale (*Physeter microcephalus*; 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, in order 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 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. After this, 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 so that they can 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 in animals 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 every hour the maximum food quantity they could ingest, and by keeping them in warm water (20-30° C; Kastelein et al., 1997a) to reduce energy loss to the environment, so that the ingested food could be used to build up their 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 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; 2018), developed to estimate population effects of disturbance for marine mammals. Information on marine mammal energetics is needed in order 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.

### Acknowledgements

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 Keurtjes, 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.

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