

High Levels of Food Intake in Harbor Porpoises (*Phocoena phocoena*): Insight into Recovery from Disturbance

Ronald A. Kastelein,¹ Lean Helder-Hoek,¹ Cormac Booth,²
Nancy Jennings,³ and Mardik Leopold⁴

¹Sea Mammal Research Company (SEAMARCO), Julianalaan 46, 3843 CC Harderwijk, The Netherlands
E-mail: researchteam@zonnet.nl

²SMRU Consulting, New Technology Centre, North Haugh, St Andrews, KY16 9SR, UK

³Dotmoth, 1 Mendip Villas, Crabtree Lane, Dundry, Bristol BS41 8LN, UK

⁴Wageningen Marine Research, Ankerpad 27, 1781 AG, Den Helder, The Netherlands

Abstract

If harbor porpoises (*Phocoena phocoena*) are impaired in their foraging ability because they need to move away from anthropogenic sound sources, their fitness may be reduced. Understanding how much harbor porpoises can eat after a disturbance, and how quickly they can replenish their energy reserves, is important for assessing the significance of disturbances. After fasting for various time periods (2 to 24 h), four captive harbor porpoises, housed in water and air temperatures similar to those encountered by wild conspecifics, were fed a structured diet of meals larger than usual (each normal meal was 20% of the daily food mass requirement). A few times they were fed *ad libitum*, but this led to severe constipation, so this feeding method was abandoned for welfare and health reasons. The food ingested over a period of one hour following fasting for 2 to 24 hours was quantified (i.e., mass, volume, and as a percentage of normal daily food mass intake in that period). The results show that, in contrast to established belief, harbor porpoises can eat a large percentage (up to ~98%) of their normal daily food mass intake in a single feeding bout without showing physical problems. Adult animals of around 155 cm in body length can eat up to ~3 kg (~2,700 ml) in one feed. If food is abundantly available after a period of fasting due to a disturbance, wild harbor porpoises could eat a large percentage of their daily energetic requirement in one feeding bout to compensate for the period of fasting. However, if food availability is limited in terms of prey numbers, size, or species, or if the fish are widely dispersed (so that more time is required to find and capture them), this may limit or reduce the speed of the recovery of body mass and blubber layer.

Key Words: odontocete, body condition, nutrition, meal size, diet, energetics, recovery from disturbance, iPCoD, DEPONS

Introduction

Harbor porpoises (*Phocoena phocoena*) are one of the smallest of all toothed whales, so they have greater body surface area to volume ratios than other, larger species (Andersen, 1981). This geometry causes them to potentially lose a great deal of energy through radiation and conduction to the surrounding water (Feldman & McMahon, 1983). To offset these losses, harbor porpoises have blubber with a relatively high insulation value (Worthy & Edwards, 1990), which is thicker in relation to their body size than that of larger odontocetes (Koopman et al., 1996; Koopman, 1998; Kastelein et al., 2018a). Due to seasonally changing water temperatures in the geographical range of the harbor porpoise, seasonal changes in blubber thickness and, thus, body mass occur regularly (Kastelein et al., 1997c, 2018a; Lockyer et al., 2003). Despite this increased insulation, harbor porpoises have a higher metabolic rate than terrestrial mammals of similar body mass and larger odontocetes (Yasui & Gaskin, 1986; Kastelein et al., 1997a, 2018a; Reed et al., 2000; Williams & Maresh, 2016; Rojano-Doñate et al., 2018), so they need to consume relatively large amounts of food to maintain a stable body temperature of ~36°C (Kastelein et al., 1990). Their high metabolic rate means that harbor porpoises are particularly sensitive to disturbance that prevents them from feeding. Harbor porpoises may stop feeding when they need to evade larger marine mammals that feed on them, such as killer whales (*Orcinus orca*; Dahlheim & White, 2010) and grey seals (*Halichoerus grypus*; Leopold et al., 2015), or when they flee from loud anthropogenic sound sources (Dähne et al., 2013).

A prominent offshore sound source in the North Sea is pile driving, which is used to place the foundations of offshore wind turbines. Currently, most offshore wind farms are constructed by means of percussion pile driving, which causes impulsive sounds with a high sound pressure level (SPL). Driving a single pile into the sea floor may take up to 3 h, and several piles can be placed per day in one wind park. Harbor porpoises are deterred from percussion piling sites at distances of up to tens of kilometers (Carstensen et al., 2006; Brandt et al., 2011; Dähne et al., 2013; Haelters et al., 2014; Rumes et al., 2017). During percussion pile driving sound exposure, harbor porpoises may swim at a speed of ~7 km/h when leaving the area, which is probably faster than their general swimming speed (Kastelein et al., 2018b). Assuming they swim away from pile driving sites in a straight line and can maintain that speed, it would take them about 1.5 to 3 h to get 10 to 20 km away from a site (see Dähne et al., 2013; Rumes et al., 2017). As porpoises likely do not forage during flight, this scenario means that a porpoise fleeing from a pile driving site would fast for up to 3 h and would subsequently need to compensate for the food missed during those 3 h and the energetic cost of fleeing.

As a small odontocete, the harbor porpoise is predated on by great white sharks (*Carcharodon carcharias*; Arnold 1972), other odontocetes such as killer whales (Ford et al., 1998), bottlenose dolphins (*Tursiops truncatus*; Ross & Wilson, 1996), and pinnipeds such as grey seals (Haelters et al., 2012). This means that porpoises often have to flee when encountering predators. Therefore, the species is probably adapted to disturbance on a certain time scale. Not feeding for 3 h is well within the normal range of behavior observed in wild harbor porpoises (Wisniewska, 2016, 2018); sometimes little foraging effort was observed for 9 to 12 h. However, if the disruption is unexpected and/or prolonged such that it impedes normal foraging behaviour, the consequences can be significant. Kastelein et al. (2019) showed that harbor porpoises lose ~4% of body mass and ~1 mm in blubber layer following a 24-h fasting period. It is not clear how readily individual harbor porpoises can make up for lost foraging opportunities through increased subsequent food intake.

Extremely high feeding rates on small fish have been observed in wild harbor porpoises (Wisniewska et al., 2016, 2018). Although this may not be representative of general porpoise feeding behavior since larger fish are found in the stomachs of many stranded or bycaught porpoises (Hoekendijk et al., 2017), it suggests that porpoises may be able to compensate after periods of fasting. Recovery (i.e., replenishing the blubber layer and regaining lost body mass) after a period of fasting depends on the availability of sufficient suitable prey, on the

energetic content of that prey, on the energy it takes to capture the prey, and on how much prey a porpoise can physically ingest. The amount of fish that harbor porpoises can eat before reaching satiation is thought to be limited by the size of the forestomach (Kastelein & Lavaleije, 1992; Figure 1). The forestomach, having an uninflated volume of around 500 ml in adult porpoises (Kastelein, pers. obs), can expand to contain food. Analysis of otoliths suggests that the forestomach of a harbor porpoise can hold at least 1.9 kg of fish (Sveegaard et al., 2012). Recovery from fasting also depends on foraging efficiency, ingestion, and digestion speed, the latter determining how soon a porpoise can feed again after it has filled its forestomach.

The goal of this study is to quantify the amount of food a harbor porpoise can eat in a short period of time (during a single feed) in order to understand how disturbance resulting in fasting might impact individuals. This information can be used to inform models that have been developed for the harbor porpoise to aid in the assessment of the population consequences of disturbance (e.g., Interim PCoD: King et al., 2015; and DEPONS: Nabe-Nielsen et al., 2018).

Methods

Study Animals

Four stranded and rehabilitated harbor porpoises were available for the study, each for a different period of time (Table 1). Their ages on arrival at the Dolfinarium Harderwijk rehabilitation center were estimated based on their length (after van Utrecht, 1978; Gaskin et al., 1984). During the study, all four animals were in good physical condition. Their age, body length, girth at axilla, and body mass ranges during the study are shown in Table 1. Three of the four were still growing, and all showed expected seasonal variation in body mass and girth.

Study Area

The study was conducted at the SEAMARCO Research Institute, the Netherlands (51° 32' N, 3° 55' 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) with an indoor pool (8 × 7 m; 2 m deep). The bottom of each pool was covered with a 20-cm-thick layer of sand on which aquatic vegetation grew and invertebrates lived. Sea water was pumped directly from the Eastern Scheldt, a semi-enclosed tidal estuary of the North Sea, into the water circulation system, with partial recirculation through biological and sand filters. The pool water temperature ranged from -2 to +24°C throughout the year. The minimum and maximum air temperatures over each 24-h period ranged from -8 to 34°C. The air and

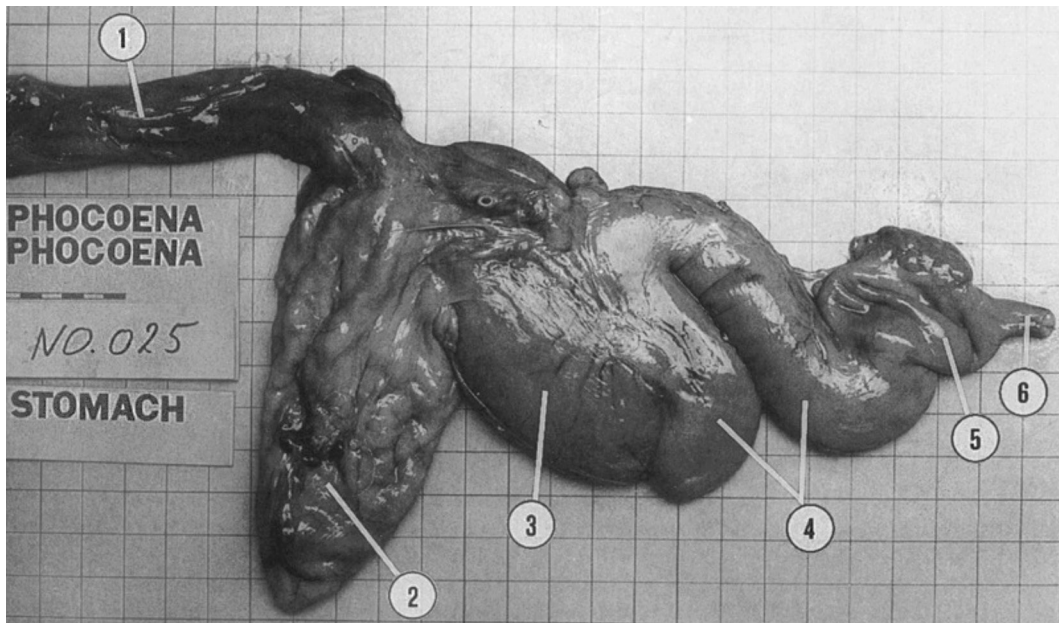


Figure 1. Part of the digestive tract of a harbor porpoise (*Phocoena phocoena*), showing from left to right (1) the esophagus, (2) the empty (expandable) forestomach, (3) the fundic (main) stomach, (4) the pyloric (connecting) stomach, (5) the duodenal ampulla, and (6) the beginning of the duodenum (small intestine) (from Kastelein & Lavaleije, 1992, with permission). The background grid squares are 2×2 cm.

Table 1. Genders, age range (giving an indication of the study period for each animal), total body length, girth at axilla, and body mass of the four study animals. Note the individual difference in body sizes per age.

Porpoise identification (M = male, F = female)	Age range (year)	Total body length range (cm)	Girth at axilla range (cm)	Body mass range (kg)
Subadult to Adult M02	3-6.5	133-147	68.0-78.0	30.6-39.1
Subadult M04	3-3.5	129-132	69.5-77.0	28.2-33.3
Adult F05	6-7	153-155	77.0-84.5	39.7-44.1
Subadult M06	3-4	127-130	73.0-81.0	27.9-32.2

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

Feeding

The harbor porpoises were routinely fed a diet of thawed sprat (*Sprattus sprattus*; 7.9 kJ/g), herring (*Clupea harengus*; 6.5 kJ/g), and mackerel (*Scomber scombrus*; 7.7 kJ/g). Based on the daily diet composition, the caloric energy density of the diet was approximately 7.1 kJ/g. The porpoises were fed fish at a temperature of $\sim 4^\circ\text{C}$. The fish were weighed digitally (1 g accuracy), and the summed mass of fish of each species eaten during each meal

was recorded. Feeding session length was usually 15 min, but occasionally up to 60 min. The volume of the fish species, as measured by water displacement, was 1,000 g sprat, ~ 950 ml; 1,000 g herring, ~ 600 ml; and 1,000 g mackerel, ~ 750 ml.

The study animals were typically (on $\sim 95\%$ of days) fed five times a day, with the daily amount divided equally over five meals ($\sim 20\%$ in each feed). No food was available to the animals during the evening and night (1600 to 0830 h). The initial food passage time in harbor porpoises is ~ 2.5 h (Kastelein et al., 1997b), and they regain their appetite (based on degree of performance in psychophysical research) starting about 2 h after eating a meal consisting of $\sim 20\%$ of the normal daily food requirement (Kastelein, pers. obs.).

When the present study began, it was the intention to feed the harbor porpoises *ad libitum* after the normal 16-h fasting period during the night: feeding would be stopped only when an animal dropped the fish that it was offered, started to play with it instead of ingesting it immediately, or swam away from the feeding station for several minutes. However, *ad libitum* feeding was done only a few times—with porpoise M02 twice, with F05 three times, and with M06 twice—during 60-min feeding sessions in which they were not asked to perform specific behaviors. Two of the animals became very lethargic after these meals and showed signs of severe constipation during the rest of the day (they experienced cramps, which were indicated by them moving their tail stocks below their bodies). After one feed, gas bubbles came out of the mouth of porpoise M06. The feces, which are normally watery and dark green, became thick and beige during the day of the *ad libitum* feeding, also indicating constipation. After this, due to welfare and health concerns, *ad libitum* feeding sessions were discontinued.

Data were collected on meals that were limited by staff but were larger than normal (> 20% of the porpoises' normal daily food mass intake). In these staff-limited meals, the amount of food offered was determined by the staff before each feeding session began. The harbor porpoises always ate all the food that was offered to them. These large meals occurred when weekly or biweekly body mass measurements were lower than expected, or when a feed had been missed (usually because staff were occupied with other animals) and was compensated for in the next feed. The large meals did not result in the animals showing any kind of discomfort. In all cases, the animals had not eaten for at least 2 h and for up to 24 h before they were fed (a broad time-frame, as these were opportunistic data), which meant that their forestomachs were likely empty when feeding began. The data were collected at various frequencies in each study animal but not more often than once a week. Staff elicited trained behaviors from the harbor porpoises during the feeds. The total amount of food ingested within 1 h (the maximum length of feeding sessions) was recorded. In these dedicated feeding sessions, the food was given quickly (generally during ~15 min), given in small increments during the hour, or given as two smaller meals during the hour (because two animals were usually fed in alternation in a training session). The data were collected between July 2008 and September 2017.

Results

When they were fed *ad libitum*, porpoises F05 and M06 ate up to 100% of their mean daily food intake during the previous week in one meal (Figure 2), but this caused severe constipation.

Porpoise M02 ate 85% of his daily food intake during the previous week in one meal without showing digestive problems.

When their food intake in one meal after at least 2 h of fasting was high, but limited by staff, the harbor porpoises ate between 38 and 98% of the normal daily food mass intake (i.e., mean daily food intake during the previous week; Figure 2). The porpoises did not suffer the digestive problems that were seen after *ad libitum* feeds. However, in staff-limited feeds, porpoise M06 ate similar amounts as during *ad libitum* feeds without showing signs of constipation, perhaps because the food given in staff-limited feeds was more spread out over the hour.

Data from both *ad libitum* and staff-limited feeds are combined and summarized in Table 2. Although we do not assume that the caloric content had an effect on the meal size ingested, the energy content of the food is also given in Table 2 and Figure 2.

Discussion and Conclusion

In this opportunistic study, variability occurred in the amount of food the harbor porpoises ate, both within and between individuals. This was as expected because the following parameters were not kept constant between feeds:

- The amount of fish offered (*ad libitum* or limited by staff)
- The time since the last meal (2 to 24 h)
- The season, which is related to energy requirements (Kastelein et al., 2018a)
- The fish given (species, size)
- The time taken to feed (15 to 60 min)
- The behavior of the animals (stationary in the water near the feeding station or free swimming)
- Whether or not the porpoises were required to perform behaviors to obtain fish
- Placement of the fish (in the porpoise's mouth or in the water)
- Individual differences (forestomach size or appetite)
- The reason for ending the feed (in the *ad libitum* feeds: dropping fish, playing with fish, or swimming away from the feeding station)

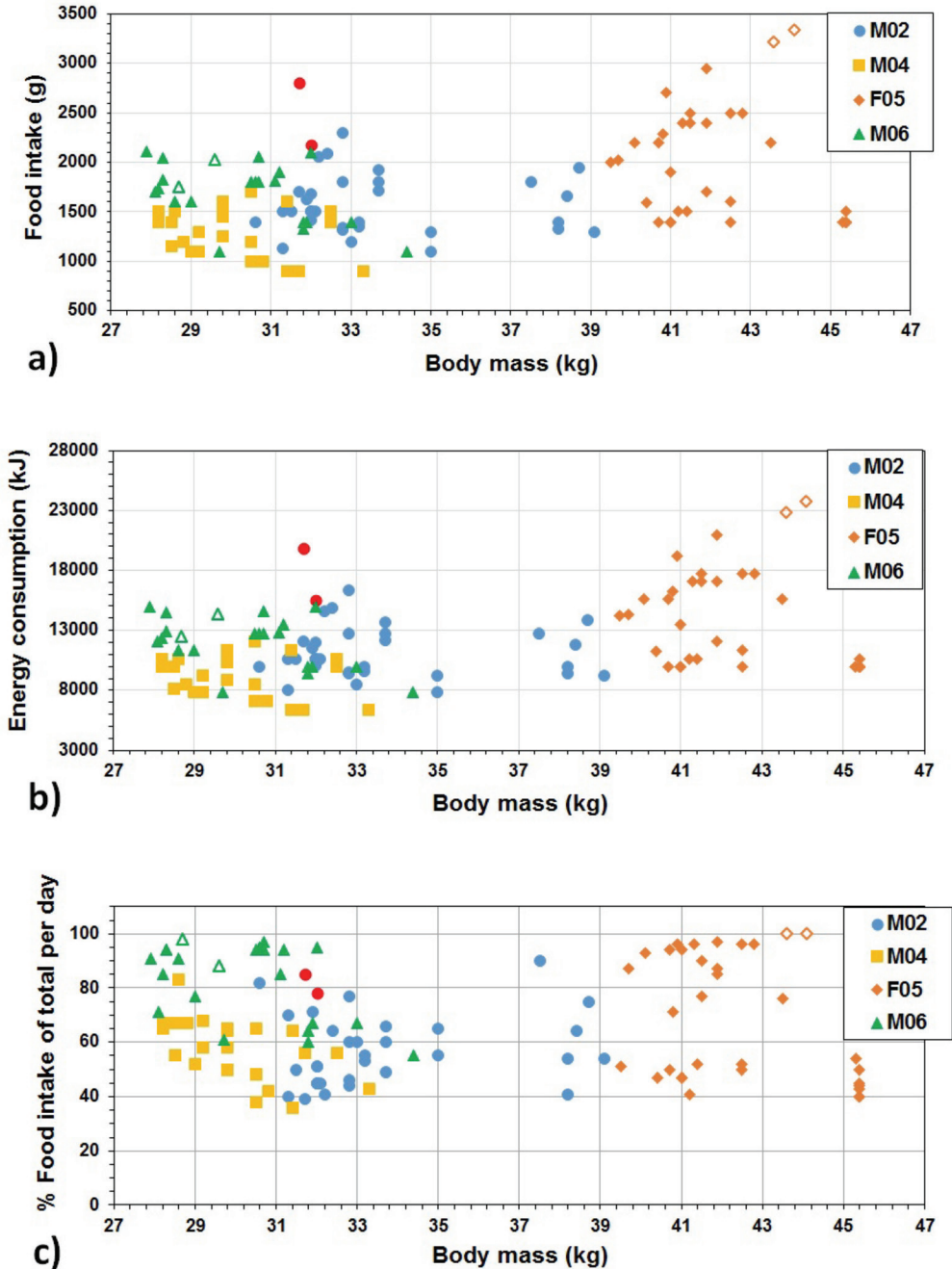


Figure 2. Food intake by four harbor porpoises in 1 h expressed in (a) grams, (b) kJ, and (c) as a percentage of mean daily food mass intake after at least 2 h of fasting. The four open symbols (porpoises F05 and M06) indicate feeds in which the animals were allowed to eat *ad libitum* (maximum food intake in one meal), becoming lethargic and showing signs of constipation (two data points from F05 overlap). The solid red dots were meals during which porpoise M02 was fed *ad libitum* but did not show signs of any discomfort afterwards. The other solid symbols show feeds that were limited in quantity by staff but larger than the usual ~20% of the normal daily food mass intake. In these staff-limited feeds, the porpoises always ate all the food that was offered.

Table 2. The mean, standard deviation (SD), and range of mass, energy content, and volumes of meals eaten in large meals by four harbor porpoises after a minimum of 2 h of fasting. Data from *ad libitum* feeds and staff-limited feeds are combined. For comparison, normal meals were ~20% of the daily food mass intake. *N* = sample size.

Porpoise	Meal mass (g)				Energy content meal (kJ)			Meal volume (ml)		% of daily food mass intake	
	Mean	SD	Range	<i>N</i>	Mean	SD	Range	Mean	Range	Min	Max
Subadult to Adult M02	1,619	365	1,100-2,800	34	11,500	2,590	7,800-19,900	1,295	880-2,240	39	90
Subadult M04	1,284	239	900-1,700	28	9,120	1,700	6,400-12,100	1,028	720-1,360	36	83
Adult F05	2,209	546	1,400-3,337	22	15,680	3,900	9,940-23,700	1,767	1,120-2,670	38	100
Subadult M06	1,635	338	1,000-2,110	22	11,600	2,400	7,100-15,000	1,308	800-1,688	44	97

Most of the data were collected opportunistically, so it is not possible to unravel the individual roles (if any) of each of these parameters. More studies would be needed to evaluate the factors affecting the amount of food harbor porpoises can eat in one meal.

While the intention of this study of captive animals was to provide insight into the maximum amount of food that wild harbor porpoises could ingest to overcome lost foraging opportunities due to disturbance, we recognize that the results may not be directly translatable. When they were fed *ad libitum* without being asked to perform trained behaviors, porpoises F05 and M06 showed signs of severe discomfort after the feed. Wild porpoises would not ingest such a large amount of fish in one meal without expending energy and time to capture the fish which might impact the speed with which the first stomach is filled and, thus, the chance of the feeling of discomfort. The study animals were kept in similar water and air temperatures to wild porpoises, in large pools with sea water, and swam most of the day like their conspecifics, so their energy requirements and food intake may have been similar. However, in common with most other captive harbor porpoises, the study animals were not fed during the night, whereas wild harbor porpoises do feed at night. The context of porpoises in the wild varies depending on geographic location (e.g., water depth, fish species preyed upon, and local temperatures), season, and year. Both wild and captive porpoises show population-related body size differences (for instance, North Sea and Baltic populations; Møhl-Hansen, 1954; Lockyer, 1995; Learmonth et al., 2014), as well as individual differences in body size, metabolism, gender, age, health, reproductive state, etc.

Sveegaard et al. (2012) estimated that the forestomach of a harbor porpoise could contain at least 1.9 kg of fish. The present study shows that

an adult porpoise (the size of the largest animal in the present study, porpoise F05) can eat ~3 kg of fish, and that the forestomach can expand to contain a volume of up to 2,700 ml (about six times the volume of an empty forestomach; Table 2). In the wild, if harbor porpoises encounter a sufficiently large school of fish when they are hungry, they can probably eat at least 85%, and possibly 100%, of their daily food mass intake in a short period of time (< 1 h). Wisniewska et al. (2016, 2018) suggest that wild harbor porpoises made up to 200 to 550 successful prey capture attempts per hour. They can digest food rapidly (initial passage time is ~2.5 h; Kastelein et al., 1997b) and then eat more. Therefore, after periods of fasting that may result from disturbances, as long as food is abundantly available, harbor porpoises can probably recover quickly. A high metabolism works both ways: when insufficient food is available, an animal can lose mass quickly; but if food is readily available and can be ingested quickly, rapid mass gain is possible.

The lowest amount of food consumed following at least 2 h of fasting was 36% of daily food mass intake in 1 h (Table 2). Wild harbor porpoises take approximately 3 h to flee a pile driving site (Dähne et al., 2013; Rumes et al., 2015). If only poor-quality prey are available, or if prey are dispersed, porpoises may need to feed almost all day and night to ingest sufficient energy to recover after fasting for a few hours. Wisniewska et al. (2016) observed that wild harbor porpoises had periods of low foraging activity (lasting 6 to 12 h, often during daylight hours) and periods of increased foraging activity (lasting 3 to 4 h, often in darkness). This suggests that harbor porpoises can increase their activity when they encounter a suitable prey patch or suitable conditions for efficient foraging. It is unclear whether these foraging patterns, observed by Wisniewska et al. (2016), are unusual for harbor porpoises in the wild or

whether they are representative of the species (Hoekendijk et al., 2017).

Given their small size and thermoregulatory constraints, harbor porpoises are believed to be under constant pressure to forage effectively and frequently to survive (Read & Hohn, 1995). Depending on the season, healthy porpoises can lose approximately 1 kg of body mass if they do not eat for 24 h, during which time they would normally eat 2 to 2.5 kg (Kastelein et al., 2019). If suitable prey is abundant, harbor porpoises are likely to be able to recuperate quickly from disturbances. However, little is known about the availability of food in areas that wild harbor porpoises may flee to or about their foraging behavior when they are disturbed. If they reduce their foraging effort or if food availability is limited (e.g., diurnally, seasonally, annually, or geographically), recovery of body mass may be compromised.

As a recommendation for future policymakers and managers, prey availability should be studied just outside a radius of ~20 km of pile driving locations (representing a 3-h swim for harbor porpoises), as part of environmental impact assessments for offshore pile driving. Each pile takes around 3 h to drive into the sea bed, and pile driving often continues for several hours each day. If disturbances occur in quick succession, if suitable prey were not abundant to begin with, or if disturbances influence prey availability, harbor porpoises may lose too much body mass and become hypothermic and susceptible to disease.

Acknowledgments

We thank all the people involved with data collection. We thank Bert Meijering (Topsy Baits) for providing space for the SEAMARCO Research Institute. We also thank Floor Heinis (Heinis Water Management & Ecology), Inger van den Bosch (Netherlands Ministry of Infrastructure and Water Management), and two anonymous reviewers for their valuable constructive comments on this manuscript. Funding for this project was obtained from Gemini, Buitengaats C.V. (PO GEM-03-185; contact Luuk Folkerts). The harbor porpoises were held under authorization of the Netherlands Ministry of Economic Affairs, Department of Nature Management, with Endangered Species Permit FF/75A/2009/039. We thank the ASPRO group for making the harbor porpoises available for this study.

Literature Cited

- Andersen, S. H. (1981). Body surface area of juvenile harbour porpoise, *Phocoena phocoena*. *Aquatic Mammals*, 8(3), 94-95.
- Arnold, P. W. (1972). Predation on harbour porpoise, *Phocoena phocoena*, by a white shark, *Carcharodon carcharias*. *Journal of the Fisheries Resources Board of Canada*, 29, 1213-1214. <https://doi.org/10.1139/f72-179>
- 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>
- Dahlheim, M. E., & White, P. A. (2010). Ecological aspects of transient killer whales *Orcinus orca* as predators in southeastern Alaska. *Wildlife Biology*, 16, 308-322. <https://doi.org/10.2981/09-075>
- 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>
- 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](https://doi.org/10.1016/0034-5687(83)90002-6)
- Ford, J. K. B., Ellis, G. M., Barrett-Lennard, L. G., Morton, A. B., Palm, R. S., & Balcomb III, K. C. (1998). Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. *Canadian Journal of Zoology*, 76, 1456-1471. <https://doi.org/10.1139/z98-089>
- 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. Report 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>
- Haelters, J., Kerckhof, F., Jauniaux, T., & Degraer, S. (2012). The grey seal (*Halichoerus grypus*) as a predator of harbour porpoises (*Phocoena phocoena*)? *Aquatic Mammals*, 38(4), 343-353. <https://doi.org/10.1578/AM.38.4.2012.343>

- 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*, 258-264. <https://doi.org/10.1111/mms.12446>
- 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., 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., Helder-Hoek, L., & Jennings, N. (2018a). 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., & Versteegen, 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., Van de Voorde, S., & Jennings, N. (2018b). Swimming speed of a harbor porpoise (*Phocoena phocoena*) during playbacks of pile driving sounds. *Aquatic Mammals*, *44*(1), 92-99. <https://doi.org/10.1578/AM.44.1.2018.92>
- Kastelein, R. A., van der Sijs, S. J., Staal, C., & Nieuwstraten, S. H. (1997c). 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., Helder-Hoek, L., Jennings, N., van Kester, R., & Huisman, R. (2019). Reduction in body mass and blubber thickness of harbor porpoises (*Phocoena phocoena*) due to near-fasting for 24 hours in four seasons. *Aquatic Mammals*, *45*(1), 37-47. <https://doi.org/10.1578/AM.45.1.2019.37>
- 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>
- 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>
- 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., Begeman, L., van Bleijswijk, J. D. L., IJsseldijk, L. L., Witte, H. J., & Gröne, A. (2015). Exposing the grey seal as a major predator of harbour porpoises. *Proceedings of the Royal Society B*, *282*, 20142429. <https://doi.org/10.1098/rspb.2014.2429>
- Lockyer, C. (1995). Investigation of aspects of the life history of the harbour porpoise, *Phocoena phocoena*, in British waters. In A. Bjørge & G. P. Donovan (Eds.), *The biology of phocoenids. Report of the International Whaling Commission, Special Issue 16*, 189-197.
- 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>
- Møhl-Hansen, U. (1954). Investigations on reproduction and growth of the porpoise (*Phocoena phocoena* (L)) from the Baltic. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjøbenhavn*, *166*, 369-396.
- 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>
- 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>
- 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>
- Rojano-Doñate, L., McDonald, B. I., Wisniewska, D. M., Johnson, M., Teilmann, J., Wahlberg, M., . . . Madsen, P. T. (2018). High field metabolic rates of wild harbour porpoises. *Journal of Experimental Biology*, *221*. <https://doi.org/10.1242/jeb.185827>
- Ross, H. M., & Wilson, B. (1996). Violent interactions between bottlenose dolphins and harbour porpoises. *Proceedings of the Royal Society of London: Biological Sciences*, *263*, 283-286. <https://doi.org/10.1098/rspb.1996.0043>

- Rumes, B., Debusschere, E., Reubens, J., Norro, A., Haelters, J., Deneudt, K., & Degraer, S. (2017). Determining the spatial and temporal extent of the influence of pile driving sound on harbour porpoises. In S. Degraer, R. Brabant, B. Rumes, & L. Vigin (Eds.), *Environmental impacts of offshore wind farms in the Belgian part of the North Sea: A continued move towards integration and quantification* (pp. 129-141). Brussels: Royal Belgian Institute of Natural Sciences, OD Natural Environment, Marine Ecology and Management Section.
- Sveegaard, S., Andreassen, H., Mouritsen, K. N., Jeppesen, J. P., Teilmann, J., & Kinze, C. C. (2012). 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>
- 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.
- Williams, T. M., & Maresh, J. L. (2016). Exercise energetics. In M. A. Castellini & J-A. Mellish (Eds.), *Marine mammal physiology: Requisites for ocean living* (pp. 47-68). Boca Raton, FL: CRC Press.
- Wisniewska, D. M., Johnson, M., Teilmann, J., Rojano-Doñate, 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>
- Wisniewska, D. M., Johnson, M., Teilmann, J., Rojano-Doñate, L., Shearer, J., Sveegaard, S., . . . Madsen, P. T. (2018). Response to “Resilience of harbor porpoises to anthropogenic disturbance: Must they really feed continuously?” *Marine Mammal Science*, *34*, 265-270. <https://doi.org/10.1111/mms.12463>
- 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., & 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>