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Resilience of harbor porpoises to anthropogenic disturbance: Must they really feed continuously?

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Harbor porpoises (*Phocoena phocoena*) are among the smallest cetaceans and have been referred to as "aquatic shrews," given their small size and rapid life history (Kanwisher and Sundnes 1965). These extreme traits impose energetic challenges on thermoregulation and metabolic rate (Lockyer 2007). Counterintuitively, harbor porpoises inhabit rather cold temperate waters of the Northern Hemisphere and are among the most abundant cetaceans (Read 1999), numbering hundreds of thousands in shelf waters of the northeast Atlantic for example (Hammond *et al*. 2013, 2017). This attests to a successful adaptation to their boreo-temperate environment. Nevertheless, due to their small size and propensity to lose heat, and their short reproductive life cycle, harbor porpoises are energetically challenged (Kanwisher and Sundnes 1965, Read and Hohn 1995, Lockyer 2007) and must avoid prolonged periods of fasting (Read 1999, MacLeod *et al*. 2007).

Recently, Wisniewska *et al.* (2016) used high-resolution digital acoustic tags (DTAGs) to monitor the foraging behavior of five harbor porpoises in Danish waters. This approach provided detailed observations on the size and quantity of targeted prey, as well as estimates of how efficiently porpoises capture their prey. Porpoises trapped in a pound net were tagged and monitored for periods between 15 and 23 h. After their release, these porpoises showed extreme feeding behaviors. Foraging was almost continuous, spanning day and night at an "ultra-high" rate (Wisniewska *et al.* 2016). Prey encounter rates varied between 0 and 200 prey items per hour during the

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day and between 50 and 550 at night. The porpoises targeted primarily small fish (3–10 cm long) and captured these with a success rate of >90%. These observations were interpreted by Wisniewska *et al.* (2016) as confirmation that porpoises are "living in the fast lane" (Kanwisher and Sundnes 1965, Read and Hohn 1995, Lockyer 2007). The authors concluded that porpoises are living on an energetic knife-edge, with little margin to compensate for any stochasticity in food availability due to anthropogenic or environmental disturbances. Furthermore, the authors concluded that porpoises did not compete with commercial fisheries given the small fishes consumed.

We agree with Wisniewska *et al*. (2016) that these small, warm-blooded mammals have one of the highest costs of living among cetaceans, and they are certainly more sensitive than other species to variability in the quality and quantity of ingested prey (Spitz *et al*. 2012). However, we argue here that the observations reported by Wisniewska *et al.* (2016) may offer a biased and extreme view of porpoise biology due to (1) the small sample size used in this study (five individuals), (2) the biased age structure of porpoises examined (four juveniles and one adult), (3) the circumstance of this monitoring (*i.e.*, after the animals had been trapped in a pound net for 24 h, prior to release), and (4) the short period of monitoring after tagging (between 15 and 23 h).

Small Sample Size and Biased Age Composition

We commend Wisniewska *et al.* (2016) for their innovative use of DTAGs to investigate the feeding ecology of harbor porpoises, but refute that their observations can be extrapolated to the species as a whole, or even to the situation in Danish waters. A sample of five individuals cannot be considered representative of an entire population, especially for such variable aspects like feeding behaviors and diet composition. Furthermore, their sampling of five individuals included only one adult, a female accompanied by a calf. The four other porpoises were identified as subadults by Wisniewska *et al*. (2016) based on their size (Table 1). However, the individual body lengths of these animals were more typical of juveniles based on growth curves established for porpoises from the inner Danish waters (Galatius 2005), from which the tagged animals were taken. Based on their lengths, these young porpoises would have been between 0.5 and 2.2 yr old, and similar estimates were obtained using other growth curves for porpoises in Danish waters (Lockyer and Kinze 2003) and other areas (Read and Tolley 1997). In fact, the capture dates of these porpoises, when combined with their size and the expected period of parturition (Lockyer and Kinze 2003), suggest that these four individuals were actually all younger than 2.2 yr (Table 1). Therefore, the small sample of mostly juvenile animals is clearly not representative of the population.

Stomach content analyses of harbor porpoises reveal strong age- and geographic-related dietary variation (Read 1999, Santos and Pierce 2003, Spitz *et al.* 2006, Leopold 2015, Andreasen *et al.* 2017). Notably in the North Sea, juveniles feed primarily on small lean fish (<10 cm) such as gobies (consistent with Wisniewska *et al.* 2016's observations). In contrast, the diet of the adults includes larger and energy-rich prey items such as gadoids and pelagic fishes (*e.g.*, clupeids, whiting, and sand eels) ranging in size from 10 to 30 cm to sustain their high metabolic requirements (Lockyer and Kinze 2003, Spitz *et al.* 2012, Leopold 2015, Andreasen *et al.* 2017). Search effort, rates of encounter, and prey capture almost certainly differ between adults and juveniles, as well as with space and time (Read 1999, Santos and Pierce 2003, Spitz *et al.* 2006, Leopold 2015, Andreasen *et al.* 2017). Furthermore, previous

Table 1. Age estimates. ID, sex capture date, and size of the five harbor porpoises studied in Wisniewska *et al.* (2016). Age A values are estimated using the individual size and the Gompertz growth curves for males and females from Galatius (2005) and provided as mean (minimum–maximum). Age B values are estimated based on the size, capture date, and most probable parturition date (*e.g.*, June–July; Lockyer and Kinze 2003).

ID	Sex	Date	Size (cm)	Age A (yr)	Age B (yr)
Hp14_226b	Male	14 August 2014	126	1.5 (0.8–2.7)	2.2
Hp13_170a	Male	19 June 2013	122	1.1 (0.5–2.1)	1 or 2
Hp13_102a	Male	12 April 2013	114	0.5 (0.1–1.2)	0.8
Hp12_272a	Female	28 September 2012	122	0.9 (0.4–1.5)	1.3
Hp12_293a	Female	19 October 2012	163	Adult	Adult

published studies on harbor porpoise diet are based on robust samples collected over large spatial and temporal scales; the five animals observed by Wisniewska *et al.* (2016) should not overshadow the analyses of the contents of several hundred stomachs. The consumption of larger, high-calorie prey provides greater rates of energy intake and releases individuals from the need to forage continuously, leaving more time for other activities (*e.g.* resting, mating, traveling; as seen in the field). Such an energetic cushion makes porpoises more resilient to anthropogenic disturbances and other environmental changes. Thus, we argue that it is highly unlikely that porpoises could maintain an ultrahigh foraging and capture rates as reported by Wisniewska *et al.* (2016) because it leaves so little time for other important behaviors. Other factors must explain the feeding rates recorded in these five porpoises, such as the conditions of the experiment.

Conditions of the Experiment

Wisniewska *et al.* (2016) stated that "upon discovering a porpoise in the net, the fishermen closed the mouth of the net to prevent the animal from escaping. Tagging personnel arrived within 24 hours." It is unlikely that animals trapped in a pound net for 24 h or more would have continued feeding. After being trapped and tagged, the porpoises would have been released both stressed and possibly starved (Neimanis *et al.* 2004). Therefore, the entire recording time period (15–23 h period after tagging) on which the authors base their conclusions should be considered as poorly representative of a "normal behavior" since the porpoises released after being trapped should still be recovering from stress and starvation. In other words, the ultrahigh feeding rates after the porpoises were released could possibly be seen as compensation for lost foraging time (while in the pound net). That porpoises can compensate by increasing their intake rate, if needed, might be suggestive that they are resilient to abnormal situations. This could suggest that porpoises have room to eat more if needed, so they are not totally stressed all the time. This is exactly what one would expect for such a successful species.

Are Such Ultrahigh Feeding Rates and Number of Consumed Prey Actually Realistic and Required for Maintenance and Survival of Harbor Porpoises?

Wisniewska *et al.* (2016) argued "that porpoises forage nearly continuously day and night, attempting to capture up to 550 small (3–10 cm) fish prey per hour." This ultrahigh feeding rate should therefore lead to the ingestion of more than 13,000 prey per day, if they feed continuously. Assuming the weight of a 3–10 cm single fish shall reach at least 1 g, the individual daily ration should exceed 13 kg per day. For an adult porpoise of 50 kg, this would correspond to more than 25% of its body weight. However, the estimates of food consumption for an average adult harbor porpoise are typically between 5% and 10% body weight, thus between 2.5 kg and 5 kg per day in normal conditions (Santos and Pierce 2003, Santos *et al.* 2014). Stomach content data suggest that porpoises (all sampled ages combined) feed on fish of typically between 10 and 30 cm in length. For instance, Borjesson *et al.* (2003) recorded mean ± SD body size and mass of herring (*Clupea harengus*) found in porpoise stomachs to be 26.1 ± 4.9 cm and 163 ± 88 g, 28.1 ± 5.8 cm and 208 ± 119 g for cod (*Gadus morhua*), and 27.8 cm and 137 g for blue whiting (*Micromesistius poutassou*). So, adult porpoises could very well sustain themselves feeding on just 2–3 fish per hour if those fish were around 100 g and 20 cm in length. This contrasts strikingly with the estimates of Wisniewska *et al.* (2016). Note however, that juvenile porpoises tend to take smaller prey, like gobies (Gobiidae) that can weigh <1 g each. Hence, a juvenile porpoise of ~20 kg would need to take 2,000 such small prey per day, and this is shown to be the case by stomach content analyses (Leopold 2015, Andreasen *et al.* 2017). Still, this would only need an intake rate of 80 prey per hour, with continuous feeding. These average feeding rates appear more realistic than porpoises feeding continuously on >10,000 fish per day as proposed by Wisniewska *et al.* (2016). That the porpoises followed in this study were young, just released from 24 h of captivity, and probably starving might provide a plausible explanation for the ultrahigh feeding rates observed by Wisniewska *et al*. (2016).

Lethal Interactions with Commercial Fisheries

Wisniewska *et al.* (2016) concluded that there is little overlap between the diet of harbor porpoises and commercial fisheries, based on the small size of the prey consumed by the porpoises in this study. It is indeed correct that no evidence of any direct competition between porpoises and fisheries has been found at the net level. Stomach contents of harbor porpoises do not generally contain fish of commercial size classes (*i.e.*, ≥30 cm, except for herring and mackerel, *Scomber scombrus*) (see for example Kindt-Larsen 2008). In fact, very few fish of that size are consumed by porpoises, as shown by previous stomach content analyses of porpoises (Read 1999, Santos and Pierce 2003, Spitz *et al.* 2006, Leopold 2015, Andreasen *et al.* 2017). However, acoustic detection cannot provide fish species identification and porpoises evidently do feed on juvenile commercial fish species alongside other noncommercial species. Moreover, some species like sand eels (Ammodytidae) are a major component of the porpoise's diet in areas like the North Sea (Santos and Pierce 2003, MacLeod *et al.* 2007, Leopold 2015). However, these species are also a major target of commercial fishery (Camphuysen 2005). This could lead to significant overlap in term of length. The porpoises included in Wisniewska *et al.* (2016)'s study were captured in pound nets that catch a wide variety of fish species, such as mackerel and cod, among other species, all are potential prey items for porpoises when those fish are young and small.

Wisniewska *et al*. (2016) emphasize that even moderate disturbance in food availability may severely impact the fitness of harbor porpoises, based on their exceptional feeding rates (despite the limitations of their sampling and the experimental conditions). Chronic food shortage is certainly cause for concern in cetacean conservation (*e.g.*, MacLeod *et al.* 2007). Some important food species, such as whiting (*Melangius* *merlangus*) and sand eels have dangerously low stock sizes, but here we insist that incidental bycatch remains a more immediate and severe threat to the survival of harbor porpoises. Even if fisheries would not suffer from competition with porpoises for the same fish (species), porpoises certainly suffer from large losses through fisheries. Thousands of porpoises are killed each year in European gill net fisheries (Read 1999, Stenson 2003, Bjørge *et al.* 2013). Efforts to assess and mitigate these bycatches have been, and still are, of paramount importance for the conservation of this species and its coexistence with human activities.

Conclusions

In summary, we applaud the creative use of DTAGs to study the feeding ecology of such an elusive species as the harbor porpoise conducted by Wisniewska *et al.* (2016), and we agree that the high cost of living for harbor porpoises implies an elevate risk of nutritional stress in case of changes in quality and quantity of available prey. However, we call for a cautious, critical, and rational assessment of the results and interpretations. The limited scope of the sampling and the likely atypical foraging of the tagged animals prevent any generalization of the observed extreme feeding patterns to the population or species level. Wisniewska *et al.* (2016) rather discovered a feeding mode which is extreme and was until now not picked up by classic diet studies, based on stomach content analyses. Juveniles tend to consume smaller prey as compared to adults, which means they should take a higher number of prey to sustain themselves. The study by Wisniewska *et al.* (2016) indicates that the lower limit of acceptable prey size is very small indeed, if these prey can be encountered at very high rates, and be ingested rapidly with a high rate of catching success. The experimental conditions likely also impacted porpoises' behaviors. Porpoises trapped in a pound net for 24 h (or even more) before tagging should have to recover from high levels of stress and starvation once released. This aspect requires serious attention and further investigation since it might explain a significant part of the exceptionally high intake rates reported in this study. The 15–23 h recorded behaviors following the release of the porpoises may not represent "normal behaviors." Consuming such large numbers of fish would not be required in a situation that allows the predator to take larger prey to meet its daily needs (~10% body weight). The exceptional intake rates reported would be unsustainable in the long run, as these would not leave the animals time to accomplish other parts of their life history, such as resting, traveling, and breeding. The conclusion by Wisniewska *et al.* (2016) that even moderate perturbation in food availability may have severe fitness consequences for porpoises might be true, and this is somewhat reflected in historical changes in the species' distribution (Hammond *et al.* 2013, Fontaine 2016). However, considering all the biases described above, this conclusion seems to be overstated in our opinion. Recovery from stress and starvation, as well as particular feeding conditions, might be equally good arguments to explain this exceptional feeding behavior. In fact, the ultrahigh feeding rates seen during recovery from having been caught could suggest resilience properties of porpoises: apparently, porpoises can step-up their feeding rates if needed as observed in other animals (*e.g.*, Swennen *et al.* 1989). We could also reason that if porpoises were on such an energetic knife-edge, they would not be such a successful and abundant species. We also want to caution that the conclusions of Wisniewska *et al.* (2016) should not overshadow the immediate threat that dramatic levels of incidental bycatch of harbor porpoises still occur in commercial fisheries each year. Harbor porpoise diet might not directly overlap with the size of the fish targeted by commercial fisheries, but they do feed upon the small size section of the commercial fish species, as well as the noncommercial species present in the reward.

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