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Letters

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

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Our recent paper on harbor porpoise (*Phocoena phocoena*) foraging (Wisniewska *et al.* 2016) has sparked an interesting discussion that has been thoughtfully summarized by Hoekendijk *et al.* (2018). In their correspondence, these authors commend our methodological approach but point out some potential shortcomings. Specifically, their concerns pertain to the small sample size used in our study, the biased age structure of porpoises examined, the potential impacts of the tagging procedure, and the short period of monitoring after tagging. Moreover, the authors put in doubt our

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findings of little overlap between the diet of the tagged porpoises and commercial fisheries, and suggest that the ability to feed at high rates makes porpoises resilient to anthropogenic disturbance. In this note, we address these points of critique.

There is, unfortunately, no unbiased way to assess the prey preference and dietary intake of free-ranging marine mammals like harbor porpoises. Although the traditional approach involving stomach content analysis of stranded and bycaught individuals provides important information, animals must either end up on a beach (*e.g.*, due to illness or navigation error) or in a net (*e.g.*, potentially due to a preference for the prey targeted by the fishery) in order to be sampled. In our paper, we took a novel and complementary approach involving analysis of echo information from prey targeted by instrumented porpoises as they hunt freely. As a result, we are reliant on animals incidentally live caught in commercial pound nets to be temporarily restrained for tagging, resulting in a small sample size comprising mostly young individuals. Although we would of course have preferred a broader sample, this does not lessen the significance of our results. Specifically, even if the "ultra-high" foraging rates demonstrated in our paper are only typical of young animals, the resulting higher vulnerability to disturbance will still give rise to a bottleneck effect: all animals are young at some point in their lives. Moreover, animals of 2 yr and younger constitute a significant proportion of the porpoise population (Lockyer and Kinze 2003).

This high proportion of young porpoises, perhaps combined with their inexperience, may explain why this age class prevails in pound nets. Unfortunately, very few of our suction cup tag deployments on adult porpoises have extended beyond a few hours without considerable sliding or detachment of the tag. However, data from an adult female of 170 cm, tagged since our paper was drafted, revealed buzz rates ranging from 35 to 140 buzzes per hour with an average of 73 buzzes per hour over the 13 h deployment, similar to the 86 buzzes per hour that we reported for another adult female in Wisniewska *et al.* (2016) (Table 1). While the buzz rates of these adults are on average lower than for juveniles (125 per hour), they, nonetheless, appear to target some 1,500–2,000 small fish per day (Table 1). Thus, although our adult sample size is small, Hoekendijk *et al.*'s concern that high feeding rates are only found in juvenile porpoises does not seem to be supported by our data.

Table 1. Buzz rates of the five harbor porpoises in Wisniewska *et al.* (2016) and two new animals not presented previously (in bold), ordered by size. Buzz rates were computed as averages of buzz counts in complete recording hours, *i.e.*, excluding the first and last incomplete hours of the recording. Time before the first foraging buzz was assumed to be the recovery period. Hence, tag duration represents here the time from start of foraging to the end of tag deployment. Total tag recording time is provided in brackets.

ID	Sex	Deployment date	Standard length (cm)	Tag duration (h)	No. of feeding buzzes	Buzzes per hour
hp16_316a	♂	11 Nov 2016	113	39.1 (39.5)	5,715	146
hp13_102a	♂	12 Apr 2013	114	22.7 (23.7)	3,405	162
hp12_272a	♀	28 Sep 2012	122	17.8 (21.9)	1,821	106
hp13_170a	♂	19 Jun 2013	122	15.3 (15.3)	1,222	60
hp14_226b	♂	14 Aug 2014	126	19.8 (20)	3,234	153
hp12_293a	♀	19 Oct 2012	163	16.4 (17.7)	1,346	86
hp15_116a	♀	24 Apr 2015	170	12.4 (13)	906	73
Mean buzz rate juveniles						125.4
Mean buzz rate adults						79.5

We also note that these authors mistakenly extrapolate the extreme value of foraging rate reported in our paper to infer that individual porpoises must be taking ">10,000 fish per day." We clearly stated in our paper that 550 prey capture attempts per hour was the maximum hourly rate recorded from any of our porpoises. In figure 1 of the paper, we showed how the hourly buzz rate changed throughout the deployment and reported the total buzz count for each tagged individual. The mean buzz rate for juveniles in our study of 125 per hour (Table 1) leads to a much lower daily ration than that erroneously inferred by Hoekendijk *et al*. Assuming the weight of each small fish to be around 1 g, and a 90% prey capture success rate, our porpoises would have consumed about 2.7 kg/24 h, which is roughly 10% of the body weight of a young porpoise (Lockyer *et al*. 2003). These numbers are consistent with stomach content analyses (Leopold 2015, Andreasen *et al*. 2017): Leopold (2015) states that "young porpoises quickly become very efficient foragers on gobies. We have seen many stomachs containing hundreds, and 30 containing the remains of over one thousand gobies (the record-holder had remains of 5,369 gobies in its stomach)." This is very much in line with our findings even if not from the same area or population.

Hoekendijk *et al*. go on to suggest that "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." This is again an extreme interpretation for which Hoekendijk *et al*. provide no supporting evidence. Porpoises likely swim into pound nets following prey, and there is always fish in the nets where the animals are trapped. We do not know to what extent porpoises feed while in the pound net nor whether they have an elevated stress level during this time. We did, however, make every effort to minimize stress during tagging. Porpoises were typically only restrained for 5 min while being instrumented with the suction cup tags and were not followed after release. Given the uncertain state of hunger of porpoises at the time of release, and the scant data on how porpoises respond to stress and starvation, it is not possible to refute Hoekendijk *et al*.'s assertion. But, it certainly seems a bit constructed to argue that the entrapped porpoises do not feed in the net and *therefore* must feed a lot after tagging (for the entire recording time) and *therefore* show large room for compensation and, *hence*, resilience to disturbance. Since our paper was published we have tagged a juvenile porpoise for 39.5 h (Fig. 1, Table 1) providing an opportunity to explore whether potential responses to tagging might attenuate over a longer interval. That animal targeted an average of 145 fish per hour, producing 2,841 buzzes in the first 24 h after release, and 2,874 buzzes in the following 15.5 h, entirely consistent with our other tagged juveniles. Although this could be interpreted as a prolonged response to the tagging circumstances, such an argument becomes increasingly difficult to sustain and we suggest that it is more tempered to view the tag data as largely representative of normal behavior of the animals sampled.

In common with many tag-based studies, our data represent a small and brief sample from a single location. While these data provide the first insight into the search and prey capture behavior of any porpoise, we certainly do not expect (nor claim in the paper) that our results must apply to porpoises as a whole. Harbor porpoises are opportunistic foragers with dietary preferences that likely differ between geographical areas, seasons, and individuals. However, we reiterate that diet analyses based on stomach contents also have several sources of bias, with the most important limitation being short and differential gastric passage time (Kastelein *et al*. 1997, Christiansen *et al.* 2005, Ross *et al*. 2016). While our tag data represent a brief period of

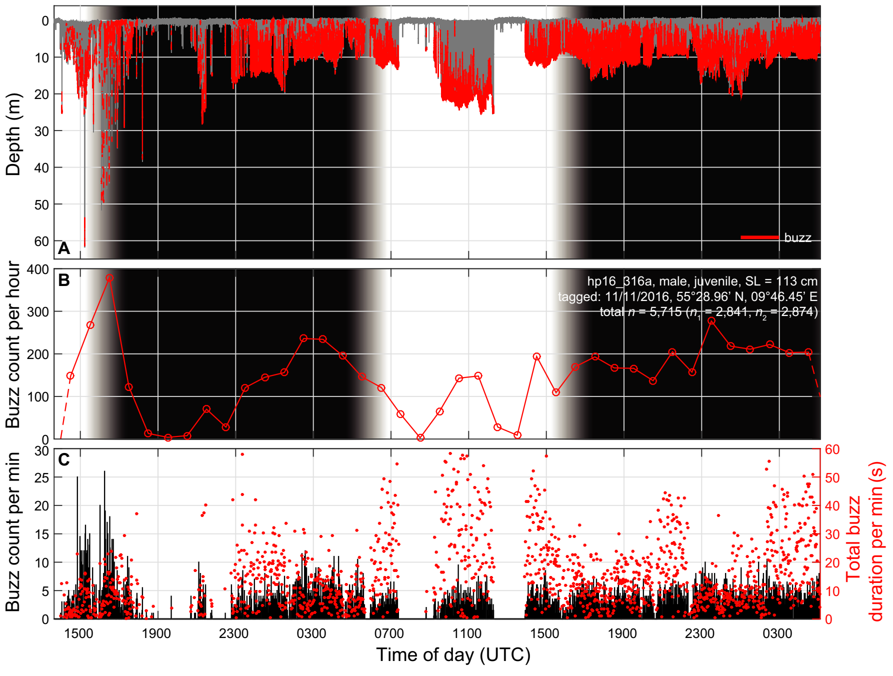

Figure 1. Foraging behavior of a juvenile harbor porpoise during a 39.5 h DTAG deployment. (A) Dive profile. Individual buzzes are marked in red. The shaded area represents twilight (gray) and night (black). See Wisniewska *et al.* (2016) for detailed methodology. (B) Hourly buzz counts as recorded by the attached tag. Numbers for the first and last incomplete hours are depicted with dashed lines. The animal's sex, age class, standard length (SL), tagging date, and location, as well as the number of buzzes recorded during the first 24 h (n_1) and the following 15.5 h (n_2) are listed in the panel. The digits in the names of the individuals indicate the year and Julian day of tag deployment. (C) Minute-wise buzz counts (black bars) and total buzz durations (red circles) illustrating the different foraging strategies employed by the porpoise with numerous short buzzes during pelagic dives, and fewer longer buzzes when targeting benthic or demersal prey.

monitoring for each animal, stomach contents represent an even shorter interval of foraging spanning a maximum of 5 h (Christiansen *et al.* 2005, Ross *et al.* 2016). This rapid digestion process contributes to the scarcity of data from stranded animals, which are often found with empty stomachs (Neimanis *et al.* 2004). Consequently, most inferences about porpoise diet are based on stomachs from individuals bycaught in fishing nets (but see, *e.g.*, Andreasen *et al.* 2017), which are likely biased towards prey in the nets they were targeting. There may also be a bias towards detecting remains of larger prey in stomach contents, as smaller otoliths may deteriorate faster (Christiansen *et al.* 2005, Ross *et al.* 2016), possibly as fast as within an hour for the 1–1.5 mm otolith of a 5 cm black goby (*Gobius niger*) (Härkönen 1986, Christiansen *et al.* 2005). Most diet studies have not accounted for the differential residence time of otoliths in the forestomach of porpoises (but see Ross *et al.* 2016 and Andreasen *et al.* 2017), therefore likely overestimating the share of larger species in porpoise diet (Ross *et al.* 2016). Thus, a complete picture of porpoise foraging will only be achieved by combining insights from a range of different methods.

Finally, we wish to clarify two important misapprehensions of Hoekendijk *et al.* (2018) with regard to our paper. Nowhere in our paper do we make the claim that porpoises do not feed on species of commercial interest: our echo analysis method provides little information on the prey species targeted. While we see how our sentence "the consistently small fish targeted by the four porpoises with measurable echograms suggest that their diet has little overlap with commercial fisheries" could have been misunderstood, our intended message was that there was little overlap, and hence competition, with commercial fisheries in terms of the sizes of targeted fish. This conclusion tallies with data from bycaught animals, as Hoekendijk *et al.* (2018) also point out: with the exception of herring (*Clupea harengus*) and sandeels (*Ammodytes tobianus*), the majority of fish found in stomachs of porpoises from Inner Danish Waters are below the sizes of commercial interest for the given species (Sveegaard *et al.* 2012). Likewise, we do not intend to dispute or draw attention away from bycatch as the prevalent anthropogenic threat to porpoises in European coastal waters, and we wonder how that conclusion can be reached from our paper. Like Hoekendijk and colleagues, we consider efforts to mitigate incidental catches of porpoises in commercial fisheries to be of paramount importance. We sincerely hope that our studies using fine-scale biologging data will complement other study methods to better define the factors that lead to such elevated bycatch and so aid in the conservation of this species.

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