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High heart rates in hunting harbour porpoises

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The impressive breath-hold capabilities of marine mammals are facilitated by both enhanced O_2 stores and reductions in the rate of O_2 consumption via peripheral vasoconstriction and bradycardia, called the dive response. Many studies have focused on the extreme role of the dive response in maximizing dive duration in marine mammals, but few have addressed how these adjustments may compromise the capability to hunt, digest and thermoregulate during routine dives. Here, we use DTAGs, which record heart rate together with foraging and movement behaviour, to investigate how O_2 management is balanced between the need to dive and forage in five wild harbour porpoises that hunt thousands of small prey daily during continuous shallow diving. Dive heart rates were moderate (median minimum 47–69 bpm) and relatively stable across dive types, dive duration (0.5–3.3 min) and activity. A moderate dive response, allowing for some perfusion of peripheral tissues, may be essential for fuelling the high field metabolic rates required to maintain body temperature and support digestion during diving in these small, continuously feeding cetaceans. Thus, despite having the capacity to prolong dives via a strong dive response, for these shallow-diving cetaceans, it appears to be more efficient to maintain circulation while diving: extreme heart rate gymnastics are for deep dives and emergencies, not everyday use.

1. Background

Marine mammals face a physiological trade-off in that they must hold their breath while expending O_2 to hunt and consume prey underwater. The remarkable breath-hold capability of marine mammals is enabled by large O_2 stores and physiological adjustments including peripheral vasoconstriction and bradycardia during diving that minimize O_2 consumption. This so-called dive response regulates the magnitude and distribution of peripheral blood flow, ultimately conserving blood O_2 for critical tissues such as the heart and brain [1–3], and is influenced by a variety of factors including dive duration, depth, exercise, age and volition [4–11]. Due to the challenge of studying blood flow and cardiac output in wild marine mammals, heart rate (f_H) is often measured as a proxy for evaluating dive response and O_2 management [12]. Heart rate is an excellent proxy because to maintain stable blood pressure, there is a strong relationship between peripheral vasoconstriction and cardiac output, and endotherms are finely tuned to maintain a relatively stable blood pressure through baroreceptors, chemoreceptors and the autonomic nervous system [12–15]. Until recently, it was not possible to even measure f_H in wild cetaceans, but with new tagging technology, f_H has now been measured in two species: a

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single foraging blue whale (8.5 h, *Balaenoptera musculus*, the largest baleen whale, approximately 70 000 kg) [16], and five narwhals (approx. five dives each, *Monodon monoceros*, mid-size toothed whale, approximately 1000–1600 kg) released from prolonged net entanglement and stranding [17]. Both species exhibited extreme bradycardia, with f_H dropping to 10–20% of surface values, but also exhibited exercise-induced increases in diving f_H [16,17]. While these recent studies have improved our understanding of O_2 management in larger cetaceans, it is still unknown how small wild cetaceans living in thermally challenging environments regulate f_H while diving and exercising to maximize foraging returns. Here, we investigate the dive heart rate response in the second smallest cetacean, the harbour porpoise (*Phocoena phocoena*), in shallow inner Danish waters.

Harbour porpoises have high metabolic rates to combat heat loss in their high-latitude habitats [18,19]. Porpoises meet these metabolic demands, at least in inner Danish waters (the so-called Belt Sea population [20]), by high-rate shallow foraging on small prey [21,22]. Understanding how they manage O_2 in active foraging dives is critical to assessing how physiological capacity may limit their ability to deal with natural environmental variation and anthropogenic disturbances. Trained porpoises are capable of extreme bradycardia as exhibited by a f_H below 15 beats per minute (bpm) (approx. 10% of surface f_H) in long dives for this species of 4 min [8]. However, dive responses in captivity are typically moderate (30–45% of surface f_H), and mildly influenced by dive duration, exercise and volition during shorter dives [7,8,23,24]. As wild porpoises in the Belt Sea population, in contrast with captive conspecifics, attempt to capture 100 prey per hour and hence must spend a higher proportion of their time engaged in active hunting dives, we hypothesized (i) that wild foraging porpoises will exhibit graded, and occasionally extreme, fluctuations between high surface and low dive f_H, potentially decreasing f_H to <10% of surface values in longer dives, and (ii) that they will display a stronger exercise response than the porpoises in captivity due to a greater range of effort between non-foraging dives and active foraging dives. Here, we test these hypotheses by quantifying f_H in relation to fine-scale movement and foraging behaviour in five wild porpoises using suction cup-attached biologging tags that can uniquely measure heart rate, breathing, exercise and foraging simultaneously in these small wild cetaceans.

2. Methods

(a) Animal handling and instrumentation

Between September 2016 and September 2018, five harbour porpoises (1 adult female, 1 adult male and 3 juvenile males; see table 1 for detail) that were incidentally trapped in pound nets in the inner Danish waters of the Kattegat and the Belt seas were instrumented with ECG-DTAG3 multi-sensor data loggers (15.5 × 8.5 × 3 cm with two 20–40 cm wires for suction cup electrodes, 265 g in air and slightly buoyant in seawater) [21,30]. Porpoises were instrumented within 24 h of being observed by the fisherman. Porpoises were free to swim within the compass of the net (10–30 m diameter and 5–10 m deep) until tagged and released. For instrumentation, porpoises were lifted onto a fishing boat and placed on a stretcher and soft pad. Standard body length and girth were measured, body condition evaluated, and sex and age class determined [25]. Mass was estimated from body length using sex-specific equations [19]. Only porpoises that appeared healthy were instrumented. Porpoises were released immediately after instrumentation, with all procedures lasting less than 17 min to minimize stress. The porpoises resumed feeding within 2 h of release.

The ECG-DTAG3 was placed approximately 5 cm behind the blow hole via four silicone suction cups and a silver chloride electrode embedded in a 5 cm suction cup was placed on each side of the porpoise, with the left electrode caudal and right electrode rostral to the heart to maximize the ECG signal. The ECG-DTAG3 recorded the differential potential between the electrodes relative to a ground in water with a sampling rate of 5 kHz (16-bit resolution and a 2-pole, 200 Hz anti-alias filter). The tag also recorded pressure at 50 Hz, 3-axis acceleration at 625 Hz and stereo sound at 500 kHz (16 bit, 0.5 to 150 kHz bandwidth), allowing determination of activity, ventilations and echolocation behaviour with precise synchrony to the f_H data (figure 1). The dataloggers detached by a pre-programmed release of air into the suction cup or passively after 10.5 to 40 h (table 1).

(b) Data processing

Data processing was performed using custom scripts in MATLAB (MathWorks, Inc.). Raw voltages recorded by pressure sensors and accelerometers were converted to depth (m) and acceleration ($m\ s^{-2}$) using calibration values. Sound files were examined aurally and visually in 5 s windows using a spectrogram display (Hamming window, 512 point fast Fourier transform, 75% overlap) (MATLAB code available at www.animaltags.org) to identify ventilations and feeding buzzes [21,31]. Dives were identified from a combination of depth and respiration data [21]. Respirations defined the start and end of each inter-breath interval. Inter-breath intervals were only considered a dive if the maximum dive depth was greater than two times the body length of the porpoise (i.e. 2.5–3.5 m). Dives with feeding buzzes were classified as foraging dives.

ECG data were decimated to a sampling rate of 250 Hz and filtered to remove excess noise (finite impulse response filter to remove 50-Hz electrical noise generated by sampling of other sensors). R-peaks in the ECG QRS-complex were identified using a peak detector script and records were visually inspected to correct for missing or spurious peaks. Instantaneous f_H for each heartbeat was determined from the R–R peak intervals (60 s divided by the difference in time between the current and previous R peak).

As an index for swimming effort, we calculated the minimum specific acceleration (MSA) from the three-axis acceleration data decimated to a sampling rate of 25 Hz. MSA is a measure of how much the total acceleration deviates from the gravity acceleration [32] and is an underestimate of the specific acceleration generated by the animal. It is calculated as the absolute value of the norm of acceleration minus the gravity acceleration. In captive porpoises, MSA and overall dynamic body acceleration (a commonly used activity metric [33,34]) were highly correlated (Pearson $r = 0.98$) [8], and in California sea lions MSA and stroke rate were highly correlated; however, MSA had explained more of the variation in dive f_H suggesting it was a better indicator of effort [9].

For each dive cycle (dive + post-dive interval), 13 variables were calculated, as follows: (i) dive duration (s); (ii) post-dive interval (s, duration between the respiration ending a dive and the respiration starting the following dive); (iii) dive cycle duration (s); (iv) maximum dive depth (m); (v) mean MSA ($m\ s^{-2}$, total dive MSA/number of samples); (vi) upper quartile (UQ) pre-dive instantaneous f_H (bpm, UQ (75%) in 10 s preceding the dive to avoid bias from decreases in f_H during surface breath-holds); (vii) lower quartile (LQ) dive f_H (bpm, 25th quantile—an outlier-robust estimate of how low the f_H was during the dive); (viii) UQ post-dive interval f_H (bpm); (ix) median

Table 1. Metadata and summary heart rate (f_H) variables for five wild porpoises instrumented with ECG-DTAG3. Median and range provided for dive duration and maximum dive depth. Median and 2.5–97.5 quantiles provided for minimum dive, median bottom-of-dive, maximum surface and dive cycle f_H.

ID	deployment ID[a]	sex (age class[b])	length (cm) mass[c] (kg)	deploy. dur. (h)	total dives	dives analysed[d] (>0.5 min)	dive dur. (min)	ind. cADL[e]/ (cADL[f]) (min)	maximum depth (m)	minimum dive f_H (bpm)	median bottom-of-dive f_H (bpm)	maximum surface f_H (bpm)	dive cycle f_H^g (bpm)	calculated resting[h]/ max[i] f_H (bpm)
AF	hp16_264a	female (adult)	163 67	12	298	214	0.9 (0.5–2.2)	5.0 (3.5–6.9)	6.3 (3.5–29.7)	60 (48–71)	75 (67–88)	191 (167–218)	104 (83–132)	84/240
AM	hp18_095a	male (adult)	143 44	16.5	382	306	1.5 (0.5–3.3)	4.2 (3.5–6.9)	6.7 (2.2–19.9)	57 (43–68)	76 (66–97)	204 (174–224)	106 (84–127)	93/257
JM1	hp18_120a	male (juvenile)	120 30	10.5	210	183	1.0 (0.5–2.4)	3.0 (3.3–6.5)	6.4 (2.9–25.3)	59 (40–73)	72 (66–87)	219 (199–250)	113 (95–136)	103/274
JM2	hp18_254a	male (juvenile)	116 28	11	572	138	0.9 (0.5–2.3)	3.6 (3.3–6.5)	5.9 (3.3–12.9)	47 (36–56)	60 (50–70)	188 (163–213)	87 (67–114)	105/278
JM3	hp16_316a	male (juvenile)	113 26	40	1252	918	0.8 (0.5–1.7)	2.2 (3.3–6.5)	9.7 (4.4–38.2)	69 (56–86)	113 (80–162)	208 (192–224)	141 (118–171)	107/280

[a] Deployment ID is a unique identification code created from species and date deployed (f.ex. hp = harbour porpoise, 16 = deployed in 2016, 264 – Julian day, a = first tag deployed on that day).

[b] Age class determined by length [25].

[c] Mass estimated using equations from [19].

[d] Only dives more than 2 h after release and longer than 30 s are included in analyses.

[e] Calculated aerobic dive limit (cADL) using porpoise mass and calculated metabolic rate [26].

[f] cADL estimated from average age class total body oxygen stores and two and four times Kleibers estimated metabolic rate [27].

[g] Dive cycle f_H is the total number of heartbeats during the dive and the following surface interval divided by the dive cycle duration (dive duration + post-dive interval duration).

[h] Resting $f_H = 241 \times \text{body mass}^{-0.25}$ [28].

[i] Maximum $f_H = 477 \times \text{body mass}^{-0.163}$ [29].

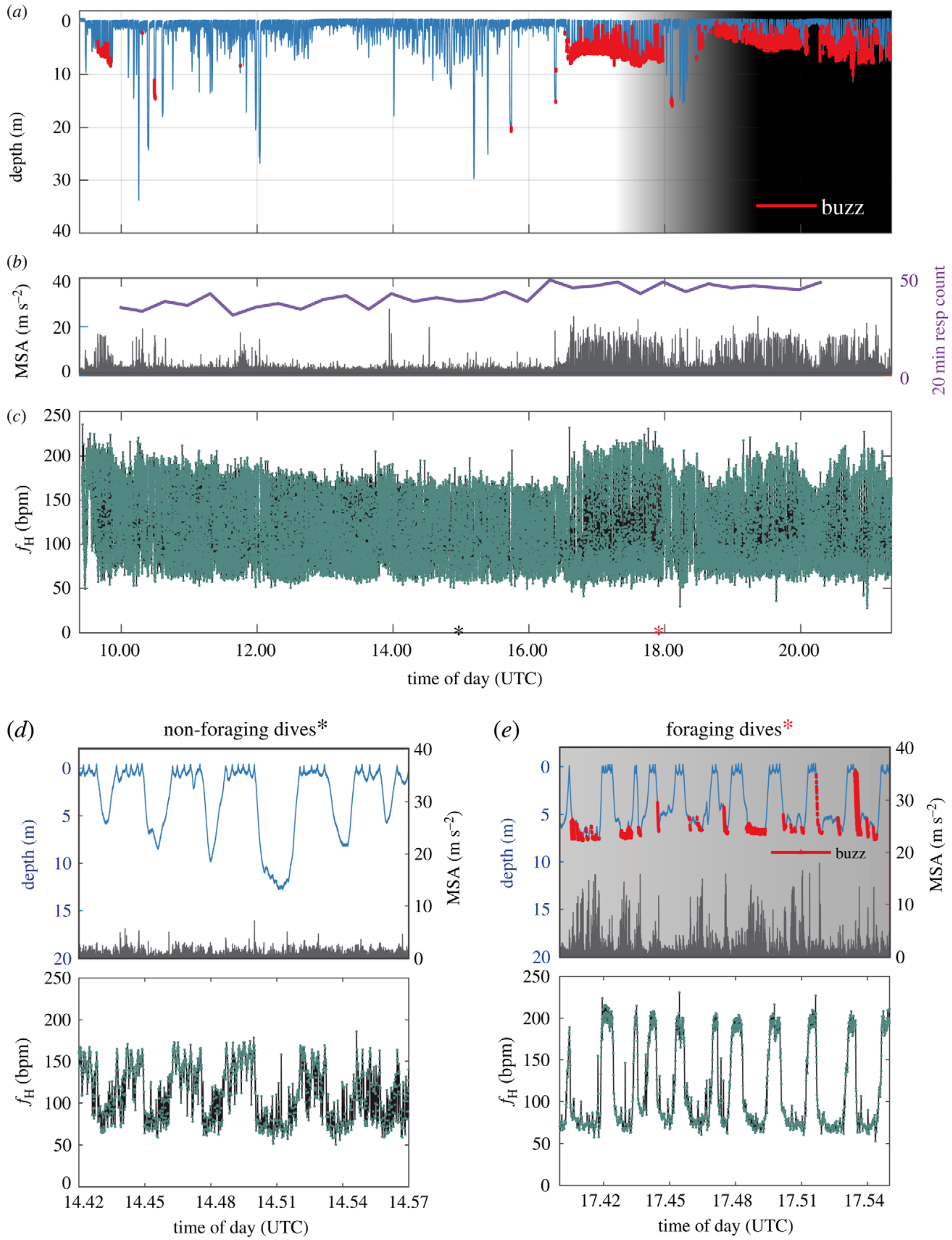

Figure 1. Diving behaviour and heart rate (f_H) of the wild adult female harbour porpoise instrumented with an ECG-DTAG. (*a*) Diving behaviour in relation to daylight (background shading). Red dots signify buzzes likely related to foraging. (*b*) MSA and 20 min respiration count [26] indicating that the porpoise was more active and had a higher metabolic rate when foraging. (*c*) Instantaneous f_H profile. Surface f_H was elevated after release and during foraging bouts. Excerpts are example dive, MSA and f_H profiles from non-foraging (*d*) and foraging dives (*e*). (Online version in colour.)

bottom-of-dive f_H (bpm, bottom-of-dive is defined as the time between when the porpoise initially reached a depth of one body length above maximum depth and when the porpoise last leaves that depth—this is a proxy for dive f_H, but avoids the influence of the initial decline and final increase in f_H); (x) minimum dive f_H (bpm); (xi) post-dive interval (PDI) f_H (bpm, total beats during post-dive interval/post-dive interval duration); (xii) dive cycle f_H (bpm, total heart beats during a dive cycle (dive + post-dive interval)/dive cycle duration); and (xiii) per cent of surface f_H during a dive (as an indicator of degree of bradycardia) was estimated by the ratio of LQ dive f_H to UQ pre-dive f_H (LQ dive f_H/UQ pre-dive f_H). In addition to the above dive variables, we divided the bottom phase of the dive into 5 s intervals and determined the mean MSA (m s^{-2}) and f_H for each interval to quantify the relationship between behaviour and f_H within dives.

(c) Statistical analysis

Statistical analyses were performed in R v. 3.5.3 (R Core Team). After release, porpoises typically swam rapidly away from the site of release primarily performing shallow swimming. During this phase, f_H was often elevated, both at the surface and submerged. Based on these observations, dives from the first 2 h post-release were excluded from analyses to reduce the influence of capture stress on results [19]. We also excluded dives less than 30 s in duration to exclude brief submergences between breaths.

We used linear mixed-effects models to investigate the effect of dive duration and mean MSA on dive and surface f_H (package 'nlme' [35]). In these models, dive duration and mean MSA were fitted as fixed-effect variables, with individual as a random effect to account for the lack of independence of dives from the same individual. Linear mixed-effects models were also used to examine the relationship between behaviour and f_H during the bottom phase of the dive. The response variable was mean dive interval heart rate. Mean interval MSA and dive duration were fitted as fixed-effect variables, with the individual as a random effect. A correlation structure (AR1) was used to account for temporal correlation in the data and the VarIdent variance function structure was used to account for the difference in variance between individuals [36]. Covariance and random effect structures of the full models were evaluated using Akaike's information criterion (AIC) and examination of residual plots [36]. Once the covariance and random effect structure was determined, the best model was selected by removing a single variable and comparing the full and reduced model using a log-likelihood chi-squared test. If the reduced model was better, another variable was removed until removing variables did not improve the model. The models with lowest AIC are reported in electronic supplementary material, tables S1 and S2. Additionally, we used linear mixed-effects ANOVAs to examine differences in f_H between foraging and non-foraging dives. Foraging state was the fixed-effect variable, and individual was fitted as a random intercept (electronic supplementary material, tables S3 and S4). All models were run with and without Juvenile Male 3 (JM3). JM3 was an outlier. His f_H was much higher and more variable than the other four porpoises, resulting in improved normality and homoscedasticity of residuals in models without JM3.

3. Results and discussion

The dive response was first discovered during forced submergence of seals and porpoises, and based on observations of deep bradycardias in such highly stressed animals, it was presented as a dramatic on–off master switch of life [2]. Subsequently, it has become clear from studies of trained animals that the dive response in marine mammals is a much more graded physiological phenomenon that is tailored to a suite of intrinsic and extrinsic conditions while diving [5–10]. Despite this deep understanding we still know very little about how the dive response is implemented during hunting in the wild where the diving animal must balance the opposing forces of physiological mechanisms enabling prolonged breath-holds and those that facilitate thermoregulation, digestion, and body maintenance as a function of a dynamic environment. Here, we use one of the smallest marine mammals, the harbour porpoise, as a model organism to address the implementation of the dive response during natural hunting behaviour in the wild. Specifically, we sought to test the hypotheses that (i) wild porpoises would exhibit a graded and occasionally extreme bradycardia tailored to the dive duration and (ii) porpoises would exhibit an exercise-modulated dive f_H response driven by hunting activity. To test these hypotheses, we obtained 10.5–40 h of DTAG data from five porpoises in Danish waters (table 1) from which we analysed 138–918 dives per individual that were longer than 30 s after excluding the 2 h following release (table 1). As typical for harbour porpoises in the Belt Sea population, dives tended to be short and shallow (median duration: 43–76 s, median maximum depth: 6–10 m) [19,21], and well within the calculated aerobic dive limit (cADL, table 1) [26,27].

(a) Wild porpoises exhibit consistent moderate dive responses

Contrary to our hypothesis that wild porpoises would exhibit a graded and occasionally extreme bradycardia, tagged porpoises displayed moderate and consistent dive f_H in dives up to 3.5 min (figures 2, 3*b*, 4 and 5). Dive heart rate only declined to 23–55% of surface values and minimum f_H was greater than 45 bpm in 95% of dives (electronic supplementary material, figure S1A). Despite a large range in estimated mass (26–67 kg), when the smallest porpoise was excluded, porpoises exhibited remarkably similar dive f_H (figures 2, 3*b* and 4, i.e. 95% of all LQ f_Hs fell between 55 and 84 bpm). This is unexpected because among mammals, small young animals generally have higher f_H than larger adults (table 1) [28]. That two juveniles (JM1 and JM2) exhibited similar dive f_H to the two adults (figures 2, 3*b*, 4 and 5 and electronic supplementary material, figures S1 and S2) suggest that the juveniles are employing a relatively more intense bradycardia, allowing them to dive similarly to adults despite smaller absolute oxygen stores due to their smaller size. These results are consistent with a previous study that determined juvenile and adult porpoises have similar cADLs [27]. For one juvenile porpoise (JM3, 26 kg), dive f_H was highly variable and higher than the other porpoises (figure 3*b*, 4, 5; electronic supplementary material, figures S1 and S2). This animal exhibited the highest respiration rate in a previous study [19]. JM3's high and variable dive f_H may be an example of the natural variability between individuals, seasonal differences due to changes in temperature or prey availability (JM3 was instrumented later in the year than other porpoises), or a result of a potential respiratory disease (common in the Belt Sea population) [37]. Because JM3 data were so distinct and strongly influenced model results, f_H was analysed with and without this porpoise (electronic supplementary material, tables S1–S3). While the porpoises only exhibited a moderate dive response, all animals displayed a true bradycardia in over 99% of the analysed dives (figure 3*b*), with f_H decreasing to below their estimated resting f_H (estimated from mass of each porpoise, table 1) [28].

Surprisingly, dive duration did not influence LQ, bottom-of-dive, minimum dive nor dive interval f_H (figures 4 and 5; electronic supplementary material, figure S1 and tables S1 and S2). Although the associations between dive duration and bottom-of-dive and LQ f_H were statistically significant when JM3 was excluded, the slope coefficient was not biologically relevant (i.e. a 1 min increase in dive duration,

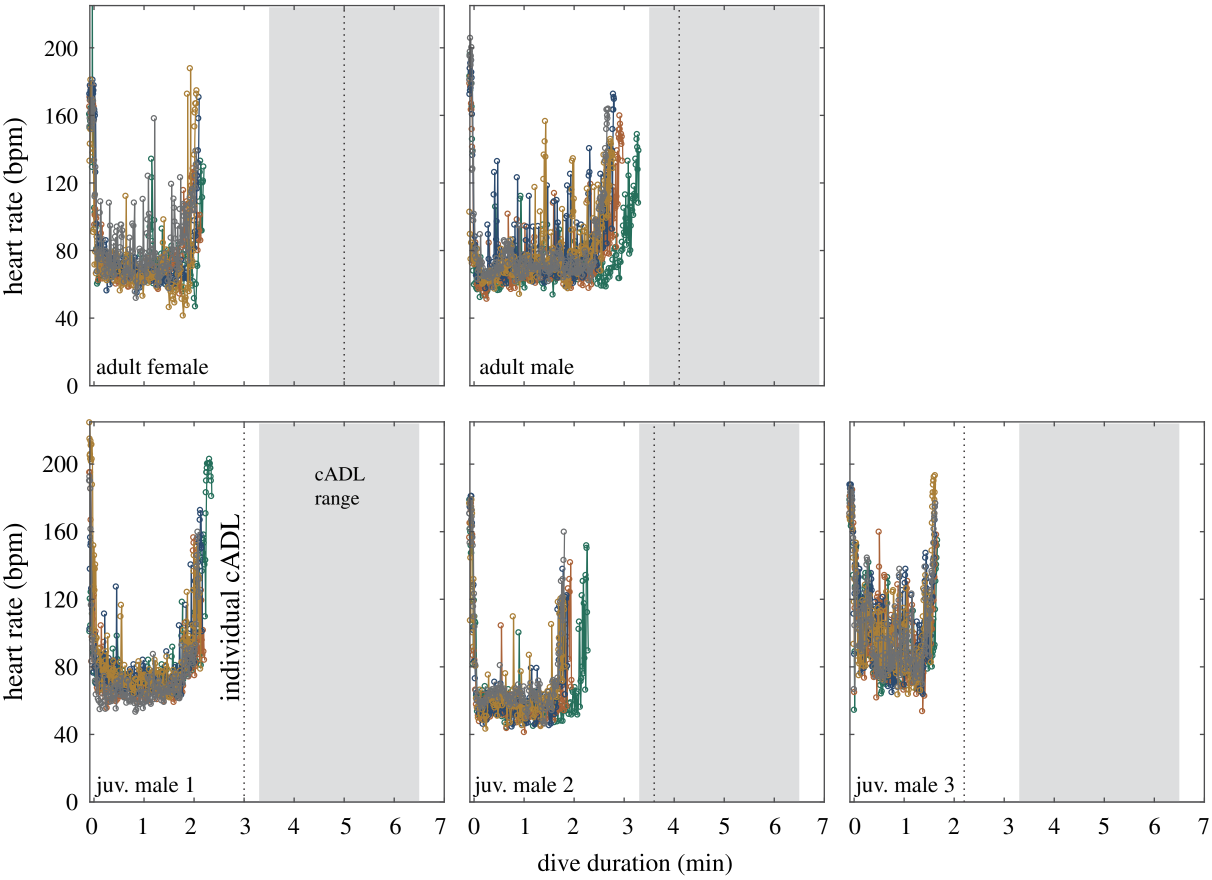

Figure 2. Dive f_H profiles from the five longest dives of each porpoise. No dives exceeded the Individual cADL or the minimum cADL estimated by age class [26,27]. While f_H profiles differed slightly between individuals, this did not appear to be due to age. Porpoises exhibited relatively consistent, moderate f_H across the range of dive durations observed. See table 1 footnotes for information about cADL calculations. (Online version in colour.)

which is a doubling of the median dive duration, only resulted in a 3 bpm decrease in LQ and bottom-of-dive f_H and dive duration explained less than 3% of the variation in f_H; electronic supplementary material, table S1) [38,39]. While Weddell seals do not appear to modify f_H with increased dive duration in aerobic dives (dives shorter than ADL) [40], f_H typically decreases with increasing dive duration during aerobic dives in other free-ranging marine mammals [4,16,41], and a decrease in f_H with increased dive duration was documented in captive porpoises performing short dives [8,23]. Low f_H in long dives is thought to be key to maximizing dive duration by minimizing blood flow to exercising muscle and other organs. Even in the longest dives performed by each porpoise of up to 3.3 min, f_H was moderate and not different from shorter dives (figure 2; electronic supplementary material, figure S2). The generally high f_H is probably required to support the high field metabolic rates documented in porpoises [19].

However, as these porpoises performed short dives that rarely approached their cADL (table 1 and figure 2), there may be no need to modify f_H to maximize dive duration. Instead, the consistent moderate bradycardia implies some blood flow to organs such as the intestine and stomach throughout the dive. The ability to digest prey while continuing to acquire more prey may be essential for small cetaceans with high metabolic demands that feed at high rates for approximately 70% of the day, but with small effective digestion systems where more food per body mass must be processed per day compared to larger cetaceans [42,43]. Larger species, or even porpoise populations that feed on larger prey, may be able to defer digestion and its metabolic cost until after foraging bouts [44–46]; captive grey seals almost completely deferred the metabolic costs of digestion until after simulated deep foraging dives, exhibiting extended surface intervals with elevated metabolic rate following foraging bouts. However, during simulated shallow dives, grey seals exhibited shorter dive durations and increased digestive costs during dives [45]. Similarly, Steller sea lions exhibit a partial deferment of digestion when actively foraging at depth, but Rosen *et al.* [46] suggest, based on differences in f_H between shallow and deep dives [47], that the degree of deferment is specific to diving conditions. For harbour porpoises in the inner Danish waters, where continuous foraging takes place at night in depths primarily less than 25 m [21,30], energy gain may be maximized by performing shorter dives with a moderate f_H allowing continued foraging while digesting. However, we predict that porpoises targeting deep-water/mesopelagic prey, such as in Greenlandic waters where porpoises dive down to 410 m [48,49], will exhibit a graded and occasionally extreme diving bradycardia with extended post-dive intervals after the longest dives.

(b) Wild porpoises exhibit an exercise-modulated surface f_H response

We hypothesized that wild porpoises would display an exercise-modulated dive f_H response and that the exercise response would be stronger than documented in captive

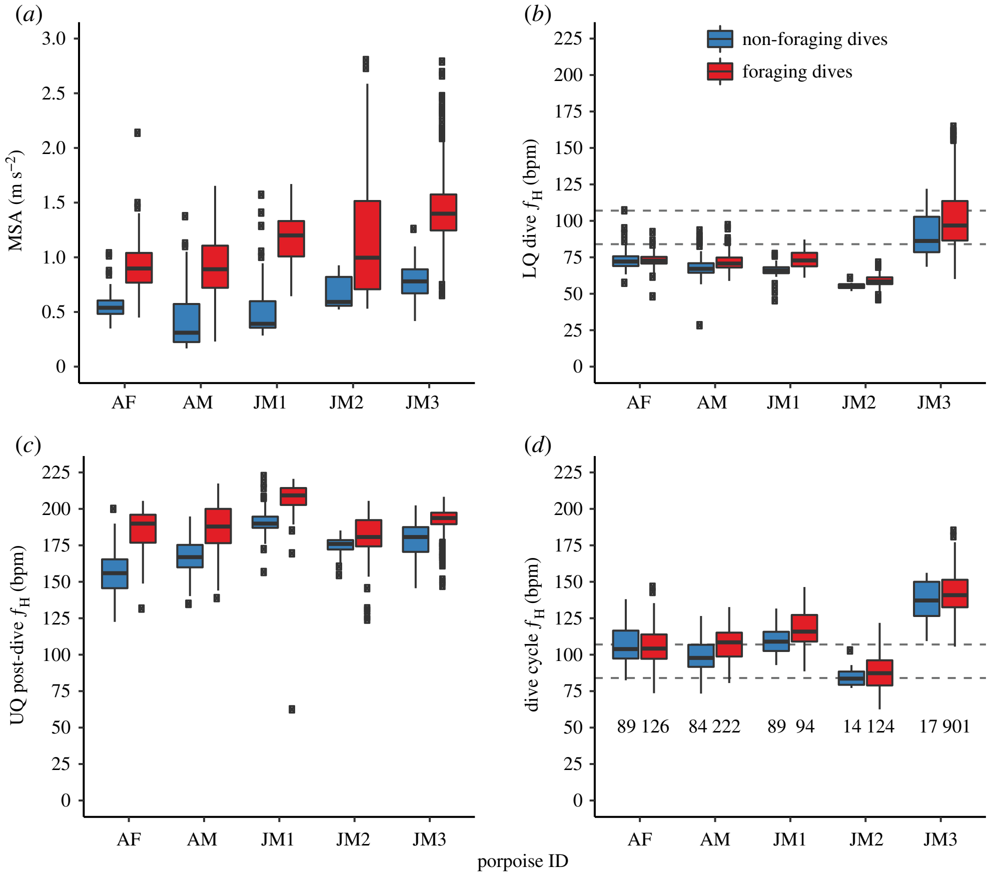

Figure 3. (*a*) Harbour porpoises exhibited higher mean MSA (activity proxy) during foraging dives compared to non-foraging dives; however, (*b*) there were likely no biologically relevant differences in LQ dive heart rate (f_{H}). (*c*) Foraging dives had higher post-dive f_{H} for most porpoises, (*d*) but there were no biologically relevant differences in f_{H} between foraging and non-foraging dives when averaged over a dive cycle (electronic supplementary material, table S3). Grey lines indicate estimated resting f_{H} from scaling [28] for a 26 kg (upper) and 67 kg (lower) mammal. Sample size provided in (*d*). The bottom and top of the box correspond to the 25th and 75th percentiles. The lower and upper whisker extend to the smallest and largest value that is no further than 1.5 × the inter-quartile range. Data beyond the end of the whiskers are outliers and are plotted individually. (Online version in colour.)

harbour porpoises [8,23,50] due to the greater diversity of behaviours exhibited in the wild. The few studies that have investigated the relationship between an activity index and dive f_{H} in pinnipeds and captive cetaceans found a positive relationship, at least in shorter aerobic dives [6,8,9,11,47], indicative of increased blood flow to exercising muscles. In wild narwhals, a positive relationship between stroke rate and f_{H} was observed once animals started to recover from prolonged capture stress [17]. Similarly, a blue whale exhibited a transient doubling of instantaneous f_{H} during costly feeding lunges [16]. By contrast, we found little support for exercise modulation of dive f_{H} in wild foraging porpoises. We used mean MSA as an index of activity [8,9,32] and, as predicted, mean MSA was higher during foraging dives compared to dives without foraging, (figure 3*a*; electronic supplementary material, table S3; mixed-effects ANOVA: 0.48 (coefficient) ± 0.02 (standard error, s.e.), $p < 0.001$). We hypothesized that this increased activity would lead to higher dive f_{H}, but there was no biologically relevant difference in LQ, median bottom-of-dive or minimum dive f_{H} between foraging and non-foraging dives (figure 3*b*; electronic supplementary material, tables S3 and S4). For example, LQ f_{H} was only 3.4 bpm higher in foraging dives, and foraging explained < 1% of the variation in f_{H}. Similarly, there was no biologically meaningful relationship between MSA and LQ f_{H} or interval MSA and interval f_{H} in the four largest porpoises (figures 4*b* and 5; electronic supplementary material, table S1 and S2): while the association between MSA and LQ f_{H} was statistically significant at the level of the dive (electronic supplementary material, table S1), an increase in mean MSA of 1 m s^{-2} only increased f_{H} by 1.8 bpm (mean dive MSA ranged between approximately 0.2–2.8 m s^{-2}). At a finer scale, there was no statistically significant relationship between interval MSA and interval f_{H} during the bottom of the dive (electronic supplementary material, table S2). The lack of relationship between activity and dive f_{H} in most of the porpoises could be a by-product of a consistent moderate dive response that allows for digestion during diving. The moderate f_{H} would be accompanied by a widespread decrease in sympathetic vasoconstriction with redistribution of blood to multiple tissues, including muscle [51]. If muscle is already moderately perfused during dives, porpoises may not increase f_{H} to provide more oxygenated blood to O_2-depleted muscle in moments of activity, at least while operating below a certain dive duration and activity threshold. In contrast with the four larger porpoises, JM3 exhibited an increase in dive f_{H} with increased activity as predicted (figure 4*b*; electronic supplementary material, figures S1 and S4).

While the diving f_{H} was moderate and not influenced by exercise, UQ instantaneous f_{H} in PDIs and PDI f_{H} (total beats during PDI/PDI duration) were high and influenced

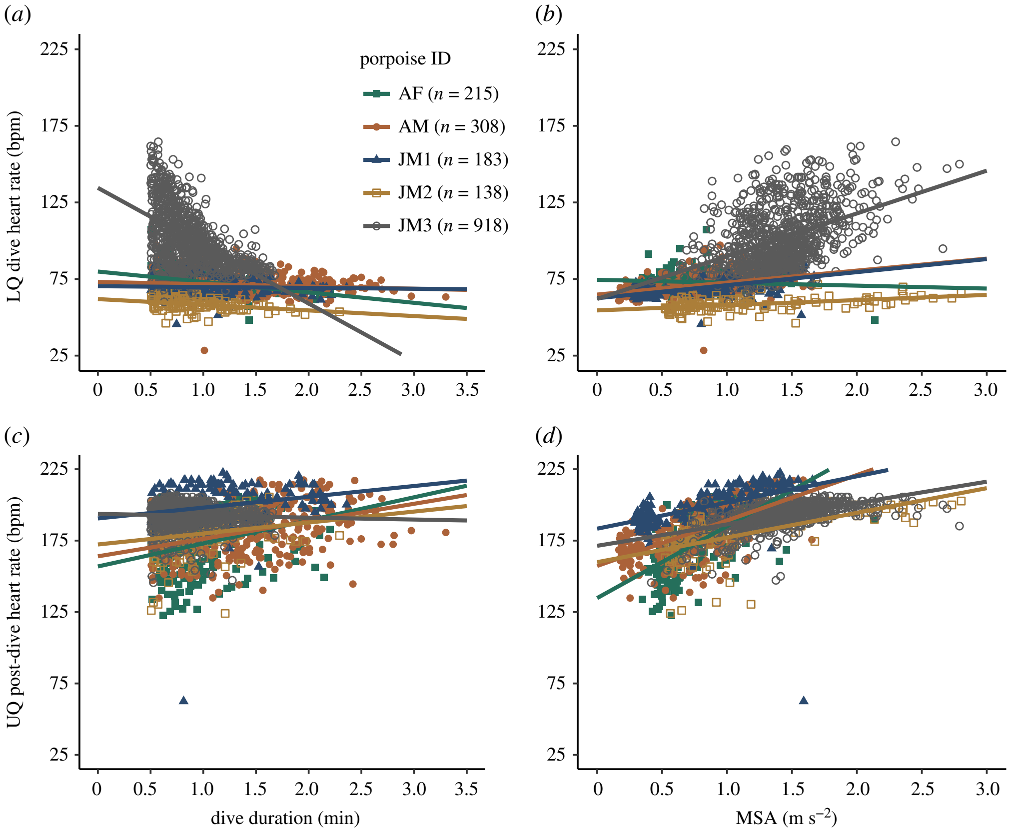

Figure 4. Influence of dive duration and mean MSA on (*a*,*b*) lower quartile dive f_H and (*c*,*d*) upper quartile post-dive surface f_H. See electronic supplementary material, table S1 for statistics. (Online version in colour.)

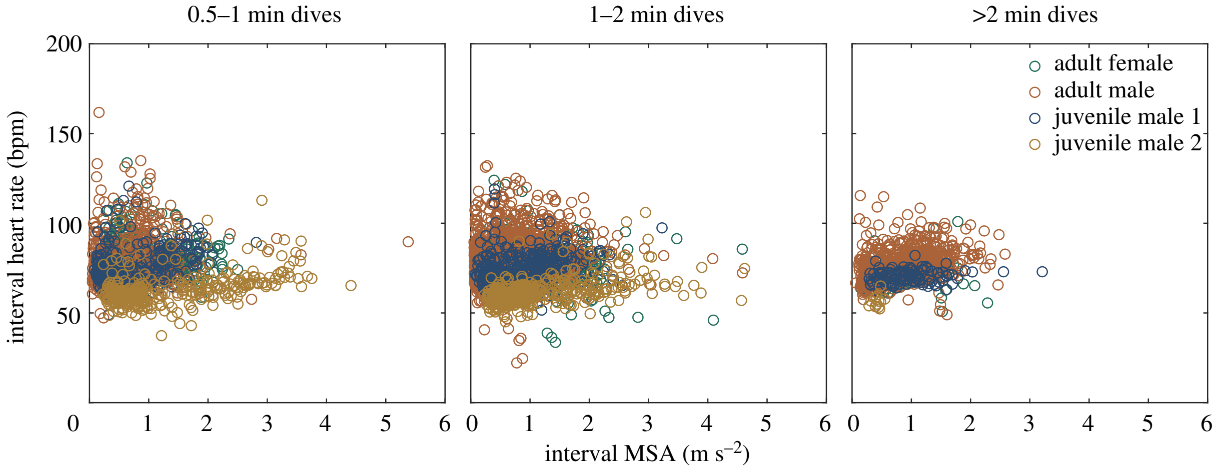

Figure 5. Interval MSA (m s^{-2}) did not influence interval heart rate (f_H) when JM3 was excluded. To facilitate visualization of the consistency of f_H across the range of dive durations observed, data are separated by dive duration category (0.5–1, 1–2 and greater than 2 min dives). Interval f_H was similar across the range of dive durations observed, but less variable in the longer dives. See electronic supplementary material, table S2 for statistics and figure S4 for JM3 data. (Online version in colour.)

by activity in all porpoises (UQ f_H is used as a proxy for surface f_H to avoid the influence of temporary decreases in f_H associated with short submergences). Post-dive UQ and PDI f_H were 11% and 23% higher, respectively, after foraging dives as compared to non-foraging dives (figure 3*c*; electronic supplementary material, table S3), and showed a positive relationship with mean MSA of the preceding dive (figure 4*d*; electronic supplementary material, figure S1 and table S1; ex. mixed effect model UQ surface f_H: 13.1 ± 4.0, $p = 0.001$, i.e. an increase in mean MSA of 1 m s^{-2} increased f_H by 13 bpm). The high post-dive UQ f_H after all dives facilitates rapid offloading of CO_2 and onloading of O_2, allowing the porpoise to maximize time submerged. The even higher post-dive UQ f_H during foraging bouts may serve to minimize time at the surface so the porpoise can quickly return to the prey patch. Although these elevated surface f_H-values after active foraging dives (median maximum f_H ranged from 188 to 219 bpm) are the highest documented for a marine mammal, they are nonetheless rarely close to the maximum f_{H} predicted from body mass of mammals (257 bpm for AF, the largest porpoise, and 280 bpm for JM3, the smallest porpoise, figure 2 and table 1) [29]. However, the porpoises occasionally exhibited f_{H} approaching the predicted maximum f_{H}, indicating they can increase f_{H} more if required.

4. Conclusion

These first longer term, continuous heart rate data from multiple, unstressed wild cetaceans demonstrate how these consummate divers juggle the conflicting demands of a deep bradycardia to prolong dives in search of prey while still delivering the O_2 needed for active hunting and digestion. We find that porpoises in shallow waters forgo deep bradycardia and instead maintain a relatively stable diving heart rate that is not influenced by dive duration or activity, and possibly size. This moderate bradycardia may be essential for providing cardiac output to support the high metabolic rate and upholding digestion during near-continuous feeding. Thus, for porpoises in this environment, extreme dive responses enabling extended dive durations, that may be critical for efficient foraging in marine mammals elsewhere, are not needed; extreme heart rate gymnastics are for deep/long dives and emergencies. Instead, shallow-feeding short duration diving porpoises have moderate dive heart rates combined with high surface heart rates that may help to balance the demands of prey capture, digestion and thermoregulation. This new understanding of how one of the smallest marine mammals manages O_2 during active foraging dives provides insight into how physiological responses are not necessarily taken to their extremes in the wild.

Ethics. Handling and instrumentation of porpoises was carried out under permission issued to J.T. from the Environmental Protection Agency (Ministry of Environment and Food of Denmark, NST-3446-0016) and the Animal Experiments Inspectorate (Ministry of Environment and Food of Denmark, 2015-15-0201-00549) during 2015–2018.

Data accessibility. Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.z612jm6cs [52]. Code used to process data is available at www.animaltags.org.

Authors' contributions. B.I.M.: conceptualization, data curation, formal analysis, funding acquisition, methodology, project administration, visualization, writing-original draft, writing-review and editing; S.L.E.: conceptualization, data curation, formal analysis, investigation, methodology, writing-original draft, writing-review and editing; M.J.: conceptualization, data curation, funding acquisition, methodology, resources, software, writing-original draft, writing-review and editing; D.M.W.: data curation, formal analysis, investigation, visualization, writing-review and editing; L.R.-D.: data curation, formal analysis, investigation, writing-review and editing; A.G.: investigation, writing-review and editing; U.S.: funding acquisition, writing-review and editing; J.T.: funding acquisition, investigation, methodology, project administration, Supervision, writing-review and editing; P.T.M.: conceptualization, funding acquisition, methodology, project administration, resources, supervision, writing-original draft, writing-review and editing. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests.

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References

1. Scholander P, Irving L, Grinnell S. 1942 Aerobic and anaerobic changes in seal muscles during diving. *Int. J. Biol. Chem.* **142**, 431–440. (doi:10.1016/S0021-9258(18)72738-5)
2. Scholander PF. 1940 Experimental investigations on the respiratory function in diving mammals and birds. *Hvalradets Skrifter* **22**, 1–131.
3. Zapol WM, Liggins GC, Schneider RC, Qvist J, Snider MT, Creasy RK, Hochachka PW. 1979 Regional blood flow during simulated diving in the conscious Weddell seal. *J. Appl. Physiol. Respir. Environ. Exerc. Physiol.* **47**, 968–973.
4. Thompson D, Fedak MA. 1993 Cardiac responses of grey seals during diving at sea. *J. Exp. Biol.* **174**, 139–154. (doi:10.1242/jeb.174.1.139)
5. Davis RW, Williams TM. 2012 The marine mammal dive response is exercise modulated to maximize aerobic dive duration. *J. Comp. Physiol. A* **198**, 583–591. (doi:10.1007/s00359-012-0731-4)
6. Williams TM *et al.* 2015 Exercise at depth alters bradycardia and incidence of cardiac anomalies in deep-diving marine mammals. *Nat. Commun.* **6**, 6055.
7. Elmegaard SL, Johnson M, Madsen PT, McDonald BI. 2016 Cognitive control of heart rate in diving harbor porpoises. *Curr. Biol.* **26**, R1175-R1176. (doi:10.1016/j.cub.2016.10.020)
8. McDonald BI, Johnson M, Madsen PT. 2018 Dive heart rate in harbour porpoises is influenced by exercise and expectations. *J. Exp. Biol.* **221**, jeb168740.
9. McDonald BI, Tift MS, Hückstädt LA, Jeffko M, Ponganis PJ. 2020 Stroke effort and relative lung volume influence heart rate in diving sea lions. *J. Exp. Biol.* **223**, jeb214163.
10. Noren SR, Cuccurullo V, Williams TM. 2004 The development of diving bradycardia in bottlenose dolphins (*Tursiops truncatus*). *J. Comp. Physiol. B* **174**, 139–147. (doi:10.1007/s00360-003-0398-9)
11. Noren SR, Kendall T, Cuccurullo V, Williams TM. 2012 The dive response redefined: underwater behavior influences cardiac variability in freely diving dolphins. *J. Exp. Biol.* **215**, 2735–2741. (doi:10.1242/jeb.069583)
12. Ponganis PJ. 2015 *Diving physiology of marine mammals and seabirds*. Cambridge, UK: Cambridge University Press.
13. Grinnell S, Irving L, Scholander P. 1942 Experiments on the relation between blood flow and heart rate in the diving seal. *J. Cell. Comp. Physiol.* **19**, 341–350. (doi:10.1002/jcp.1030190309)
14. Jobsis PD, Ponganis PJ, Kooyman GL. 2001 Effects of training on forced submersion responses in harbor seals. *J. Exp. Biol.* **204**, 3877–3885. (doi:10.1242/jeb.204.22.3877)

15. Butler PJ, Brown JA, Stephenson DG, Speakman JR. 2020 *Animal physiology: an environmental perspective*. Oxford, UK: Oxford University Press.
16. Goldbogen J *et al*. 2019 Extreme bradycardia and tachycardia in the world's largest animal. *Proc. Natl Acad. Sci. USA* **116**, 25 329–25 332. (doi:10.1073/pnas.1914273116)
17. Williams TM, Blackwell SB, Richter B, Sinding MH.S, Heide-Jørgensen MP. 2017 Paradoxical escape responses by narwhals (*Monodon monoceros*). *Science* **358**, 1328–1331. (doi:10.1126/science.aao2740)
18. Williams TM, Maresh JL. 2015 Exercise energetics. In *Marine mammal physiology: requisites for ocean living* (eds MA Castellini, JA Mellish), pp. 47–68. Boca Raton, FL: CRC Press.
19. Rojano-Doñate L, McDonald BI, Wisniewska DM, Johnson M, Teilmann J, Wahlberg M, Højer-Kristensen J, Madsen PT. 2018 High field metabolic rates of wild harbour porpoises. *J. Exp. Biol.* **221**, jeb.185827. (doi:10.1242/jeb.185827)
20. Sveegaard S *et al.* 2015 Defining management units for cetaceans by combining genetics, morphology, acoustics and satellite tracking. *Glob. Ecol. Conserv.* **3**, 839–850. (doi:10.1016/j.gecco.2015.04.002)
21. Wisniewska DM, Johnson M, Teilmann J, Rojano-Doñate L, Shearer J, Sveegaard S, Miller LA, Siebert U, Madsen PT. 2016 Ultra-high foraging rates of harbor porpoises make them vulnerable to anthropogenic disturbance. *Curr. Biol.* **26**, 1441–1446. (doi:10.1016/j.cub.2016.03.069)
22. Wisniewska DM, Johnson M, Teilmann J, Rojano-Doñate L, Shearer J, Sveegaard S, Miller LA, Siebert U, Madsen PT. 2018 Response to 'Resilience of harbor porpoises to anthropogenic disturbance: must they really feed continuously?' *Mar. Mammal. Sci.* **34**, 265–270. (doi:10.1111/mms.12463)
23. Reed J, Chambers C, Hunter C, Lockyer C, Kastelein R, Fedak M, Boutilier R. 2000 Gas exchange and heart rate in the harbour porpoise, *Phocoena phocoena*. *J. Comp. Physiol. B* **170**, 1–10. (doi:10.1007/s003600050001)
24. Teilmann J, Tougaard J, Miller LA, Kirketerp T, Hansen K, Brando S. 2006 Reactions of captive harbor porpoises (*Phocoena phocoena*) to pinger-like sounds. *Mar. Mammal. Sci.* **22**, 240–260. (doi:10.1111/j.1748-7692.2006.00031.x)
25. Lockyer C, Kinze C. 2003 Status, ecology and life history of harbour porpoise (*Phocoena phocoena*), in Danish waters. *NAMMCO Sci. Publ.* **5**, 143–175. (doi:10.7557/3.2745)
26. Rojano-Doñate L. 2020 *Acoustics and energetics of echolocators in a noisy world*. Aarhus, Denmark: Aarhus Universitet.
27. Noren SR, Noren DP, Gaydos JK. 2014 Living in the fast lane: rapid development of the locomotor muscle in immature harbor porpoises (*Phocoena phocoena*). *J. Comp. Physiol. B* **184**, 1065–1076. (doi:10.1007/s00360-014-0854-8)
28. Stahl WR. 1967 Scaling of respiratory variables in mammals. *J. Appl. Physiol.* **22**, 453–460. (doi:10.1152/jappl.1967.22.3.453)
29. Bishop CM. 1997 Heart mass and the maximum cardiac output of birds and mammals: implications for estimating the maximum aerobic power input of flying animals. *Phil. Trans. R. Soc. Lond. B* **352**, 447–456. (doi:10.1098/rstb.1997.0032)
30. Sveegaard S, Teilmann J, Tougaard J, Dietz R, Mouritsen KN, Desportes G, Siebert U. 2011 High-density areas for harbor porpoises (*Phocoena phocoena*) identified by satellite tracking. *Mar. Mammal. Sci.* **27**, 230–246. (doi:10.1111/j.1748-7692.2010.00379.x)
31. Wisniewska DM, Johnson M, Teilmann J, Siebert U, Galatius A, Dietz R, Madsen PT. 2018 High rates of vessel noise disrupt foraging in wild harbour porpoises (*Phocoena phocoena*). *Proc. R. Soc. B* **285**, 20172314. (doi:10.1098/rspb.2017.2314)
32. Simon M, Johnson M, Madsen PT. 2012 Keeping momentum with a mouthful of water: behavior and kinematics of humpback whale lunge feeding. *J. Exp. Biol.* **215**, 3786–3798. (doi:10.1242/jeb.071092)
33. Wilson RP, White CR, Quintana F, Halsey LG, Liebsch N, Martin GR, Butler PJ. 2006 Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *J. Anim. Ecol.* **75**, 1081–1090. (doi:10.1111/j.1365-2656.2006.01127.x)
34. Halsey L, Shepard E, Quintana F, Laich AG, Green J, Wilson RP. 2009 The relationship between oxygen consumption and body acceleration in a range of species. *Comp. Biochem. Phys. A* **152**, 197–202. (doi:10.1016/j.cbpa.2008.09.021)
35. Pinheiro J, Bates D, DebRoy S, Sarkar D, Heisterkamp S, Van Willigen B, Maintainer R. 2017 Package 'nlme': linear and nonlinear mixed effects models, version 3.1–131. See https://cran.r-project.org/web/packages/nlme.
36. Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM. 2009 *Mixed effects models and extensions in ecology with R*. Berlin, Germany: Springer Science & Business Media.
37. Siebert U *et al.* 2020 Health assessment of harbour porpoises (*Phocoena phocoena*) from Baltic area of Denmark, Germany, Poland and Latvia. *Environ. Int.* **143**, 105904. (doi:10.1016/j.envint.2020.105904)
38. Edwards LJ, Muller KE, Wolfinger RD, Qaqish BF, Schabenberger O. 2008 An R2 statistic for fixed effects in the linear mixed model. *Stat. Med.* **27**, 6137–6157. (doi:10.1002/sim.3429)
39. Wasserstein RL, Lazar NA. 2016 The ASA statement on *p*-values: context, process, and purpose. *Am. Stat.* **70**, 129–133. (doi:10.1080/00031305.2016.1154108)
40. Hill RD *et al.* 1987 Heart rate and body temperature during free diving of Weddell seals. *Am. J. Physiol. Reg. I* **253**, R344–R351.
41. McDonald BI, Ponganis PJ. 2014 Deep-diving sea lions exhibit extreme bradycardia in longduration dives. *J. Exp. Biol.* **217**, 1525–1534. (doi:10.1242/jeb.098558)
42. Chivers DJ, Hladik CM. 1980 Morphology of the gastrointestinal tract in primates: comparisons with other mammals in relation to diet. *J. Morphol.* **166**, 337–386. (doi:10.1002/jmor.1051660306)
43. Schmidt-Nielsen K, Knut SN. 1984 *Scaling: why is animal size so important?* Cambridge, UK: Cambridge University Press.
44. Crocker DE, Le Boeuf BJ, Costa DP. 1997 Drift diving in female northern elephant seals: implications for food processing. *Can. J. Zool.* **75**, 27–39. (doi:10.1139/z97-004)
45. Sparling CE, Fedak MA, Thompson D. 2007 Eat now, pay later? Evidence of deferred food-processing costs in diving seals. *Biol. Lett.* **3**, 95–99. (doi:10.1098/rsbl.2006.0566)
46. Rosen DA.S., Gerlinsky CD, Trites AW. 2015 Evidence of partial deferment of digestion during diving in Steller sea lions (*Eumetopias jubatus*). *J. Exp. Mar. Biol. Ecol.* **469**, 93–97. (doi:10.1016/j.jembe.2015.04.017)
47. Hindle AG, Young BL, Rosen DA, Haulena M, Trites AW. 2010 Dive response differs between shallow- and deep-diving Steller sea lions (*Eumetopias jubatus*). *J. Exp. Mar. Biol. Ecol.* **394**, 141–148. (doi:10.1016/j.jembe.2010.08.006)
48. Nielsen NH, Teilmann J, Heide-Jørgensen MP. 2019 Indications of mesopelagic foraging by a small odontocete. *Mar. Biol.* **166**, 78. (doi:10.1007/s00227-019-3525-1)
49. Nielsen NH, Teilmann J, Sveegaard S, Hansen RG, Sinding M-HS, Dietz R, Heide-Jørgensen MP. 2018 Oceanic movements, site fidelity and deep diving in harbour porpoises from Greenland show limited similarities to animals from the North Sea. *Mar. Ecol. Prog. Ser.* **597**, 259–272. (doi:10.3354/meps12588)
50. Elmegaard SL, McDonald BI, Madsen PT. 2019 Drivers of the dive response in trained harbour porpoises (*Phocoena phocoena*). *J. Exp. Biol.* **222**, jeb208637. (doi:10.1242/jeb.208637)
51. Elsner R, Franklin DL, Van Citters RL, Kenney DW. 1966 Cardiovascular defense against asphyxia. *Science* **153**, 941–949. (doi:10.1126/science.153.3739.941)
52. McDonald BI, Elmegaard SL, Johnson M, Wisniewska DM, Rojano-Donate L, Galatius A, Siebert U, Teilmann J, Madsen PT. 2021 Data from: High heart rates in hunting porpoises. Dryad Digital Repository. (doi:10.5061/dryad.z612jm6cs)