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Scaling of heart rate with breathing frequency and body mass in cetaceans

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Plasticity in the cardiac function of a marine mammal facilitates rapid adjustments to the contrasting metabolic demands of breathing at the surface and diving during an extended apnea. By matching their heart rate (f_H) to their immediate physiological needs, a marine mammal can improve its metabolic efficiency and maximize the proportion of time spent underwater. Respiratory sinus arrhythmia (RSA) is a known modulation of f_H that is driven by respiration and has been suggested to increase cardiorespiratory efficiency. To investigate the presence of RSA in cetaceans and the relationship between f_H, breathing rate (f_R) and body mass (M_b), we measured simultaneous f_H and f_R in five cetacean species in human care. We found that a higher f_R was associated with a higher mean instantaneous f_H (if_H) and minimum if_H of the RSA. By contrast, f_H scaled inversely with M_b such that larger animals had lower mean and minimum if_Hs of the RSA. There was a significant allometric relationship between maximum if_H of the RSA and M_b, but not f_R, which may indicate that this parameter is set by physical laws and not adjusted dynamically with physiological needs. RSA was significantly affected by f_R and was greatly reduced with small increases in f_R. Ultimately, these data show that surface f_Hs of cetaceans are complex and the f_H patterns we observed are controlled by several factors. We suggest the importance of considering RSA when interpreting f_H measurements and particularly how f_R may drive f_H changes that are important for efficient gas exchange.

This article is part of the theme issue 'Measuring physiology in free-living animals (Part I)'.

1. Introduction

Marine mammals are known to demonstrate dramatic changes in heart rate (f_H) associated with diving behaviour [1–3]. In the blue whale (*Balaenoptera musculus*), the largest extant animal, regular diving f_Hs of 4 beats min^{-1} have been measured [4]. The reduction in f_H, or bradycardia, during a dive reduces both the rate of oxygen consumption of the heart and, in conjunction with peripheral vasoconstriction, limits the supply of oxygen-rich blood to peripheral tissues [5,6]. By temporarily reducing the oxygen supply to the peripheral tissues and the metabolic needs of the heart, marine mammals prolong the duration of aerobic metabolism and can, in theory, extend dive duration [5,7]. The dive response is universal among marine mammals and is known to be modulated in proportion to dive depth and duration. Both harbour porpoises (*Phocoena phocoena*) and bottlenose dolphins (*Tursiops truncatus*) trained to perform dives of varying durations demonstrated a physiological anticipatory preparation in the modulation of their f_Hs according to the expected dive duration [8,9]. In Weddell seals (*Leptonychotes weddellii*) forced to dive, the degree of bradycardia was increased compared to spontaneous dives of similar durations, which is thought to reflect that the animal responds more conservatively when its ability to plan in advance is removed [10]. The ability to modulate f_H on a fine temporal scale allows a marine mammal to match its cardiovascular changes to the needs associated with its behavioural state, thereby maximizing energetic intake through increased foraging time while minimizing energetic output through reduced metabolic costs [11]. Importantly, a marine mammal's ability to modulate its instantaneous heart rate (if_H) has been correlated with increased apnea duration [12–14]. In addition, conditioned variation in if_H has been proposed as an important part of the selective gas exchange hypothesis that explains how cetaceans may exchange metabolic gases while minimizing uptake of N_2 [15,16].

Marine mammals also show considerable plasticity in cardiac function during surface intervals. While breathing at the surface marine mammals demonstrate respiratory sinus arrhythmia (RSA), like other terrestrial mammals including humans, where the if_H oscillates in synchrony with the respiratory rate (f_R) [13,17–22]. The mechanism of RSA is understood to be a central phenomenon of respiratory modulation via cardiac vagal stimulation, but its physiological role is less well understood [23–25]. The dominant hypotheses based on work in humans and dogs suggest that RSA functions to improve cardiorespiratory efficiency by increasing ventilation/perfusion matching and/or reducing cardiac work [26–28]. In cetaceans, which have evolved into a fully aquatic lifestyle, these functions could have downstream effects on an individual's ability to maximize time spent underwater. This is due to the effect of f_H modulation on perfusion and oxygen supply to the tissues via cardiac output, which are two of the primary factors that determine an individual's aerobic dive limit during diving and affect oxygen transport during surface recovery time [13,20,29–31]. RSA has been observed in several cetacean species including the grey whale (*Eschrichtius robustus*), killer whale (*Orcinus orca*), short-finned pilot whale (*Globicephala macrorhynchus*), beluga (*Delphinapterus leucas*), common dolphin (*Delphinus delphis*), bottlenose dolphin and harbour porpoise [13,20,32–39]. In bottlenose dolphins, recent work demonstrated that the resting f_H corrected for f_R was comparable to that during some apneas and underscored the potential utility of using the magnitude of RSA as an index of diving ability, as has previously been supported by studies of pinnipeds [12,13]. If the magnitude of RSA does indeed reflect diving ability because of its potential relationship to cardiorespiratory efficiency, quantifying a baseline value and estimating how it could vary in a cetacean in response to changes in f_R during disturbance are necessary for its utility as a conservation tool.

In addition to the known effect of respiration on f_H and RSA, f_H also scales allometrically across vertebrate taxa making body mass (M_b) critical in the interpretation of f_H measurements [13,20,40,41]. In previous analyses examining the relationship between M_b and f_H in mammals, a scaling exponent of −0.25 has been suggested [42]. Given the relationship of metabolic rate and f_H through Fick's principle [43], differences in f_H are expected to estimate differences in metabolic rate when accounting for M_b [44–46]. Although this relationship may be more complicated in breath-holding marine mammals [46–48], a lower rate of mass-specific oxygen consumption coupled with an isometric relationship between M_b and body oxygen stores suggests that larger animals should have increased diving capacity [49–51]. In fact, many studies in marine mammals have shown that M_b does positively correlate with dive duration, but M_b alone does not explain all of the observed inter-species variation in diving patterns nor the variation across taxa [50,52–54]. In cetaceans, other ecological and physiological factors have been suggested to play a role in determining diving behaviour including diel patterns [55], foraging ecology [56,57] and the biochemical structure of respiratory pigments [58,59].

Given the potential importance of RSA in contributing to efficient cardiorespiratory patterns of cetaceans, we aimed to investigate the scaling of RSA and f_H across cetacean species to examine inter-species variation in the degree of RSA. Our specific objectives were to collect simultaneous f_H and f_R data from five species of cetaceans in human care across a range of M_bs and determine how f_H and the degree of RSA vary allometrically with f_R and M_b.

2. Methods

(a) Animals

We collected data from six bottlenose dolphins, a beluga whale, a false killer whale (*Pseudorca crassidens*), four killer whales (*Orcinus orca*) and three short-finned pilot whales in human care for inclusion in this study. All procedures described were performed in strict accordance with the US Animal Welfare Act for the care of Marine Mammals (US-based facilities) or the European Association for Aquatic Mammals (EAAM) (Europe-based facilities). Additionally, animals were housed in outdoor facilities with access to shade whose size met or exceeded the standards set by the Alliance of Marine Mammal Parks & Aquariums (AMMPA) and the EAAM. All animals were adults and considered non-reproductive during the period of data collection. A summary of the animals that participated in the study can be found in electronic supplementary material, table S1.

(b) Data collection

All data were collected during stationary, non-fasted, resting trials with cetaceans in human care (table 1). Prior to the study, animals were desensitized to the research equipment using operant conditioning. All research trials began with a 2 min period of slow swimming or resting poolside prior to the start of data collection. To start a trial, the animal was positioned next to the trainer and rolled into dorsal recumbency to allow placement of three electrocardiogram (ECG) electrodes. The three-lead ECG used gold-plated electrodes (Disposable GoldSelect Cup Electrodes, DE-003710, Rochester Med, FL, USA), which were mounted inside custom silicone suction cups (Smooth-Sil 940, Smooth-On, Inc., PA, USA). The ECG electrodes were connected to a custom-built bio-amplifier (UUB/1-ECGb, UFI, Morro Bay, CA, United States), and then, with a BNC connector, to the data acquisition system (Powerlabs 8/35, ADInstruments, Colorado Springs, CO, USA). Conductive paste (Ten20 Conductive Paste, Weaver and Company, Aurora, Colorado, USA) was applied to each suction cup before being placed on the skin (see electronic supplementary material, figure S1). With the electrodes placed, the animal then rolled back, dorsal side up while the electrodes continued to stay attached and were submerged on the ventral side. A trial began when the animal was in ventral recumbency and positioned next to the trainer in a resting position. One trial consisted of 5–10 min of stationary rest at the surface while the ECG and breaths were recorded. From the ECG, the R–R interval was used to determine the if_H during post-processing.

For trials with bottlenose dolphins, the false killer whale and the beluga whale, f_R was recorded using a Fleisch-type pneumotachometer (Mellow Design, Valencia, Spain) developed to measure breath-to-breath exhaled and inhaled respiratory flow

Table 1. Average age, body mass (M_b), breathing frequency (f_R), heart rate (f_H), degree of RSA, maximum if_H of the RSA, and minimum if_H of the RSA across all individuals of each species. The number of breaths is indicated by *n* and the number of individuals is indicated in parentheses.

species	age (years)	M_b (kg)	f_R (breaths min^{-1})	f_H (beats min^{-1})	RSA (%)	max. if_H (beats min^{-1})	min. if_H (beats min^{-1})
Bottlenose dolphin ($n = 246$ (6))	23.8 ± 7.9	189.3 ± 36.3	5.6 ± 3.8	77.8 ± 16.9	41.7 ± 18.9	92.3 ± 13.6	60.9 ± 14.2
False killer whale ($n = 27$)	30	520.0	4.1 ± 2.7	59.4 ± 13.7	43.4 ± 23.5	73.5 ± 9.4	48.3 ± 12.7
Beluga whale ($n = 18$)	24	800.0	4.3 ± 2.7	54.6 ± 14.1	58.4 ± 23.3	69.0 ± 14.4	37.8 ± 12.6
Short-finned pilot whale ($n = 8$ (3))	8	843.3 ± 242.1	0.7 ± 0.2	38.3 ± 12.1	90.9 ± 14.2	62.1 ± 10.2	27.1 ± 3.1
Killer whale ($n = 25$ (4))	20.0 ± 15.3	2217.4 ± 344.1	1.3 ± 0.6	46.7 ± 14.0	77.0 ± 17.3	64.2 ± 4.3	28.6 ± 5.1

in small- and medium-sized cetaceans [60]. The start of a breath was determined from the flow signal and the f_R was determined from the duration between successive breaths. Further analysis of the respiratory flow was not performed for this study. For the larger species (short-finned pilot whales and killer whales), the breaths were recorded manually and verified by a change in the baseline ECG signal, which was indicative of both movement and muscle electrical activity associated with exhalation. All data were collected during the day when the feeding state of the animals was considered non-fasted. All experiments were conducted across a 2-year period between autumn 2017 and autumn 2019.

(c) Data processing

The respiratory flow and ECG were sampled at 400 Hz by a data acquisition system (Powerlabs 8/35, ADInstruments, Colorado Springs, CO, USA), which displayed all data streams in real-time on a laptop computer running LabChart (v. 8.1, ADInstruments, Colorado Springs, CO, USA). The ECG Analysis Module in LabChart was used to extract if_H from the ECG signal. All further data analysis and processing were done using MATLAB (version 2018b, © 2018 The MathWorks, Inc., Natick, MA, USA). Maximum if_H and minimum if_H were the maximum or minimum f_H measured during a given inter-breath interval (IBI), respectively. Mean if_H was the average if_H measured during an IBI, whereas mean f_H was the average of all if_Hs measured for an individual. The degree of RSA was estimated using RSA $(\%) = \Delta f_H/(\bar{f}_H)$, where Δf_H = maximum if_H of the IBI – minimum if_H of the IBI as has previously been described [61].

(d) Statistical analysis

All statistical analyses were conducted using R version 3.6.2 [62]. Linear mixed-effects models (*nlme* package) were used to evaluate the effects of f_R and M_b simultaneously and individually on f_H and the degree of RSA across all individuals, with species and animal ID included as random effects. Individual relationships between predictor and outcome variables were evaluated, with the predictor variables, f_R and M_b, $\log_{10}$-transformed to improve the normality of both variables. The outcome variables, RSA and all f_H variables were normally distributed without being $\log_{10}$-transformed and therefore were not transformed for the initial models. However, to be able to compare these data with previously published allometric relationships, the outcome variables were $\log_{10}$-transformed in subsequent models to model power law relationships between individual predictor and outcome variables. The Akaike information criterion (AIC) was used to determine the most parsimonious model for each dependent variable by selecting the model with the lowest associated AIC. For nested models, a likelihood ratio test was used to evaluate whether the most parsimonious model variable was significantly better than the nested model with the next-lowest AIC and one less predictor variable. In determining the most parsimonious model for each outcome variable, predictor variables were $\log_{10}$-transformed to improve the normality of both variables, but outcome variables were not transformed given that they were normally distributed without transformation. A model that included the interaction of f_R and M_b was considered for all dependent variables to account for the known mass dependence of f_R [63]. All statistical tests were done assuming that a *p*-value < 0.05 indicated a significant difference. Values are presented as average ± s.d. unless stated otherwise.

3. Results

Average values for age, M_b, f_R, f_H and RSA (%) are reported for each species in table 1. The killer whales were the largest cetaceans in the study and approximately 13 times larger than the average mass of the bottlenose dolphins studied (table 1). In total, 18 trials with 15 individuals were conducted, which contained a total of 324 breaths. All species and all individuals displayed a clear RSA, although there was some variation in the shape of the f_H patterns throughout the IBI (figure 1). The average f_R was lowest in the short-finned pilot whales and highest in the bottlenose dolphins (table 1). Short-finned pilot whales also displayed the lowest mean f_H (38.3 ± 12.1 beats min^{-1}) and the greatest degree of RSA, while bottlenose dolphins displayed the highest mean f_H (77.8 ± 16.9 beats min^{-1}) and the lowest degree of RSA of the five species studied (table 1).

Possible allometric relationships were evaluated by examining the relationship between individual predictor

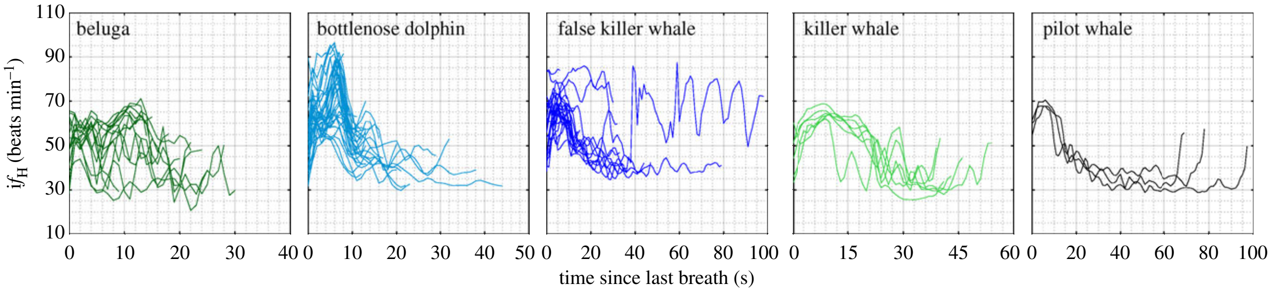

Figure 1. A representative trial for one individual of each species showing changes in heart rate (f_H) during the IBI. (Online version in colour.)

Table 2. Results of linear mixed effects models with species and animal ID included as random effects determine the allometric relationships between f_R, M_b, f_H and RSA. Values of the coefficient of the predictor variable, standard error of the coefficient, *t*-value and *p*-value are presented for each model. *p*-value indicates significance of the linear relationship between the predictor and outcome variable. Models are shown in the form $\log_{10}(y) \sim \log_{10}(x)$.

model	coeff. ± s.e.	*t*-value	*p*-value
$\log_{10}(\text{RSA}) \sim \log_{10}(f_R)$	−0.56 ± 0.03	−20.3	<0.0001
$\log_{10}(\text{RSA}) \sim \log_{10}(M_b)$	0.35 ± 0.11	3.3	<0.01
$\log_{10}(\text{Mean } if_H) \sim \log_{10}(f_R)$	0.11 ± 0.01	9.6	<0.0001
$\log_{10}(\text{Mean } if_H) \sim \log_{10}(M_b)$	−0.24 ± 0.07	−3.2	0.01
$\log_{10}(\text{Max. } if_H) \sim \log_{10}(f_R)$	−0.0 ± 0.01	−0.7	0.49
$\log_{10}(\text{Max. } if_H) \sim \log_{10}(M_b)$	−0.16 ± 0.03	−4.1	<0.001
$\log_{10}(\text{Min. } if_H) \sim \log_{10}(f_R)$	0.21 ± 0.02	12.8	<0.0001
$\log_{10}(\text{Min. } if_H) \sim \log_{10}(M_b)$	−0.34 ± 0.05	−6.3	<0.0001

variables and outcome variables with both variables $\log_{10}$-transformed (table 2). RSA was significantly related to f_R with a scaling coefficient of −0.56 ± 0.03 (coefficient ± s.e.) and to M_b with a scaling coefficient of 0.35 ± 0.11 (figure 2*a*,*b*). Similarly, both mean if_H and minimum if_H of the RSA were significantly related to both f_R and M_b. Both mean if_H and minimum if_H were positively related to f_R and scaled with coefficients of 0.11 ± 0.01 and 0.21 ± 0.02, respectively (figure 3*a*,*c*). Maximum if_H of the RSA was not significantly related to f_R. There was a significant negative relationship between f_H and M_b and maximum if_H, mean if_H, and minimum if_H of the RSA were related to M_b by the scaling coefficients −0.16 ± 0.03, −0.24 ± 0.07 and −0.34 ± 0.05, respectively (figures 2*c* and 3*b*,*d*).

Linear mixed models revealed the most parsimonious model for each outcome variable that best described the variation in the outcome variable with the fewest predictor variables (table 3). Before models were constructed, we examined the individual relationships between each predictor variable and outcome variable. There was a significant relationship between f_R and all outcome variables except for the maximum if_H of the RSA. f_R showed a negative relationship with RSA ($p < 0.0001$) and a positive relationship with mean if_H ($p < 0.0001$) and minimum if_H ($p < 0.0001$) of the RSA. M_b was significantly related to all outcome variables and showed a positive relationship with RSA ($p = 0.01$) and a negative relationship with maximum if_H ($p < 0.001$), mean if_H ($p < 0.01$) and minimum if_H ($p = 0.0001$) of the RSA. The most parsimonious model of the degree of RSA included both f_R, M_b and their interaction, such that the relationship between f_R and RSA varied with M_b (table 3). In the most parsimonious models for both mean if_H and minimum if_H of the RSA, f_H increased with increasing f_R (figure 3*a*,*c*) and decreased with increasing M_b (figure 3*b*,*d*). Minimum if_H increased more rapidly with increasing f_R as compared with mean if_H but decreased less rapidly with increasing M_b than mean if_H and maximum if_H (table 3). M_b was the only predictor variable included in the most parsimonious model of maximum if_H of the RSA (table 3).

4. Discussion

Cardiorespiratory coupling has been suggested to help cetaceans maximize gas exchange during short surfacing intervals by producing a large cardiac response, or a brief tachycardia followed by a gradual decrease in f_H, following respiration [20]. Studies in humans and dogs have suggested that RSA reduces cardiac work and/or increases ventilation/perfusion matching, both of which could benefit cetaceans that are dually constrained by their need to conduct gas exchange at the surface and forage underwater [26,27]. Here, we quantify RSA and make the first comparisons of the degree of RSA across several species of cetaceans. The data not only demonstrate that all five cetacean species studied exhibit RSA and that there are large differences in the degree of RSA across species, but also that these differences scale with M_b and f_R.

While this study is constrained by a limited sample size, particularly with one individual beluga and false killer whale, analyses were conducted on a breath-by-breath basis and therefore multiple data points were used in calculating variables both within and between individuals and species. All data used in this study were collected under resting conditions when the animals were stationary at the surface and

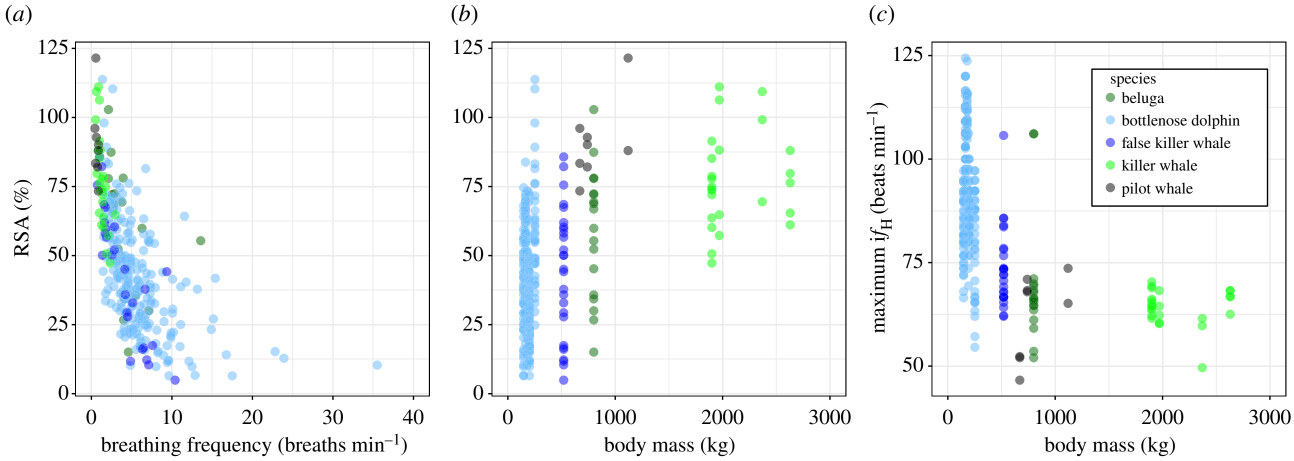

Figure 2. (*a*) RSA versus breathing frequency (f_R) and (*b*) RSA versus body mass (M_b). (*c*) Maximum if_H of the RSA versus body mass (M_b) (324 IBIs from 15 individuals).

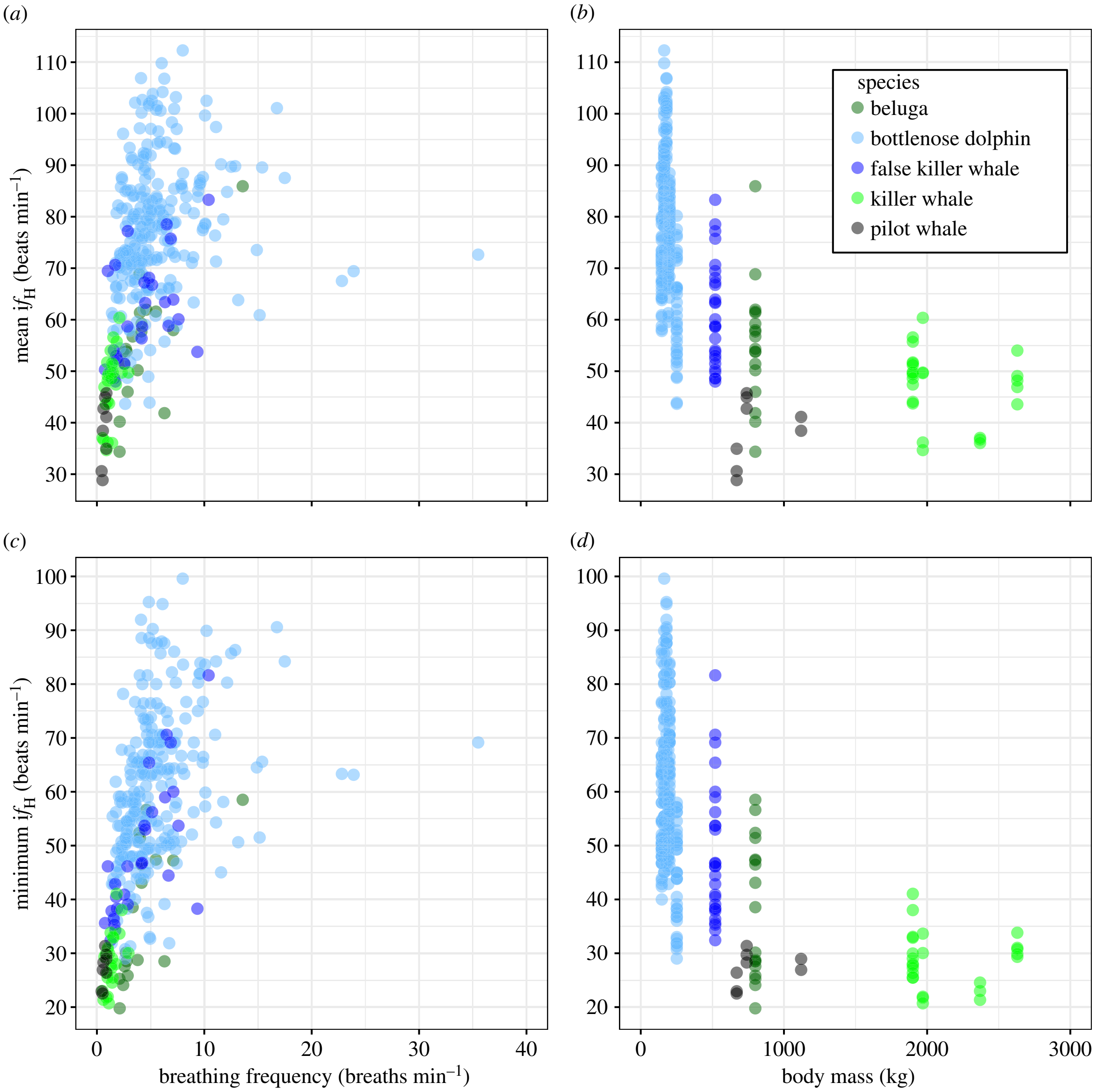

Figure 3. (*a*) Mean if_H versus breathing frequency (f_R) and (*b*) mean if_H versus body mass (M_b). (*c*) Minimum if_H versus breathing frequency (f_R) and (*d*) minimum if_H versus body mass (M_b) (324 IBIs from 15 individuals).

breathing spontaneously, so the patterns of cardiorespiratory coupling observed may not be extended to diving conditions. Additionally, variation in f_R likely does not capture the overall variation in gas exchange and therefore an examination of f_R alone in an analysis of cardiorespiratory coupling is incomplete. Both tidal volume (V_T) and O_2 extraction (E_{O2}) are

Table 3. Results of linear mixed effects models with species and animal ID included as random effects reveal the most parsimonious model of f_{H} and RSA. Predictor variables were $\log_{10}$-transformed prior to model fit. Each most parsimonious model was evaluated against the nested model with the next smallest AIC using a log-likelihood ratio test. The most parsimonious model for each outcome variable is indicated in bold and the predictor variables in that model are shown on the right.

model	AIC	predictor	coeff ± s.e.	*t*-value	*p*-value
RSA $\sim \log_{10}(f_{\mathrm{R}})$	2426.2	$\log_{10}(f_{\mathrm{R}})$	60.4 ± 24.5	2.5	0.01
RSA $\sim \log_{10}(M_{\mathrm{b}})$	2629.4	$\log_{10}(M_{\mathrm{b}})$	12.6 ± 6.3	2.0	0.08
RSA $\sim \log_{10}(f_{\mathrm{R}}) + \log_{10}(M_{\mathrm{b}})$	2426.3	$\log_{10}(f_{\mathrm{R}})$*$\log_{10}(M_{\mathrm{b}})$	−47.0 ± 10.3	−4.6	<0.0001
RSA $\sim \log_{10}(f_{\mathrm{R}})$*$\log_{10}(M_{\mathrm{b}})$	**2410.9**	intercept	43.8 ± 17.5	2.5	0.01
Mean i$f_{\mathrm{H}} \sim \log_{10}(f_{\mathrm{R}})$	2059.2	$\log_{10}(f_{\mathrm{R}})$	20.0 ± 1.7	11.6	<0.0001
Mean i$f_{\mathrm{H}} \sim \log_{10}(M_{\mathrm{b}})$	2165.1	$\log_{10}(M_{\mathrm{b}})$	−21.7 ± 5.3	−4.1	<0.0001
Mean i$f_{\mathrm{H}} \sim \log_{10}(f_{\mathrm{R}}) + \log_{10}(M_{\mathrm{b}})$	**2054.4**	intercept	112.6 ± 14.9	7.6	<0.01
Mean i$f_{\mathrm{H}} \sim \log_{10}(f_{\mathrm{R}})$*$\log_{10}(M_{\mathrm{b}})$	2055.3				
Max. i$f_{\mathrm{H}} \sim \log_{10}(f_{\mathrm{R}})$	2355.0	$\log_{10}(M_{\mathrm{b}})$	−29.4 ± 5.8	−5.1	<0.001
Max. i$f_{\mathrm{H}} \sim \log_{10}(M_{\mathrm{b}})$	**2347.8**	intercept	157.1 ± 15.9	9.9	<0.0001
Max. i$f_{\mathrm{H}} \sim \log_{10}(f_{\mathrm{R}}) + \log_{10}(M_{\mathrm{b}})$	2349.3				
Max i$f_{\mathrm{H}} \sim \log_{10}(f_{\mathrm{R}})$*$\log_{10}(M_{\mathrm{b}})$	2349.4				
Min. i$f_{\mathrm{H}} \sim \log_{10}(f_{\mathrm{R}})$	2367.0	$\log_{10}(f_{\mathrm{R}})$	25.2 ± 2.1	12.3	<0.0001
Min. i$f_{\mathrm{H}} \sim \log_{10}(M_{\mathrm{b}})$	2484.3	$\log_{10}(M_{\mathrm{b}})$	−17.9 ± 4.7	−3.8	<0.01
Min. i$f_{\mathrm{H}} \sim \log_{10}(f_{\mathrm{R}}) + \log_{10}(M_{\mathrm{b}})$	**2361.4**	intercept	84.3 ± 13.3	6.4	<0.0001
Min. i$f_{\mathrm{H}} \sim \log_{10}(f_{\mathrm{R}})$*$\log_{10}(M_{\mathrm{b}})$	2363.0				

known to vary in cetaceans during resting and active behaviours in addition to f_{R} [20,64–67]. However, given that f_{R} is a common metric used to evaluate respiratory physiology in free-ranging cetaceans because it can be determined from visual observation and/or tag data [55,68–70], we decided to use f_{R} in this preliminary study.

All animals studied exhibited RSA, which was observed as an increase in if_{H} directly following a breath and a gradual decrease in if_{H} until the next breath, although there was some variation in the degree of RSA between species (figure 1). The peak in if_{H} consistently occurred between 5–10 s in all species. If the brief tachycardia in cetaceans is driven by lung inflation, as has been suggested in seals [71], this result could suggest that the post-respiration tachycardia is secondary to an absolute change in intrathoracic pressure during breathing. Given that intrapleural pressure and air velocity in the trachea are known to be size-independent in terrestrial mammals [40] and that changes in intrathoracic pressure are known to result in changes in f_{H} during breath holds in humans [72], the brief post-respiration tachycardia may be related to changes in local pressure gradients surrounding the heart.

The mixed effects analyses allowed us to determine that both f_{R}, M_{b} and their interaction are included in the most parsimonious model of RSA (table 3 and figure 2*a*,*b*). Thus, RSA is affected by f_{R} but this relationship varies depending on M_{b}. The effect of f_{R} on the degree of RSA was expected given that RSA is driven by breathing; however, the effect of M_{b} on this relationship provides valuable information about how RSA varies, particularly at low f_{R}s. Given the variation in f_{R}s in free-ranging cetaceans [68,69,73,74], especially following a dive, this model suggests that the magnitude of the RSA varies during regular diving behaviour and that following a dive, when f_{R} is elevated, the benefits of a high f_{R} may dominate over the potential cardiorespiratory benefits of a large RSA.

For both mean if_{H} and minimum if_{H} of the RSA, f_{R} and M_{b} were included in the most parsimonious model (table 3). Because mean if_{H} was largely determined by the duration over which f_{H} decreased during the IBI, the effect of these predictors on mean if_{H} was likely secondary to their effect on minimum if_{H}. Like maximum if_{H}, mean if_{H} and minimum if_{H} scaled negatively with M_{b}, such that bigger animals displayed lower maximum if_{H}, mean if_{H} and minimum if_{H} (table 3 and figures 2*c*, 3*b*,*d*). f_{R} was positively related to both mean if_{H} and minimum if_{H}, but minimum if_{H} increased more quickly with increasing f_{R}. The results of this model suggest that even when differences in f_{R} are accounted for, M_{b} describes additional variation in mean if_{H} and minimum if_{H}. The most parsimonious model of maximum if_{H} included M_{b}, but not f_{R} (table 3 and figure 2*b*). This result agrees with our previous work in bottlenose dolphins where the maximum if_{H} did not vary across f_{R}s for a given individual [75]. This could reflect that the maximum if_{H} of the RSA is determined largely by physical constraints of body size, and that any if_{H} lower than the maximum if_{H} is a result of changes to the 'default' neural controls on f_{H}. Interestingly, a previous study noted that an adult Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) and two adult bottlenose dolphins under anaesthesia with nitrous oxide displayed steady f_{H}s averaging 80–120 beats min^{-1}, with larger animals displaying lower f_{H}s [76]. Although the M_{b}s of these animals were not reported, this range is comparable to the measured maximum if_{H}s measured in the bottlenose dolphins in this study. It is important to note that it is also possible that the maximum if_{H} of the RSA may be affected by other respiratory parameters that were not included in our analyses, like V_{T}.

RSA scaled allometrically with f_R with a scaling exponent of −0.56 (table 2). This pattern can be understood by examining figure 1. Given that the maximum if_H of the RSA appears to occur at approximately the same time (5–10 s) regardless of the IBI, this suggests that the degree of RSA, or oscillation in if_H, is largely dependent on the time over which f_H can decrease before the next breath is taken. M_b was positively related to RSA by the mass exponent of 0.35, such that bigger animals showed a higher degree of RSA. Interestingly, this is comparable to the exponent of 0.33 reported for many diving variables [50]. This perhaps suggests that the degree of RSA reflects a relationship between cardiorespiratory function and diving. Mean if_H and minimum if_H were related to f_R by the scaling exponents 0.11 and 0.21, respectively (table 2). These exponents are, to our knowledge, the first reported coefficients relating f_R and if_H in cetaceans. This relationship may be driven by the greater effect of lung inflation over the IBI as f_R increases, therefore resulting in higher if_Hs during more rapid breathing [71]. We suggest that the influence of both f_R and M_b, which is negatively related to f_H, on mean if_H and minimum if_H of the RSA may be explained as follows: f_R determines the degree to which the if_H decays to a stable, low f_H following a respiration, but M_b ultimately determines the value of this low f_H. In this case, the effect of M_b could reflect a physical scaling constraint on the minimum if_H during an IBI.

Kleiber originally proposed an allometric mass exponent of 0.75 for metabolic rate, although there is considerable controversy as to whether this value is 0.67 or 0.75, or whether a universal mass exponent is valid at all [41,77–79]. Because the action of the heart controls the supply of oxygen to the tissues, we would expect the cardiovascular variables to follow this allometry. White and Kearney [41] suggested that the sum of the mass exponents of f_H and stroke volume should equal the mass exponent of metabolic rate. Because stroke volume scales allometrically by 1.03, this implies that f_H should scale with an allometric mass exponent in the range of −0.36 to −0.28, depending on the value assumed for the allometric exponent of metabolic rate [41]. The allometric analyses in this study allow us to compare these expected values with the exponents we obtained. Both the mass exponents for mean i$f_{H,}$ −0.24, and minimum if_H, −0.34, determined in this study make this equality true; however, the mass exponent for maximum if_H, −0.16, does not. While it is important to consider the standard errors associated with the coefficients, this could indicate that, at least in cetaceans, the periods of reduced f_H during an IBI better reflect metabolic rate than the tachycardia of the respiration. In addition, the mass exponent for mean if_H is comparable to the −0.25 proposed by Stahl for scaling of f_H in terrestrial mammals and the mass exponents calculated for pinnipeds, which ranged from −0.20 to −0.24 [42,80]. However, when the predicted f_H for each species is calculated using Stahl's equation based on the average M_b of individuals of that species in this study, we found that our measured f_Hs were 17%, 15%, 17% and 4% higher than predicted for the bottlenose dolphins, false killer whale, beluga and killer whales, respectively and 17% lower than predicted for the short-finned pilot whales. Because all of the data included in this study were recorded under non-fasted conditions, the f_Hs measured could be affected by metabolic changes associated with digestion [75,81]. We should also consider the possibility that species-specific differences likely result in natural variation around the predicted values.

Though exploration of RSA in free-ranging cetaceans is critical to further determine the role of RSA during active, diving behaviours, this study suggests that cardiorespiratory coupling plays a role in determining f_Hs across species of different sizes as it scales both with body size, M_b, and with f_R. We show that RSA scales with M_b similarly to that of other diving-related parameters and suggest the potential for RSA to reflect a relationship between cardiorespiratory function and diving capacity. We also compare allometric exponents with previously published mass exponents in terrestrial mammals and pinnipeds and identify similarities and differences in predicted values of f_H. Because the various components of the RSA are differentially affected by f_R and M_b, we suggest that there may be multiple controls that determine the modulation of f_H that cetaceans exhibit. Given the importance of f_H in determining oxygen consumption during diving, the known variation in f_Rs in cetaceans and the coupling of f_H and f_R through RSA, we recommend that M_b and f_R should be accounted for when attempting to understand f_H measurements in relation to the diving capacities of cetaceans.

Ethics. The study protocols were accepted at each facility and also by the Animal Care and Welfare Committee at the Oceanografic (OCE-17-16, amendments OCE-29-18 and OCE-3-19i), the Bureau of Medicine (BUMED, NRD-1015) and the Institutional Animal Care and Use Committee at Duke University (A045-17-02 and A251-19-11). This study complies with the ARRIVE guidelines.

Data accessibility. The data and code used for this analysis can be found at https://osf.io/7kmcn/.

Authors' contributions. A.M.B. and A.F. conceptualized the study; A.M.B., A.F., J.R.-L. and T.R. collected the data; A.M.B. conducted the data analysis; A.M.B., A.F., J.R.L., T.R. and DPN wrote and edited the manuscript; A.F. and D.P.N. supervised the work. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests.

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