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RESEARCH ARTICLE

Short-finned pilot whales modulate surfacing and breathing patterns more strongly in response to dives than in anticipation

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Abstract

Diving marine mammals must allocate time between respiring at the surface and foraging underwater. Previous studies of optimal diving theory have attempted to predict such patterns, but the amount of time divers must spend at the surface before and after dives of varying durations remains difficult to assess. Here, we examined the surfacing and breathing patterns of short-finned pilot whales (*Globicephala macrorhynchus*) from biologger data to examine their use of anticipatory versus reactive strategies. We used linear mixed-effects models to examine the effect of dive characteristics on surface interval (SI) durations and breathing rate. Pilot whales increased SI duration before dives of increasing duration and after dives of increasing activity. Instantaneous breathing rates (f_Rs) of pilot whales demonstrated little anticipation but rather a strong reactive pattern seen by the modulation of f_R in response to the previous rather than upcoming dive. During typical SIs, f_R was predicted by time since previous dive, duration of the previous dive, time until upcoming dive, and activity of the previous dive. Short-finned pilot whales in our study area exhibit both benthic and pelagic foraging, which may compel anticipation when prey capture is predictable and reaction when prey capture is difficult to predict. The observed surfacing and breathing patterns therefore likely reflect a balance of the needs for blood gas homeostasis, aerobic metabolism, and the variability of foraging opportunities. An improved understanding of how animals make decisions about diving is critical for informing predictions of how they will contend with changing ocean landscapes.

NEW & NOTEWORTHY A new study reveals how short-finned pilot whales balance the conflicting demands of foraging underwater with breathing at the surface. Using data from digital tags, scientists found that pilot whales rely more on surfacing strategies that react to the effort of a dive rather than anticipate. Their use of such strategies may reflect variation in the ability to predict prey capture in benthic and pelagic habitats.

diving physiology; respiration; short-finned pilot whales

INTRODUCTION

The challenges an aquatic lifestyle presents to mammalian physiology are numerous, but perhaps most consequential is the requirement to perform breath-hold dives. Aquatic mammals must dive to forage at depths that are often hundreds of meters away from the air they breathe. As breathing and diving are mutually exclusive activities, a diver's behavior is constrained and requires prioritization of these two behaviors on short time scales (1). The question of how diving mammals make decisions about apportioning their time at the surface and depth has, therefore, been the focus of many theoretical and empirical studies. Models of optimal diving suggest that surfacing and diving patterns should maximize some combination of the proportion of time spent foraging, net energetic gain, and energetic efficiency (1–3). Many empirical studies of diving mammals and birds provide evidence to support this theory under certain circumstances (4–9). However, time allocation models are limited in their ability to make quantitative predictions about diving (6, 7, 10). This is, in part, due to the complexity of several physiological parameters that are not entirely accounted for in most optimal diving models, including variation in O_2 uptake at the surface (6, 10, 11), the importance of CO_2 versus O_2 in influencing diving behavior (7, 10, 12–14), variation in diving metabolic rate caused by swim speed, dive duration, and body condition, (10, 15–19), and the possibility of using both aerobic and anaerobic cellular respiration during a dive (10, 20, 21). To better understand the relationship between diving and surface behavior, more fine-scale physiological

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information is needed including patterns of gas exchange on a surface interval (SI)-by-SI basis (e.g., respiratory rate, breath count, tidal volume, and oxygen extraction) and subsurface behavior and physiology on a dive-by-dive basis (e.g., swim speed, activity level, and heart rate).

For dives shorter than the aerobic dive limit (ADL), time spent at the surface should primarily be a function of rates of gas exchange, rather than the need to process byproducts of anaerobic metabolism (22). Gas exchange during a surfacing interval is influenced by the alveolar minute ventilation, the product of respiratory frequency and tidal volume minus the dead-space volume. These factors can be controlled voluntarily, but they are predominantly driven by central and peripheral chemoreceptors that monitor local changes in blood gases (23–25). In mammals, it is largely believed that CO_2, which rapidly dissociates in the blood to form H^+ and HCO_3^- therefore lowering pH, is the driver of ventilation, rather than O_2 (26). Recent work in gray seals, however, has suggested the opposite, as seals exposed to experimental gas concentrations responded more strongly to O_2 concentrations in modulating their dive behavior than CO_2 (27). Some evidence indicates that marine mammals have a higher capacity to buffer increased CO_2 in the blood (28–30), but CO_2 still may play a role in determining when a diver must surface to breathe (13, 31, 32). Much of the literature concerning surface duration has focused on the recovery of O_2 as a major driver, although CO_2 elimination takes longer than O_2 uptake following a dive (12, 13, 33, 34). In a study of free diving Weddell seals, three breaths were required following a dive for CO_2 levels to be elevated in the exhalate and the rate of CO_2 elimination did not reach a maximum until 2–3 min after surfacing (35). O_2 uptake is also nonlinear during a surface period and is dependent on the degree of O_2 depletion on a dive and the number and timing of breaths at the surface (12, 36). Therefore, allocation of time at the surface is likely greatly influenced by the number, timing, and depth of breaths during that SI and the accumulated CO_2 load and O_2 debt. No technology currently exists to measure CO_2 elimination and O_2 uptake in free-ranging cetaceans, but reasonable proxies can be used to attempt to understand the dynamics of gas exchange during an SI. For example, if the respiratory stimulus of increased P_{CO_2} is the primary cause for an elevated breathing rate and increased ventilation depth, then we may indirectly understand changes in gas exchange by examining changes in the number, frequency, and tidal volume of breaths following a dive. Importantly, however, most of these variables are impossible to measure on free-ranging animals with current biologging sensors limiting our ability to validate these assumptions.

One framework within which these changes can be evaluated is that of anticipatory versus reactive breathing, which has previously been used to understand the behavior of diving birds in relation to the duration of their surfacing intervals (37, 38). Anticipatory breathing is defined by a positive correlation between a dive's duration and/or activity level and the duration of the SI preceding that dive—as though the animal is anticipating the duration of the upcoming dive or the amount of activity that while be required in the upcoming dive. In contrast, reactive breathers are defined by a strong correlation between a dive's duration/activity level and the duration of the SI following that dive. This concept can be extended to measurements of instantaneous change in breathing rate and ventilation depth. Work on free-diving Magellanic penguins showed that both respiratory frequency and tidal volume are elevated following a dive, fall gradually during the SI, but rise again before the next dive, potentially suggesting a linkage to both pre- and postdive O_2 and CO_2 levels, although these were not measured (39). The authors also hypothesized that this type of breathing may act to efficiently renew O_2 and eliminate CO_2. Several studies in marine mammals have looked at changes in breathing rate in relation to diving, providing insight into the physiological nature of SIs. Dives of trained belugas and bottlenose dolphins revealed patterns of predive hyperventilation (40) and increasing postdive breathing rate with increasing dive duration (41–43). A novel method for detecting breathing rate from heart rate data showed a positive correlation between postdive breathing rate during the first minute of the SI and dive duration in northern elephant seals (44). Finally, the breathing rate of long-finned pilot whales was found to increase directly before and after a dive (45). In particular, the increase in breathing rate after a dive was positively correlated with dive duration, as was the duration of the period needed for breathing rate to recover to normal levels. A robust investigation of changes in breathing patterns in the context of dive preparation and recovery should shed light on how divers make decisions about the allocation of time at the surface and depth.

Using a method that incorporates kinematics to detect breathing events from archival acoustic and movement tags, we investigated the relationship between SI duration, breathing rate, and diving behavior in short-finned pilot whales. Previous models of optimal diving have suggested that an anticipatory strategy should be used, whereby oxygen stores are only loaded to support the extent of the upcoming dive, although such predictions fail to explain the reactive breathing patterns of some seabirds with more unpredictable foraging styles (1, 38). Short-finned pilot whales are deep divers that utilize a mix of foraging strategies, feeding both pelagically and benthically (46). Unlike many other marine animals, who tend to feed on fewer, larger prey items during benthic dives compared with pelagic dives (47, 48), pilot whales in the Cape Hatteras area perform twice as many prey capture attempts on benthic compared with pelagic dives (46). Although it is unknown exactly what prey distribution pilot whales may encounter on the benthos, the seafloor provides a consistent landmark for locating prey thus limiting the overall search area. In contrast, pelagic dives lack any physical structure and prey patchiness is likely due to more ephemeral characteristics that might be less predictable when whales are at the surface preparing for a dive. Therefore, we expected that short-finned pilot whales should display a mix of anticipatory and reactive strategies matching their variable dive context.

METHODS

Tag Deployment

We deployed 40 digital acoustic recording tags, or DTAGs (49), on short-finned pilot whales off Cape Hatteras, North Carolina, between 2010 and 2018. DTAG version 2s were used for 38 deployments between 2010 and 2014 and in 2016, and DTAG version 3s were used for two deployments in 2015 and 2018. We deployed these suction cup-attached tags to the dorsal fin or dorsal surface of the animal using a carbon fiber pole from a small (<10 m) rigid hulled inflatable boat. DTAGs contain a suite of sensors including a pressure sensor to measure depth, a 3-axis accelerometer and a 3-axis magnetometer to infer animal orientation, all which sampled at 50 Hz (version 2) or 250 Hz (version 3). Depth and kinematic data streams were all downsampled to 50 Hz for analysis. Audio was recorded by tag-embedded hydrophones with 16-bit resolution at a sampling rate of 96–192 kHz (depending on tag version and settings).

Depth Analysis

We used custom MATLAB tools to transform the raw DTAG data into animal-frame for further analysis (50). Data were calibrated using previously collected bench calibrations to set the tag-specific axis conventions (51). Depth data were corrected for variation in temperature at the pressure sensor. We identified dives as any submergence greater than or equal to 20 m, a threshold which has been used in previous studies of this species (52). This depth is ~4–6 body lengths and excludes shallow submersions between respirations as dives. We defined SIs as the period between two dives.

Movement Analysis

We transformed the accelerometer and magnetometer data into an animal-fixed reference frame and used the transformed data to calculate pitch, roll, and heading throughout the dive record. Acceleration was used to calculate the magnitude of the three-dimensional jerk vector. To do so, we filtered acceleration using a zero-phase, 5th-order Butterworth band-pass filter with cutoff frequencies of 2 Hz and 15 Hz. The norm-jerk was determined from filtered acceleration. The Shannon entropy (SE) of differentiated acceleration in the surge direction and differentiated jerk were calculated and then smoothed with a moving mean filter using a window length of 5 s. Pitch was similarly filtered using a zero-phase, 5th-order Butterworth band-pass filter with cutoff frequencies of 2 Hz and 15 Hz to remove noise and then differentiated. The SE of differentiated pitch was calculated and then smoothed with a moving mean filter using a window length of 5 s. Smoothed SE of differentiated acceleration in the surge direction, differentiated three-dimensional jerk, and differentiated pitch were used for later breath detections.

Breath Detections

We detected breathing events using a combination of two methods using the published MATLAB tool *respdetect* (53). To reduce high-frequency noise in the depth data and facilitate more precise identification of surfacings, we first smoothed depth with a moving average filter using a window length of 50 samples. For the first breath detection method, "single-breath surface events" were identified as periods when the animal was within 0.5 m of the surface for a duration ≥1 s and ≤10 s. If the depth minima of a surfacing was more than 0.15 m deeper than the average depth minima of the two shallowest in a neighborhood of four surfacings around this detection, this event was not considered a surfacing. For single-breath surfacing events, a breathing event was recorded at the depth minimum of the surface event. The second breath detection method, "logging surface events" were identified as periods when the animal was within 0.5 m of the surface for a duration >10 s. For these events, breathing events were identified as the co-occurrence of two of the following three criteria: local maxima in the *1*) smoothed SE of three-dimensional jerk, *2*) smoothed SE of acceleration in the surge direction, and *3*) smoothed SE of pitch (Fig. 1). After local maxima were identified for each signal, a 5-s window centered around each local maximum was established. A breathing event was then recorded at the center of each data segment where the windows (at least two of the three) overlapped. Single-breath surface events were assumed to be accurate based on previous use of a 1 surfacing:1 breath assumption in stereotypic (i.e., all single-breath surface events) breathing baleen whales (54). To ensure the accuracy of logging breath detections, 10% of the total duration of logging intervals were randomly sampled. These periods were acoustically audited for audible breaths which were marked by their start and end. Given the use of a 5 s window to identify breaths from kinematic data, an audible logging breath was considered "detected" if a kinematic detection was made within 5 s of the start or end of the audible breath. For accuracy, a detection rate of all audible breaths during randomly sampled logging periods is reported.

Statistical Analysis

All statistical analyses were conducted using R version 4.1.0 (R Core Team, 2020). We categorized SIs as typical or extended surfacings by identifying the local minimum of the bimodal distribution calculated from the kernel density estimate with a bandwidth calculated using Silverman's "rule of thumb" (density, stats package). Analyses of SIs and breathing rates (fRs) were conducted separately for typical versus and extended SIs, as we made the a priori assumption that physiological drivers would be different between these two types of surfacings. It is not possible to know the start of an SI directly following tag deployment nor the end of an SI at the end of a tag record, so these periods, and their associated breaths, were not included in analyses. We used Wilcoxon rank-sum tests (Wilcox.test, stats package) to examine differences in characteristics of typical and extended SIs.

We used linear mixed-effects models (*lme, nlme* package) with individual as a random intercept using restricted likelihood estimation to evaluate the effect of pre- and post-SI dive duration and dive ODBA on SI duration. We also constructed models to determine the effect of pre- and post-SI dive duration, dive ODBA, the interaction of dive duration and dive ODBA, time since last dive, and time until next dive on f_R during the SI for both typical and extended SIs. Due to high multicollinearity of time since last dive and time until next dive for extended SIs and our interest in patterns related to diving, we chose to examine separate models for the 10 min immediately following a dive (postdive f_Rs) and the 10 min immediately preceding a dive (predive f_Rs) during extended SIs and use time since last dive in the former and time until next dive in the latter. Otherwise, we retained all predictors in the model of each outcome variable given our interest in testing an established theoretical framework rather than constructing the most parsimonious model. SI number nested in individual was included as a random

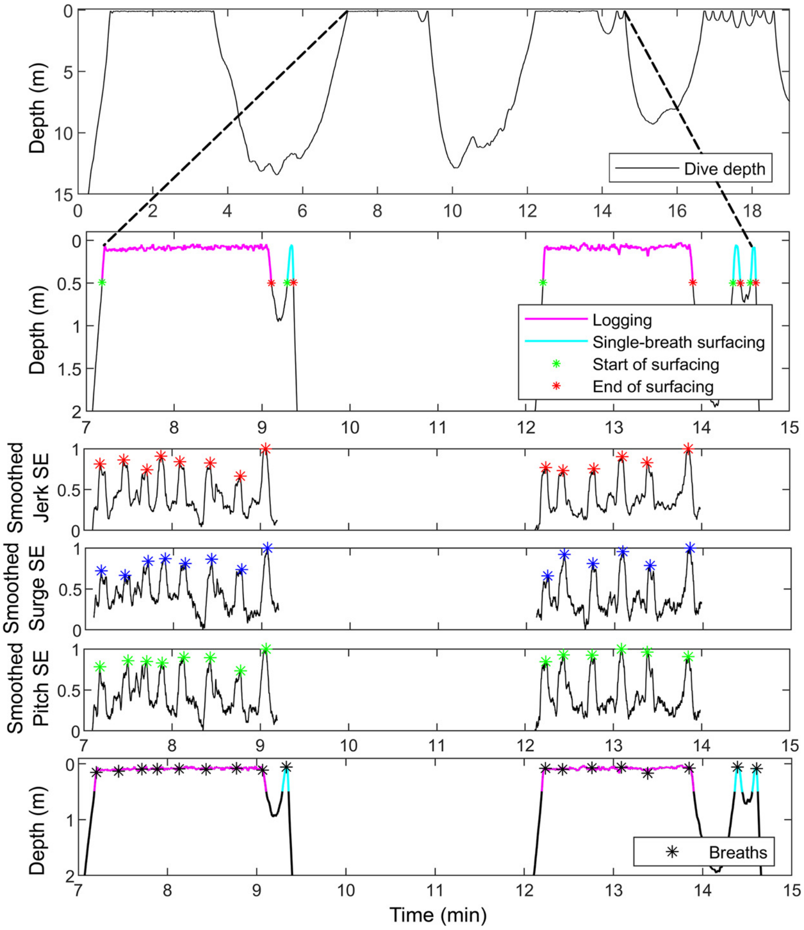

Figure 1. Detecting breathing events from kinematic data. Surfacings are classified as either single-breath surfacings or logging periods. During logging periods, breaths are identified as the cooccurrence of local maxima in 3 movement parameters: smoothed Shannon entropy of jerk, smooth Shannon entropy of surge, and smooth Shannon entropy of pitch.

intercept in all models of f_R. We included a 1st-order autoregressive serial correlation structure of SI number within a tag deployment (i.e., individual) and breath number within SI number within a tag deployment to account for temporal autocorrelation of dives for models of SI duration and f_R during typical SIs. Residual plots were visually examined to ensure all fixed effects met assumptions of linearity, normality, and homoscedasticity. Q-Q plots showed that the distribution of SI durations were right-skewed, so we applied a $\log_{10}$-transformation to meet the assumption of normality. To increase the interpretability and comparability of model coefficients, we also centered and standardized all predictor variables in all models.

To provide real-world context to the model effects, we used the mixed-effects model results to make predictions about the influence of varying dive parameters (i.e., duration, ODBA, and time since last dive/time until next dive) on both SI duration and f_R. We only made predictions using parameters that were significant in the full model of each respective outcome variable. For each prediction, we held every other predictor at its mean value while varying only the predictor of interest.

Due to the challenge of defining a clear cutoff between the postdive period for one dive and the predive period for the next dive within an SI, we took a two-faceted approach to analyzing f_Rs. In addition to continuous linear models, which allowed dive duration and activity level to explain the variation in f_R in addition to time relative to dive end or dive start, we also employed fixed binned comparisons of f_R by time relative to dive end or dive start across dive durations. We chose to analyze absolute time rather than relative time (e.g., time relative to the SI duration) to avoid standardizing across variable SI durations, which assumes that recovery and preparation scale proportionally with SI duration and is, likely, not biologically accurate. The fixed binned approach, which only captures variation explained by time, provides a clearer framework for highlighting differences in f_R at moments of interest across dives of all durations and activity levels.

Thus, to examine fine-scale changes in pre- and postdive f_R during typical SIs for dives of different durations, we binned dive durations into five 5-min intervals and f_Rs into 2-min intervals for the 10 min before and after dives within each dive duration bin. Notably, many short-finned pilot whale SIs were shorter than 10 min in duration, thus breathing rate data was often included in the postdive analysis for one dive and the predive analysis for the subsequent dive. However, this cutoff was chosen to avoid diluting the signal of interest during long SIs where recovery or preparation processes are unlikely to occur throughout the entire duration of the SI. We used a Kruskal–Wallis rank sum test (kruskal.test, stats package) followed by a post hoc Dunn test (dunnTest, *FSA* package) to make comparisons of f_R during each pre- and postdive interval across dive duration bins. We used a significance level of $\alpha = 0.05$ for all statistical tests.

RESULTS

Dives

Tagged pilot whales performed 469 dives with a mean dive duration of 9.9 min (range = 1.0–22.5 min), a mean dive depth of 316.9 m (range = 20.1–1077.0 m), and a mean dive ODBA of 0.03 g (range = 0.003–0.15 g) (Supplemental Fig. S1).

Breaths

A total of 15,647 breaths were detected across all 40 tag deployments during analyzed SIs. Of this, 11,135 occurred during typical SIs (71%) and 4,512 occurred during extended SIs (29%). Acoustic validation of 10% of randomly selected logging breaths resulted in audits of 1.6 h of logging periods, which included 217 audible breaths and resulted in a 95% true positive rate for respdetect breath detections (Supplemental Fig. S2) (53). As single-breath surface events, which are assumed to have 100% accuracy (54), contribute to the overall breath detections, the accuracy of all detections is expected to be well above 95% across all breaths. The overall mean instantaneous f_R for all f_Rs from all animals was 4.7 ± 2.2 breaths·min^{-1} and the range of individual mean f_Rs was 2.7–5.8 breaths·min^{-1} (Supplemental Fig. S3). The total number of breaths taken during typical SIs was lower than that during extended SIs (Wilcoxon rank sum: W = 134, $P < 0.0001$, Supplemental Fig. S4*A*), whereas the number of breaths taken per minute of the SI during typical SIs was higher than during extended SIs (Wilcoxon rank sum: W = 11,177, $P < 0.0001$, Supplemental Fig. S4*B*).

SI Duration

SIs displayed a right-skewed, bimodal distribution (Fig. 2*A*). The local minimum of the bimodal distribution occurred at 31.4 min, which was used to distinguish typical from extended SIs. A total of 93% of SIs were considered typical (<31.4 min) and 7% of SIs were considered extended (≥31.4 min) (Table 1). Whether the SI preceding a dive was typical or extended did not affect the duration of the upcoming dive (Wilcoxon rank sum test: W = 6,515, $P = 0.27$, Fig. 2*B*), but extended SIs followed dives shorter than those followed by typical postdive SIs (Wilcoxon rank sum test: W = 6,921, $P = 0.04$, Fig. 2*C*). We examined whether extended SIs tended to occur more closely in time to the longest dives, calculated as the 95th percentile of dive durations, or those ≥18.4 min. The time since the last dive ≥18.4 min was lower for extended SIs than typical SIs (Wilcoxon rank sum test: W = 398, $P = 0.02$) as was the time until the next dive ≥18.4 min (Wilcoxon rank sum test: W = 398, $P = 0.03$).

Results of the linear mixed-effects model revealed a positive effect of the activity level of the dive before an SI ($\beta = 0.07 \pm 0.03$, $P = 0.01$) and the duration of the dive after an SI ($\beta = 0.09 \pm 0.02$, $P < 0.001$) on typical SI duration (Supplemental Table S1). In other words, the duration of a typical SI is modulated by the activity level of the preceding dive and the duration of the upcoming dive, but the effect of the post-SI dive's duration level is 28% stronger than that of the pre-SI dive's activity level (Table 2).

During extended SIs, neither dive duration nor dive ODBA during the dive before or after a SI affected SI duration

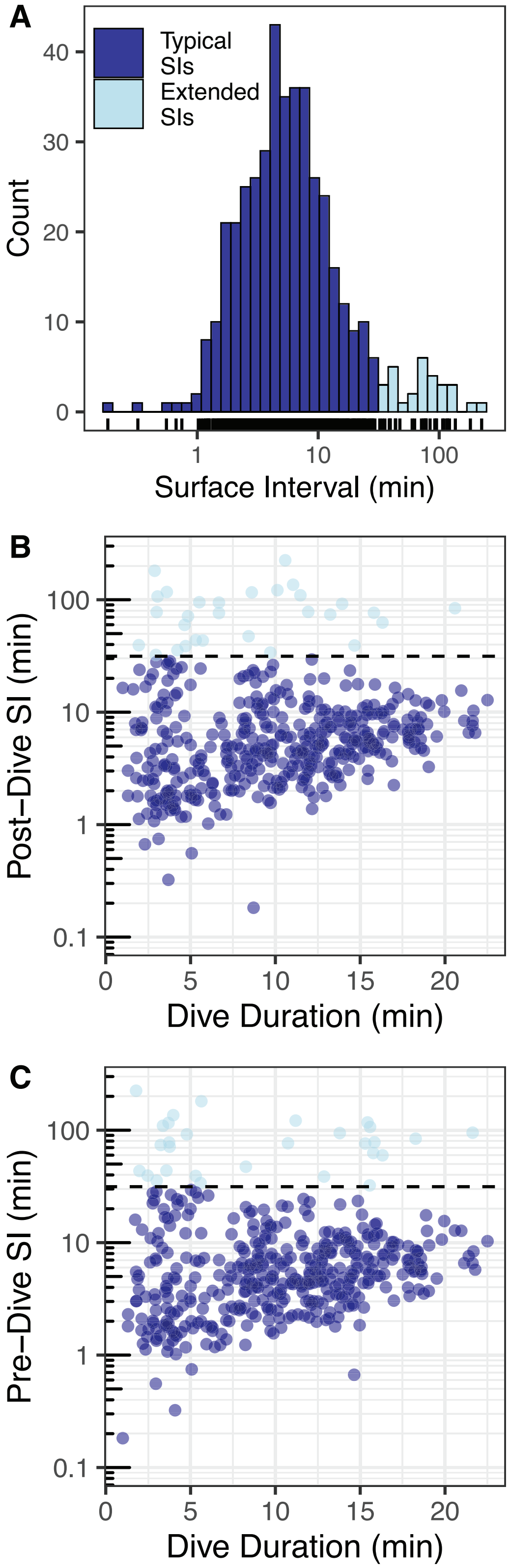

Figure 2. The distribution of surface interval (SI) durations (*A*) (*n* = 429) of short-finned pilot whales and their relation to dive duration (*B* and *C*). The dark blue bars and points represent typical SI durations, which are <31.4 min, and the light blue bars and points represent extended SI durations, which are ≥31.4 min (*A*). The horizontal dashed line in *B* and *C* represents the 31.4 min cutoff used to distinguish between typical and extended SIs.

Table 1. *Characteristics of 429 SIs by short-finned pilot whales*

SI Type	*n*	Mean Duration, Min	Min – Max Duration, Min	Time Since Last Dive ≥ 18.4 Min, Min	Time Until Next Dive ≥ 18.4 Min, Min	Mean Number of Breaths	Mean Number of = Breaths per Minute of SI, Breaths·Min^{-1}
Typical, <31.4 min	400	6.9 ± 5.7	0.2–29.4	196.6 ± 166.1	105.5 ± 89.7	27.8 ± 15.9	4.8 ± 1.5
Extended, ≥31.4 min	29	83.1 ± 44.9	32.3–224	55.4 ± 62.2	49.9 ± 37.0	155.6 ± 93.1	1.9 ± 0.5

SIs, surface intervals.

(Supplemental Table S2). A nonzero model intercept, however, revealed that for an extended SI preceded and followed by dives of average duration and ODBA, extended SI duration was predicted to be 63.6 min.

f_Rs

In the linear mixed-effects model of f_R during typical SIs, time since last dive, time until next dive, their interaction, the duration and activity level of the dive before the SI, and the interaction of dive duration and ODBA of the dive before the SI all affected f_R (Supplemental Table S1). There was no effect of the duration or activity level, or their interaction, of the upcoming dive on f_R. Generally, f_R decreased as time since last dive increased and time until next dive increased (i.e., the next dive was further away in time). Longer and more active dives before the SI resulted in higher f_Rs (Table 3). The effect of time since last dive was the strongest ($\beta = -0.92 \pm 0.03$, $P < 0.001$), followed by the effect of the preceding dive duration ($\beta = 0.36 \pm 0.046$, $P < 0.001$), time until next dive ($\beta = -0.34 \pm 0.031$, $P < 0.001$), and then preceding dive ODBA ($\beta = 0.22 \pm 0.072$, $P < 0.01$).

During extended SIs, postdive f_R was only affected by time since last dive ($\beta = -0.93 \pm 0.078$, $P < 0.001$) and predive f_R was only affected by time until next dive ($\beta = -0.56 \pm 0.076$, $P < 0.001$) (Supplemental Table S2). The effect of time on recovery was nearly twice as strong as that of anticipation with f_R falling from 5.5 to 2.3 breaths·min^{-1} in the 10 min after a dive of average duration and ODBA and increasing from 2.4 to 4.3 breaths·min^{-1} in the 10 min before a dive of average duration and ODBA.

Table 2. *Predicted duration of a typical surface interval for a specified change in the predictor conditions*

Full Model	
SI Duration ~ Previous Dive Dur. * Previous Dive ODBA + Upcoming Dive Dur. * Upcoming Dive ODBA	
Predictor Condition	**Predicted SI Duration, Min**
All mean values	5.5
Previous dive was 25th percentile ODBA	4.9
Previous dive was 75th percentile ODBA	6.1
Previous dive doubles in ODBA	8.5% increase
Upcoming dive is 5 min	4.6
Upcoming dive is 25 min	7.7
Upcoming dive doubles in duration	25.2% increase

The full model of SI duration for typical surface intervals (Sis) is provided with significant predictors in bold. Predictions are only provided based on altering predictors that were significant in the full model of SI duration. Predictors were standardized (centered and scaled) and $\log_{10}$-transformed before model fitting, but the table displays the model outputs without explicitly showing these transformations to focus on the predictor effects. The *operator indicates inclusion of both main effects and their interaction (e.g., A * B is equivalent to A + B + A:B). Mean values of each predictor were Previous Dive Dur. = 10.1 min, Previous Dive ODBA = 0.03 g, Upcoming Dive Dur. = 10.2 min, and Upcoming Dive ODBA = 0.04 g.

For typical SIs, binned postdive f_R was elevated in the first 2 min following a dive but fell to a consistently lower value for the rest of the 10 min after dive (Fig. 3*A*). f_Rs following longer dives were higher out to 4 min following a dive, but after 4 min there were minimal differences in binned postdive f_Rs by dive duration. There were few differences in binned predive f_R, though f_Rs 2–8 min before intermediate dives (10–20 min) tended to be higher than those 10 min before the shortest dives (Fig. 4*A*). There were few differences in binned postdive f_R during extended SIs in by time bin or dive duration bin, but elevated rates did tend to occur immediately following longer dives (Fig. 3*B*). There were no differences in binned predive f_Rs for any time bins or dive duration bins during extended SIs (Fig. 4*B*).

DISCUSSION

The aim of our study was to examine the surfacing and breathing patterns of short-finned pilot whales in anticipation of and reaction to dives of varying durations and activity levels. We hypothesized that individuals would use a mix of anticipatory and reactive strategies that match their mixed benthic and pelagic foraging strategy (46). In birds, anticipatory strategies have been associated with species that forage benthically, consume their prey underwater, and require high capture effort (37, 38, 55), as these foraging characteristics allow for predictable diving patterns. In contrast, reactive strategies are more often observed in divers that demonstrate pelagic foraging, consuming prey at the surface, and with low capture effort, all of which contribute to a dive being less predictable (37, 38, 55). Our result of both an anticipatory and reactive SI duration response and a limited anticipatory but strong reactive f_R response highlights short-finned pilot whales' mixed use of these strategies, supporting both predictable and unpredictable dives.

SI Duration

Short-finned pilot whales exhibit two distinct types of surfacing behavior that can be categorized as typical SIs during continual diving and extended SIs that represent 30-min to multihour periods at the surface (<20 m). Pilot whales demonstrated modulation of typical SI durations related to the activity level of the dive before the SI and the duration of the dive after the SI, with the anticipatory response to dive duration being 28% higher than the reactive response to dive

Table 3. *Predicted instantaneous breathing rates (f_Rs) and changes in f_R during typical SIs for a specified change in the predictor conditions*

Full Model				
f_R ~ Time Since Last Dive * Time Until Next Dive + Previous Dive Dur. * Previous Dive ODBA + Upcoming Dive Dur. * Upcoming Dive ODBA				
	f_R (Breaths·Min^{-1})			
Predictor Condition	**0 Min after Dive**	**10 Min after Dive**	**10 Min before Dive**	**0 Min before Dive**
All mean values	5.9	3.9	4.7	5.4
Previous dive was 5 min	5.4	3.5	3.6	5.5
Previous dive was 25 min	6.8	4.9	5.0	6.9
Previous dive dur. increases by 1 min	0.07 breaths·min^{-1} increase			
Previous dive was 25th percentile ODBA	5.8	3.8	4.0	5.8
Previous dive was 75th percentile ODBA	6.0	4.0	4.2	6.0
Previous dive ODBA increases by 0.1 g	1.2 breaths·min^{-1} increase			

The full model of SI duration for typical SIs is provided with significant predictors in bold. Predictions are only provided based on altering predictors that were significant in the full model of f_R. Predictors were standardized (centered and scaled) before model fitting, but the table displays the model outputs without explicitly showing these transformations to focus on the predictor effects. The * operator indicates inclusion of both main effects and their interaction (e.g., A * B is equivalent to A + B + A:B). Mean values of each predictor were Time Since Last Dive = 4.5 min, Time Until Next Dive = 5.1 min, Previous Dive Dur. = 11.6 min Previous Dive ODBA = 0.04 g, Upcoming Dive Dur. = 11.6 min, Upcoming Dive ODBA = 0.04 g.

ODBA. Lea et al. (1, 38) suggest that Kramer's model of optimal diving necessitates an anticipatory breathing strategy as time spent at the surface should be limited to what is required for the upcoming dive and not necessarily to fully recover from the previous dive. O_2 uptake at the surface diminishes as stores recover, and therefore the rate of O_2 gain can be maximized and surface time reduced by only replenishing O_2 to the level needed for the upcoming dive (1). Optimal divers are expected not to dive at a maximal physiological limit continuously, but instead, dive until blood O_2 falls to a certain level (12, 13, 56). As short-finned pilot whales anticipate diving by increasing the duration of typical SIs before longer dives, our results suggest some agreement with optimal diving theory.

However, short-finned pilot whales also demonstrate a reactive surfacing strategy as the duration of typical SIs is increased following more active dives. The influence of both post-SI dive duration and pre-SI dive ODBA suggests that although it may be feasible to anticipate dive duration, the amount of activity a dive requires may be more difficult to anticipate, thereby requiring a reactive strategy. The lack of a stronger effect of dive ODBA or duration of the previous dive on typical SI duration could also suggest that typical SIs are not used for full physiological recovery, as hypothesized by optimal diving theory, and instead supports the use of extended SIs for longer recovery processes like lactate processing. If lactate processing requires extended SIs, this could help to explain why pilot whales limit their activity underwater through their use of short sprints and extended gliding (52). In this case, we would predict logging pilot whales should maintain high heart rates (f_Hs) during some portion of extended SIs to facilitate perfusion to muscles and lactate metabolism.

Extended SIs appear to reflect a more basal physiological state for pilot whales. Although these extended surface periods do not appear to serve a role in immediate anticipation or recovery from a dive, extended SIs may instead support anticipation and recovery from a series of long dives which supports the possibility that marine mammals can delay the requirement to process lactate. Traditionally, it has been assumed that dives beyond the ADL (22) require extra time at the surface to replenish O_2 stores and to process accumulated lactate (57). However, diving northern and southern elephant seals as well as Australian sea lions routinely decouple long dives from long SIs, indicating individuals may be able to tolerate lactate and/or significantly reduce their metabolic rates during diving (58–60). Furthermore, lactate levels in diving seals can decrease during short, shallow dives (22, 61), and this has been proposed as a functional role for the repeated "shallow" dives that can last for multiple hours in beaked whales and occur in between deeper dives (62). If short, shallow dives support a similar function in short-finned pilot whales, they may have decoupled the need to immediately process lactate from remaining at the surface for an extended period. Alternatively, like elephant seals and Australian sea lions, pilot whales may have other mechanisms by which blood lactate remains lower than otherwise expected and the relationship between the longest dive durations and longest SI durations becomes decoupled. Yet the association between the occurrence of extended SIs and the longest dives in this study could mean that, although the clearing of lactate is delayed in the short term, over a series of dives lactate accumulation requires extended periods of recovery at the surface. Ultimately, a larger sample size and more complex autoregressive correlation structure are required to explore surfacing and diving patterns on longer time scales.

Alternatively, extended SIs may serve a role in social coordination of the group before travel. Short- and long-finned pilot whales are believed to use surface periods to rest, socialize, and travel (63–65) and display synchronicity of breathing, implying the importance of social cohesion when at the surface (66). Groups of pilot whales travel together (67), so these long SIs may be required to coordinate with an individual's group to initiate transit to a new foraging area.

f_Rs

f_Rs during typical SIs indicate that short-finned pilot whales demonstrate a much stronger reactive breathing response to diving than an anticipatory response. Though f_Rs were predicted by the time until the next dive, suggesting some amount of preparation, time since the previous dive

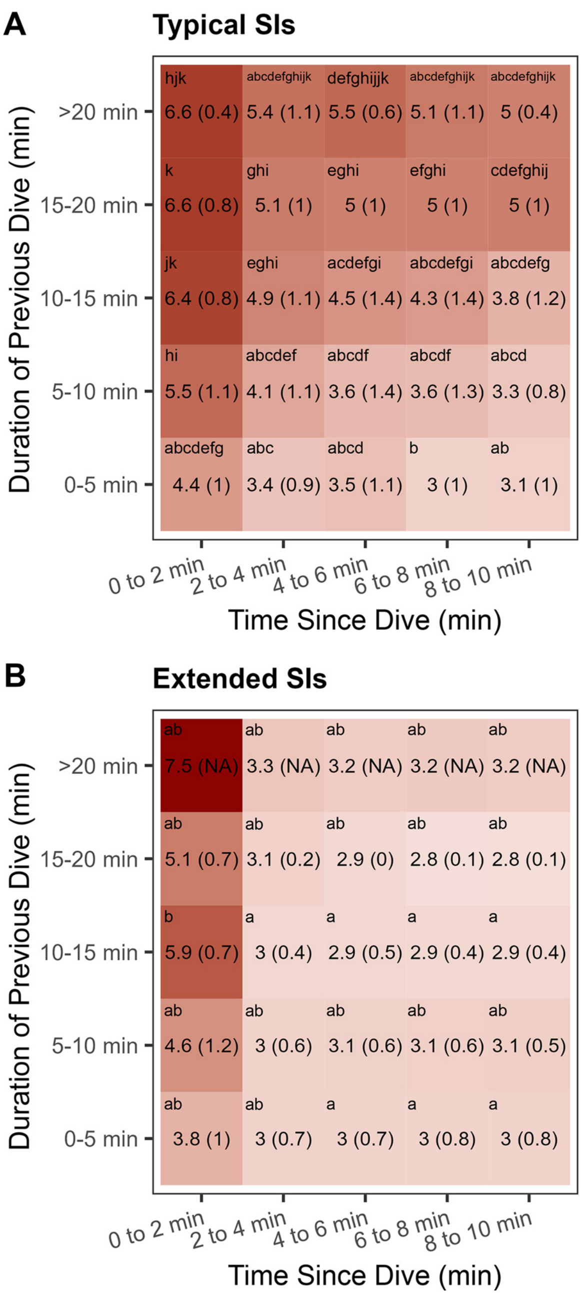

Figure 3. Mean instantaneous breathing rates (f_Rs) following dives of varying durations in 2-min intervals presented as means (SD) during typical ($n = 11{,}135$ breaths) and extended ($n = 4{,}512$ breaths) surface intervals (SIs). Grid cells are colored by the mean value of the cell with the highest mean value represented by dark red and the lowest mean value represented as white. Letters indicate the results of a Dunn test for pairwise comparisons where cells with the same letter are not detectably different.

had a three times stronger effect. Similarly, the duration and activity level of the previous dive influenced f_R, whereas that of the upcoming dive did not. Thus, pilot whales' anticipatory response to diving via modulation of breathing patterns during typical SIs appears limited and they instead rely on respiring to recover from dives based on the energetic demands of each individual dive.

Fine-scale changes f_R at the start of typical SIs support a strong reactive breathing response. Postdive f_Rs decreased over time following a dive, with substantial differences in immediate postdive f_R for dives of varying durations but few differences after 2 min at the surface. This pattern indicates an immediate physiological response upon surfacing from a dive and a rapid recovery of f_R with 2 min of continuous respiration. The lack of substantial differences in postdive f_R for dives ≥10 min (Fig. 3*A* and Supplemental Fig. S5*A*) suggests that these f_Rs may represent an optimal respiratory timing for maximizing O_2 uptake when O_2 stores have been depleted. These f_Rs could represent an optimized f_R-f_H

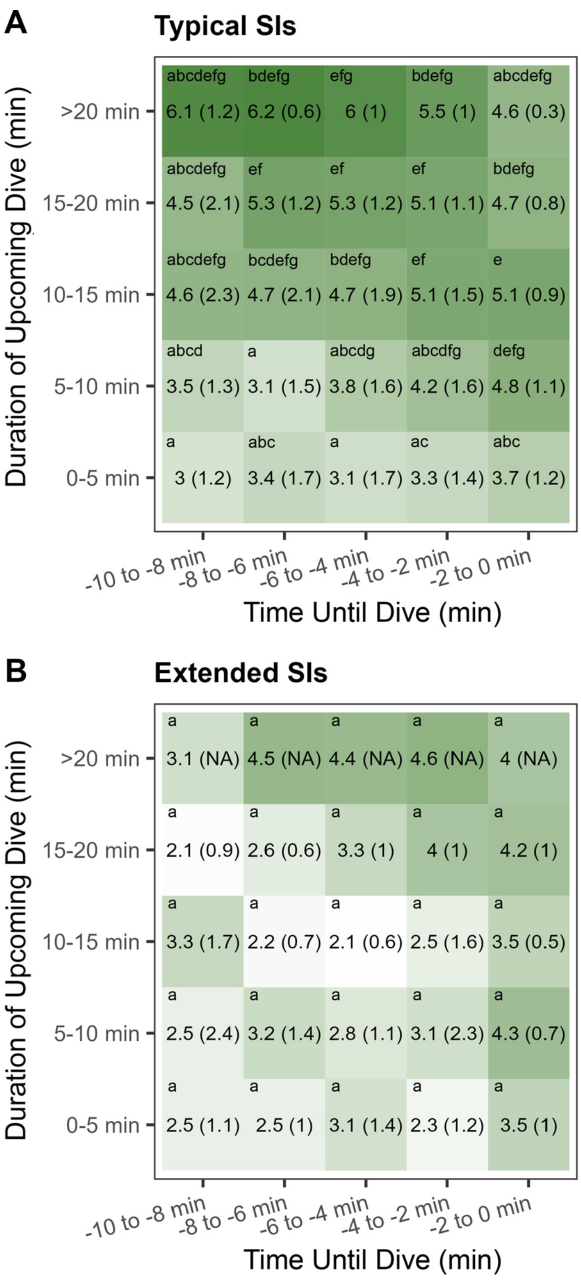

Figure 4. Mean instantaneous breathing rates (f_Rs) leading up dives of varying durations in 2-min intervals presented as means (SD) during typical ($n = 11{,}135$ breaths) and extended ($n = 4{,}512$ breaths) surface intervals (SIs). Grid cells are colored by the mean value of the cell with the highest mean value represented by dark green and the lowest mean value represented as white. Letters indicate the results of a Dunn test for pairwise comparisons where cells with the same letter are not detectably different.

relationship at which cardiac output is maximized and more rapid breathing would not improve ventilation but would incur the cost of respiration as has been suggested in juvenile elephant seals (44, 68). Yet, there were some differences in f_Rs 10 min out from dives of different durations. In our view, it is unlikely that O_2 dynamics are the primary driver of f_R patterns >10 min after a dive has concluded. A study of respiratory timing in killer whales suggests that O_2 stores in diving killer whales are likely renewed after only six respirations (36). In bottlenose dolphins, recovery of end-tidal O_2 to prebreath hold level requires 10 breaths and occurs in 1.2 min (41). The respiratory system is also responsible for eliminating CO_2 and N_2 at the surface, and gas exchange during recovery reflects a trade-off between replenishing O_2 and limiting the accumulation of CO_2 and N_2 (69). Thus, the driver of an f_R that is elevated from basal levels >10 min since the previous dive could instead be related to CO_2 offload, which has been shown to require longer recovery times in harbor porpoises, gray seals, and Steller sea lions (12, 13, 34, 56). The modulation of both SI duration and f_R during typical SIs in a reactive response to the previous dive's characteristics could reflect such differing time requirements for recovery toward blood gas homeostasis. If short-finned pilot whales require a similar number of breaths to recover O_2 as dolphins and killer whales, then the additional breaths afforded to pilot whales during longer SIs following more active dives may be more important for CO_2 recovery and/or lactate processing.

In the final 10 min of typical SIs, binned values of f_R appeared to decrease particularly in the final 2 min before diving. Still, predive f_Rs before the longest dives were elevated across most predive intervals compared with the shortest dives. This could reflect a sustained reactive breathing response to the previous dive, where f_R continues to recover toward a basal level as the upcoming dive approached but remains elevated enough that a distinct anticipatory effort is not required to increase f_R. Notably, f_R during typical and extended SIs immediately before diving was similar, around 4.3–4.5 breaths·min^{-1}. This suggests that though pilot whales may use a limited anticipatory breathing strategy before short-duration dives, predive hyperventilation is not utilized when f_R remains elevated from a reactive response to the previous dive (Figs. 4*A* and Supplemental S5*B*). The effect of f_R on f_H (70–72), and ultimately perfusion, suggests that a high f_R could allow pilot whales to maintain a higher degree of perfusion in advance of diving, which should maximize the predive loading and unloading of O_2 and CO_2, respectively, via increased ventilation-perfusion matching.

In contrast to typical SIs, during extended SIs pilot whales did not exhibit a reactive nor anticipatory breathing strategy that was modulated by dive duration or dive ODBA. Instead, they demonstrated a dive duration and ODBA-independent decrease in postdive f_R (from 5.5 to 2.3 breaths·min^{-1} for a dive of average duration and ODBA) and increase in predive f_R (from 2.4 to 4.3 breaths·min^{-1} for a dive of average duration and ODBA) during the first and last 10 min of an extended SI, respectively. Thus, although pilot whales exhibit changes in f_R that suggest recovery and anticipation of diving in general, that these were not modulated by the energetic demands the neighboring dives suggests no true reactive or anticipatory response, per se. For breaths immediately following dives this could indicate that there is a cost of rapid breathing at the surface and, in the absence of the need to rapidly recover from a dive, it is preferable to utilize an optimal respiratory timing that is independent of O_2 store depletion (Figs. 3*B* and Supplemental S5*C*). This result emphasizes the importance of recovery in preparing for the next dive in that, if the next dive will not occur within a typical time interval, there is less demand to recover quickly. That short-finned pilot whales demonstrate a true dive characteristic-dependent reactive f_R response during typical SIs, but not extended SIs, suggests possible expectation or planning of upcoming extended SIs. If long SIs are used to coordinate with an individual's group to initiate travel, perhaps these could be vocally coordinated in advance.

Because overall f_R was typically lower during extended SIs, the "ramp up" in f_R at the end of extended SIs (Figs. 4*B* and Supplemental S5*D*) could serve two potential functions. First, predive hyperventilation could serve to reduce alveolar and arterial CO_2 and delay the urge to breathe. This is a common goal of predive hyperventilation "purges" by free divers. Theoretical work suggests hyperventilation could add as much as 10 min to maximum apneas in humans (73) and has also been observed in penguins (39). Predive hyperventilation has been observed to result in a lower end-apneic arterial CO_2 value after long dives compared with end-apneic arterial CO_2 after shorter surface apneas in Weddell seals (74). Recently, hyperventilation has also been revealed as one of two mechanisms for controlling the ratio of brain O_2 to CO_2 by modulating tissue CO_2 and thus supporting normal ATP synthesis (75). Alternatively, predive hyperventilation could serve to increase perfusion before a dive, perhaps to facilitate maximal loading of O_2 in the blood and muscle if the extended SI was used for travel, for example, and therefore resulted in some minor accumulated O_2 debt. Increased ventilation and perfusion could also function to "arterialize" venous blood to create a venous O_2 reserve (76). The lack of association between f_R during extended SIs and dive duration and ODBA of the upcoming dive suggests that the dive immediately following an extended SI may be unpredictable and possibly exploratory in nature.

Further Considerations

It should be noted that if SI duration before a long, active dive is predicted to be long, it is possible the overall number of breaths in the predive SI will be high though timing of these breaths may not necessarily be more rapid. Magellanic penguins appear to modulate their number of predive breaths with the number of prey captured on the previous dive implying anticipation of foraging effort (77) and agreeing with predictions of optimal diving. Therefore, although short-finned pilot whales may not strongly modulate f_R in an anticipatory manner, they still display anticipatory breathing secondary to the positive effect of dive duration of predive SI duration.

Another important consideration is that this study does not capture any information about changes in tidal volume. Tidal volume remains a physiological variable that is critically important for determining energetics (78), but is difficult to estimate in free-ranging whales. Only recently have bioenergetics approaches incorporated estimates of tidal volume and its expected variation. This approach has been used in energetic models for species where measurements of tidal volume in individuals under human care have not been made (79, 80). Changes in tidal volume have a larger effect on ventilation at the alveoli (i.e., alveolar ventilation) than changes in f_R so it is plausible that pilot whales also modulate their tidal volume during SIs. Measurements of nares area and breath duration of humpback whales and Antarctic minke whales demonstrate that breaths are highly variable within an SI, highlighting the potential for breath-to-breath variability in oxygen uptake that is not captured by f_R alone (81). In the future, the novel application of existing imaging methods from tags or unoccupied aerial systems (UAS) may be able to provide useful information on variation in tidal volume on a per breath basis.

Notably, mean f_R for extended SIs was 1.9 breaths·min^{-1} (Table 1), which is elevated above the resting f_R predicted for a 3,000 kg individual inactive in 22°C water of 1.1 breaths·min^{-1} (82). If instead the pilot whales are considered minimally active or active, their predicted mean f_R increases to 1.3 and 1.6 breaths·min^{-1}, respectively. In this study, we had no way to determine whether individual pilot whales were postprandial (i.e., fasted) and nonreproductive; thus, it is likely that the individuals in our study may have additional, nonbasal metabolic demands during extended SIs. In addition, it is important to consider that when including dive time in estimates of f_R across dive-surface cycles (i.e., breaths per day), overall f_R will be expected to decrease. However, the close agreement of our empirical data with phylogenetic allometric analyses suggests that these scaling relationships are useful for reflecting real physiology of animals in situ.

Finally, that pilot whales rely more on a reactive response in their modulation of f_R supports its use as an indicator of real-time oxygen need and thus metabolic demand. Current models of field metabolic rate (FMR) that rely on breathing rates can only be used over long enough time scales that an individual can be assumed to have reached physiological steady state due to assumptions about tidal volume and oxygen extraction fraction (79, 80). If future studies can characterize fine-scale changes in tidal volume and oxygen extraction fraction such that bioenergetic models no longer have to rely on long-term averages, reactive f_Rs ensure that short-term metabolic estimates will truly reflect real-time oxygen demand and not demands of future dives.

Conclusions

Short-finned pilot whales modulate the duration of SIs and f_R before and after dives according to the duration and activity level of the dive, supporting a limited anticipatory and strong reactive response to diving. The combination of strategies used by these pilot whales indicates that they may take advantage of multiple diving strategies, presumably during foraging, where some dives can be anticipated (e.g., benthic diving to a predictable depth where the seafloor may help to limit the search area) and others are less predictable in their duration and activity level (e.g., pelagic foraging where the oceanographic conditions that drive prey distribution may be more ephemeral), requiring a reactive response. Short-finned pilot whales in Cape Hatteras demonstrate both benthic and pelagic feeding, so a combined surfacing and breathing strategy could support the use of different types of foraging dives. In addition to making decisions related to the variability in foraging opportunities, the surfacing and breathing patterns observed in this study seem to reflect a balance of the needs for blood gas homeostasis and aerobic metabolism while diving. Understanding how aquatic mammals make decisions about diving can inform our understanding of how their physiology may be affected by the need to change their behavior during a dive if exposed to an unexpected disturbance such as a predation attempt or anthropogenic disturbance. These findings reveal important information about the connection between vital rates, like f_R, and diving behavior in free-ranging cetaceans and ultimately help to understand how marine mammals efficiently divide their time between the surface and depth.

ETHICAL APPROVALS

All research was conducted under NOAA Permits 14241 (issued to Peter Tyack) and 14809 (issued to D.P.N.) and the research protocols were approved by the Institutional Animal Care and Use Committee of Duke University (A194-09-07, A163-12-06, and A158-2018).

DATA AVAILABILITY

Data will be made available upon reasonable request.

SUPPLEMENTAL MATERIAL

Supplemental Figs. S1–S5 and Tables S1 and S2: https://doi.org/10.25740/fq946kg2345.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

A.M.B., A.J.R., and D.P.N. conceived and designed research; A.J.R. and D.P.N. performed experiments; A.M.B. and J.M.S. analyzed data; A.M.B. and A.F. interpreted results of experiments; A.M.B. prepared figures; A.M.B. drafted manuscript; A.M.B., J.M.S., A.F., A.J.R., and D.P.N. edited and revised manuscript; A.M.B., J.M.S., A.F., A.J.R., and D.P.N. approved final version of manuscript.

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