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1 Behavioral data suggest adaptive buoyancy control during 2 shallow dives in humpback whales

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14 **Abstract**

15 Marine mammals have been proposed to have a passively changing buoyancy that influences their
16 swimming efforts depending on the depth due to pulmonary alveolar compression/expansion as ambient
17 pressure changes. Mysticetes have been described to have the same passive mechanism without
18 considering their unique respiratory system, which may provide the ability to change their buoyancy
19 actively to enhance vertical movements. Here, we present behavioral evidence supporting that adult
20 mysticetes actively change buoyancy during shallow dives by analyzing diving data from multi-sensor
21 tags placed on humpback whale (HW) mother-calf pairs. We show that adult female HW displays low
22 effort to swim downward and upward regardless of the depth and can stay perfectly static (stationary) at
23 different depths. In contrast, calves display depth-dependent swimming efforts and only remain stationary

24 with external help or at a specific depth. Our study adds to the body of evidence regarding the unique
25 features of mysticetes' dives.

26 **Keywords**

27 Active buoyancy control, baleen whale, cetacean, mother-calf, respiratory system, swimming behavior

28 **Introduction**

29 Aquatic animals have evolved various adaptations for vertical movement in the water column (Alexander,
30 1982; Pelster, 2009). Sharks and squids adjust the angle of their fins for depth control and must swim
31 continuously to maintain depth or ascend due to their bodies being denser than water. Most teleost fish
32 regulate their body density by altering the gas volume in their swim bladder, allowing for near-effortless
33 vertical movement and neutral buoyancy at various depths. Marine mammals are thought to use the
34 passive depth/hydrostatic pressure-related compression and expansion of air in their respiratory system
35 (primarily involving pulmonary alveoli), which modify their density/buoyancy, to aid descent/ascent
36 (Miller et al., 2004; Skrovan et al., 1999; Williams et al., 2000). Near the surface, where hydrostatic
37 pressure is low, a high buoyant force counters weight (positive buoyancy) due to the internal air's large
38 volume (thus low density)—increased air compression then balances buoyant force with weight, achieving
39 neutral buoyancy at a specific depth D_{neutral} . Deeper than D_{neutral} , further compression reduces buoyant
40 force below weight, causing sinking (negative buoyancy). Marine mammals overcome (and then take
41 advantage of) these changes in buoyancy by actively swimming above D_{neutral} and gliding past it during
42 descent. Below D_{neutral} , they actively swim to ascend and glide after reaching D_{neutral} . The relationship
43 between hydrostatic pressure, buoyancy, and swimming kinematics has been extensively demonstrated in
44 pinnipeds and odontocetes (Miller et al., 2004; Skrovan et al., 1999; Williams et al., 2000).

45

46 Mysticetes (baleen whales) are often compared to odontocetes (toothed whales) regarding buoyancy and are
47 expected to exhibit similar hydrostatic pressure-related diving patterns (Goldbogen et al., 2006; Nowacek
48 et al., 2001; Williams et al., 2000). However, previous studies overlooked their unique respiratory anatomy,
49 which might allow for active buoyancy control (Adam et al., 2013; Gandilhon et al., 2015; Reidenberg,
50 2018; Reidenberg, 2022). Mysticetes have a laryngeal sac, an air-filled organ connected to the lungs, which
51 is absent in other marine mammal groups. It acts as an additional air reservoir of significant volume
52 (comparable to a fully inflated lung) (Reidenberg, 2018; Reidenberg, 2022; Reidenberg and Laitman, 2007)
53 and was initially suggested to improve apnea duration and to be involved in sound production (Adam et al.,
54 2013; Elemans et al., 2024; Gandilhon et al., 2015; Reidenberg, 2018; Reidenberg, 2022). Gandilhon et al.
55 (2015) theorized that mysticetes can actively adjust buoyancy by controlling the laryngeal sac volume (and,
56 to a lesser extent, lung volume), intentionally compressing it for buoyancy reduction or expanding it to
57 increase buoyancy (Figure 1, Video S1). They may also change their center of gravity and thus adjust pitch
58 when shunting air cranially or caudally between the various respiratory chambers (Reidenberg, 2018).
59 Current evidence suggests adaptations in their respiratory system allow for air pressure/volume control
60 despite external pressure changes due to depth. Their respiratory tract features structural reinforcements that
61 isolate internal air from external ambient pressure and regulate air volume (Figure 1). Additionally, several
62 Closure mechanisms within the respiratory tract enable independent control of internal pressures in various
63 portions (e.g., laryngeal sac + nasal cavities, trachea + lungs, Figure 1, Video S1) (Damien et al., 2019;
64 Elemans et al., 2024; Reidenberg and Laitman, 2007). Gandilhon et al. (2015) proposed that lung
65 pressure/volume is regulated independently through the diaphragm and intercostal muscle contractions,
66 while laryngeal sac volume adjusts via circumferential muscle contractions (Figure 1).

67 Testing the theoretical role of mysticetes' unique respiratory system in buoyancy control remains difficult
68 due to the challenges of directly observing its function in live animals. Furthermore, regardless of the
69 mechanism involved (air sac adjustments, controlled air release, or other physiological adaptations),
70 empirical evidence supporting the notion that mysticetes can actively control their buoyancy is sparse.

71 Observers often note their ability to stabilize at various depths to sing or rest and move vertically without
72 visible effort from their fins, but formal documentation remains rare. Gandilhon et al. (2015) provided
73 convincing but limited observation ($N = 1$).

74 Here, we tested the hypothesis that mysticetes can actively adjust their buoyancy to position at different
75 depths and optimize vertical movements (active buoyancy control hypothesis or ABC hypothesis), using
76 humpback whale (HW) mother-calf pairs in their breeding ground. By analyzing diving data from multi-
77 sensor tags, we analyzed changes in swimming efforts at various depths during upward (ascent) and
78 downward (descent) movements. We also identified the depth at which whales maintained static, neutrally
79 buoyant positions. According to the ABC hypothesis, we predicted that HWs do not vary their swimming
80 efforts with depth/hydrostatic pressure during dives and that their neutral buoyancy depth is flexible, varying
81 even within a single dive. Thus, their buoyancy operates independently of ambient pressure, optimizing
82 vertical swimming effort at any depth.

83 **Materials and methods**

84 **Dataset**

85 We used data from animal-borne multi-sensor tags deployed on 47 HW mother-calf pairs off Sainte Marie
86 Island, Madagascar, during winter 2013-2019 and 2021-2022. Tags were placed on the (31 mother-calf
87 pairs), the mother (10 pairs), or simultaneously on both (6 pairs). Most whales carried the Acousonde 3B
88 tag, while 12 calves had CATS cam tags. The Acousonde tags include a pressure sensor, a temperature
89 sensor, a hydrophone, a 3D accelerometer, and a 3D magnetometer. The CATS cam tags include the same
90 sensors plus a video camera. Tagging procedures and specifications have been published previously
91 (Huetz et al., 2022; Ratsimbazafindranahaka et al., 2022; Ratsimbazafindranahaka et al., 2023; Saloma et
92 al., 2022). Each deployment (individual) was associated with an age class (Ratsimbazafindranahaka et al.,
93 2023): C1 ($N = 2$) – neonate, C2 ($N = 14$) – very young non-neonate, C3 ($N = 21$) – older calves < 3

94 months old, or Adult ($N = 16$) – mothers. C1s were grouped with C2s as category C1-C2 due to the
95 limited sample size.

96 For each deployment, we extracted depth (in meters), depth rate (rate of change in depth or vertical speed,
97 in meters/second), vertical acceleration (in meters/second²), body posture (body pitch and roll, in degree)
98 and fluke stroke signals (in degrees) (Ratsimbazafindranahaka et al., 2022; Simon et al., 2012) at a
99 sampling rate of 10 Hz. Stroking was identified when fluke stroke signals exceeded a threshold set for
100 each individual (mean = $1.5 \pm 0.8^\circ$, range = $0.5\text{--}5^\circ$) by visual inspection, as there are evident differences in
101 stroking and non-stroking periods (López et al., 2015). We calculated the Fluke Stroke Rate (FSR, in Hz)
102 from these strokes based on half-strokes (López et al., 2015; Ratsimbazafindranahaka et al., 2022).
103 Finally, we computed two proxies for forward speed: (1) relative speed from flow noise recorded by the
104 tag's hydrophone (66-94 Hz frequency band) (Cade et al., 2017) and (2) absolute speed as the pitch-
105 corrected depth rate, $\Delta\text{depth}/\sin(\text{pitch})$ (Cade et al., 2021; Miller et al., 2004). The flow noise was rescaled
106 to represent relative speed from 0 to 1, corresponding to the minimum and the maximum detected speed,
107 respectively. The absolute speed was only calculated when $|\text{pitch}|$ exceeded 30° (Narazaki et al., 2018).

108 Data analysis

109 *Comparison of the swimming effort during downward and upward swimming*

110 We subdivided all continuous periods with known absolute speed into 5-s segments that were then used as
111 the units of analysis, categorizing each as either downward (pitch $< -30^\circ$) or upward (pitch $> 30^\circ$)
112 swimming and discarding segments between -30° and 30° . Then, we calculated the ratio of FSR to
113 absolute speed as a proxy for the swimming effort (Noren et al., 2006). We also calculated the average
114 depth. A total of 2072 downward (428 from C1-C2 calves, 1388 from C3 calves, and 256 from adults) and
115 1549 upward (308 from C1-C2 calves, 1107 from C3 calves and 134 from adults) segments from 993
116 dives (about 2 ± 1 downward segments and 2 ± 2 upward segments per dive on average, range: 1–8 and 1–16
117 segments per dive, respectively) were extracted and analyzed. The depth corresponding to these analyzed
118 segments was comparable among the three age classes, with the downward segments closer to the surface

119 (mean = 8 ± 6.1 m, range = 1–45.9 m) compared to the upward segments (mean = 13.5 ± 7.7 m, range = 1.8–
120 45.3 m, Figure S1, Table S1). The speed was also comparable across the three age classes, with the speed
121 during downward segments being slightly lower (mean = 1.1 ± 0.4 m s⁻¹, range = 0.5–3.1 m s⁻¹) compared
122 to upward segments (mean = 1.3 ± 0.5 m s⁻¹, range = 0.5–3.3 m s⁻¹, Figure S1, Table S1). However, there
123 was a significant difference in the swimming effort across the three age classes (Figure S1, Table S1). The
124 effort was on average higher for segments from C1-C2 (mean = 0.29 ± 0.12 beat m⁻¹, range = 0.07–0.87 beat
125 m⁻¹) and C3 (mean = 0.29 ± 0.12 , range = 0.06–1.09 beat m⁻¹) than for segments from Adults
126 (mean = 0.2 ± 0.1 beat m⁻¹, range = 0.02–0.69 beat m⁻¹). Moreover, the effort corresponding to downward
127 swimming was significantly higher than upward swimming both for segments from C1-C2 (downward:
128 mean = 0.31 ± 0.12 beat m⁻¹, range = 0.1–0.87 beat m⁻¹; upward: mean = 0.26 ± 0.12 beat m⁻¹, range = 0.07–
129 0.79 beat m⁻¹) and C3 (downward: mean = 0.3 ± 0.12 beat m⁻¹, range = 0.09–0.85 beat m⁻¹; upward:
130 mean = 0.27 ± 0.12 beat m⁻¹, range = 0.06–1.09 beat m⁻¹) but similar for segments from Adults (downward:
131 mean = 0.2 ± 0.1 beat m⁻¹, range = 0.02–0.69 beat m⁻¹; upward: mean = 0.2 ± 0.1 beat m⁻¹, range = 0.03–
132 0.49 beat m⁻¹).

133 To model the relationships between swimming effort (log-transformed response), depth, age class, and
134 swimming vertical direction (fixed effects), we used a linear mixed-effects model (LMM) in R (R core
135 team, <https://www.r-project.org/>) with the *lme4* package (Bates et al., 2015), followed by a Type II
136 ANOVA test. We included the interactions between fixed effects and added individuals as random effects.
137 Model assumptions, including homoscedasticity and normality, were verified graphically. The LMM was
138 followed by Tukey's post-hoc tests (R package *emmeans*) (Lenth et al., 2018) to compare the swimming
139 effort across directions at 5, 15, 30, and 45 m depth for each age class. Segments with absolute speeds of
140 0.5 m s⁻¹ or less were excluded as these were considered stationary or quasi-stationary behavior.

141 *Description of the stationary behavior*

142 We identified periods when the individual was stationary for each deployment and calculated the
143 corresponding average depth. We also calculated the signed difference in average depth between successive

144 stationary periods within the same dive if multiple periods occurred. A stationary period was conservatively
145 defined as a > 10 s continuous interval with relative speed < 0.2 (less than 20% of maximum recorded
146 forward speed for the animal), $|\text{depth rate}| < 0.05 \text{ m s}^{-1}$, and $|\text{vertical acceleration}| < 0.05 \text{ m s}^{-2}$. For each
147 calf tagged with a CATS cam tag (thus with video data), we screened the corresponding video for each
148 stationary period using BORIS v.7.9.22 (Friard and Gamba, 2016) to assess the calf's position relative to its
149 mother at that time.

150 **Results and discussion**

151 Mothers exert similar effort to swim downward and upward while calves do not, and adult
152 females are able to stay stationary at varying depths

153 As predicted, our data show that mothers do not vary their swimming efforts with hydrostatic pressure
154 during dives (Figure 2A), unlike odontocetes and pinnipeds (Miller et al., 2004; Skrovan et al., 1999;
155 Williams et al., 2000). Additionally, their neutral buoyancy depth is highly variable and can shift within
156 the same dive cycle (Figures 2B and 2C). Mothers exhibited consistent effort when swimming downward
157 and upward across all depths (Figure 2A, Table 1) and showed stationary periods > 10 s at various depths
158 (overall range = 0–36.9 m, intra-individual depth variation > 5 m in 10 of 16 mothers, Figures 2C). Rather
159 than experiencing passive buoyancy changes related to hydrostatic pressure, adult HWs can minimize or
160 eliminate opposing buoyancy effects during vertical movements and achieve neutral buoyancy at any
161 depth. Buoyancy changes were possible even within a single dive, as indicated by the intra-dive stationary
162 depth change data (182 observations from 10 mothers). Typically, intra-dive stationary depth changes
163 were small (-0.3 and 0.1 m, first and third quartiles, respectively) but could range from -4 (going up) to 4
164 m (going down) (Figure 2B). Furthermore, as illustrated in Figure 2B, top panel, there were instances
165 where, after successively going down and staying stationary three times within the same dive, the whale
166 still demonstrated almost no effort to go up during the initial phase of ascent, suggesting an initial upward
167 movement involving buoyancy change instead of pure fluke effort.

168 Unlike mothers, calves' swimming patterns resembled those of odontocetes (Miller et al., 2004; Skrovan et
169 al., 1999; Williams et al., 2000), exhibiting positive buoyancy near the surface (less effort swimming
170 upward than downward) and negative buoyancy at depth (more effort swimming upward than downward),
171 with specific neutral buoyancy depth (i.e., where the switch occurs, around 38 m for C1-C2s and 18 m for
172 C3s, Figure 2A). Additionally, while calves remained stationary at various depths like their mothers
173 (Figure 2C), they only did so independently within a narrow range aligned with their predicted specific
174 neutral buoyancy depth, as shown by video data (C3s observed stationary and not touching their mother at
175 18 ± 0.9 m, range = 16.1–19.4 m, Figures 2C, 2E). Near the surface, they pressed against their mothers
176 from below (Figure 2C, 2D), seemingly to prevent involuntary surfacing due to positive buoyancy. At
177 depth, they rested on support (Figure 2C, 2F).

178 **Active Buoyancy Control (ABC): The unique respiratory system of baleen whales as an**
179 **explanation**

180 Our data support the ABC hypothesis for HWs. The potential underlying mechanism may lie in
181 mysticetes' unique respiratory system, particularly the occurrence of an additional controllable air
182 reservoir (Adam et al., 2013; Damien et al., 2019; Elemans et al., 2024; Gandilhon et al., 2015;
183 Reidenberg, 2018; Reidenberg, 2022; Reidenberg and Laitman, 2007). By modulating the air
184 pressure/volume in their respiratory system through their laryngeal sac muscle (laryngeal sac volume) and
185 their diaphragm and intercostal muscles (lung volume), mysticetes could precisely regulate their body
186 density and buoyancy at various depths. This ability would allow them to maintain consistent swimming
187 effort regardless of whether they are ascending, descending, near the surface, or at depth and to remain
188 stationary at any chosen depth or transition between depths without significant external effort. Calves (C1-
189 C2 and C3, which are still relatively young) may still be developing these skills because they require
190 learning, practice, and mature organs; hence, their swimming kinematics depend on depth, and they need
191 assistance to maintain stationary positions.

192 An alternative mechanism for the ABC is that whales use air exhalation to adjust buoyancy. However, this
193 does not clarify how the whales in our data achieve three successive stationary periods at decreasing
194 depths or initiate ascent immediately with minimal effort (Figure 2B). It is also insufficient to explain their
195 consistent effort levels during both descent and ascent at any depth, especially since whales typically do
196 not produce bubbles during vertical movements but rather in other specific contexts (Croll et al., 2018;
197 Hain et al., 1982; Tyack and Whitehead, 1982). Furthermore, Gandilhon et al. (2015) documented a
198 humpback whale adjusting its buoyancy without exhaling or using fluke or fin movements. Similarly,
199 findings in pygmy blue whales (Davenport et al., 2022) show a whale repeatedly rising and dropping
200 between 17 and 23 m within a dive, with some depth changes occurring without apparent fluke movement.
201 These observations support that whale buoyancy control likely involves mechanisms beyond simple air
202 exhalation.

203 All mysticetes likely exhibit ABC due to their shared respiratory system (Damien et al., 2019; Elemans et
204 al., 2024; Reidenberg, 2022; Reidenberg and Laitman, 2007), but past studies overlooked it. For example,
205 among the dive profiles analyzed by Williams et al. (2000), only the blue whale showed significant depth
206 overlap between descent and ascent terminal glides (Figure 1 in Williams et al., 2000). This could be
207 attributed to initial momentum from active swimming or suggest a varying D_{neutral} if mysticetes actively
208 manage their buoyancy.

209 Based on current knowledge of the cardio-respiratory physiology of terrestrial mammals, pinnipeds, and
210 odontocetes, several questions remain however regarding buoyancy control via lungs and laryngeal sacs,
211 including physiological challenges from excessive trans-thoracic pressure (the necessity of chest collapse,
212 Brown and Butler, 2000) and selective gas exchange requiring alveoli collapse (Fahlman, 2024).

213 Mysticetes may have developed yet unknown adaptations to address these issues. Alternatively,
214 mysticetes may rely primarily on the laryngeal sac volume to control buoyancy and allow the chest (and
215 pulmonary alveoli) to compress under pressure. In any case, data from this study are limited to dives
216 <60 m, so conclusions cannot be extended to greater depths. Buoyancy control in mysticetes may still face

217 structural or anatomical limits under the high pressure of deep dives, forcing them just to let their
218 laryngeal sacs and alveoli compress or collapse, leading to a negative buoyancy and extended descent
219 glides at great depth, as observed in deep-diving right whales (Nowacek et al., 2001). Future research
220 should thus examine deep dives (down to 616 m for HWs, Derville et al., 2020). Nonetheless, even if
221 limited to shallow depths, buoyancy control can impact energetic costs for non-deep diving mysticetes.
222 For instance, a study on the energetic costs of breaches in mysticetes and odontocetes, without considering
223 potential vertical movement management differences, found exceptionally high values (Segre et al., 2020).
224 Given that most mysticetes rely on their energetic reserves during the breeding season, yet they frequently
225 breach, such energy-expensive activity seems counterintuitive, particularly for lactating females. The
226 buoyancy control via lungs and laryngeal sacs could help explain this, allowing minimal effort for surface
227 acceleration during breaches through buoyancy adjustments.

228 It is important to note that despite the general trends we observed, significant intra-age class variability in
229 swimming effort was observed in our model. These variations could result from unaccounted factors like
230 pitch (Nowacek et al., 2001), effects of preceding segments, individual motivations (e.g., urgency,
231 behavioral differences between young and adults), inhaled air quantity, and body lipid proportions (Biuw
232 et al., 2003). Our model also did not account for repeated individual dive-level measurements due to
233 limited observations per swimming direction per dive. Furthermore, depth changes between successive
234 stationary periods within the same dive were rare (and 50% of 182 observations from 10 mothers being
235 between 0.3 and 0.1 m only), likely because of our conservative criteria. Further studies are encouraged,
236 for instance, regarding estimating buoyancy, drag effects, slow pectoral fin movements, and the potential
237 coexistence of air exhalation and variations in inhaled air quantity with the suggested system as a
238 buoyancy control mechanism, as well as exploring alternative explanations. Further anatomical studies
239 should inform these investigations.

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247 and complies with the European Union Directive on the Protection of Animals Used for Scientific
248 Purposes (EU Directive 2010/63/EU).

249 **Competing interests**

250 The authors declare no competing interests.

251 **Author contributions**

252 M. N. R., O. A., C. H., I. C. and A. S. conceived the ideas and designed methodology; M. N. R., O. A., C.
253 H., I. C. and A. S. collected the data; M. N. R. and O. A. led the writing of the manuscript. All authors
254 interpreted the data, contributed critically to the drafts, and gave final approval for publication.

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260 **Data availability**

261 The dataset generated and analyzed during the current study are available in the Supplemental Data S1.

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357 **Figure legends**

358 **Figure 1.** Schematic representation of the respiratory tract of mysticetes (adapted from Gandilhon et al.,
359 2015). Reinforcements isolating the internal air from ambient pressure are in bold, with black indicating
360 semi-rigid structures and red indicating structures under voluntary control (skeletal muscles). Closure
361 mechanisms isolating portions of the respiratory tract when closed are in blue. Mysticetes are theorized to
362 control buoyancy by managing air pressure within their respiratory system, affecting overall density using
363 closure mechanisms and skeletal muscles around the laryngeal sac and lungs. Closing the blowholes
364 isolates internal air from ambient pressure, leaving it mainly subject to the whale's internal pressure (P_i)
365 control. Muscle contractions adjust the volumes of the respiratory chambers (lungs + trachea and laryngeal
366 sac + nasal cavities if the separating closure mechanism is closed), changing P_i . Compressing both
367 chambers increases density, reducing buoyancy, while expanding them decreases density, increasing
368 buoyancy. Independently adjusting the two chambers allows fine-tuned volume/ P_i control (compensating
369 for the volume change in one chamber with the other, using only the laryngeal sac for buoyancy control,
370 or shifting the center of gravity to adjust the pitch).

371 **Figure 2.** (A) Relationship between swimming effort, depth, and direction for calves (C1-C2s and C3s)
372 and adult females (Type II ANOVA, $\chi^2 = 18.88$, $df = 2$, $P < 0.001$). Each point represents a 5-second

373 swimming segment (partial residuals), with red dots for upward swimming (pitch > 30°) and blue dots for
374 downward swimming (pitch < -30°). The regression lines from the linear mixed-effects model (LMM) are
375 solid red for upward and dashed blue for downward swimming. Yellow stars indicate the transition depth
376 around which the calves likely switch from positively to negatively buoyant. (B) Data showing an adult
377 female (dep27) stationary (gray bands) >10 s at different depths within the same dive, with both upward
378 and downward movements possible. The dive profiles are colored by relative swimming speed. Blue
379 silhouettes (~12 m long scaled by depth axis) show the whales' posture based on pitch and roll data during
380 the stationary periods (gray bands). The lower limit of the depth axis represents the maximum depth
381 recorded for the individual. The Overall Dynamic Body Acceleration (ODBA, yellow), as in (Wilson et
382 al., 2006), is also shown, with the overall median for the whole track of the individual indicated by the
383 horizontal line. It indicates minimal effort, even during transitions between periods defined as stationary.
384 (C) Depths of stationary periods for seven C1-C2s (red), 13 C3s (green), and 16 adult females (blue).
385 Most individuals stayed stationary at varying depths. Cross symbols indicate data without video (from
386 Acousonde tags or misdirected CATS cam tags). Circles indicate calves below their mothers, pressed
387 against them (mainly C1-C2, with one instance in a C3, dep09), as indicated by available video data.
388 Diamonds indicate calves near but not touching their mothers. (D) A C1-C2 below its mother at 7.1 m
389 depth. (E) A C3 stationary at 17.3 m depth next to its mother without touching her. (F) A C3 stationary at
390 23 m depth, resting on the seafloor (see Video S2). (D-F) Red and blue arrows indicate each individual's
391 longitudinal axis, pointing towards the snout.

392 **Tables**

393 **Table 1.** Comparison of the swimming effort between downward (Down) and upward (Up) swimming at
394 5, 15, 25, 35, and 45 m using Tukey's post-hoc multiple comparisons tests following a linear mixed-effects
395 model (LMM) for three age classes C1-C2, C3 (calves), and adult females. Bold *P*-values indicate
396 statistically significant differences.

Depth (m)	C1-C2		C3		Adult	
	Down/Up	<i>P</i>	Down/Up	<i>P</i>	Down/Up	<i>P</i>
5	1.438	< 0.001	1.387	< 0.001	1.031	0.995
15	1.277	< 0.001	1.087	< 0.001	1.009	1
25	1.134	0.649	0.853	< 0.001	0.988	1
35	1.007	1	0.668	< 0.001	0.967	> 0.999
45	0.894	0.989	0.524	< 0.001	0.947	> 0.999



