

High suckling rates and acoustic crypsis of humpback whale neonates maximise potential for mother-calf energy transfer

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HIGH SUCKLING RATES AND ACOUSTIC CRYPSIS OF HUMPBACK

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WHALE NEONATES MAXIMISE POTENTIAL FOR MOTHER-CALF

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ENERGY TRANSFER

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22 **SUMMARY**

- 23 1. The migration of humpback whales to and from their breeding grounds results in a
24 short, critical time period during which neonatal calves must acquire sufficient energy
25 via suckling from their fasting mothers to survive the long return journey.
- 26 2. Understanding neonate suckling behaviour is critical for understanding the energetics
27 and evolution of humpback whale migratory behaviour and for informing conservation
28 efforts, but despite its importance, very little is known about the details, rate and
29 behavioural context of this critical energy-transfer.
- 30 3. To address this pertinent data gap on calf suckling behaviour we deployed multi-sensor
31 Dtags on eight humpback whale calves and two mothers allowing us to analyse detailed
32 suckling and acoustic behaviour for a total of 68.8 hours.
- 33 4. Suckling dives were performed $20.7 \pm 7\%$ of the total tagging time with the mothers
34 either resting at the surface or at depth with the calves hanging motionless with roll and
35 pitch angles close to zero.
- 36 5. Vocalisations between mother and calf, which included very weak tonal and grunting
37 sounds, were produced more frequently during active dives than suckling dives,
38 suggesting that mechanical stimuli rather than acoustic cues are used to initiate nursing
- 39 6. Use of mechanical cues for initiating suckling and low level vocalisations with an active
40 space of less than 100 meters indicate a strong selection pressure for acoustic crypsis.
- 41 7. Such inconspicuous behaviour likely reduces the risk of exposure to eavesdropping
42 predators and male humpback whale escorts that may disrupt the high proportion of
43 time spent nursing and resting, and hence ultimately compromise calf fitness.

44 8. The small active space of the weak calls between mother and calf is very sensitive to
45 increases in ambient noise from human encroachment thereby increasing the risk of
46 mother-calf separation.

47

48 **Key-words** Humpback whale, nursing, suckling, neonate, migration, bio-energetics

49

50 **INTRODUCTION**

51

52 Cetaceans are fully adapted to an aquatic environment, and yet they must still breathe air and
53 suckle their young as terrestrial mammals. The lack of physical maternal support to calves for
54 transport and nursing means that neonate cetaceans must have sufficient motor skills to
55 suckle, swim and breath-hold immediately after birth (McBride & Kritzler 1951;
56 Wahrenbrock *et al.* 1974; Peddemors 1990; Peddemors, Fothergill & Cockcroft 1992). To
57 facilitate the critical transfer of energy during nursing, cetaceans have evolved milk with a
58 higher fat content compared to that of terrestrial mammals (Chittleborough 1958; Slijper
59 1966; Harrison 1969), active nursing where milk is ejected into the mouth of the calf
60 (McBride & Kritzler 1951; Slijper 1966; Drinnan & Sadlier 1981; Ridgway *et al.* 1995), and
61 rapidly improving breath-holding capabilities, thereby enabling neonates to suckle for longer
62 durations within hours of birth (Asper, Young & Walsh 1988; Peddemors 1990; Cartwright &
63 Sullivan 2009a).

64 Several species of large baleen whales undertake long annual migrations
65 between high latitude feeding grounds and low latitude breeding grounds. It is likely they
66 embark on this migration to reduce predation pressure and seek sheltered, warm and calm
67 waters for the neonates. While travelling long distances might not pose large energetic costs

68 for mothers (Corkeron & Connor 1999), the cessation of foraging while lactating does impose
69 a large energetic challenge for them, resulting in a significant decline in body condition
70 (Chittleborough 1958; Lockyer 2007; Christiansen *et al.* 2016). This creates a short critical
71 time window on the breeding grounds (Dawbin 1966; Herman & Antinaja 1977; Clapham &
72 Mayo 1987; Clapham 1996, 2000) to transfer sufficient energy to the calf for it to grow and
73 survive the long migration back to the foraging grounds. Indeed, the growth rate of humpback
74 whale calves is remarkably fast; studies have found a growth rate of 0.5-1m/month in length
75 (Glockner & Venus 1983; Christiansen *et al.* 2016) suggesting a need for substantial time
76 investment in suckling.

77 An increase in size gives the calf not only an energetic advantage during the
78 subsequent migration, but it also increases its probability of surviving predation attempts.
79 Rapid weight gain is optimised by having frequent access to the mother for nursing and by
80 minimising energy expended in travelling and diving. Humpback whale (*Megaptera*
81 *novaeangliae*) mothers modify their dive durations on foraging grounds corresponding to the
82 dive capability of the calf, presumably to allow the calf to stay in close contact (Szabo &
83 Duffus 2008; Tyson *et al.* 2012). By maintaining close proximity to its mother, the calf gains
84 access to maternal provisioning and protection, while reducing the risk of separation. Close
85 proximity also allows for hydrodynamic advantages by slipstreaming, thereby conserving
86 energy during swimming (Noren & Biedenbach 2008; Tyson *et al.* 2012). The use of acoustic
87 cues between mother and calf could help maintain this close contact and facilitate the
88 coordination of behavioural transitions such as initiating suckling.

89 Acoustic signals from mother-calf pairs have been reported previously for
90 humpback whales (Silber 1986; Dunlop, Cato & Noad 2008; Zoidis *et al.* 2008). These may
91 serve not only as a vehicle of communication between mother and calf but may also have

92 unwanted consequences such as attracting potential eavesdropping predators or male
93 humpback whale escorts (Tyack 1983; Deecke, Ford & Slater 2005). Predation poses a risk to
94 both mothers and calves (Pitman *et al.* 2014), whereas male escorts may be a mixed blessing
95 to the mothers; they may disrupt energy transfer to the calves, but in turn also represent
96 potential fathers for their next calf (Cartwright & Sullivan 2009b). For the calves, male
97 escorts may primarily be a source of disturbance that make the mothers move and hence cause
98 higher calf energy expenditure and fewer suckling opportunities. As such, we hypothesise that
99 calves seek to signal in a way that maintains critical contact, protection and nursing
100 opportunities from the mother, while minimising the risk of eavesdropping by predators and
101 escorts.

102 A detailed understanding of mother-calf behaviours is important not only from a
103 biological standpoint, but is also needed to guide conservation efforts and manage human
104 activities such as whale watching in breeding grounds. Despite the importance of these
105 behaviours, our knowledge of suckling in neonate baleen whales is sparse being based largely
106 on limited surface and underwater observations (Glockner-Ferrari & Ferrari 1984; Clapham &
107 Mayo 1987; Cartwright & Sullivan 2009b). Both approaches carry the risk of disrupting
108 natural behaviour of study subjects (Constantine 2001), potentially leading to biased
109 interpretations. To obtain fine-scale data on nursing behaviour while minimising vessel
110 proximity, we deployed multi-sensor tags, Dtags, on neonate humpback whales and their
111 mothers in Exmouth Gulf in Western Australia. Specifically, we aimed to: i) quantify where
112 and how often young calves suckle to better understand their resilience to disturbance, and ii)
113 investigate how mother-calf pairs solve the need for maintaining contact in a low visibility
114 environment while keeping risks of detection by predators and male humpback escorts low.

115

116 MATERIALS AND METHODS

117 Field site, study animals and tagging

118 Field work was conducted in Exmouth Gulf, Western Australia (22.16° S,
119 114.30° E) during August and September 2014. Exmouth Gulf is a known breeding and
120 resting ground for the Stock D humpback whale population (Bejder *et al.* 2015) during their
121 southbound migration (Chittleborough 1953; Jenner, Jenner & McCabe 2001). Calves are
122 usually less than three months of age when they reach Exmouth Gulf and have a body length
123 of about 4-7 meters (Chittleborough 1958; Christiansen *et al.* 2016). Exmouth Gulf is shallow
124 compared to the waters outside the gulf with depths less than 25m.

125 We approached and tagged mother-calf pairs that were logging or travelling
126 slowly. We conducted an hour of behavioural focal follow (Altmann 1974) on the mother-calf
127 pair before and after tagging, during which we maintained a distance of >200m with the
128 engine of the observation platform turned off. This allowed for noting the overall behaviour of
129 the tagged animal and its mother, and more specifically to identify visually when calves
130 performed peduncle dives which served as a proxy for suckling dives (Gordon *et al.* 1998;
131 Gero & Whitehead 2007). Travelling bouts, during which both calf and mother were
132 swimming actively, were classified as active dives.

133 During tagging attempts, the logging mother-calf pair was approached slowly
134 (<2 knots) with a 5.5m aluminium-hulled boat powered by an 80 HP Yamaha four-stroke
135 engine in forward idle. All of the study animals were tagged with non-invasive, digital
136 archival Dtags (Johnson & Tyack 2003) using a 9m carbon fibre pole. On the two occasions
137 where we tagged both mother and calf, the calf was always tagged first. We then conducted a
138 2hr focal follow before tagging the mother. Version 3 Dtags were attached between the
139 blowhole and the dorsal fin with four 50 mm diameter soft silicone suction cups (Fig 1a).

140 These tags have a frontal cross-sectional area of 20 cm² and a net buoyancy in water of 10g
141 and so are unlikely to add drag that could have an energetic impact on the calves. Tags were
142 programmed to release after a pre-programmed period of 22h using a timed galvanic release
143 which vented the cups, but some detached prematurely due to whales rubbing (Johnson &
144 Tyack 2003). The tags were retrieved the following day using radio tracking of the 220 MHz
145 VHF beacon in the tag. The Dtags sampled three-axes accelerometers, magnetometers and a
146 pressure sensor at 200Hz with 16-bit resolution, and stereo sound at 240kHz also with 16-bit
147 resolution. Sound was treated with a 6-pole anti-alias filter at 70kHz and a 1-pole high pass
148 filter at 150Hz prior to conversion and was then decimated to a sampling rate of 120kHz
149 before storing in memory giving flat (± 2 dB) frequency response from 0.15 to 50kHz. The
150 gentle slope of the 1-pole high-pass filter de-emphasizes flow noise while allowing for
151 detection and quantification of sounds down to at least 40 Hz.

152

153 **Data analysis**

154 *Behavioural classification*

155 Data analyses were performed using custom scripts in Matlab 8.4 2014b. Sensor
156 data were decimated to a sampling rate of 25 Hz using identical symmetric finite impulse
157 response low-pass filters on each channel. Accelerometer and magnetometer data were then
158 calibrated and rotated to account for the orientation of the tag on the animal using the
159 intervals of logging at the surface as an orientation reference (Johnson & Tyack 2003).
160 Behavioural observations recorded during focal follows of mother-calf pairs were used to
161 identify suckling and active dives in the Dtag data. Movement effort of tagged animals during
162 suckling and non-suckling dives was measured using the minimum specific acceleration
163 (MSA). The MSA provides a measure of how much the total acceleration deviates from the

164 gravity acceleration and is an under-bound on the specific acceleration generated by the
165 animal (Simon, Johnson & Madsen 2012). MSA is calculated by taking the absolute value of
166 the norm of the tri-axial acceleration minus the gravitational force of earth (9.81 m/s^2). Jerk
167 peaks in contrast to MSA are used for locating sudden movement changes made by the animal
168 and is calculated by taking the differential to the acceleration (Ydesen *et al.* 2014).

169 The median dive MSA recorded from calves during suckling dives, as identified
170 during focal follows, was calculated from the start to end time of each dive as determined
171 from the tag pressure measurements. The grand median MSA for each whale during these
172 suckling dives was used to normalise the MSA for each tagged whale to account for overall
173 differences in the acceleration between animals due to tag placements on different parts of the
174 body. Focal follow suckling dives were characterised by a much lower MSA distribution
175 (median normalised MSA=1.04) compared to active dives (median normalised MSA=4.36)
176 (Wilcoxon rank-sum test, $Z=-228.2$, $p < 0.01$) (Fig 1 b,e,f,i). We therefore used the median
177 normalised MSA recorded in active and suckling dives as classified from the focal follows to
178 establish thresholds for classifying the remaining dives of each tag out. To avoid the
179 confounding effects of a few very strong acceleration peaks from water splashes or contact
180 with the mother in both suckling and active dives, we used the receiver operating
181 characteristic (ROC) curve approach (Fawcett 2006) to identify an upper trimming level for
182 MSA data in identified focal follow suckling dives ($n=43$) and focal follow active dives
183 ($n=231$) that minimised classification errors. For a given trimming level, all instantaneous
184 MSA values above the trimming level were excluded before calculating the median MSA of
185 each trimmed dive. A set of ROC curves was then formed from the trimmed median MSAs
186 with each curve having a different trimming level (expressed as a percentile of the normalised
187 MSA). This was done for each percentile in the range from 70 to 99, and the area under curve

188 (AUC) was calculated for each resulting ROC curve as an indicator of the potential
189 classification performance. The AUC was found to be largest (0.98) for a 91% trimming level,
190 thus this was chosen to calculate median MSAs for classification of suckling dives in the tag
191 data outside of focal follow periods. To find an appropriate detection threshold, we then used
192 a maximum likelihood criterion on the empirical probability density distributions of the
193 trimmed median MSAs for the visually observed dives. The threshold giving the fewest total
194 errors was found as the MSA value at the intersection point of the two distributions. This
195 yielded a threshold of 1.5, giving proportions of true positives and false positives of 0.86 and
196 0.004, respectively. The threshold was then used to distinguish between active (i.e., those with
197 a median trimmed and normalised MSA > 1.5) and suckling dives (i.e., those with a median
198 trimmed and normalised MSA < 1.5).

199 All dives were located for each tag out and suckling and active dives were
200 distinguished according to the determined MSA criteria. Additionally, a depth threshold for
201 dives was set to avoid misclassifying occasional short and shallow dives. Suckling dives were
202 only scored if the maximum dive depth was >1.5m corresponding roughly to the ventral-
203 rostral body width of the mother, and the dive duration was >1min. In comparison, focal
204 follow suckling dives had a mean maximum depth of (\pm s.d.) 3.8 \pm 2.6m and a mean duration of
205 (\pm s.d.) 2.4 \pm 0.2min. The same depth threshold was imposed on active dives but no minimum
206 duration was set, to include short energetic dives. Dives were divided into descent, bottom
207 and ascent phases based on the vertical velocity (i.e., the differential of depth taken from the
208 pressure sensor). Bottom phases were located by taking the differential of depth, the first and
209 last periods of the dive with a depth difference larger than zero were classified as descent and
210 ascent respectively. Orientation of the calves was only calculated during the bottom phase of

211 dives. In dives classified as suckling, the bottom phase duration was interpreted as time spent
212 on suckling or attempts thereof.

213

214 *Sound analysis*

215 Sound data (68.8h from 10 whales) was examined acoustically and visually in
216 successive 15s segments using a spectrogram display (Hamming window, nfft: 4096 and 90%
217 overlap). We identified and marked start time and duration of sonic events such as
218 vocalisations, rubbing and breaching. Vocalisations were classified as either grunting or tonal
219 sounds following established definitions (Zoidis *et al.* 2008). Sound cues were only noted
220 during dives: surface breathing and logging bouts were not included in the analysis because of
221 the high probability of missing sounds when the tag was out of the water or splashed. Given
222 the close proximity between mother and calf it is not possible to reliably identify which is
223 vocalising; therefore, our call rates represent the total vocal output of mother-calf pairs. A
224 large proportion of the sound data from the tag outs on the two mother humpback whales was
225 unavailable for meaningful acoustic analysis, due to the high proportion of time spent logging
226 at the surface, during which the tag was out of the water.

227 Only vocalisations with a signal to noise ratio (SNR) greater than 10dB were
228 retained for further analysis. To estimate the signal to noise ratio, the RMS ambient noise
229 level of a 1s segment starting 2s before each vocalisation was calculated and compared to the
230 RMS sound level in a 0.125s window covering the strongest section of the call. Ambient noise
231 and calls were low-pass filtered at 5 kHz using a 4th order Butterworth bandpass filter before
232 RMS calculations. The centroid frequency and RMS bandwidth of calls were calculated as per
233 established definitions (Au 1993; Madsen & Wahlberg 2007).

234 To get an estimate of the ambient noise level in Exmouth Gulf, a SoundTrap
235 (Ocean Instruments Ltd) was deployed for seven days. The SoundTrap was deployed at 8m
236 depth and set to record continuously at a sampling rate of 288kHz for the entire deployment.

237 To test the hypothesis that an acoustic signal functions as a cue for i) initiating
238 suckling or ii) keeping contact we examined the quantity of vocalisations and rubbing sounds
239 during suckling (n=404) and active dives (n=2095). Generalised linear mixed models
240 (GLMM) were used to compare the number of vocalisations and rubbing sounds between
241 suckling and active dives. Specifically, we modelled the number of vocalisations or rubbing
242 sounds per dive as a function of dive type and duration using the Automatic Differentiation
243 Model Builder (glmmADMB) package in R software version 3.3.1, which accounts for over-
244 dispersed data (Bolker *et al.* 2009). The error distribution was Poisson with a log link
245 function. Dive type (i.e., active or suckling dive), and duration of dive were included in the
246 model as fixed effects and calf ID was included in both models as a random effect.

247

248 **RESULTS**

249 Ten humpback whales were tagged in Exmouth Gulf, WA, between August 26th
250 and September 3rd 2014 (Table 1). Eight of the ten humpback whales were young calves,
251 while the remainder were mothers accompanying two of the tagged calves. Tags were all
252 placed between the blowhole and the dorsal fin of the whale and stayed attached for a mean
253 (\pm s.d.) of 7.5 ± 6.4 h. All calves were accompanied by their mothers and two mother-calf pairs
254 (mn242a, mn247b) were also associated with an escort during tagging and the behavioural
255 focal follow. In the two instances the mother-calf pairs were joined by one or more escorts
256 their overall activity level increased significantly. Besides those two instances no other
257 conspecifics were observed near the mother-calf pairs during the focal follows.

258 All calves and mothers had a mild reaction to the tagging process. Typical
259 reactions included a couple of slow dives away from the tagging boat after which the whales
260 resumed their pre-tagging logging behaviour (normally within 15min).

261

262 **Suckling dives**

263 An example of suckling dives and active dives recorded from a mother-calf pair
264 (mn239a, mn239b) is shown in Fig. 1. A typical suckling dive begins with the calf making
265 three to four fluke strokes to dive some 1.6m below the dorsal surface of the stationary mother
266 (Fig 1b-e). The calf then initiates suckling which continues for approximately 2min during
267 which both the mother and calf are stationary and horizontally orientated (Fig 1b-e). When
268 suckling is complete the calf slowly ascends and returns to the surface to breathe. Suckling
269 was performed at a wide range of mean depths (1.1-19.2m) (Fig 2) and over half of suckling
270 dives for each animal ($65\pm 44\%$) occurred at a depth greater than 2.5m i.e. when the mother
271 was submerged (Fig 2). However, suckling dive depth varied widely by individual with some
272 calves only suckling near the surface while other calves only suckled at depth during the
273 intervals that the tags were attached.

274 Eight tagged calves performed 2499 dives deeper than 1.5m (Fig 5). Of those
275 dives 404 were classified as suckling dives giving an overall mean proportion of time spent in
276 suckling position of $20.7\pm 7\%$ ($n=8$) (Table 1). Independent of dive depth, the vertical depth
277 offset between mother and calf during suckling dives (Fig 1) was $1.7\pm 0.6\text{m}$ ($n=21$) for
278 mn238a and mn238b and $1.6\pm 0.4\text{m}$ ($n=11$) for mn239a and mn239b. The overall mean calf
279 depth in suckling dives in which the mother was submerged (i.e., with calf depths greater than
280 2.5m, ensuring the mother is at least a half body width beneath the surface) was $8.3\pm 2.3\text{m}$.
281 Calves adopted a consistently horizontal posture during suckling dives with overall mean

282 (\pm s.d.) roll and pitch angles during the bottom phase of 8.4 ± 6.1 and 9.1 ± 5.9 degrees
283 respectively. As indicated by the low MSA, calves make little movement during suckling (Fig
284 1e) and in effect remain stationary beneath their mother. The vertical speed during ascent and
285 descent in suckling dives (grand mean vertical speed of 0.6 ± 0.1 m s⁻¹) is in accordance with
286 previous dive data of young humpback whale calves on breeding grounds (Stimpert *et al.*
287 2012). Suckling dives had a grand mean duration of 2.1 ± 0.9 min of which 47-88% (Table 1)
288 of the total dive duration was spent in suckling position on average.

289

290

291 **Vocalisations**

292 Vocalisations recorded by the tags were classified as either grunting sounds
293 (Zoidis *et al.* 2008) or tonal sounds (Table 2). Tonal sounds were longer in duration and had a
294 distinctive sinusoidal wave shape compared to the grunting sounds (Fig 4 b, c). Mean centroid
295 frequencies of tonal and grunting sounds were 910 ± 580 Hz and 500 ± 310 Hz, respectively. The
296 mean RMS bandwidth for tonal sounds was 1350 ± 800 Hz and for grunting sounds
297 730 ± 390 Hz. The two call types differed little in received levels on the tag with a mean of
298 141 ± 1 dB re 1μ Pa RMS for tonal sounds and 136 ± 4 dB re 1μ Pa RMS for grunting sounds.
299 Given the consistent received levels on the calves, it is very likely that most calls were
300 produced by the calves (Table. 2). To estimate the masking noise from the environment, the
301 mean noise spectral density from a week of recordings from a deployed SoundTrap was
302 calculated over the approximate 1000 Hz RMS bandwidth of the two call types giving an
303 estimated masking noise level (N_{masking}) of 109 dB re 1μ Pa RMS.

304 Dive type had a significant influence on number of vocalisations per dive
305 (GLMM, $p = 0.0079$, Table 3), with ~ 4 times more calls during active dives (Fig. 3a).

306 However, there was no relationship between dive duration and number of vocalisations. To
307 account for individual variance among animals we included ID as a random effect in the
308 model, which explained 41% of the variance in number of calls.

309 Vocalisations were produced throughout the tag deployment (Fig 6) with a
310 tendency for call rate to increase with activity level during active dives (as measured by
311 MSA) as seen in Fig. 4a, where vocal output as a function of time and depth for one calf
312 (mn247a) is shown. However, when considering all eight calves that trend was not
313 statistically significant (Fig. 5). Three tags stayed on the calves after sundown, indicated by
314 the grey patched areas. No particular diurnal trend was evident amongst these three animals in
315 either call rates or suckling dive rates but the sample size is too small to be conclusive.

316 In contrast to the vocalisations, rubbing sounds per dive were produced 1.3
317 times more frequently during suckling dives than active dives (GLMM, $p < 0.01$, Table 3)
318 (Fig 3b). Additionally, there was a positive relationship between dive duration and number of
319 rubbing sounds per dive (GLMM, $p < 0.01$, Table 3). 69% of the variance in rubbing sounds
320 was explained by individual. The presence of jerk peaks (indicating a sudden change in
321 motion) in association with rubbing sounds indicated that the rubbing sounds are good proxies
322 for physical contact between mother and calf (Fig. 6).

323

324 **DISCUSSION**

325 Observing suckling in an aquatic medium is challenging, since surface and
326 underwater observations are potentially biased by the presence of nearby observers
327 (Constantine 2001; Best *et al.* 2015). Here we sought to overcome these limitations by
328 deploying suction-cup attached multi-sensor tags on humpback whale neonates, enabling a
329 detailed analysis of their behaviour (Johnson, Aguilar de Soto & Madsen 2009). Although

330 tagging young animals must be undertaken with great care, the mild reactions in this study
331 suggest that tagging offers a low disturbance approach to detailed studies of natural calf
332 behaviour. Most importantly, the use of tags allowed us to remain >200m away from calves
333 during visual follows and to track suckling behaviour at night-time. A drawback of this
334 protocol is that not all of the suckling dives recorded by the tags can be verified by direct
335 observation. Here we used tag-recorded movement signatures during a subset of verified dives
336 to distinguish active and suckling dives in the remainder of the data. Although effective, this
337 technique inevitably leads to a small percentage of dives being miss-classified but this will
338 likely have little impact on the conclusions drawn here.

339 Time spent at low latitudes is critical for the growth of humpback whale calves
340 to sustain the upcoming migration (Brodie 1975) from the calm temperate waters of the
341 breeding grounds to rougher, colder and more predator dense environments (Corkeron &
342 Connor 1999; Clapham 2000). Previously, Herman & Antinaja (1977) reported that mother-
343 calf pairs spent a large percentage (26%) of their time on breeding grounds resting, but they
344 could not distinguish how much of that time was spent nursing. Here we show that tagged
345 neonate humpback whales are in suckling position, and so potentially suckling, on average
346 20% of the time (Table 1). This large time investment in suckling is consistent with the short
347 time window for energy transfer before humpback whales migrate back to high latitude
348 feeding grounds (Dawbin 1966). Distinguishing between actual suckling i.e., on-teat time
349 where milk is transferred as opposed to suckling attempts is difficult, since there were no
350 distinct signals in the accelerometer data indicating a successful transfer of milk from mother
351 to calf. Moreover, time spent suckling does not translate directly into milk intake as milk
352 transfer within a suckling bout is affected by maternal quality and age/size of the offspring
353 (Trillmich 1986; Cameron 1998). Thus our results are likely an upper bound on the actual

354 suckling time; nevertheless, our estimate of 20% time investment in suckling is consistent
355 with findings for other marine mammals, despite differences in nursing strategies (Ofedal,
356 Boness & Tedman 1987).

357 The overall suckling and diving behaviour documented here is in line with
358 previous visual observations of neonate humpback whales (Glockner & Venus 1983;
359 Glockner-Ferrari & Ferrari 1984). The calf dives slowly beneath the mother where it
360 maintains a horizontal, motionless position for a duration of 2.5 ± 0.5 min before slowly
361 returning to the surface to breathe (Table 1, Fig 1). Taber & Thomas (1984) found a similar
362 pattern in suckling neonate southern right whales, where they observed the mother logging at
363 the surface, while the calf performed successive suckling dives with modal durations of 1.5-
364 4.5 min depending on the age of the calves. This stationary suckling behaviour is in contrast
365 with the suckling behaviour of small toothed whales, where mothers nurse their young while
366 swimming or gliding (McBride & Kritzler 1951; Asper *et al.* 1988; Peddemors *et al.* 1992;
367 Miles & Herzing 2003). Stationary suckling is energetically advantageous for both the mother
368 and the calf, allowing the mother, who is solely dependent on stored body reserves, to
369 conserve energy, and permitting the calf to allocate energy to growth rather than movement
370 (Harrison 1969; Herman & Tavolga 1980). This stationary behaviour may be facilitated by
371 calm waters, potentially explaining why mother-calf pairs seek out sheltered areas such as
372 Exmouth Gulf.

373 However, suckling does occur not only in our data when mothers are logging at
374 the surface: more than fifty percent of the inferred suckling dives of the tagged calves took
375 place with the mother submerged at depths greater than 2.5m (Table 1). Suckling at depth was
376 performed by six of eight calves in this study and was the dominant suckling mode in five of
377 these. This large component of deep-water suckling would be missed in studies relying only

378 on visual observations of logging mothers. The consistent offset in dive depth between
379 mothers and calves of around 1.6 m (Fig 1) implies that the mother is resting at depth while
380 the calf dives down beneath her to suckle. Although diving to these depths only requires a few
381 fluke strokes, the large percentage of suckling occurring at depth is surprising, since both the
382 mother and the calf should have an interest in conserving energy. Deeper dives may make it
383 easier to maintain suckling position for the calf via the more compressed lungs that at a mean
384 depth of 7.3 meters will be some 40% less buoyant than at 1.5 m depth due to hydrostatic
385 compression of air in the lungs, assuming that calves dive on inspiration. This reduced
386 buoyancy could result in calves spending less energy on maintaining position during suckling,
387 compared to near-surface suckling dives. Alternatively, buoyant calves may simply support
388 themselves on the ventral surface of the mother while suckling to minimise effort.

389 Another possible explanation for suckling at depth relates to the
390 thermoregulation of mothers. Given their dark skin colour, logging at the surface for long
391 periods during warm daylight hours in the tropics may lead to overheating (Scholander &
392 Schevill 1955). The slightly cooler deeper waters and absence of direct insolation may
393 provide some relief. However, this would imply that deep-water suckling dives should be
394 absent at night. Our limited night data show some deep-water suckling dives in the dark (Fig
395 5), leading us to question this explanation. The deeper suckling depths could also be driven by
396 wind and sea state conditions; in rougher seas it may be easier to maintain position at depth
397 than near the surface, but we do not have detailed sea state data to test that hypothesis. A final
398 possibility is that suckling at depth could give an acoustic advantage since surface related
399 noise is significantly lowered, resulting in an improvement of acoustic vigilance.

400 Irrespective of the depth at which it is performed, suckling under water requires
401 mother-calf coordination to ensure that milk is ejected successfully into the mouth of the calf,

402 likely calling for cues to initiate this behaviour (Triossi *et al.* 1998). We hypothesised that
403 acoustic cues could aid such coordination, but found that few calls and grunts were produced
404 by mother and calf during suckling dives and that these were not more prevalent immediately
405 before suckling was inferred to commence. Thus, even though humpback whales are normally
406 highly vocal (Payne & McVay 1971; Winn & Winn 1978; Dunlop *et al.* 2007) these findings
407 suggest that suckling is not initiated by acoustic communication. Rather, frequent rubbing
408 sounds closely related with acceleration transients suggest that mechanical stimulation is used
409 by the calf to initiate lactation by its mother (Fig 6). Tactile cues to initiate lactation are also
410 used by other cetacean species including bottlenose dolphins (*Tursiops truncatus*) (McBride
411 & Kritzler 1951; Drinnan & Sadlier 1981; Peddemors *et al.* 1992), Atlantic spotted dolphins
412 (*Stenella frontalis*) (Miles & Herzing 2003), killer whales (*Orcinus orca*) (Asper *et al.* 1988)
413 and southern right whales (*Eubalaena australis*) (Taber & Thomas 1984). In southern right
414 whales, calves have been observed to head-butt their mothers if their suckling attempts are
415 rejected (Taber & Thomas 1984). Such mammary bumps are common across all mammals as
416 one of several cues to initiate lactation (Lent 1974; Appleby, Weary & Chua 2001), but unlike
417 some terrestrial mammals (Sèbe *et al.* 2008), humpback whales seemingly do not also use
418 acoustic cues in this process. Acoustic signals may provide inadvertent information to
419 eavesdropping male humpback whale escorts or predators. Killer whales especially have been
420 reported to have a high success rate in predating on neonatal humpback whale calves in the
421 area (Pitman *et al.* 2014). In comparison, mechanical stimulation is an inconspicuous way of
422 communicating, allowing the calf to covertly signal its mother of its readiness to suckle.
423 Therefore we hypothesise that silence in mother-calf pairs serves to reduce the risk of
424 predation or dangerous escort attention (Aguilar de Soto *et al.* 2012).

425 Although the low call rates during suckling dives support the notion that silence
426 is maintained to avoid detection, mother-calf pairs do in fact vocalise occasionally, albeit in a
427 different behavioural context (Fig 3a,4,5). Vocalisations are mainly associated with active
428 dives, where they likely function as cohesive calls between mother and calf to maintain
429 contact as also reported for other cetacean species (McBride & Kritzler 1951; Janik & Slater
430 1998). The disadvantage of such vocalisations is that they may serve as homing cues for
431 predators and other eavesdroppers with negative consequences for calf fitness. However, in
432 low visibility waters, such as Exmouth Gulf, the calf and mother are unlikely to see each other
433 beyond a few body lengths of the mother, and separation would also have severe fitness
434 consequences, requiring a means of maintaining contact. When resting, such a need is limited
435 (Fig 4), but when moving there is likely an increased impetus for cohesion calls explaining
436 why calls were more frequent during active dives. Increased vocalisation rates among mother-
437 calf pairs have been reported when pairs are with one or multiple escorts suggesting that an
438 increase in distraction level results in an increased vocal rate to maintain contact (Tyack &
439 Whitehead 1983; Baker & Herman 1984; Dunlop *et al.* 2008; Cartwright & Sullivan 2009b).

440 Another way to reduce detection of acoustic signals by distant listeners is to
441 produce them at low source levels (Nakano *et al.* 2009; Dunlop 2016). Assuming that the
442 received levels recorded by the tags, placed approximately 1 m behind the blow hole, serve as
443 reasonable proxies for source levels, the vocalisations, irrespective of whether produced by
444 the calf or mother, are very weak. RLs were some 40 dB lower than sounds recorded with a
445 similar tag on a singing humpback male in the same area (unpublished data), and also much
446 weaker (20-70 dB) than the social sounds reported for adult humpback whales (Thompson,
447 Cummings & Kennison 1977; Thompson, Cummings & Ha 1986; Dunlop *et al.* 2008).
448 Assuming that the quiet vocalisations can be detected by other animals at an SNR of 0 dB the

449 low source levels translate into an active space of some 30m for the measured ambient noise
450 level, assuming spherical spreading, and negligible absorption over these short ranges. Thus,
451 low level vocalisations may serve to keep contact without attracting unwanted attention, at the
452 expense of a very small communication range between mother-calf pairs meaning that
453 mothers and calves must keep close. Supporting this, we and others have observed that
454 humpback whale calves rarely separate from their mother by more than a few tens of meters.
455 (Glockner & Venus 1983; Zoidis *et al.* 2014). Other humpback whale calls are produced at
456 levels appropriate to the intended audience: a long communication range is favoured for songs
457 to reach a large audience while the quieter social sounds are intended for the immediate group
458 (Dunlop *et al.* 2013). Additionally, groups of humpback whales amplitude modulate their
459 social calls presumably to avoid unwanted attention from potential singers nearby (Dunlop
460 2016).

461 The broader implications of this behaviour are that an increase in the
462 disturbance level from noise-generating human activities, such as whale watching, shipping
463 and fishing, may increase the risk of mother-calf pair separation, reducing the time available
464 for suckling, or require that louder contact calls are made which, in turn increases the
465 possibility of detection. In either case, increased ambient noise could have negative
466 consequences for calf fitness (Cartwright & Sullivan 2009b; Craig *et al.* 2014).

467

468 **Conclusion**

469 A massive energy transfer occurs between mother and calf humpback whales
470 during the few months between birth and migration, as demonstrated by significant body loss
471 of the mother in synchrony with calf growth. Here we show that humpback whale calves are
472 in a position to suckle on average 20% of their time. The high proportion of time spent on

473 suckling emphasises that humpback mother-calf pairs are vulnerable to disturbance that may
474 increase energy expenditure and reduce energy transfer from mother to calf. Calves suckle by
475 positioning themselves nearly motionlessly beneath their resting mothers. This low effort
476 suckling behaviour may only be supported in calm waters possibly explaining why humpback
477 whales often seek sheltered waters for nursing their calves, highlighting the conservation
478 importance of such areas. Although suckling depths varied between calves, some 50% of
479 suckling took place when the mother was submerged; a behaviour that may relate to
480 thermoregulation, buoyancy, a reduction of wave action to facilitate suckling, or that
481 submerged mothers may be in a better listening position for detecting singing escort males
482 and predatory killer whales. However, this shallow diving behaviour also makes them more
483 vulnerable to collisions with deep-draft vessels, as they are not visible from moving vessels.

484 Vocalisations were detected between mother-calf pairs but we found no support
485 for the hypothesis that suckling is initiated by sound cues. Rather, calves appeared to use
486 mechanical stimulation, presumably head bumps of the mammae area, as has been
487 documented in other mammals. Sounds in the form of grunts and tonal calls were, however,
488 predominantly produced when the mother and calf were moving suggesting that they are used
489 as contact calls. These weak calls have an estimated active space of much less than 100
490 meters reducing the risk of attracting eavesdropping male escorts and killer whales. A
491 problem of such weak calls is that even moderate increases in ambient noise will create a very
492 small active space that may increase the risk of the calf being separated from the mother.

493

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495 MJ build the Dtags and developed analytical tools in Matlab. SV analysed the data, and
496 drafted the manuscript with input from LB, MJ and PTM.

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742 **Figure Legends**

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744 Fig. 1. (a) Overall dive profiles of a tagged mother (mn239b, red line) and calf (mn239a, blue line)
745 pair (b-e) Enlargement showing two suckling dives during which the mother is logging at the
746 surface. (f-i) Enlargement showing two active dives in which both mother and calf are diving. In
747 each 4-panel frame, plot (b) and (f) show the dive profiles of the two animals, (c) and (g) show the
748 roll angles (degrees), (d) and (h) show the pitch angles (degrees), and (e) and (i) show the MSA
749 (m/s^2). The inset photo shows the tagged mother and calf logging at the surface

750 Fig. 2. Histograms of mean maximum depth of inferred suckling dives by calves (N=8). Calf ID and
751 sample size per animal are given on each histogram.

752 Fig. 3. Boxplot of acoustic cues per minute for all calves during suckling dives and active dives. (a)
753 grunting and tonal sounds (b) rubbing sounds.

754 Fig. 4. (a) Dive profile of mn247a, depth in meters from surface (blue), MSA (m/s^2) (grey),
755 grunting sounds (red) and tonal sounds (dark blue) plotted on top of dive profile (b, c) spectrograms
756 (Hamming window, nfft: 4096, 90% overlap) of a grunting sound (b) and a tonal sound (c). For
757 both, the power spectrum is shown to the right and the waveform beneath.

758

759 Fig. 5. Subplot of dive profiles for eight tagged calves (n=8), MSA (grey), grey areas indicate sun
760 down, tonal sounds (dark blue) and grunting sounds marked (red). To the right a histogram of depth
761 distribution for each calf

762 Fig. 6. (a) Segment of the dive profile of mn241a with occurrence of rubbing sounds indicated in
 763 red. (b) spectrogram (Hamming window, nfft: 4096, 90% overlap) of a rubbing sound (c) Norm jerk
 764 (i.e., magnitude of the tri-axial differential of acceleration, $m\ s^{-3}$) recorded by the tag at the same
 765 time as the rubbing sound in (d) Mean normalised jerk for all calves during rubbing sounds. The
 766 jerk from 1 second before to 4 seconds after the start of each rub sound was extracted and the mean
 767 of these jerk segments was calculated for each animal. The red solid line is the average jerk for all
 768 calves.

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771 Table 1. Summary of tagging and suckling details for each tagged whale.

| Tag ID | Animal | Tag duration (h) | Tagging coordinates | # of suckling dives | Suckling dive depth (m) median (IQR) | % time in suckling position | % time in suckling position during suckling dive mean \pm std |
|--------|--------|------------------|---------------------|---------------------|--------------------------------------|-----------------------------|---|
| mn238a | Calf | 5.3 | 22.27'S 114.19'E | 30 | 2.3 (1.5-7.1) | 25.6 | 79.3 \pm 7.7 |
| mn238b | Adult | 2.9 | 22.25'S 114.19'E | - | - | - | - |
| mn239a | Calf | 4.1 | 22.14'S 114.14'E | 25 | 1.7 (1.5-1.9) | 19.9 | 81.5 \pm 8.7 |
| mn239b | Adult | 3.6 | 22.15'S 114.14'E | - | - | - | - |
| mn241a | Calf | 3 | 22.37'S 114.23'E | 10 | 2.1 (2.0-2.2) | 14.3 | 87.7 \pm 4.6 |
| mn242a | Calf | 6.2 | 22.30'S 114.26'E | 15 | 10.2 (9.7-12.2) | 12.2 | 63.1 \pm 12.5 |
| mn243a | Calf | 7.6 | 22.34'S 114.26'E | 41 | 7.9 (7.3-8.3) | 24.9 | 69 \pm 14.5 |
| mn246b | Calf | 24 | 22.31'S 114.24'E | 149 | 10.5 (8.2-13.9) | 15.8 | 47 \pm 16.6 |
| mn247a | Calf | 6.3 | 22.20'S 114.25'E | 25 | 7.5 (5.6-9.5) | 19.5 | 74.1 \pm 13.2 |
| mn247b | Calf | 12.1 | 22.22'S 114.25'E | 109 | 4.7 (3.4-7) | 33.1 | 74 \pm 14.7 |

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773 Suckling dives: inferred suckling dives (see Methods).

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Table 2. Summary of acoustic parameters of the two types of vocalisations: tonal and grunting sounds.

| Tag ID | Grunting Sounds Total | Tonal Sounds Total | Grunting Sounds pr. hour | Tonal Sounds pr. hour | Received level grunting sounds dB re 1µPa | Received level tonal sounds dB re 1µPa | Centroid freq. grunting sounds (Hz) mean±s.d. | Centroid freq. tonal sounds (Hz) mean±s.d. | RMS Bandwidth grunting sounds (Hz) mean±s.d. | RMS Bandwidth tonal sounds (Hz) mean±s.d. |
|---------|-----------------------|--------------------|--------------------------|-----------------------|---|--|---|--|--|---|
| mn238a | 113 | 0 | 21.5 | 0 | 131±0 | - | 233±0 | - | 304±0 | - |
| mn239a | 65 | 0 | 15.7 | 0 | 131±0 | - | 451±0 | - | 724±0 | - |
| mn241a | 159 | 5 | 52 | 1.6 | 142±7 | 142±0 | 241±126 | 300±0 | 447±190 | 455±0 |
| mn242a | 346 | 34 | 55.3 | 5.4 | 141±5 | 141±6 | 384±359 | 536±330 | 618±397 | 840±405 |
| mn243a | 179 | 4 | 23.5 | 0.5 | 138±5 | 142±0 | 992±566 | 1463±0 | 1263±580 | 2170±0 |
| mn246b | 555 | 87 | 23 | 3.6 | 136±4 | 139±5 | 879±585 | 1592±473 | 1273±778 | 2225±552 |
| mn247a | 591 | 156 | 92.9 | 24.5 | 135±4 | 140±5 | 306±359 | 646±548 | 512±438 | 1060±828 |
| mn247b* | 277 | 16 | 22.8 | 1.3 | - | - | - | - | - | - |

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* The tag used on mn247b had a faulty hydrophone connection and sound cues were therefore excluded from acoustic analysis for this individual.

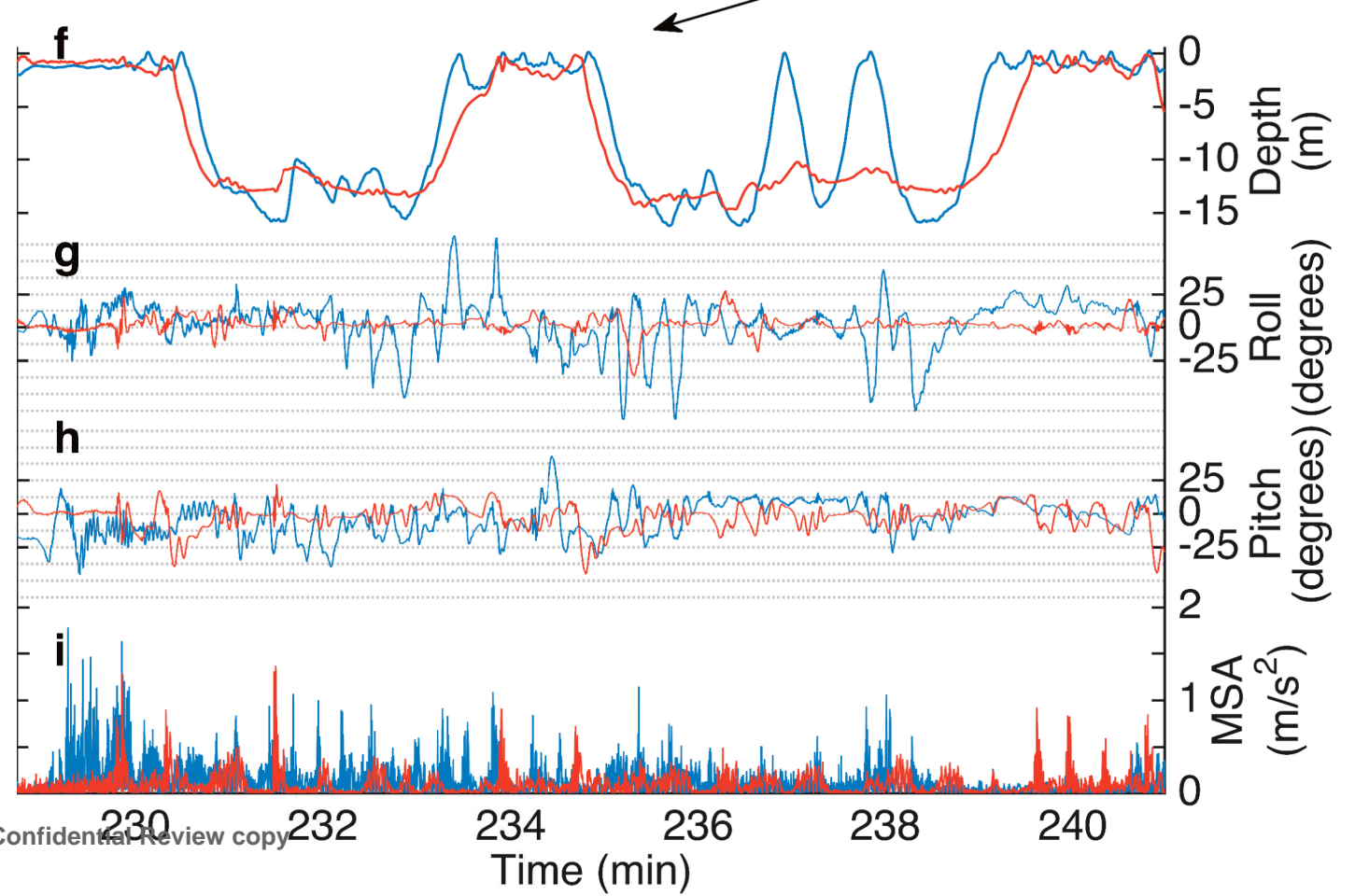
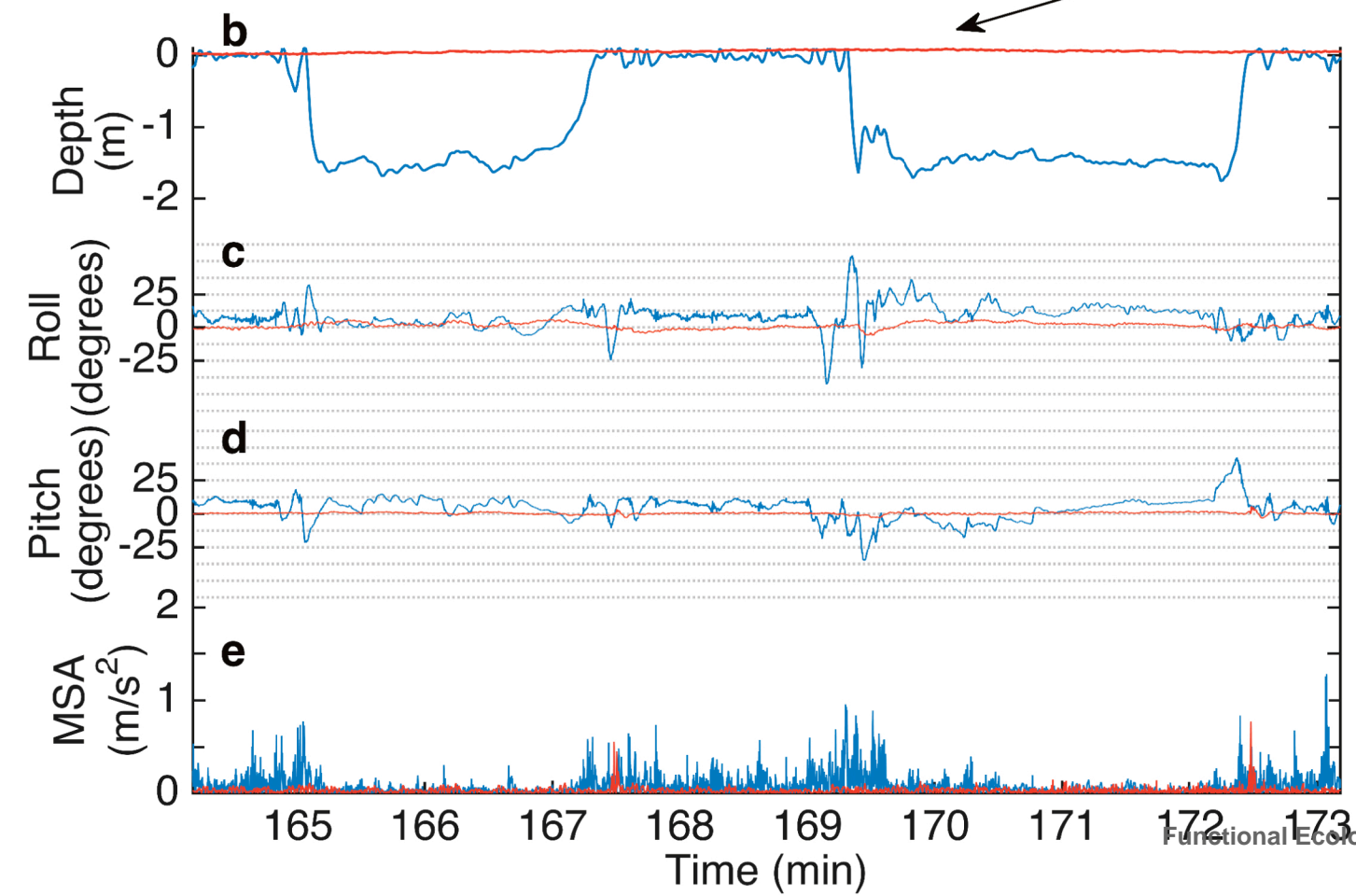
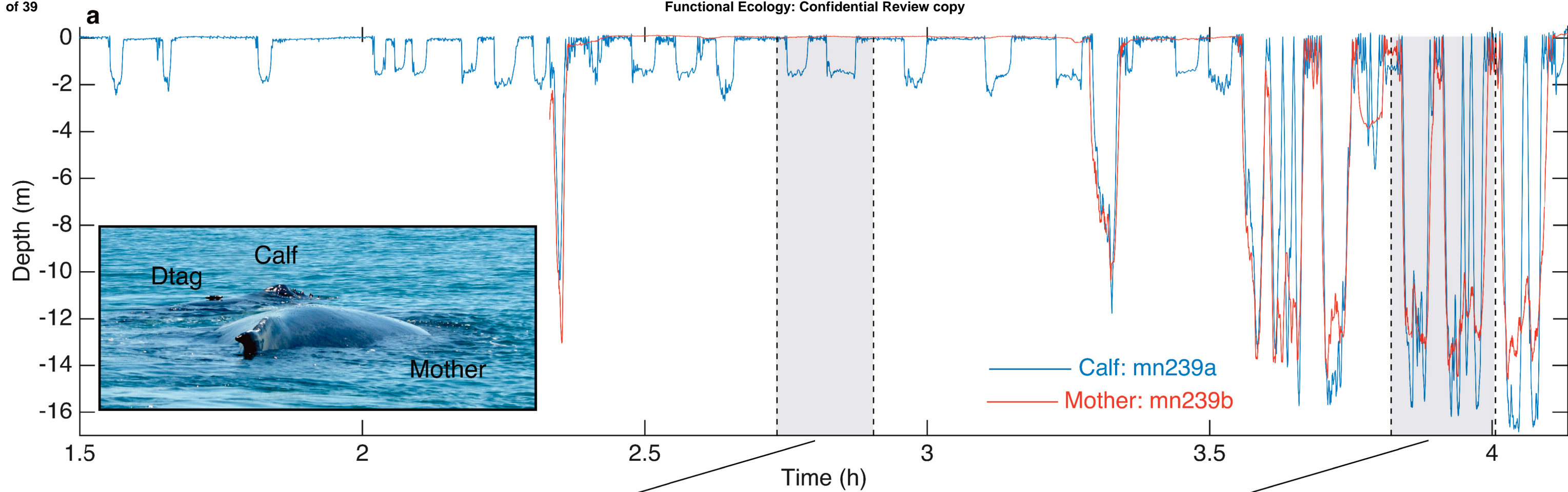
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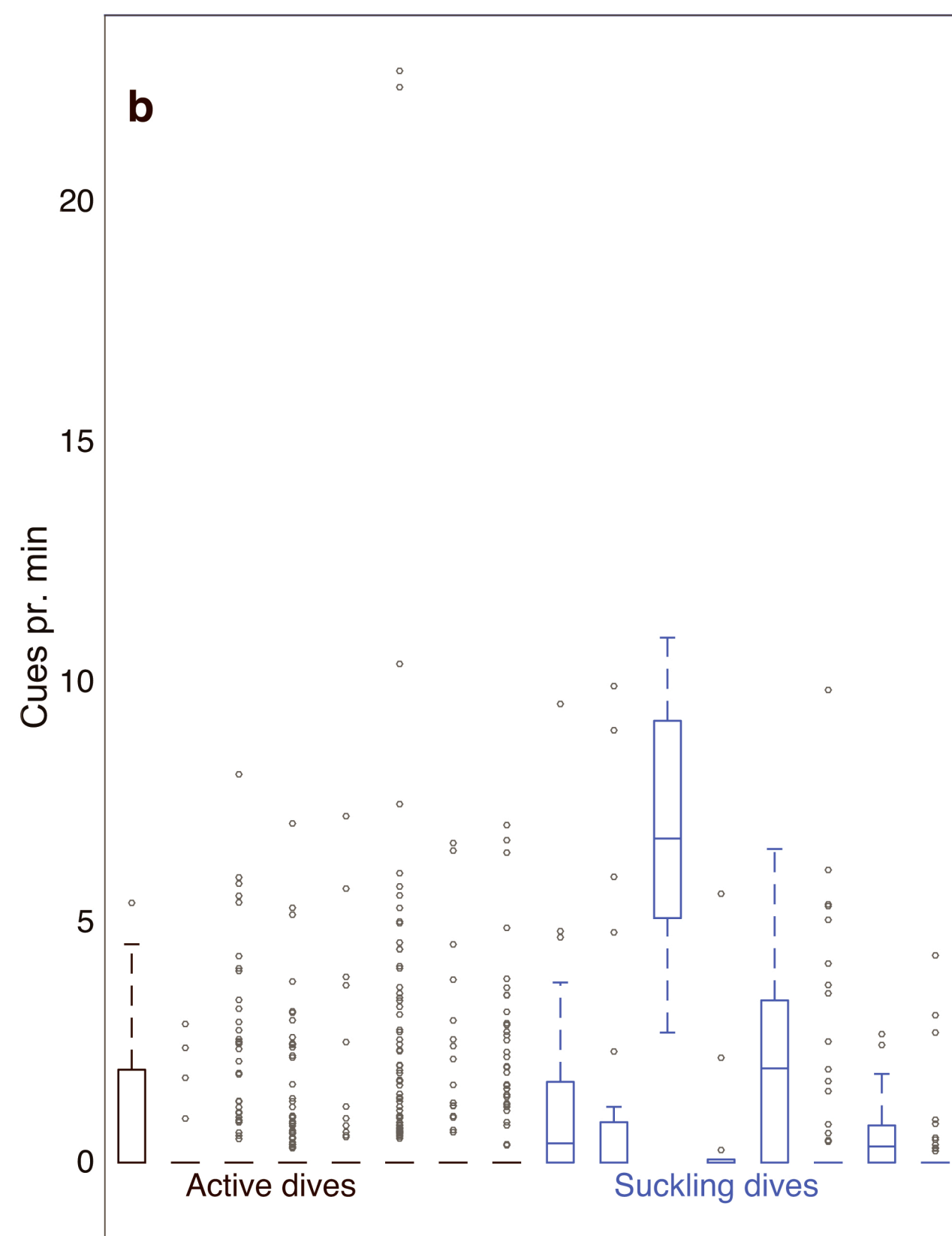
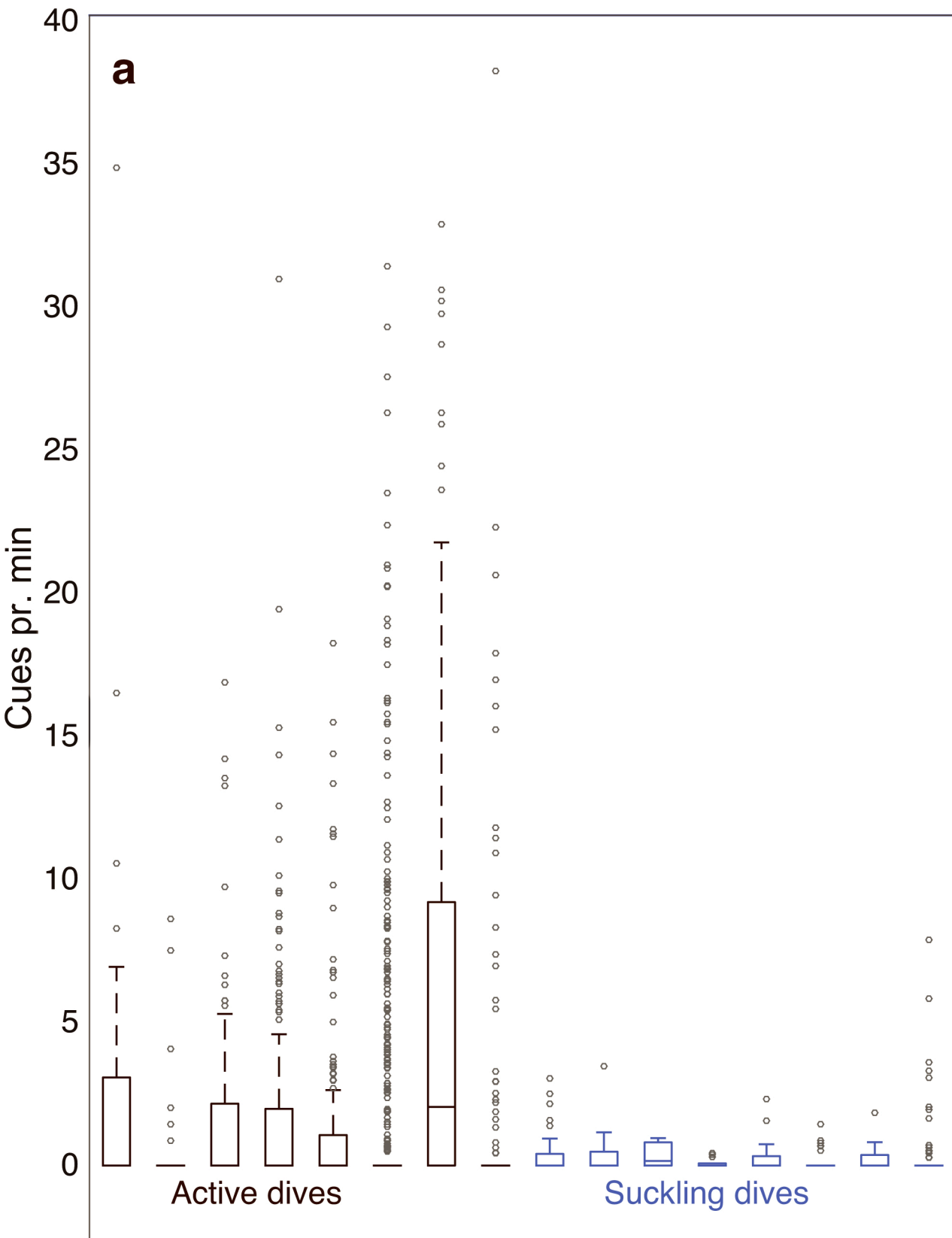
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Table 3. Results of the generalised linear mixed models exploring the relationship of vocalisations and rubbing sounds between active and suckling dives.

| Factor | Response | | | | | |
|----------------|---------------|-------|---------|----------------|--------|--------|
| | Vocalisations | | | Rubbing sounds | | |
| | Estimate | SE | p | Estimate | SE | p |
| Intercept | -0.257 | 0.229 | 0.26 | -2.482 | 0.302 | <0.01* |
| Dive type | -0.274 | 0.103 | 0.0079* | 1.339 | 0.0829 | <0.01* |
| Length of dive | -0.0319 | 0.035 | 0.357 | 0.754 | 0.0316 | <0.01* |

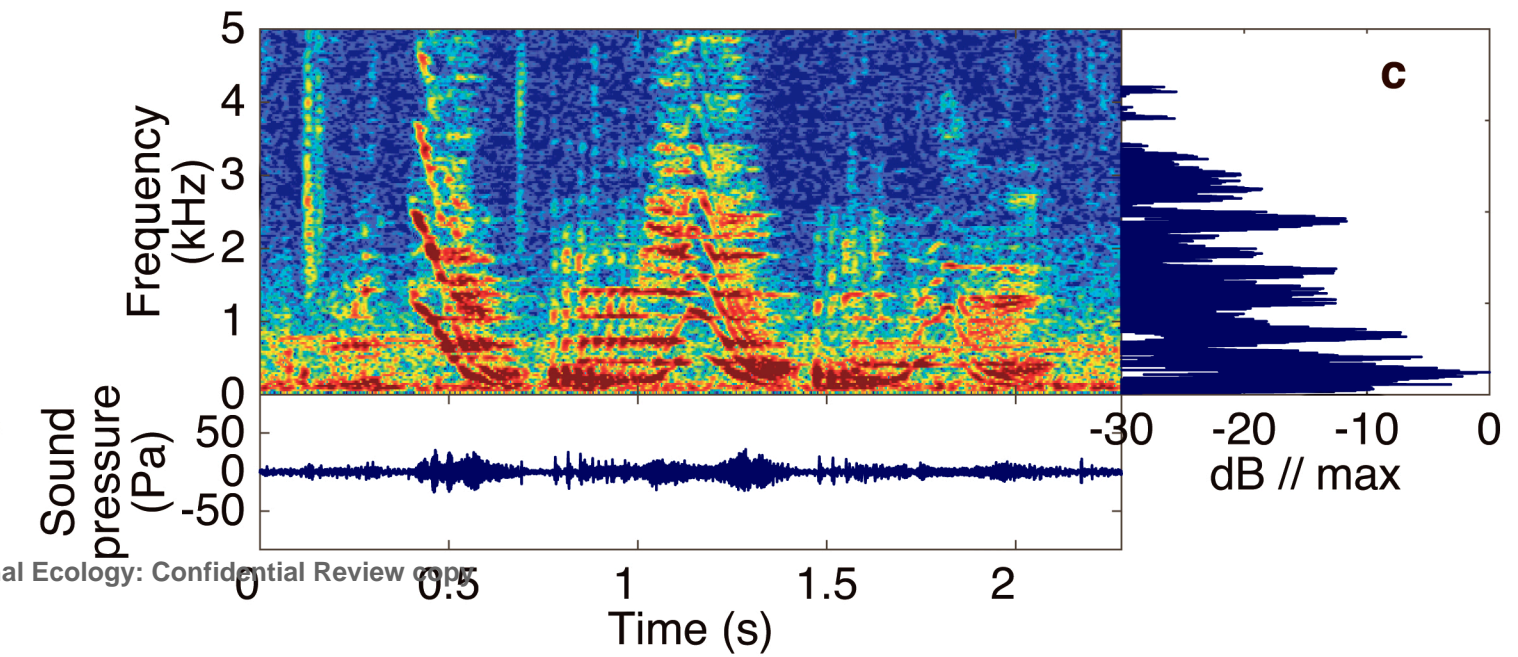
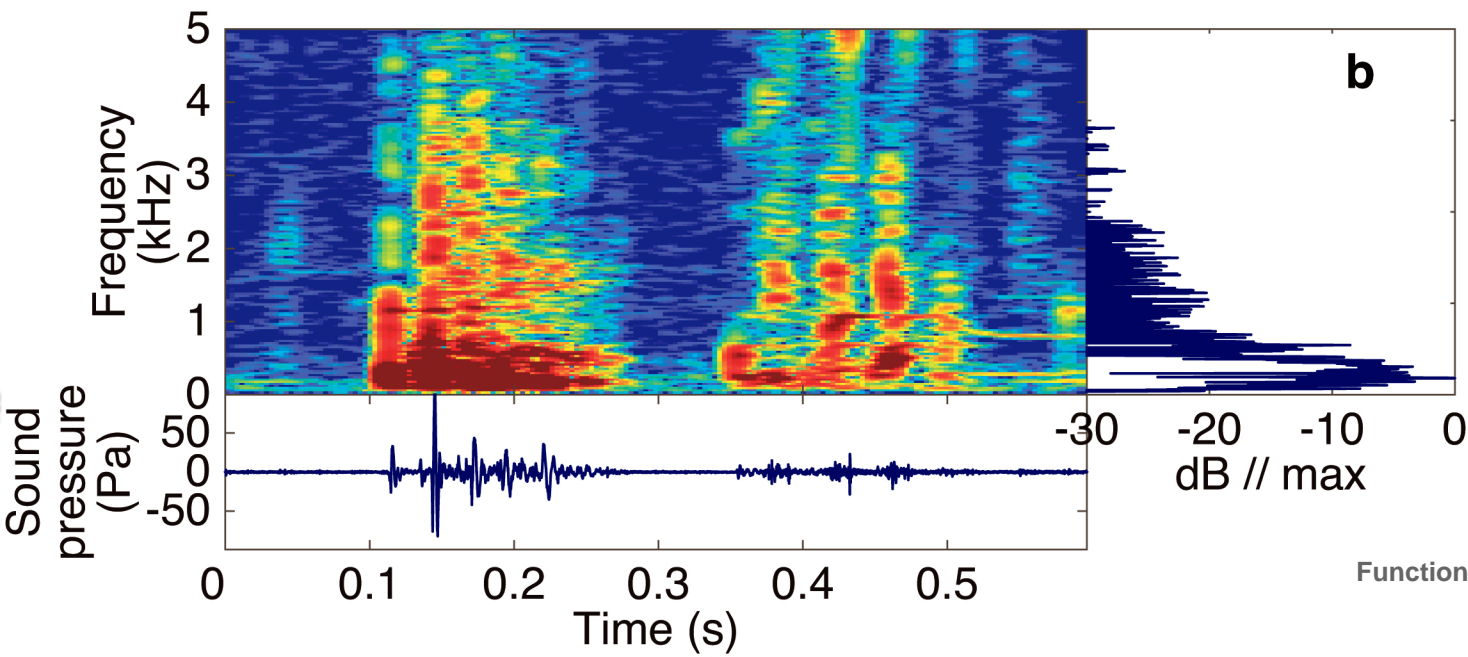
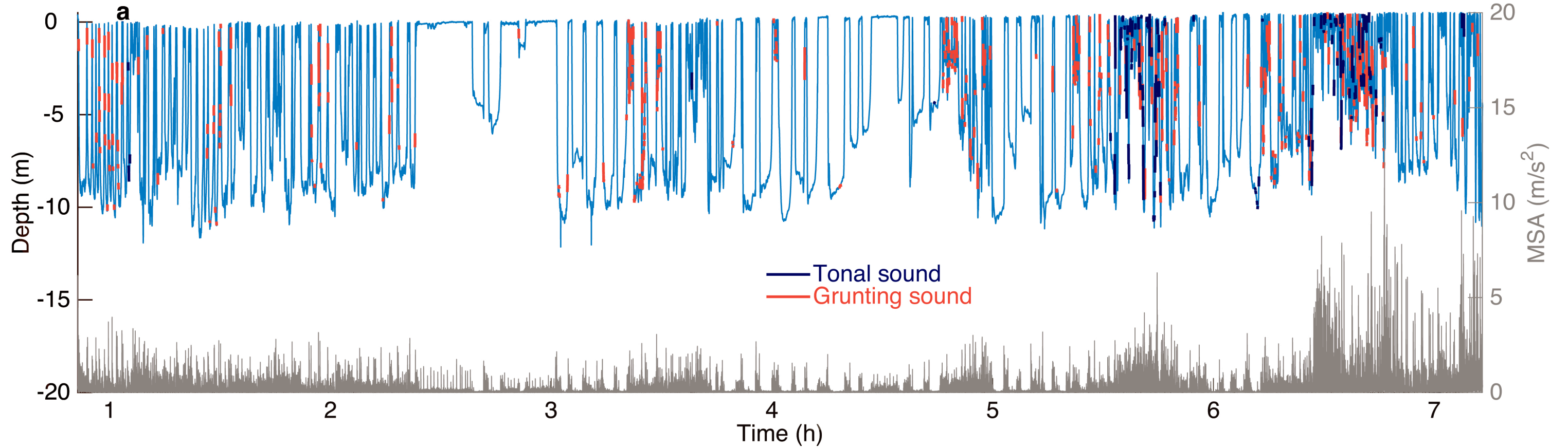
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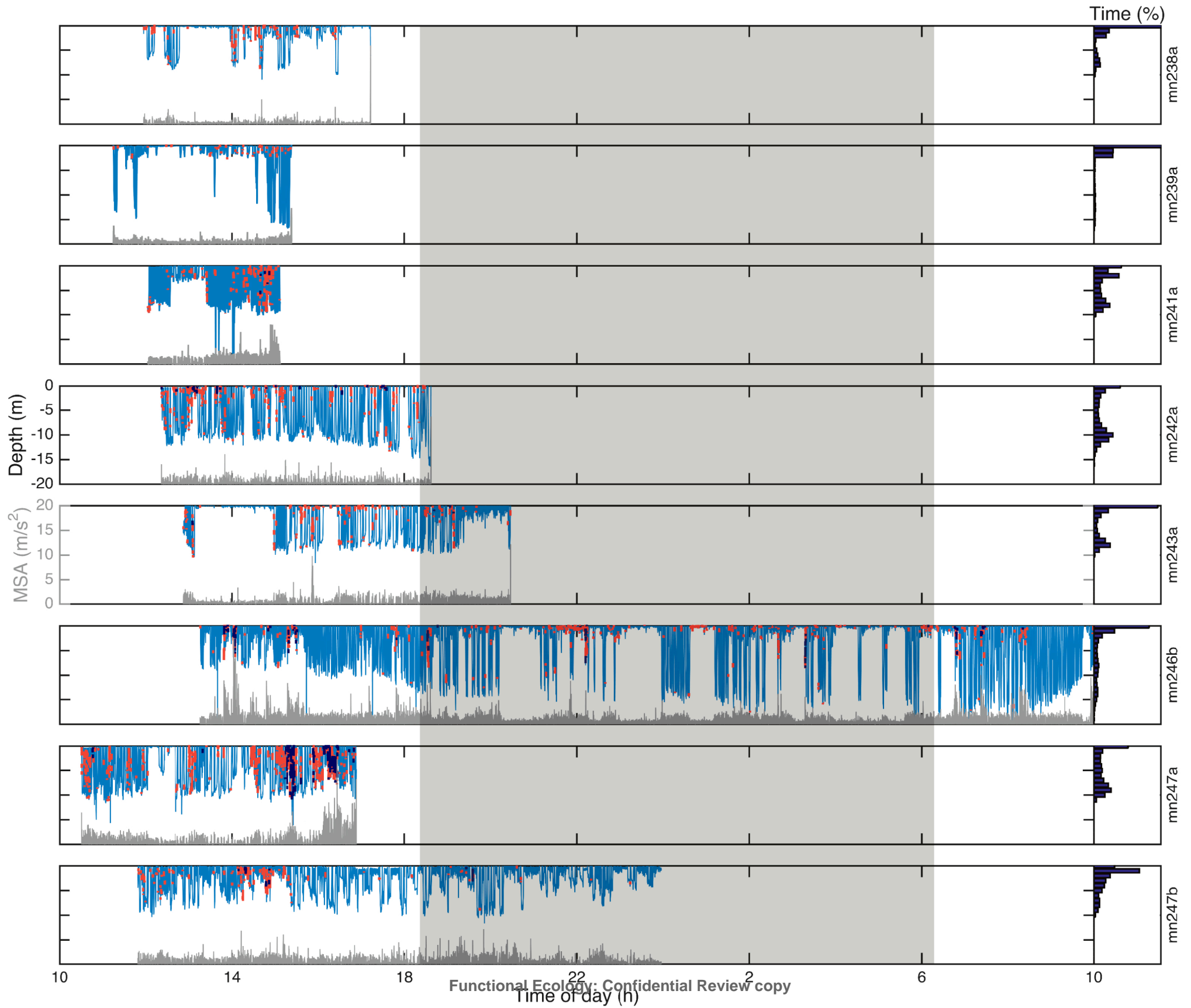


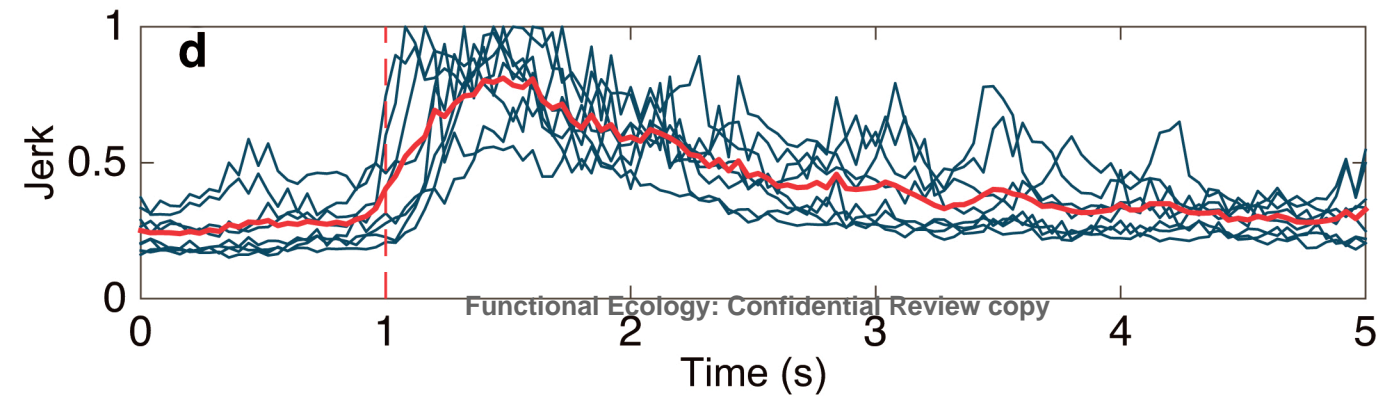
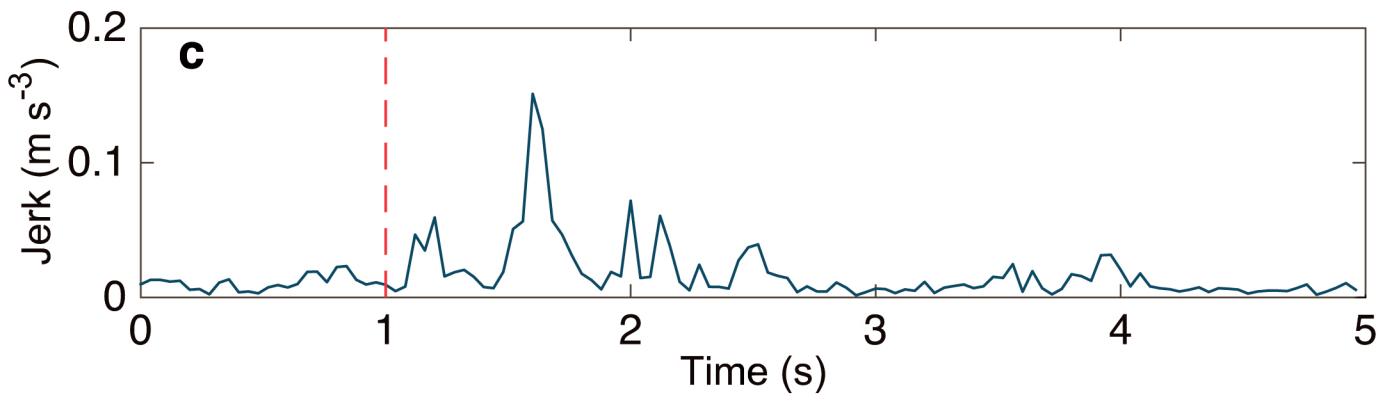
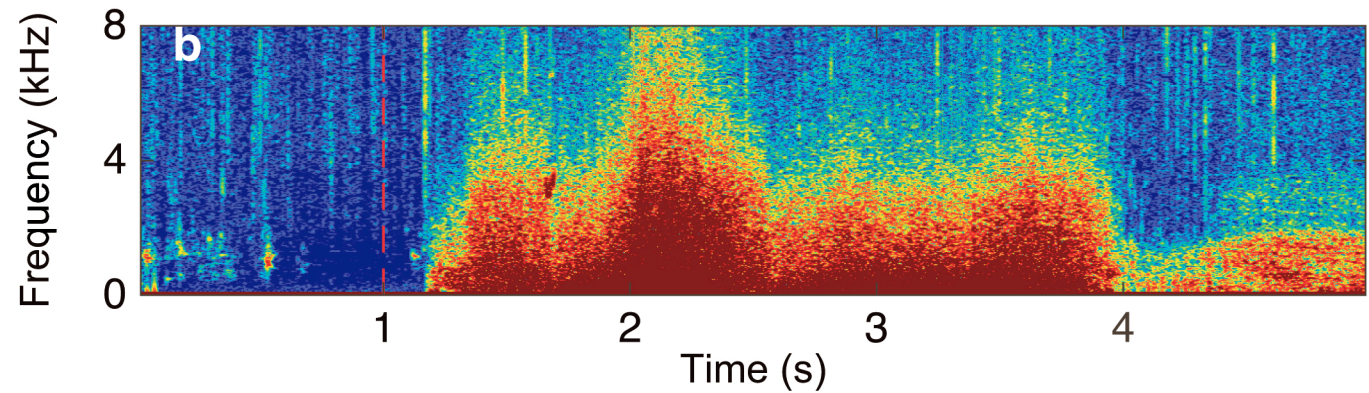
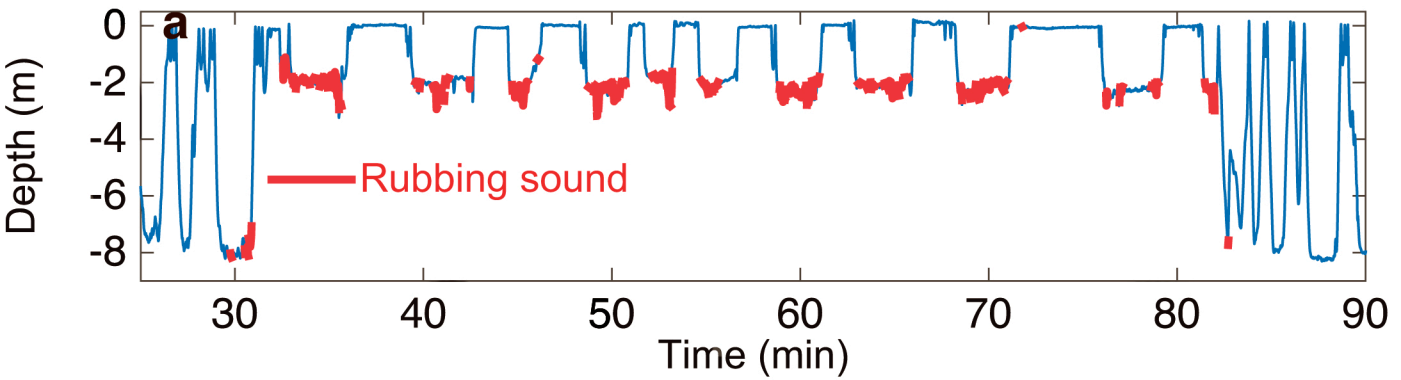


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| Tag ID | Animal | Tag duration (h) | Tagging coordinates | # of suckling dives | Suckling dive depth (m) median (IQR) | % time in suckling position | % time in suckling position during suckling dive mean \pm std |
|--------|--------|------------------|---------------------|---------------------|--------------------------------------|-----------------------------|---|
| mn238a | Calf | 5.3 | 22.27'S 114.19'E | 30 | 2.3 (1.5-7.1) | 25.6 | 79.3 \pm 7.7 |
| mn238b | Adult | 2.9 | 22.25'S 114.19'E | - | - | - | - |
| mn239a | Calf | 4.1 | 22.14'S 114.14'E | 25 | 1.7 (1.5-1.9) | 19.9 | 81.5 \pm 8.7 |
| mn239b | Adult | 3.6 | 22.15'S 114.14'E | - | - | - | - |
| mn241a | Calf | 3 | 22.37'S 114.23'E | 10 | 2.1 (2.0-2.2) | 14.3 | 87.7 \pm 4.6 |
| mn242a | Calf | 6.2 | 22.30'S 114.26'E | 15 | 10.2 (9.7-12.2) | 12.2 | 63.1 \pm 12.5 |
| mn243a | Calf | 7.6 | 22.34'S 114.26'E | 41 | 7.9 (7.3-8.3) | 24.9 | 69 \pm 14.5 |
| mn246b | Calf | 24 | 22.31'S 114.24'E | 149 | 10.5 (8.2-13.9) | 15.8 | 47 \pm 16.6 |
| mn247a | Calf | 6.3 | 22.20'S 114.25'E | 25 | 7.5 (5.6-9.5) | 19.5 | 74.1 \pm 13.2 |
| mn247b | Calf | 12.1 | 22.22'S 114.25'E | 109 | 4.7 (3.4-7) | 33.1 | 74 \pm 14.7 |

| Tag ID | Grunting Sounds | Tonal Sounds | Grunting Sounds pr. hour | Tonal Sounds pr. hour | Received Ecological Received dB re 1 μ Pa | Received Ecological Received dB re 1 μ Pa | Caribbifreq. grunting sounds (Hz) mean \pm s.d. | Caribbifreq. tonal sounds (Hz) mean \pm s.d. | RMS Bandwidth grunting sounds (Hz) mean \pm s.d. | RMS Bandwidth tonal sounds (Hz) mean \pm s.d. |
|---------|-----------------|--------------|--------------------------|-----------------------|---|---|---|--|--|---|
| mn238a | 113 | 0 | 21.5 | 0 | 131 \pm 0 | - | 233 \pm 0 | - | 304 \pm 0 | - |
| mn239a | 65 | 0 | 15.7 | 0 | 131 \pm 0 | - | 451 \pm 0 | - | 724 \pm 0 | - |
| mn241a | 159 | 5 | 52 | 1.6 | 142 \pm 7 | 142 \pm 0 | 241 \pm 126 | 300 \pm 0 | 447 \pm 190 | 455 \pm 0 |
| mn242a | 346 | 34 | 55.3 | 5.4 | 141 \pm 5 | 141 \pm 6 | 384 \pm 359 | 536 \pm 330 | 618 \pm 397 | 840 \pm 405 |
| mn243a | 179 | 4 | 23.5 | 0.5 | 138 \pm 5 | 142 \pm 0 | 992 \pm 566 | 1463 \pm 0 | 1263 \pm 580 | 2170 \pm 0 |
| mn246b | 555 | 87 | 23 | 5.6 | 136 \pm 4 | 139 \pm 5 | 819 \pm 585 | 1592 \pm 473 | 1273 \pm 778 | 2225 \pm 552 |
| mn247a | 591 | 156 | 92.9 | 24.5 | 135 \pm 4 | 140 \pm 5 | 306 \pm 359 | 646 \pm 548 | 512 \pm 438 | 1060 \pm 828 |
| mn247b* | 277 | 16 | 22.8 | 1.3 | - | - | - | - | - | - |

| Factor | Vocalisations | | | Response | | |
|----------------|---------------|-------|---------|----------|--------|--------|
| | Estimate | SE | p | Estimate | SE | p |
| Intercept | 0.257 | 0.229 | 0.26 | 2.482 | 0.302 | <0.01* |
| Dive type | -0.274 | 0.103 | 0.0079* | 1.339 | 0.0829 | <0.01* |
| Length of dive | -0.0319 | 0.035 | 0.357 | 0.754 | 0.0316 | <0.01* |