

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

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Summary

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

Key-words: bio-energetics, humpback whale, migration, neonate, nursing, suckling

Introduction

Cetaceans are fully adapted to an aquatic environment, and yet they must still breathe air and suckle their young as terrestrial mammals. The lack of physical maternal support to calves for transport and nursing means that neonate cetaceans must have sufficient motor skills to suckle, swim and breath-hold immediately after birth (McBride & Kritzler 1951; Wahrenbrock *et al.* 1974; Peddemors 1990;

Peddemors, Fothergill & Cockcroft 1992). To facilitate the critical transfer of energy during nursing, cetaceans have evolved milk with a higher fat content compared to that of terrestrial mammals (Chittleborough 1958; Slijper 1966; Harrison 1969), active nursing where milk is ejected into the mouth of the calf (McBride & Kritzler 1951; Slijper 1966; Drinnan & Sadlier 1981; Ridgway *et al.* 1995), and rapidly improving breath-holding capabilities, thereby enabling neonates to suckle for longer durations within hours of birth (Asper, Young & Walsh 1988; Peddemors 1990; Cartwright & Sullivan 2009a).

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Several species of large baleen whales undertake long annual migrations between high latitude feeding grounds and low latitude breeding grounds. It is likely they embark on this migration to reduce predation pressure and seek sheltered, warm and calm waters for the neonates. While travelling long distances might not pose large energetic costs for mothers (Corkeron & Connor 1999), the cessation of foraging while lactating does impose a large energetic challenge for them, resulting in a significant decline in body condition (Chittleborough 1958; Lockyer 2007; Christiansen *et al.* 2016). This creates a short critical time window on the breeding grounds (Dawbin 1966; Herman & Antinoya 1977; Clapham & Mayo 1987; Clapham 1996, 2000) to transfer sufficient energy to the calf for it to grow and survive the long migration back to the foraging grounds. Indeed, the growth rate of humpback whale calves is remarkably fast; studies have found a growth rate of 0.5–1 m per month in length (Glockner & Venus 1983; Christiansen *et al.* 2016) suggesting a need for substantial time investment in suckling.

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

Acoustic signals from mother–calf pairs have been reported previously for humpback whales (Silber 1986; Dunlop, Cato & Noad 2008; Zoidis *et al.* 2008). These may serve not only as a vehicle of communication between mother and calf but may also have unwanted consequences such as attracting potential eavesdropping predators or male humpback whale escorts (Tyack 1983; Deecke, Ford & Slater 2005). Predation poses a risk to both mothers and calves (Pitman *et al.* 2015), whereas male escorts may be a mixed blessing to the mothers; they may disrupt energy transfer to the calves, but in turn also represent potential fathers for their next calf (Cartwright & Sullivan 2009b). For the calves, male escorts may primarily be a source of disturbance that make the mothers move and hence cause higher calf energy expenditure and fewer suckling opportunities. As such, we hypothesise that calves seek to signal in a way that maintains critical contact, protection and

nursing opportunities from the mother, while minimising the risk of eavesdropping by predators and escorts.

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

Materials and methods

FIELD SITE, STUDY ANIMALS AND TAGGING

Field work was conducted in Exmouth Gulf, Western Australia (22.16°S, 114.30°E) during August and September 2014. Exmouth Gulf is a known breeding and resting ground for the Stock D humpback whale population (Bejder *et al.* 2016) during their southbound migration (Chittleborough 1953; Jenner, Jenner & McCabe 2001). Calves are usually <3 months of age when they reach Exmouth Gulf and have a body length of about 4–7 m (Chittleborough 1958; Christiansen *et al.* 2016). Exmouth Gulf is shallow compared to the waters outside the gulf with depths <25 m.

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

During tagging attempts, the logging mother–calf pair was approached slowly (<2 knots) with a 5.5 m aluminium-hulled boat in forward idle. All of the study animals were tagged with non-invasive, digital archival Dtags (Johnson & Tyack 2003) using a 9 m carbon fibre pole. On the two occasions where we tagged both mother and calf, the calf was always tagged first. We then conducted a 2 h focal follow before tagging the mother. Version 3 Dtags were attached between the blowhole and the dorsal fin with four 50 mm diameter soft silicone suction cups (Fig. 1a). These tags have a frontal cross-sectional area of 20 cm² and a net buoyancy in water of 10 g and so are unlikely to add drag that could have an energetic impact on the calves. Tags were programmed to release after a preprogrammed period of 22 h using a timed

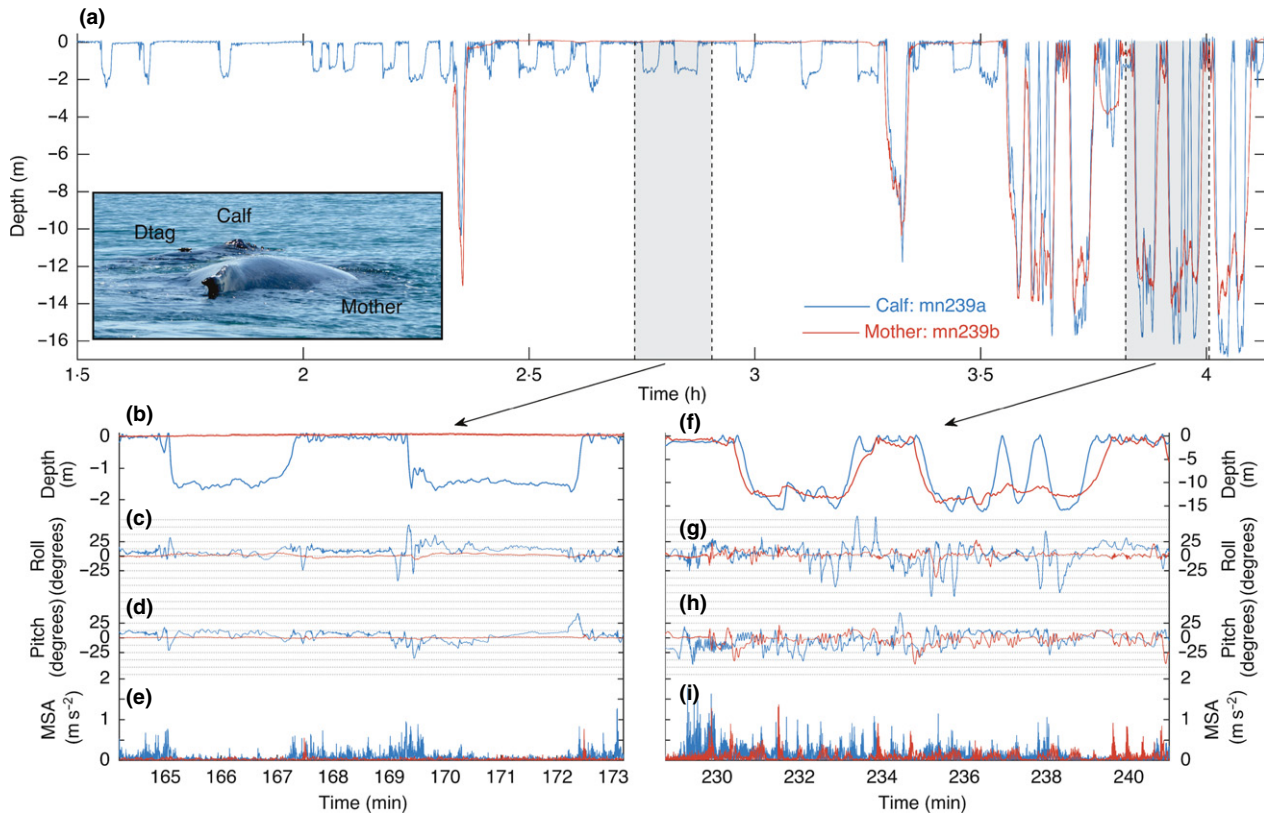


Fig. 1. (a) Overall dive profiles of a tagged mother (mn239b, red line) and calf (mn239a, blue line) pair (b–e) Enlargement showing two suckling dives during which the mother is logging at the surface. (f–i) Enlargement showing two active dives in which both mother and calf are diving. In each 4-panel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

galvanic release which vented the cups, but some detached prematurely due to whales rubbing (Johnson & Tyack 2003). The tags were retrieved the following day using radiotracking of the 220 MHz VHF beacon in the tag. The Dtags sampled three-axis accelerometers, magnetometers and a pressure sensor at 200 Hz with 16-bit resolution, and stereo sound at 240 kHz also with 16-bit resolution. Sound was treated with a 6-pole anti-alias filter at 70 kHz and a 1-pole high pass filter at 150 Hz prior to conversion and was then decimated to a sampling rate of 120 kHz before storing in memory giving flat (± 2 dB) frequency response from 0.15 to 50 kHz. The gentle slope of the 1-pole high pass filter de-emphasises flow noise while allowing for detection and quantification of sounds down to at least 40 Hz.

DATA ANALYSIS

Behavioural classification

Data analyses were performed using custom scripts in MATLAB Release 2014b (The MathWorks, Inc., Natick, MA, USA). Sensor data were decimated to a sampling rate of 25 Hz using identical symmetric finite impulse response low-pass filters on each channel. Accelerometer and magnetometer data were then calibrated and rotated to account for the orientation of the tag on the animal using the intervals of logging at the surface as an orientation reference (Johnson & Tyack 2003). Behavioural observations recorded during focal follows of mother–calf pairs were used to identify suckling and active dives in the Dtag data. Movement effort of tagged animals during suckling and nonsuckling dives was

measured using the minimum specific acceleration (MSA). The MSA provides a measure of how much the total acceleration deviates from the gravity acceleration and is an under-bound on the specific acceleration generated by the animal (Simon, Johnson & Madsen 2012). Minimum specific acceleration is calculated by taking the absolute value of the norm of the tri-axial acceleration minus the gravitational force of earth (9.81 m s^{-2}). Jerk peaks in contrast to MSA are used for locating sudden movement changes made by the animal and is calculated by taking the differential to the acceleration (Ydesen *et al.* 2014).

The median dive MSA recorded from calves during suckling dives, as identified during focal follows, was calculated from the start to end time of each dive as determined from the tag pressure measurements. The grand median MSA for each whale during these suckling dives was used to normalise the MSA for each tagged whale to account for overall differences in the acceleration between animals due to tag placements on different parts of the body. Focal follow suckling dives were characterised by a much lower MSA distribution (median normalised MSA = 1.04) compared to active dives (median normalised MSA = 4.36) (Wilcoxon rank-sum test, $Z = -228.2$, $P < 0.01$) (Fig. 1b,e,f,i). We therefore used the median normalised MSA recorded in active and suckling dives as classified from the focal follows to establish thresholds for classifying the remaining dives of each tag out. To avoid the confounding effects of a few very strong acceleration peaks from water splashes or contact with the mother in both suckling and active dives, we used the receiver operating characteristic (ROC) curve approach (Fawcett 2006) to identify an upper trimming level for MSA data in identified focal follow suckling dives ($n = 43$) and focal follow active dives ($n = 231$) that minimised

classification errors. For a given trimming level, all instantaneous MSA values above the trimming level were excluded before calculating the median MSA of each trimmed dive. A set of ROC curves was then formed from the trimmed median MSAs with each curve having a different trimming level (expressed as a percentile of the normalised MSA). This was done for each percentile in the range from 70 to 99, and the area under curve (AUC) was calculated for each resulting ROC curve as an indicator of the potential classification performance. The AUC was found to be largest (0.98) for a 91% trimming level, thus this was chosen to calculate median MSAs for classification of suckling dives in the tag data outside of focal follow periods. To find an appropriate detection threshold, we then used a maximum likelihood criterion on the empirical probability density distributions of the trimmed median MSAs for the visually observed dives. The threshold giving the fewest total errors was found as the MSA value at the intersection point of the two distributions. This yielded a threshold of 1.5, giving proportions of true positives and false positives of 0.86 and 0.004, respectively. The threshold was then used to distinguish between active (i.e. those with a median trimmed and normalised MSA > 1.5) and suckling dives (i.e. those with a median trimmed and normalised MSA < 1.5).

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

Sound analysis

Sound data (68.8 h from 10 whales) were examined acoustically and visually in successive 15s segments using a spectrogram display (Hamming window, nfft: 4096 and 90% overlap). We

identified and marked start time and duration of sonic events such as vocalisations, rubbing and breaching. Vocalisations were classified as either grunting or tonal sounds following established definitions (Zoidis *et al.* 2008). Sound cues were only noted during dives: surface breathing and logging bouts were not included in the analysis because of the high probability of missing sounds when the tag was out of the water or splashed. Given the close proximity between mother and calf, it is not possible to reliably identify which is vocalising; therefore, our call rates represent the total vocal output of mother–calf pairs. A large proportion of the sound data from the tag outs on the two mother humpback whales was unavailable for meaningful acoustic analysis, due to the high proportion of time spent logging at the surface, during which the tag was out of the water.

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

To get an estimate of the ambient noise level in Exmouth Gulf, a SoundTrap (Ocean Instruments, Auckland, New Zealand) was deployed for 7 days. The SoundTrap was deployed at 8 m depth and set to record continuously at a sampling rate of 288 kHz for the entire deployment.

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

Results

Ten humpback whales were tagged in Exmouth Gulf, WA, Australia, between 26 August and 3 September 2014

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

Tag ID	Animal	Tag duration (h)	Tagging coordinates	No. of suckling dives	Suckling dive depth (m) median (IQR)	% time in suckling position	% time in position during suckling dive mean \pm SD
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

Suckling dives: inferred suckling dives (see Materials and methods).

(Table 1). Eight of the ten humpback whales were young calves, while the remainder were mothers accompanying two of the tagged calves. Tags were all placed between the blowhole and the dorsal fin of the whale and stayed attached for a mean (\pm SD) of 7.5 ± 6.4 h. All calves were accompanied by their mothers and two mother–calf pairs (mn242a, mn247b) were also associated with an escort during tagging and the behavioural focal follow. In the two instances, the mother–calf pairs were joined by one or more escorts their overall activity level increased significantly. Besides those two instances, no other conspecifics were observed near the mother–calf pairs during the focal follows.

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

SUCKLING DIVES

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

Eight tagged calves performed 2499 dives deeper than 1.5 m (Fig. 5). Of those dives, 404 were classified as suckling dives giving an overall mean proportion of time spent in suckling position of $20.7 \pm 7\%$ ($n = 8$) (Table 1). Independent of dive depth, the vertical depth offset between mother and calf during suckling dives (Fig. 1) was

1.7 ± 0.6 m ($n = 21$) for mn238a and mn238b and 1.6 ± 0.4 m ($n = 11$) for mn239a and mn239b. The overall mean calf depth in suckling dives in which the mother was submerged (i.e. with calf depths >2.5 m, ensuring the mother is at least a half body width beneath the surface) was 8.3 ± 2.3 m. Calves adopted a consistently horizontal posture during suckling dives with overall mean (\pm SD) roll and pitch angles during the bottom phase of $8.4 \pm 6.1^\circ$ and $9.1 \pm 5.9^\circ$, respectively. As indicated by the low MSA, calves make little movement during suckling (Fig. 1e) and in effect remain stationary beneath their mother. The vertical speed during ascent and descent in suckling dives (grand mean vertical speed of 0.6 ± 0.1 m s^{-1}) is in accordance with previous dive data of young humpback whale calves on breeding grounds (Stimpert *et al.* 2012). Suckling dives had a grand mean duration of 2.1 ± 0.9 min of which 47–88% (Table 1) of the total dive duration was spent in suckling position on average.

VOCALISATIONS

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

Dive type had a significant influence on number of vocalisations per dive (GLMM, $P = 0.0079$, Table 3), with ~ 4 times more calls during active dives (Fig. 3a). However, there was no relationship between dive duration and

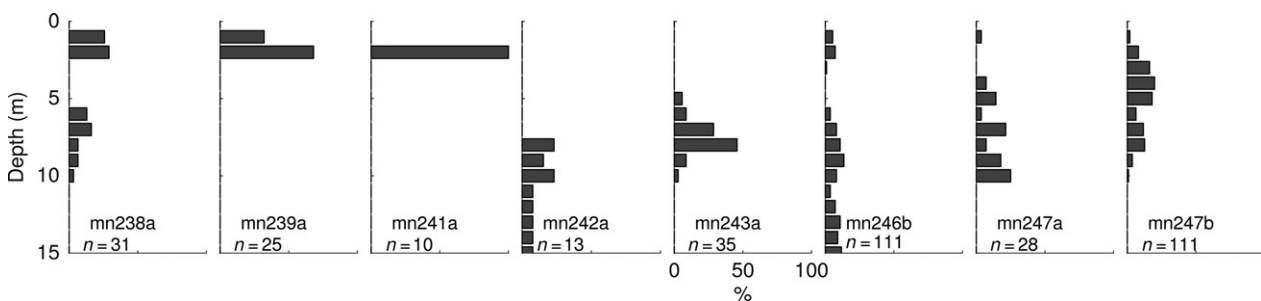


Fig. 2. Histograms of mean maximum depth of inferred suckling dives by calves ($N = 8$). Calf ID and sample size per animal are given on each histogram.

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 per hour	Tonal sounds per hour	Received level	Received level	Centroid freq.	Centroid freq.	RMS	RMS
					grunting sounds dB re 1 μ Pa	tonal sounds dB re 1 μ Pa	grunting sounds (Hz) mean \pm SD	tonal sounds (Hz) mean \pm SD	bandwidth grunting sounds (Hz) mean \pm SD	bandwidth tonal sounds (Hz) mean \pm SD
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	3.6	136 \pm 4	139 \pm 5	879 \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	–	–	–	–	–	–

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

Factor	Response					
	Vocalisations			Rubbing sounds		
	Estimate	SE	<i>P</i>	Estimate	SE	<i>P</i>
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*

*Indicate that $P < 0.05$.

number of vocalisations. To account for individual variance among animals, we included ID as a random effect in the model, which explained 41% of the variance in number of calls.

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

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

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

Discussion

Observing suckling in an aquatic medium is challenging, since surface and underwater observations are potentially biased by the presence of nearby observers (Constantine 2001; Best *et al.* 2015). Here, we sought to overcome these limitations by deploying suction-cup attached multi-sensor tags on humpback whale neonates, enabling a detailed analysis of their behaviour (Johnson, Aguilar de Soto & Madsen 2009). Although tagging young animals must be undertaken with great care, the mild reactions in this study suggest that tagging offers a low disturbance approach to detailed studies of natural calf behaviour. Most importantly, the use of tags allowed us to remain >200 m away from calves during visual follows and to track suckling behaviour at night-time. A drawback of this protocol is that not all of the suckling dives recorded by the tags can be verified by direct observation. Here, we used tag-recorded movement signatures during a subset of verified dives to distinguish active and suckling dives in the remainder of the data. Although effective, this technique inevitably leads to a small percentage of dives being misclassified but this will likely have little impact on the conclusions drawn here.

Time spent at low latitudes is critical for the growth of humpback whale calves to sustain the upcoming migration

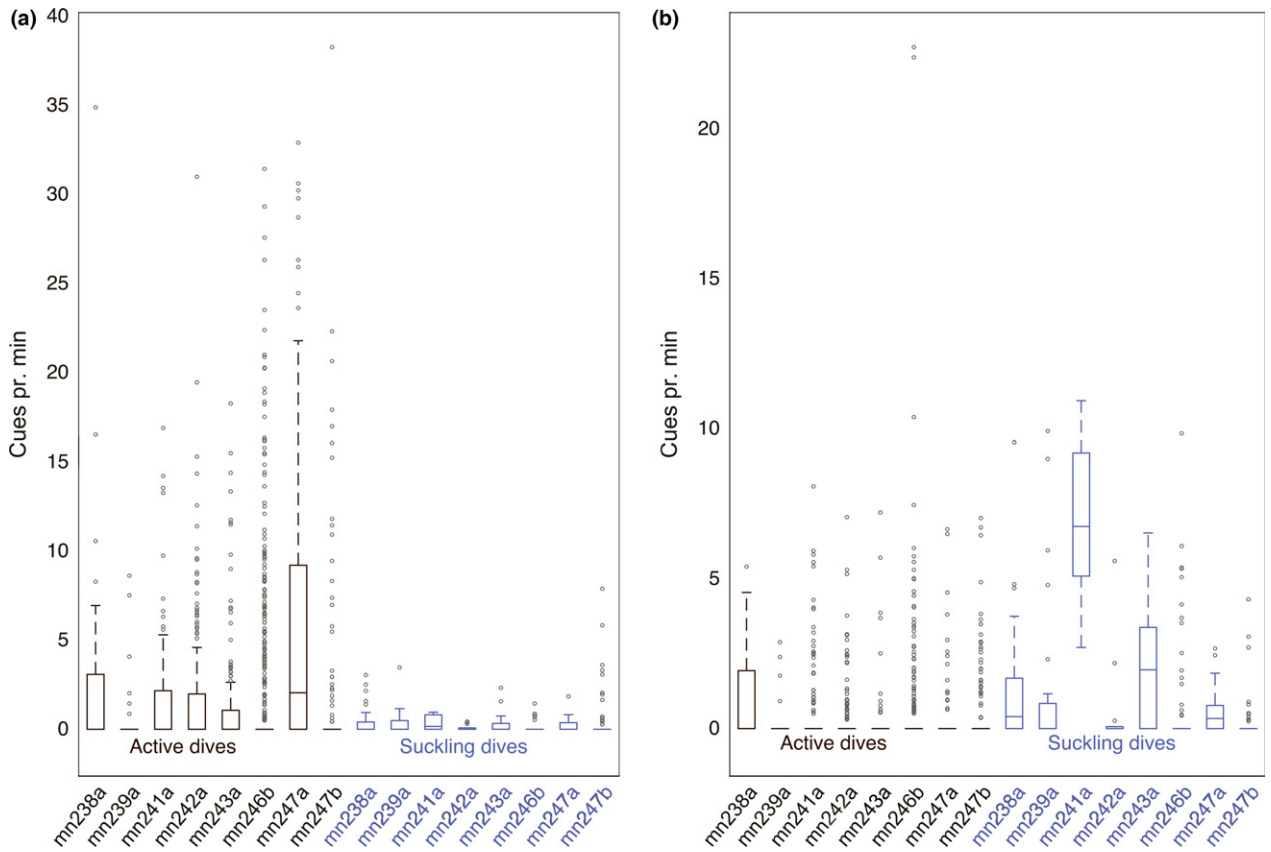


Fig. 3. Boxplot of acoustic cues per minute for all calves during suckling dives and active dives. (a) Grunting and tonal sounds (b) rubbing sounds.

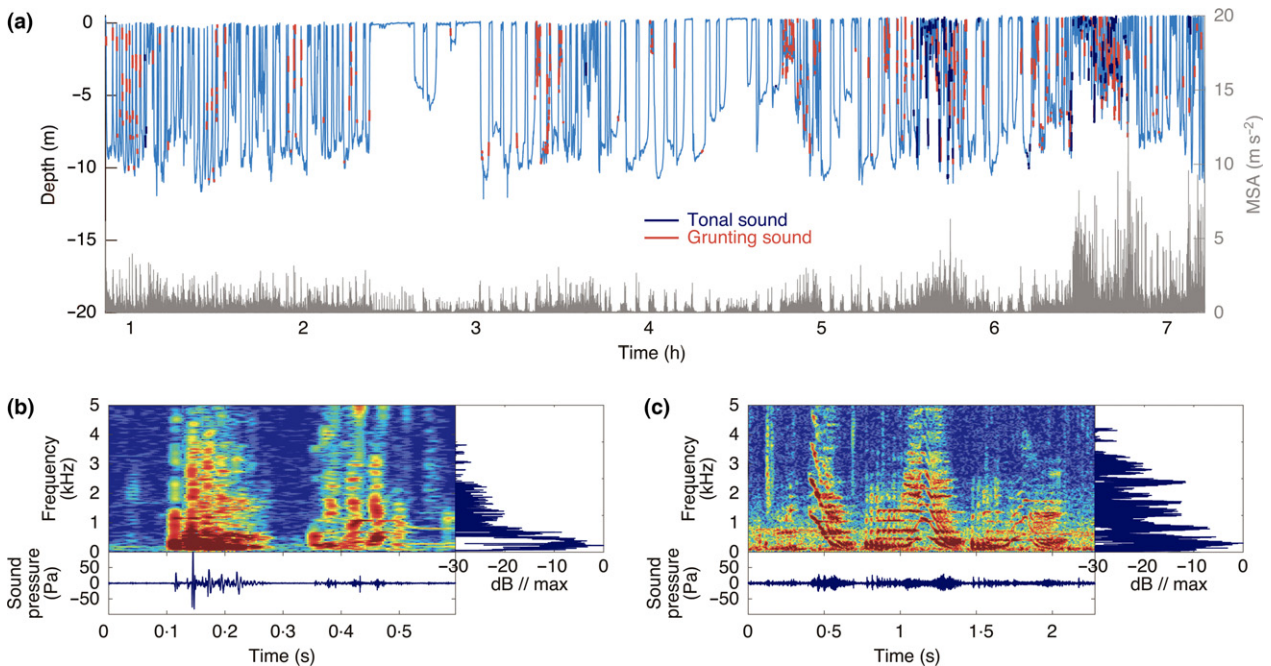


Fig. 4. (a) Dive profile of mn247a, depth in metres from surface (blue), minimum specific acceleration (MSA) ($m s^{-2}$) (grey), grunting sounds (red) and tonal sounds (dark blue) plotted on top of dive profile (b, c) spectrograms (Hamming window, nfft: 4096, 90% overlap) of a grunting sound (b) and a tonal sound (c). For both, the power spectrum is shown to the right and the waveform beneath.

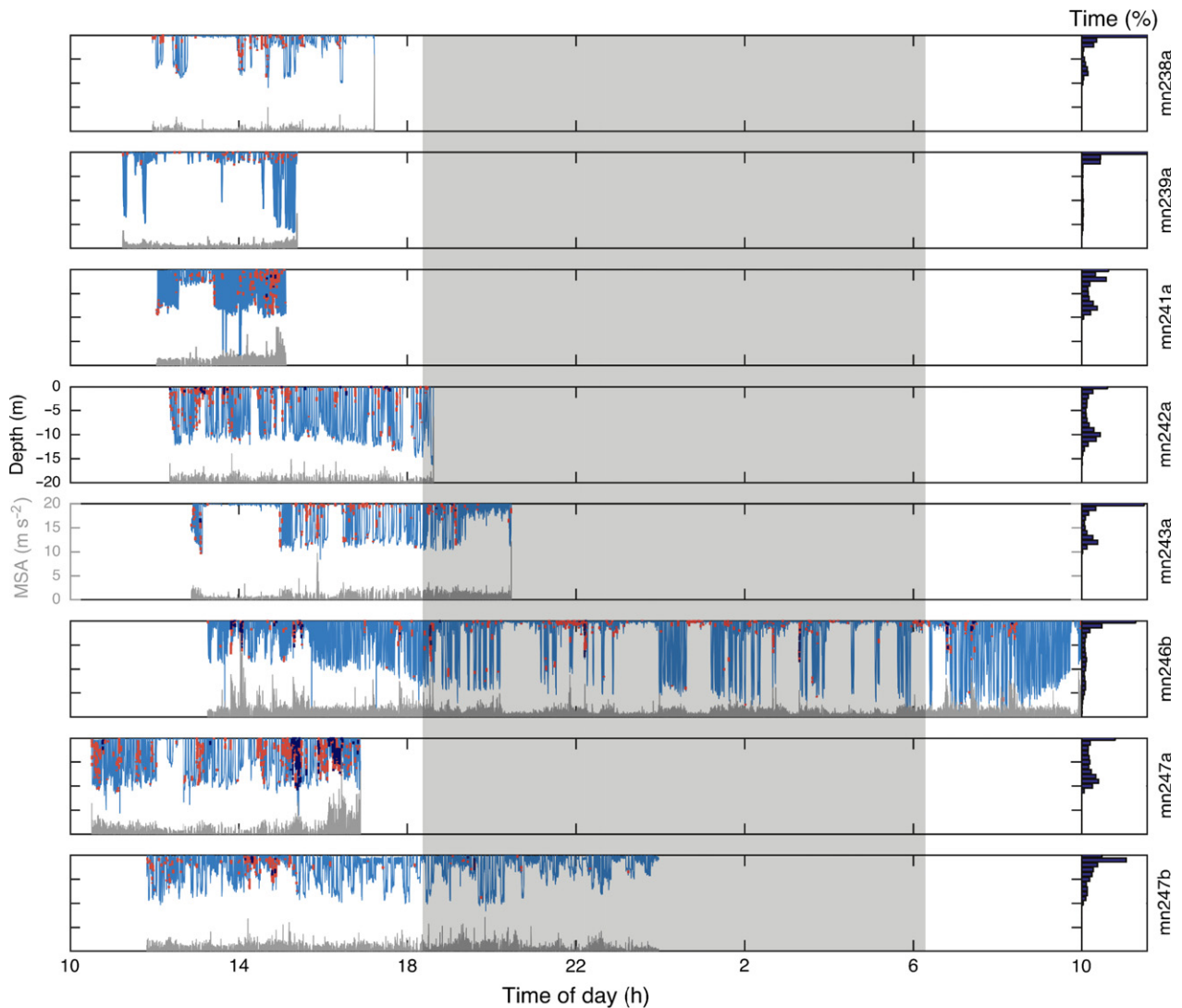


Fig. 5. Subplot of dive profiles for eight tagged calves ($n = 8$), minimum specific acceleration (MSA) (grey), grey areas indicate sun down, tonal sounds (dark blue) and grunting sounds marked (red). To the right a histogram of depth distribution for each calf.

(Brodie 1975) from the calm temperate waters of the breeding grounds to rougher, colder and more predator dense environments (Corkeron & Connor 1999; Clapham 2000). Previously, Herman & Antinaja (1977) reported that mother–calf pairs spent a large percentage (26%) of their time on breeding grounds resting, but they could not distinguish how much of that time was spent nursing. Here, we show that tagged neonate humpback whales are in suckling position, and so potentially suckling, on average 20% of the time (Table 1). This large time investment in suckling is consistent with the short time window for energy transfer before humpback whales migrate back to high latitude feeding grounds (Dawbin 1966). Distinguishing between actual suckling i.e. on-teat time where milk is transferred as opposed to suckling attempts is difficult, since there were no distinct signals in the accelerometer data indicating a successful transfer of milk from mother to calf. Moreover, time spent suckling does not translate directly into milk intake as milk transfer within a suckling bout is affected by

maternal quality and age/size of the offspring (Trillmich 1986; Cameron 1998). Thus, our results are likely an upper bound on the actual suckling time; nevertheless, our estimate of 20% time investment in suckling is consistent with findings for other marine mammals, despite differences in nursing strategies (Oftedal, Boness & Tedman 1987).

The overall suckling and diving behaviour documented here is in line with previous visual observations of neonate humpback whales (Glockner & Venus 1983; Glockner-Ferrari & Ferrari 1984). The calf dives slowly beneath the mother where it maintains a horizontal, motionless position for a duration of 2.5 ± 0.5 min before slowly returning to the surface to breathe (Table 1, Fig. 1). Taber & Thomas (1984) found a similar pattern in suckling neonate southern right whales, where they observed the mother logging at the surface, while the calf performed successive suckling dives with modal durations of 1.5–4.5 min depending on the age of the calves. This stationary suckling behaviour is in contrast with the suckling behaviour

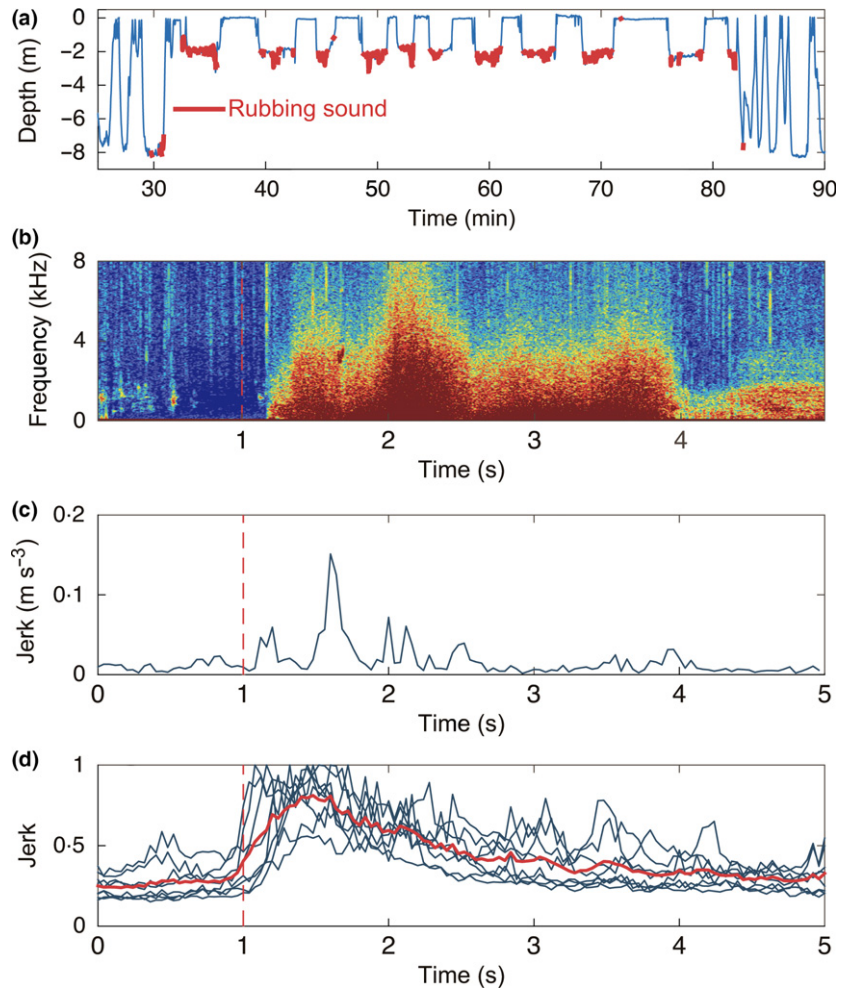


Fig. 6. (a) Segment of the dive profile of mn241a with occurrence of rubbing sounds indicated in red. (b) spectrogram (Hamming window, nfft: 4096, 90% overlap) of a rubbing sound (c) Norm jerk (i.e. magnitude of the tri-axial differential of acceleration, m s^{-3}) recorded by the tag at the same time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

of small toothed whales, where mothers nurse their young while swimming or gliding (McBride & Kritzler 1951; Asper, Young & Walsh 1988; Peddemors, Fothergill & Cockcroft 1992; Miles & Herzing 2003). Stationary suckling is energetically advantageous for both the mother and the calf, allowing the mother, who is solely dependent on stored body reserves, to conserve energy, and permitting the calf to allocate energy to growth rather than movement (Harrison 1969; Herman & Tavolga 1980). This stationary behaviour may be facilitated by calm waters, potentially explaining why mother–calf pairs seek out sheltered areas such as Exmouth Gulf.

However, suckling does occur not only in our data when mothers are logging at the surface: more than 50% of the inferred suckling dives of the tagged calves took place with the mother submerged at depths >2.5 m (Table 1). Suckling at depth was performed by six of eight calves in this study and was the dominant suckling mode in five of these. This large component of deep-water suckling would be missed in studies relying only on visual observations of logging mothers. The consistent offset in dive depth between mothers and calves of around 1.6 m (Fig. 1) implies that the mother is resting at depth while the calf dives down beneath her to suckle. Although diving to these

depths only requires a few fluke strokes, the large percentage of suckling occurring at depth is surprising, since both the mother and the calf should have an interest in conserving energy. Deeper dives may make it easier to maintain suckling position for the calf via the more compressed lungs that at a mean depth of 7.3 m will be some 40% less buoyant than at 1.5 m depth due to hydrostatic compression of air in the lungs, assuming that calves dive on inspiration. This reduced buoyancy could result in calves spending less energy on maintaining position during suckling, compared to near-surface suckling dives. Alternatively, buoyant calves may simply support themselves on the ventral surface of the mother while suckling to minimise effort.

Another possible explanation for suckling at depth relates to the thermoregulation of mothers. Given their dark skin colour, logging at the surface for long periods during warm daylight hours in the tropics may lead to overheating (Scholander & Schevill 1955). The slightly cooler deeper waters and absence of direct insolation may provide some relief. However, this would imply that deep-water suckling dives should be absent at night. Our limited night data show some deep-water suckling dives in the dark (Fig. 5), leading us to question this explanation. The

deeper suckling depths could also be driven by wind and sea state conditions; in rougher seas it may be easier to maintain position at depth than near the surface, but we do not have detailed sea state data to test that hypothesis. A final possibility is that suckling at depth could give an acoustic advantage since surface-related noise is significantly lowered, resulting in an improvement of acoustic vigilance.

Irrespective of the depth at which it is performed, suckling under water requires mother–calf coordination to ensure that milk is ejected successfully into the mouth of the calf, likely calling for cues to initiate this behaviour (Triossi *et al.* 1998). We hypothesised that acoustic cues could aid such coordination, but found that few calls and grunts were produced by mother and calf during suckling dives and that these were not more prevalent immediately before suckling was inferred to commence. Thus, even though humpback whales are normally highly vocal (Payne & McVay 1971; Winn & Winn 1978; Dunlop *et al.* 2007) these findings suggest that suckling is not initiated by acoustic communication. Rather, frequent rubbing sounds closely related with acceleration transients suggest that mechanical stimulation is used by the calf to initiate lactation by its mother (Fig. 6). Tactile cues to initiate lactation are also used by other cetacean species including bottlenose dolphins (*Tursiops truncatus*) (McBride & Kritzler 1951; Drinnan & Sadlier 1981; Peddemors, Fothergill & Cockcroft 1992), Atlantic spotted dolphins (*Stenella frontalis*) (Miles & Herzing 2003), killer whales (*Orcinus orca*) (Asper, Young & Walsh 1988) and southern right whales (*Eubalaena australis*) (Taber & Thomas 1984). In southern right whales, calves have been observed to head-butt their mothers if their suckling attempts are rejected (Taber & Thomas 1984). Such mammary bumps are common across all mammals as one of several cues to initiate lactation (Lent 1974; Appleby, Weary & Chua 2001), but unlike some terrestrial mammals (Sèbe *et al.* 2008), humpback whales seemingly do not also use acoustic cues in this process. Acoustic signals may provide inadvertent information to eavesdropping male humpback whale escorts or predators. Killer whales especially have been reported to have a high success rate in preying on neonatal humpback whale calves in the area (Pitman *et al.* 2015). In comparison, mechanical stimulation is an inconspicuous way of communicating, allowing the calf to covertly signal its mother of its readiness to suckle. Therefore, we hypothesise that silence in mother–calf pairs serves to reduce the risk of predation or dangerous escort attention (Aguilar de Soto *et al.* 2012).

Although the low call rates during suckling dives support the notion that silence is maintained to avoid detection, mother–calf pairs do in fact vocalise occasionally, albeit in a different behavioural context (Figs 3a, 4 and 5). Vocalisations are mainly associated with active dives, where they likely function as cohesive calls between mother and calf to maintain contact as also reported for other cetacean species (McBride & Kritzler 1951; Janik & Slater 1998). The disadvantage of such vocalisations is that

they may serve as homing cues for predators and other eavesdroppers with negative consequences for calf fitness. However, in low visibility waters, such as Exmouth Gulf, the calf and mother are unlikely to see each other beyond a few body lengths of the mother, and separation would also have severe fitness consequences, requiring a means of maintaining contact. When resting, such a need is limited (Fig. 4), but when moving there is likely an increased impetus for cohesion calls explaining why calls were more frequent during active dives. Increased vocalisation rates among mother–calf pairs have been reported when pairs are with one or multiple escorts suggesting that an increase in distraction level results in an increased vocal rate to maintain contact (Tyack & Whitehead 1983; Baker & Herman 1984; Dunlop, Cato & Noad 2008; Cartwright & Sullivan 2009b).

Another way to reduce detection of acoustic signals by distant listeners is to produce them at low source levels (Nakano *et al.* 2009; Dunlop 2016). Assuming that the received levels recorded by the tags, placed c. 1 m behind the blow hole, serve as reasonable proxies for source levels, the vocalisations, irrespective of whether produced by the calf or mother, are very weak. Received levels were some 40 dB lower than sounds recorded with a similar tag on a singing humpback male in the same area (P.T. Madsen, unpubl. data), and also much weaker (20–70 dB) than the social sounds reported for adult humpback whales (Thompson, Cummings & Kennison 1977; Thompson, Cummings & Ha 1986; Dunlop, Cato & Noad 2008). Assuming that the quiet vocalisations can be detected by other animals at an SNR of 0 dB, the low source levels translate into an active space of some 30 m for the measured ambient noise level, assuming spherical spreading, and negligible absorption over these short ranges. Thus, low level vocalisations may serve to keep contact without attracting unwanted attention, at the expense of a very small communication range between mother–calf pairs meaning that mothers and calves must keep close. Supporting this, we and others have observed that humpback whale calves rarely separate from their mother by more than a few tens of metres (Glockner & Venus 1983; Zoidis *et al.* 2014). Other humpback whale calls are produced at levels appropriate to the intended audience: a long communication range is favoured for songs to reach a large audience while the quieter social sounds are intended for the immediate group (Dunlop *et al.* 2013). Additionally, groups of humpback whales amplitude modulate their social calls presumably to avoid unwanted attention from potential singers nearby (Dunlop 2016).

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

Conclusion

A massive energy transfer occurs between mother and calf humpback whales during the few months between birth and migration, as demonstrated by significant body loss of the mother in synchrony with calf growth. Here, we show that humpback whale calves are in a position to suckle on average 20% of their time. The high proportion of time spent on suckling emphasises that humpback mother–calf pairs are vulnerable to disturbance that may increase energy expenditure and reduce energy transfer from mother to calf. Calves suckle by positioning themselves nearly motionlessly beneath their resting mothers. This low effort suckling behaviour may only be supported in calm waters possibly explaining why humpback whales often seek sheltered waters for nursing their calves, highlighting the conservation importance of such areas. Although suckling depths varied between calves, some 50% of suckling took place when the mother was submerged; a behaviour that may relate to thermoregulation, buoyancy, a reduction of wave action to facilitate suckling, or that submerged mothers may be in a better listening position for detecting singing escort males and predatory killer whales. However, this shallow diving behaviour also makes them more vulnerable to collisions with deep-draft vessels, as they are not visible from moving vessels.

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

Authors' contributions

S.V., L.B. and P.T.M. designed the experiment and collected the data. M.J. build the Dtags and developed analytical tools in Matlab. S.V. analysed the data, and drafted the manuscript with input from L.B., M.J. and P.T.M.

Acknowledgements

We warmly thank L. Hermannsen, F. Christiansen, J. Tyne, J. Totterdal and staff from the Department of Parks and Wildlife in Exmouth for their assistance and support during field work. We also thank K. Beedholm for help with analysis and A. Stimpert, F. Christiansen, A. Werth and B. McDonald for helpful comments on earlier versions of the manuscript. This work was funded by a Sir Walter Murdoch Honorary Professorship along with Carlsberg and FNU funding to P.T.M. L.B. was funded by Murdoch University, and M.J. was funded by the Marine Alliance for Science and Technology, Scotland, and by a Marie Curie Career Integration Grant.

Conflict of interest

None.

Data accessibility

Data for this paper are deposited in the Dryad Digital Repository <https://doi.org/10.5061/dryad.m8j17> (Videsen *et al.* 2017).

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Received 22 August 2016; accepted 15 March 2017

Handling Editor: Jeremy Goldbogen