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Mother–Calf vocal communication in Atlantic walrus: a first field experimental study

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Abstract In all colonial pinnipeds studied, mother–young vocal recognition exists and allows rapid and reliable meetings in spite of the confusing environment of the breeding colony. The efficiency of this recognition process guarantees pup survival, especially in species where females alternate foraging sea trips and lactation periods on land. The Atlantic Walrus (*Odobenus rosmarus rosmarus*) is a highly gregarious pinniped with females attending their calves for an extended period of time (2–3 years). Although we expect mother–calf vocal recognition to occur in this species due to the high density of individuals packed in herds, it has never been experimentally demonstrated. Here, we assessed the individual stereotypy of both mother and calf barks recorded in the wild by measuring frequency and temporal acoustic parameters. Both discriminant function and artificial neural network analyses resulted in high correct classification rates, underlying a well-defined individual stereotypy in parameters related to frequency modulation and frequency values. Playback experiments showed that mothers were more responsive to the barks of their own calf than to those of unrelated young. Finally, propagation experiments revealed that barks propagate at greater distances over water surface than over ice, acoustic features such as frequency modulation and frequency spectrum being highly resistant to degradation during propagation. Thus, acoustic analysis and propagation experiments suggest that these frequency parameters might be the key acoustic features involved in the individual identification process. This experimental study clearly demonstrates that Atlantic walrus has developed a highly reliable mother–calf vocal communication allowing such strong social bond.

Keywords Vocal communication · Mother–young interaction · Maternal care · Individual recognition · Signature · Pinnipeds

Introduction

In many mammals, mother and young have developed the ability to identify each other (Halliday 1983; Tang Halpin 1991), inducing mutual fitness benefits (Trivers 1972). By avoiding misdirected maternal care, females reduce their energy expenditure and enhance their reproductive success. For offspring, such recognition is essential to their survival since in most mammals mothers nurse only their own offspring and can be highly aggressive towards non-offspring (McArthur 1982; Harcourt 1991). Mother–offspring recognition is therefore crucial to reproductive success/offspring survival, especially for those animals breeding in large groups where a mother's ability to locate its offspring is compromised, and for colonial species where allo-nursing does not occur. To better understand the relationships between mother and offspring recognition systems (nature of communication channels, coding of individual signatures, modalities of maternal response) and social systems, it is essential to study closely related species experiencing various ways of life (social structure, mating system). In this regard, Pinnipeds (Phocids, Otariids and Odobenids) are models of choice: (1) females come

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ashore (on land or on ice) to breed and nurse their own young (2) individual vocal recognition between mother and young is reported in most studied species (see Insley et al. 2003 for a review) and (3) species vary dramatically in breeding density from solitary individuals to densely packed colonies. As reported in Insley et al. (2003), recognition ability between mother and offspring seems to depend on two factors: phylogeny and the difficulty for mother and young to meet (depending on, e.g. degree of animal density, duration of pup dependence, likelihood and predictability of separations). From the species that have been studied up to now, mother–offspring recognition appears more frequent in Otariids than in Phocids and more efficient in highly colonial species than in less gregarious ones (Insley et al. 2003; Charrier and Harcourt 2006).

Pinnipeds are myopic in air (Wartzok and Ketten 1999) and olfactory signals can only be used at short distance to confirm recognition when mother and offspring come in contact (Bonner 1968; Stirling 1971). Visual and olfactory cues being less efficient and reliable at long range, acoustic signals are the primary cues used for (mediating) individual recognition. Up to now, studies on mother–young vocal communication in pinnipeds focused on the two largest families, Phocids and Otariids (see Insley et al. 2003 for review), with the third family, the Odobenids (walruses) being very poorly studied. Only Miller (1985) described the vocal repertoire of Pacific walrus (*Odobenus rosmarus divergens*) and Atlantic walrus (*Odobenus r. rosmarus*). Two other studies, performed with two and one captive animals, respectively (Kastelein et al. 1995; Kibal'chich and Lisitsina 1979) gave a brief description of female and offspring calls, and a recent study showed the ability of captive walruses to produce novel sounds (Schusterman and Reichmuth 2008). To comprehend the mother–offspring recognition processes in walruses, there is a need for experimental investigations.

Walruses breed in Arctic areas are highly gregarious, forming herds of several hundreds or thousands of individuals (Fay 1982; Miller and Boness 1983; Sjare and Stirling 1996; COSEWIC 2006). The range of gregariousness varies between subspecies, period of the year and sex. For instance, during summer, Atlantic walruses form large mixed groups of individuals (Miller and Boness 1983; COSEWIC 2006), whereas Pacific walruses form large sex-segregated herds (Fay 1982).

Mating occurs during winter (January–March), and in spring of the following year, the birth occurs. Females give birth to a single calf (gestation period: 15–16 months with 4–5 months delayed implantation) that they will nurse for 18–24 months or more (25–27 months, Fisher and Stewart 1997). In Otariids and Odobenid, females nurse their own young for an extended period (4–24 months) compared to most Phocids (5 days to 2.5 months; Riedman 1990; Renouf 1991). In Odobenid mother and calf always stay together, even when the female forages at sea (Stewart and Fay 2001; Kovacs and Lavigne 1992) with no lengthy periods of separation as in Otariids (Nowak 2003). As in Otariids, females are highly protective of their young and they can be very aggressive to and may even kill non-related young (Harcourt 1991, 1992). As in Otariids too, adoption and allo-maternal care are extremely rare (Otariids: Riedman 1990; Georges et al. 1999; Odobenid: Fay 1982; Nowak 2003).

In walrus, the mother–calf bond is probably one of the strongest among pinnipeds. Mother and offspring almost never separate, and bonding can persist several years after weaning (Knudtson 1998; Nowak 2003). Females are very protective, and such strong maternal attachment for the young leads females to be very attentive and responsive to calls of their calves. Walrus produce diverse types of social vocalisations: aggressive vocalisations such as grunts, roars and guttural sounds, produced by adults, barks produced by both adults and young animals, and non-intentional sounds such as motorboat sound, sneeze, cough and flatulent sound (see Miller 1985 for details). Females and calves exchange barks when they are separated but also when reunited (Miller 1985).

Since barking seems to actively ensure the maintenance of the mother–calf bond, but also the maintenance with other members of the herd (either males or females), our study focuses on this particular vocalisation. Our investigations on mother–young vocal communication are the first performed on wild walruses in their natural environment. Although mother–calf vocal recognition has already been suggested (Fay 1982; Miller and Boness 1983; Miller 1985), it has never been investigated or experimentally demonstrated.

In the present study, we first performed an acoustic analysis of the barks produced by Atlantic walrus calves and mothers using different statistical methods to verify if these vocalisations are individually distinguishable, and to determine the acoustic parameters which can potentially support individual identity. Second, we carried out playback experiments on females in the field to assess whether they recognise their calf by their vocalisations. Third and last, we performed sound propagation tests with natural mother and calf barks over ice and over water, to investigate the preservation over distance of the acoustic features likely involved in the vocal identification process.

Materials and methods

Study site and animals

This study was carried out in the Foxe Basin, near Igloolik (69°21′53″N 81°48′58″W—Fig. 1), Nunavut, Canada, during

Fig. 1 Study location—Igloolik is located in the Foxe Basin, Nunavut, Canada (*lower panel*). Each flag (*upper panel*) represents a given spot where a group of walrus has been recorded during June 2006 ($n = 38$ groups recorded in 1 month). The study area represents about 5.000 km^2

two 1-month fieldtrips in June 2006 (sound recordings and playback experiments) and June 2008 (propagation tests). The walrus population in the Foxe Basin is estimated to be 5,500 individuals (DFO 2000; NAMMCO 1995). At this time of the year, the Atlantic walruses were hauling out on floating ice in groups of varying sizes (i.e. from 3 to more than 50 individuals), and they went to the water for feeding only. Groups were composed of adults (males and females) and young of varying ages (i.e. from newborns to 2–3 year old juveniles). We focused on females attending calves of the year, most of them being less than 1-month old (estimation based on the size of the calf, its greyish colour and on the presence of the umbilical cord, Qamaniq, personal communication; see Fay 1982 for similar age determination in Pacific walrus calves).

Recording procedure

Walruses were carefully approached by boat when resting on floating ice. In most of the cases (87% of the approaches, $n = 104$), the group stayed on ice and no striking behavioural change was noticed. Thus, walruses appeared not to be disturbed by our approach. Mothers' and calves' barks were recorded when interacting with each other at a distance ranging from 5 to 25 m, depending on sea conditions. Recording sessions of a mother–calf pair did not last more than 15 min to minimise or avoid any potential disturbance. Vocalisations recordings were made using a shotgun microphone [Sennheiser MKH 70, frequency response: 60–20.000 Hz (−3 dB)] connected to a digital recorder (Marantz PMD 670, sampling frequency: 22.050 Hz). Barks were downloaded to a laptop to set up playback tracks and for further analysis.

Call analysis

We could differentiate three sub-categories or graded barks (Miller 1985; Charrier, personal observation): "barks" produced in non-distress context, "distress barks" produced in fast long trains by calves, and "soft barks" or "contact calls" were low amplitude barks produced by mothers and calves when they were in a close contact, most of the time with the mouth closed. We selected barks produced in non-stressful mother–young interactions and rejected any distress barks and soft barks. Indeed distress barks presented different characteristics: they were produced in long trains at a fast rate louder than regular barks, and thus exhibited more harmonics than regular barks with an emphasis on high frequencies. Soft barks, produced with a closed mouth, were very faint, and thus showed almost no harmonics. Under non-distress conditions, mother and calf usually exchanged single barks or short bark series. We selected barks with a good signal-to-noise ratio and without overlap with other vocalising animals. Each individual was the focus of a unique recording session in which barks from several calling bouts were recorded.

Because barks produced by walrus calves and females were low-pitched (Figs. 2, 3), we resampled the original recording from 22.050 to 11.025 Hz to process to an accurate analysis in the frequency domain. Acoustic measurements were made using Avisoft SAS-Lab Pro (Avisoft Bioacoustics, Berlin, Germany, R. Specht—version 4.36). For each bark, several variables were considered to describe the temporal and frequency patterns of the recorded signals (Fig. 4). The total duration of the call (Dur, s) was measured on the oscillogram. Variables relative to energy spectrum such as the frequency values (Hz) of the first, second and third energy peak (Fmax1, Fmax2 and Fmax3, respectively—Fig. 4) were measured on the amplitude spectrum of the entire call (Hamming window, frequency resolution: 0.6 Hz). Lastly, frequency values of the fundamental frequency (fo) were automatically measured every 10 ms from the beginning to the end of the call

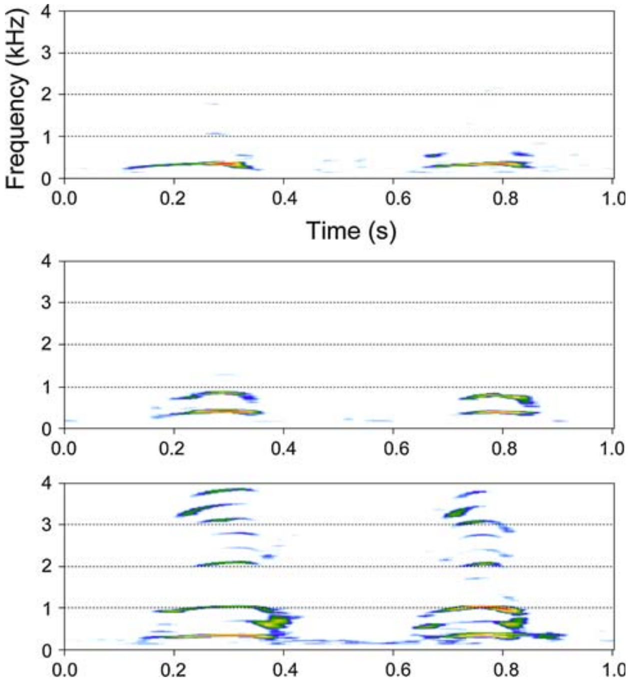

Fig. 2 Barks from three different Atlantic walrus calves. These calls are composed of a fundamental frequency and few relative harmonics with a chevron-shape frequency modulation (hamming window size: 512 points; overlap 75%)

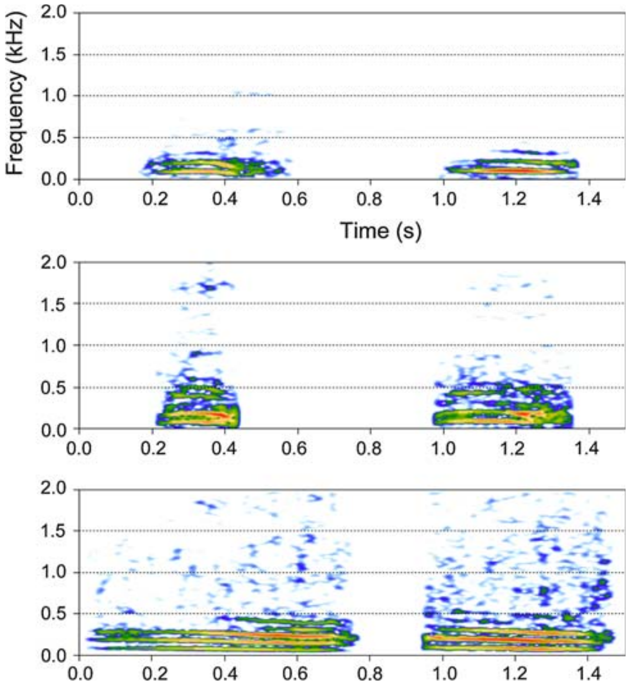

Fig. 3 Barks from three different Atlantic walrus mothers. The acoustic structure is similar to the one observed for calves except that mother barks are longer in duration and lower pitched (hamming window size: 1,024 points; overlap 90%)

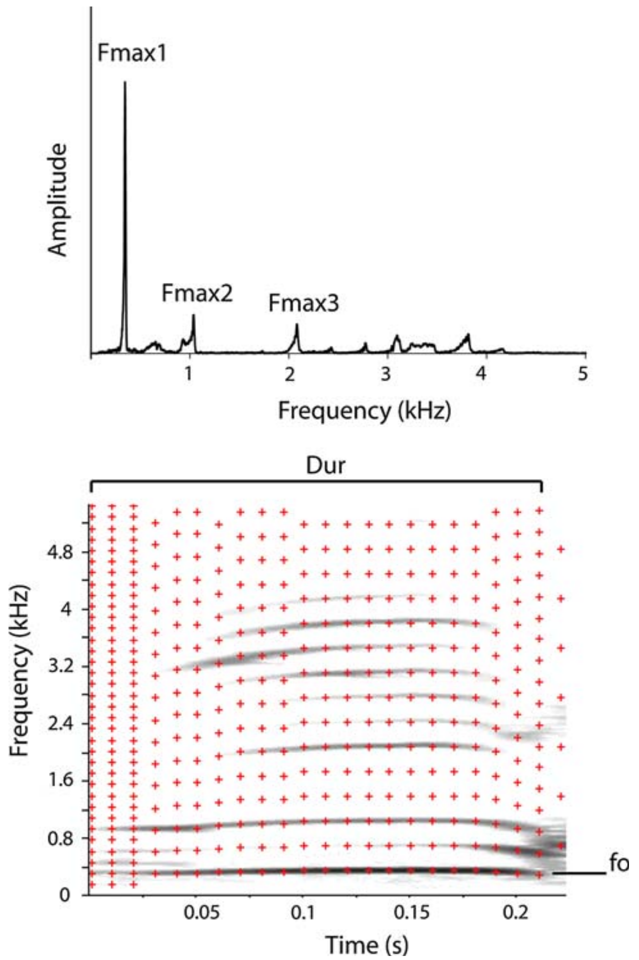

Fig. 4 Acoustic parameters measured on walrus barks. Spectral measurements such as *Fmax1–3* were performed on the averaged energy spectrum. Duration (*Dur*) and temporal variations of the fundamental frequency fo1–*n* (calculated by the auto-correlation method) were automatically measured from the spectrogram (hamming window size: 512 points, overlap 96.87%—automatic measurements module in Avisoft-SASlab Pro)

(fo 1–*n* (Hz); *n* is the number of measured frequency values and depends on the duration of each bark, *n* = [total duration of the bark (ms)/10] + 1). These frequency values were derived by calculation directly from the spectrogram (FFT size: 512 points, 98.30% overlap—Fig. 4). These measurements allowed us to follow the temporal variations of the fundamental and then gave an accurate view of the evolution of the frequency modulation pattern of the call.

Statistical analysis methods

To assess if females' and calves' barks were individually stereotyped, and thus could potentially be used in mother–calf recognition, we analysed the call acoustic cues using three different methods. For the analysis of single acoustic variables, we calculated the potential of individuality coding (PIC) based on the between- and within-individual coefficients of variation (CVb and CVw, respectively) and a one-way ANOVA using individual as a categorical predictor variable (Robisson et al. 1993; Charrier et al. 2002, 2003; Charrier and Harcourt 2006). Besides this univariate approach, two multivariate analyses (discriminant function analysis—DFA—and artificial neural network analysis—ANN) provided classification procedures that assigned each recorded call to its appropriate emitter (correct assignment) or not (incorrect assignment).

The within-individual and between individual coefficients of variation (CVw and CVb, respectively) were calculated using the formula: $CV = 100 \times (SD/X)$, where SD was the standard deviation, X was the mean of the sample (Sokal and Rohlf 1995). To assess the potential of individual coding (PIC) for each parameter, we calculated the ratio CVb/mean CVw (mean CVw being the mean value of the CVw of all individuals). For a given parameter, a PIC value >1 meant that this parameter was individually specific since the intra-individual variability was smaller than the inter-individual variability (Robisson et al. 1993). For each acoustic parameter, we used one-way ANOVA to assess differences between individuals. We employed Welch's correction for unequal variances for all ANOVAs (Welch 1938) regardless of the results of heteroscedasticity diagnostic tests (Moser et al. 1989; Moser and Stevens 1992). Because we were measuring several acoustic features on each call and performing multiple tests on the same data set, we adjusted the level of significance using the sequential Bonferroni adjustment (Keppel 1991; Quinn and Keough 2002).

We further tested individuality in the calves' calls by performing cross-validated discriminant function analyses (DFA). For the cross-validation, 2/3 of the data were used for the training and the remaining 1/3 for the testing. By using this analysis, we determined which acoustic features can be used to differentiate individuals, and we also assessed the percentages of correct call classification to individuals. This analysis was performed using Statistica v.6 (StatSoft Inc. 2001).

Artificial neural network (ANN) is also a powerful data modelling tool to classify vocalisations into categories such as species, individuals or call types (Reby et al. 1997; Parsons and Jones 2000; Deecke and Janik 2006). We used a multilayer feed-forward networks with online-standard back-propagation epoch training and adaptive learning (Rumelhart et al. 1986) using the ANN Toolbox version 0.4.2 (Copyright© 1998, 2001 Ryurick M. Hristev) for Scilab version 2.6 (Copyright© 1989–2005. INRIA ENPC). The inputs of the network were the acoustic variables measured from the calves' barks, and the outputs were the different individual calves. Our network used only one hidden neuron layer. This network was trained with 2/3 of the input data (2/3 of the date for each individual was chosen randomly), and after training, the remaining 1/3 of the input data was used to test the network. Since all the acoustic variables were in different units (s or Hz), we transformed the data before training. For each variable, we divided the data by its maximum value, so that all data ranged between 0 and 1. To obtain the best performance with the network, we performed several runs in which we changed the number of epochs during the training process (from 500 to 3,000) and the number of neurons in the hidden layer (from 4 to 16). The reliability of call classification obtained with the ANN method was then compared with the one of DFA to assess if one method might outperform the other.

Playback test procedure on mothers

All recordings and playback tests were performed from the boat, and all tested females were not alone on ice but always with other animals (males, females and mother–calf pairs). The age of the tested females could not be assessed. Playback stimuli were prepared on the laptop by one researcher (the experimenter), while another researcher (the observer) was continually monitoring the female to be tested since it was not possible to individually mark the animals. Playback tests on mothers were done in the 15–20 min following the recordings of their own calf. Females were tested in the presence of their calf since it was impossible to temporarily remove the young during the playback session as it has been done in previous experiments with Subantarctic fur seals *Arctocephalus tropicalis* (e.g. Charrier et al. 2001). Calls were broadcast using the Marantz digital recorder (frequency response: 0–20 kHz: −0.5 dB; dynamic range: 86 dB) connected to an Audax unidirectional loudspeaker via a customised 10-W amplifier (frequency response 0.1–9 kHz ± 4 dB). For each tested female, we broadcast two different series, one composed of her own calf's calls and another one composed of calls from a non-filial calf (stranger). Each experimental series consisted of 5–6 calls separated by silences ranging from 0.2 to 0.5 s, matching the natural call rate (i.e. based on the recording of the natural bark sequence). Since the calves' calls could be different in duration between the two experimental series (own calf/stranger calf), we chose 5 or 6 calls to ensure that the total duration of each series would be the same. Before the beginning of the playback, we waited until both mother and calf were calm. The order of presentation of both series (own calf and unaffiliated calf) was balanced among tested females. While the experimenter was playing the series, the observer was assessing the female's behavioural response to the playback series and was not aware of the series order (blind test). To avoid pseudo-replication, all the tested mothers received "stranger" calls coming from different individuals (i.e. calls from calves recorded previously to the playback on a different group). The distance between the loudspeaker and the tested mother was about 10–15 m, and calves' calls were played at an approximate natural sound pressure level (78 ± 4 dB_{SPL} measured at 1 m using a Bruel and Kjaer sound level metre type 2235, slow setting, linear scale). The female's behaviour was observed during 60 s after the end of the playback series, and we waited at least 5 min before playing the second experimental series (i.e. until the female returned to a relaxed behaviour).

Behavioural responses measures

Preliminary field observations showed that under natural conditions, the mother responded to her calf's barks by searching (head) movements, looking to her young, calling and smelling it. To characterise the behavioural responses of the mothers to our playback tests, we thus used a 5-point ethological scale: 0 = no reaction; 1 = the female looked once towards the speaker during the playback; 2 = she looked towards the speaker and searched around (head movements); 3 = she looked towards the speaker, searched around and smelt/touched her calf during the playback; 4 = she looked towards the speaker, searched around, called during the playback and smelt/touched her calf (strong reaction). Mothers' behavioural responses to the calls of their own calf versus calls of a stranger were compared using Wilcoxon signed ranks tests (Sokal and Rohlf 1995).

Propagation tests

Walruses occupy several types of environments such as sea ice (fast ice and floating ice), water and land. We studied the two most typical and representative environments in which mother–calf vocal communications take place, over ice and water surface, to determine at which maximal distance the mother–calf individual recognition remains reliable.

To proceed, we played back two calls series: one of mother barks and the second of calf barks. Each series consisted of ten identical natural calls from a given mother or from a given calf separated by a 1-s silence. At the beginning and the end of each series, a synthetic sound showing an inverted V-shape frequency modulation (0.2–2 kHz) has been added to help in the synchronisation in time of the different recordings. The calls series were broadcast at a natural SPL (82 ± 3 dB_{SPL} at 1 m for the mother series, 78 ± 4 dB_{SPL} at 1 m for the calf series, SPL measurements were made with a Bruel and Kjaer sound level metre type 2235, slow setting, linear scale) and propagated calls were re-recorded at different distances using an Edirol R-09 digital recorder (sampling frequency = 44.1 kHz; frequency response: 20–22 kHz). The propagation distances were 1 m (control), 8, 32, 64, 128, 256 and 512 m (last distance: only on water surface). The speaker was placed at about 50 cm above ice or water surface (to mimic the location of the head). Distances between the speaker and the microphone were measured with a graduated rope for distances till 32 m and with a Garmin eTrex Legend GPS for longer distances (distance precision ± 2 m).

The ice environment was a flat fast ice area covered by 5 cm of snow. Propagation tests in both studied environments were performed under similar weather conditions (no wind, temperature = 0.5–2°C; air pressure = 100.5 kPa) To quantify the modifications undergone by the barks during propagation, we measured three main acoustic parameters: amplitude and frequency modulations (AM and FM) and the frequency spectrum of the entire bark. For each acoustic variable, we compared the averaged data from the ten stimuli at a given propagation distance to those obtained at 1 m (control) by using Pearson's r product-moment correlation coefficient. To assess the modification of the amplitude modulations at the different distances, we calculated the smoothed envelope of the entire bark using the analytical signal method using Hilbert transform. To characterise the change in FM pattern of the barks during propagation, we used Avisoft Correlator based on the digital spectrographic cross-correlation (SPCC) method. This method, described in detail by Clark et al. (1987) and Khanna et al. (1997), simultaneously analysed the frequency, amplitude and time components of a signal by sliding the averaged spectrograms (FFT size 512, overlap 87.5%) of the propagated signal along the time axis of the averaged spectrogram of the non-propagated signal.

Results

We analysed a total of 544 barks from 22 calves (14–73 calls per individual) and 164 barks from 11 mothers (8–20 calls per individual). To maintain a consistent number of variables describing the frequency modulation pattern, we kept the first eight measured values of the fundamental frequency for calves (i.e. fo1–8) and the first 16 values for the mothers (i.e. fo1–16). These numbers corresponded to the minimum available data for all individuals (for instance, calf barks' duration ranged from 72 to 317 ms in the 16 individuals data set used for DFA and ANN analyses). Then a total of 12 and 20 acoustic variables were kept for the different data analyses on calves (Dur, Fmax1–3 and fo1–8.) and mothers (Dur, Fmax1–3 and fo1–16), respectively.

Descriptive analysis and PIC values

As a general rule, barks produced by Atlantic walrus calves (Fig. 2) and mothers (Fig. 3) were composed of a

Table 1 Analysis of the different acoustic parameters measured in barks of calf and mother walrus

Var		N_{ind}	N_{calls}	Mean ± SD	CV_{b}	$\text{CV}_{\text{w mean}}$	PIC	ANOVA
Dur (s)	Calf	22	544	0.139 ± 0.044	32.05	23.04	1.39	$F_{21,519} = 18.91$*
	Mother	11	164	0.322 ± 0.123	38.13	23.71	1.61	$F_{10,153} = 18.68$*
Fmax_1 (Hz)	Calf	22	544	420 ± 110	26.32	11.49	2.29	$F_{21,519} = 42.53$*
	Mother	11	164	168 ± 71	42.11	19.40	2.17	$F_{10,153} = 10.16$*
Fmax_2 (Hz)	Calf	22	492	744 ± 368	49.49	29.69	1.67	$F_{21, 519} = 25.81$*
	Mother	11	164	197 ± 121	61.24	41.55	1.47	$F_{10,153)} = 7.88$*
Fmax_3 (Hz)	Calf	22	392	1017 ± 554	54.50	38.58	1.41	$F_{21,519} = 24.97$*
	Mother	11	164	337 ± 160	47.33	40.62	1.17	$F_{10,153} = 10.88$*
fo (Hz) averaged	Calf	22	544	400 ± 104	25.93	10.17	2.55	$F_{21,519} = 94.14$*
	Mother	11	164	118 ± 24	24.94	14.25	1.75	$F_{10,153} = 67.07$*

fo averaged is the average value of the 8 data and 16 data measured on the fundamental frequency of calf and mother barks, respectively

ANOVA: for all acoustic variables, *F* values are indicated in the table with their respective *P* values (* $P < 0.001$)

fundamental frequency (fo) and harmonics, and showed a chevron-shape frequency modulation.

In calf barks, the fundamental frequency ranged between 120 and 689 Hz, with an average at 379 Hz. Most of barks had few harmonics (1–4 additional harmonics, Fig. 2) and a mean duration of 139 ± 44 ms (range: 72–349 ms). The main energy frequency band (i.e. Fmax1–3) ranged from 420 to 1017 Hz, and the highest energy peak frequency (Fmax1, 420 ± 110 Hz) was mainly concentrated on the fundamental frequency (Table 1). Mother barks were longer in duration (322 ± 123 ms, Table 1) and lower pitched with an averaged fundamental frequency at 118 Hz (based on the whole data set). As in calves' barks, the energy was concentrated in the lower frequencies. Indeed, the average Fmax1–3 values ranged from 168 to 337 Hz, with the highest energy peak frequency (Fmax1, 168 ± 71 Hz) corresponding also to the fundamental frequency (Table 1). In both calf and mother barks, the fundamental frequency showed a slow frequency modulation pattern composed of an ascending part at the beginning followed by a plateau in the middle and ended by a descending part (Figs. 2, 3). As summarised in Table 1, for all variables, the coefficients of variation within individuals were smaller than those among individuals, resulting in PIC values >1. This means that all measured variables could potentially support "individual" information. For both mother and calf vocalisations, the highest PIC values were obtained for the temporal variation of the fundamental frequency fo1–*n* (i.e. frequency modulation pattern) and Fmax1.

Discriminant function analysis

For both DFA and ANN, we kept individuals for which we had recorded at least 14 calls. This resulted in a calf data set composed of 450 barks from 16 individuals, and a mother data set composed of 135 barks from eight individuals.

For the calf data set, cross-validated DFA performed on 12 acoustic variables revealed a significant difference among calves (Wilk's $\lambda = 0.0043$, $F_{180,4014} = 17.37$, $P < 0.001$). The overall DFA extracted three discrimination roots (eigenvalues: 11.7, 1.27 and 1.23, respectively) that contributed to 90.2% of the total variance (74.3, 8 and 7.9%, respectively). Parameters relative to fo were mainly correlated with the first root (coefficients of correlation > 0.5), Fmax2–3 were correlated with the second one, and, Fmax1 and Dur were correlated with the third one. Temporal variation of the fundamental frequency fo (i.e. frequency modulation pattern) contributed the most to distinguish the different calves. In addition, the classification matrix revealed that barks were correctly assigned to individuals with an averaged classification rate of 67% (range: 19–100%—Table 2, cross-validated DFA). Only one calf had a low classification rate (i.e. 19%), however, this rate was still greater than those expected by chance (1/16 = 6.25%).

For the mother data set, cross-validated DFA performed on 20 acoustic variables revealed a significant difference among mothers (Wilk's $\lambda = 0.0000471$, $F_{140,728} = 18.10504$ $P < 0.001$). Three discrimination roots were extracted (eigenvalues: 470.71, 9.73 and 1.70%, respectively) that contributed to 99.6% of the total variance (97, 2 and 0.4%, respectively). Most fundamental frequency parameters (fo) were strongly correlated with the first and second roots, Fmax2–3 were correlated with the first root, Fmax1 and Dur with the third root as well as some fundamental frequency parameters. The temporal variation of fo contributed the most to distinguish the different females. Moreover, the classification matrix indicated that barks were correctly assigned to individual females with an averaged

Table 2 Percentages of correct classification rates (calves: $n = 16$ individuals, 450 barks; mothers: $n = 8$ individuals, 135 barks) with two different statistical methods: cross-validated discriminant function analysis (DFA) and artificial neural network (ANN)

Calf ID	*N* calls (total)	DFA (%)	ANN (%)	Mother ID	*N* calls (total)	DFA (%)	ANN (%)
cA	19	84	71	mA	16	60	20
cB	46	83	63	mB	18	80	83
cC	15	80	100	mC	14	100	100
cD	16	63	100	mD	14	25	75
cE	18	72	100	mE	17	83	67
cF	23	48	50	mF	19	50	100
cG	15	67	60	mG	18	50	50
cH	27	52	56	mH	19	67	100
cI	17	41	17				
cJ	72	81	100				
cK	16	100	83				
cL	27	85	100				
cM	19	58	86				
cN	42	62	7				
cO	21	19	43				
cP	57	79	95				
Classification rates		67	71			64	74

classification rate of 64% (range: 25–100%—Table 2, cross-validated DFA).

Artificial neural network

For the calf data set, the back-propagation network was trained with the 12 acoustic variables, and the best performance was obtained with a hidden layer composed of 12 neurons and a training of 3,000 iterations. Using these network characteristics, we obtained an overall correct classification rate of 71% (range: 7–100%, Table 2), with only one calf showing a very low classification rate, but greater than that expected by chance (1/16 = 6.25%).

For the mother data set, the back-propagation network was trained with the 20 acoustic variables, and the best performance was obtained with a hidden layer composed of 20 neurons and trained for 2,000 iterations. Using these network characteristics, we obtained an overall correct classification rate of 74% (range: 20–100%, Table 2).

Individual classification rates obtained with DFA and ANN were not significantly different (*t*-tests for dependant samples: $t_{16} = -0.58$, $P = 0.57$ for calves and $t_8 = -6.72$, $P = 0.41$ for mothers).

Playback test on mothers

We performed 16 playback sessions (i.e. 16 tested females), but three females did not react to both experimental series (own calf and stranger calf) and were therefore removed from our analysis. Based on the 13 remaining females (Fig. 4), behavioural responses to the own calf's calls were significantly stronger than those obtained with calls from a stranger calf (Wilcoxon matched pairs test, $Z = 3.06$, $P = 0.002$). Typically, during the playback of their own calf barks, females looked towards the speaker, searched around and checked their own calf. Only one of the 13 females gave the strongest behavioural response (score of 4) by emitting several calls in reply to our playback (Figs. 4, 5).

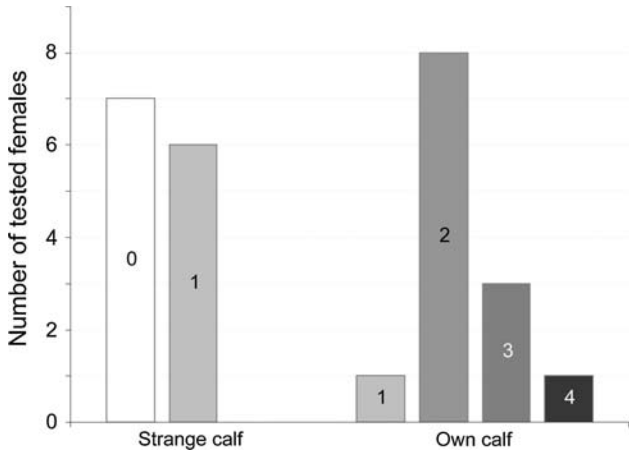

Fig. 5 Behavioural responses of walrus females obtained during the playback tests. The use of a 5-point ethological scale (from *0*: no reaction to *4*: strong reaction) allowed us to characterise the behavioural response of the tested females to calls from non-filial calves (i.e. strange calf) and from their filial calf (i.e. own calf). Comparison between responses to strange and own calf calls was found significant (Wilcoxon matched pairs test; $Z = 3.06$, $P < 0.01$)

Table 3 Pearson's product moment correlations for averaged spectra (FFT), averaged spectrograms (FM) and averaged envelopes (AM) between the reference signal (1 m) and the propagated signal at different distances (from 8 to 128 m) and in two different environments (over ice and over water) for both calf and mother barks

Distance of propagation (m)		8	16	32	64	128	256
Ice							
Calf	Averaged spectra (FFT)	0.99	0.96	0.80	0.29	NC	
	Averaged spectrograms (FM)	0.98	0.91	0.70	0.35	NC	
	Averaged envelopes (AM)	0.90	0.81	0.83	0.18	NC	
Mother	Averaged spectra (FFT)	0.82	0.72	0.33	0.15	0.12	
	Averaged spectrograms (FM)	0.74	0.65	0.28	0.14	0.12	
	Averaged envelopes (AM)	0.69	0.61	0.28	0.19	0.25	
Water							
Calf	Averaged spectra (FFT)	0.99	0.99	0.99	0.99	0.79	0.03^{NS}
	Averaged spectrograms (FM)	0.99	0.99	0.98	0.98	0.70	0.05
	Averaged envelopes (AM)	0.89	0.91	0.87	0.89	0.71	0.04
Mother	Averaged spectra (FFT)	0.97	0.93	0.94	0.87	0.64	0.08
	Averaged spectrograms (FM)	0.95	0.90	0.89	0.79	0.59	0.12
	Averaged envelopes (AM)	0.93	0.92	0.91	0.88	0.71	0.18

For each acoustic variable, averages were calculated on the ten broadcast stimuli (*NC*: not calculated. All correlations were all significant at $\alpha = 0.0083$ except one marked as *NS*, non-significant)

Propagation experiments over ice and water

Over ice, propagated bark series could be detected from background noise out to 128 m for mothers and out to 64 m for calves. At greater distances, the signal-to-noise ratio was <1, and it was impossible to find the propagated calls on our recordings (Table 3). Correlations between the propagated signals and the control signal for the three studied parameters (AM, FM and frequency spectrum) were decreasing as distance increases. Pearson's *r* coefficients were found >0.5 out to 32 m for the calf series and out to 16 m for the mother series. The highest correlations were obtained for the frequency spectrum (FFT). Propagation results were not symmetrical between mother and calf indicating that degradations of acoustic features were stronger for mother barks than for calf barks.

Over water, propagated bark series were detectable from background noise out to 256 m for both mother and calf series. At 512 m, we could not detect the calls on the recordings. As expected, the correlations between the non-propagated signal and the propagated ones for the three studied parameters decreased also when distance increases but, surprisingly, all the Pearson's *r* coefficients were >0.70 up to 128 m. Again, the highest values were found for the frequency spectrum. However, at 256 m, a drastic change occurred since all Pearson's *r* correlation coefficients were found lower than 0.18 whatever the studied acoustic variable. In this environment, both calf and mother barks showed the same propagation efficiency.

Discussion

Our acoustic analyses demonstrated that barks produced by walrus calves and mothers showed an individual stereotypy which is a prerequisite to individual vocal recognition. Univariate analyses showed that all acoustic variables measured in barks had PIC values >1 meaning that each studied variable can be potentially used by mothers or calves to recognise each other. Corroborating the results of univariate analyses, the percentages of correct classification rates obtained with cross-validation DFA and ANN methods were high since around 70% for both mothers and calves. We had two calves for which we obtained low classification rates. This could be explained by a very young age of these individuals causing a lack of vocal stability, or a particular motivational state (i.e. hunger, cold, fear) that could not be observed or controlled during our recordings.

This level of stereotypy in vocalisations has been mainly found in Otariids and supports mother–pup vocal recognition (Insley 1992; Phillips and Stirling 2000; Page et al. 2002; Charrier and Harcourt 2006). Although it is not entirely valid to compare these DFA results to those of previous studies since the number of acoustic variables measured and the number of individuals or calls per individual vary between studies, comparisons gave interesting outcomes on the individual stereotypy of vocalisations in mammal species. For instance, the DFA correct classification rates obtained for walrus barks were similar to some found in Otariid pups (ranging from 52 to 95%, for review see Charrier and Harcourt 2006), but greater than those found in Phocids (ranging from 14 to 64%, for review see Charrier and Harcourt 2006). It appears that colonial living, high degrees of polygyny, no allo-suckling, prolonged maternal absences, and thus high selective pressures for mother–offspring recognition have lead to strong vocal stereotypy (Charrier and Harcourt 2006). Walrus presents similar selective pressures for mother–young recognition except short but frequent mother–calf separation while the mother is feeding and an extended maternal attendance (Fay 1982; Riedman 1991; Knudtson 1998). Thus, individual vocal stereotypy seems to strongly depend on both ecological and biological traits.

In the Atlantic walruses in the present study, the highest PIC values were found for the parameters relative to the fundamental frequency fo and Fmax1, and the DFA showed that these parameters contributed the most to the total variance. Such a result was not surprising because spectral characteristics are strongly correlated to the anatomical structure of the vocal tract, specific to each individual (Kelemen 1963). These results are consistent with those previously found in other mammal species such as Otariids (Insley 1992; Phillips and Stirling 2000; Charrier et al. 2002, 2003; Charrier and Harcourt 2006) and ungulates (Reby et al. 1999; Torriani et al. 2006). Although our analyses revealed that fundamental frequency, its temporal variation (i.e. frequency modulation) and energy spectrum could be potentially used for individual recognition, only playback experiments with modified or synthesized signals could prove their real use by individuals for identification. It should also be noted that the frequency modulation pattern was an important feature for individual discrimination processes in numerous colonial/social species where parent–offspring vocal recognition occurs such as colonial seabirds (Charrier et al. 2001; Aubin and Jouventin 2002), seals (Charrier et al. 2002, 2003), bats (Scherrer and Wilkinson 1993) and dolphins (Janik et al. 2006).

From a methodological point of view, we used two difference statistical methodologies to classify calls by individuals: a DFA and an ANN. Although the classification rates obtained by both methodologies often depend on the type of studied vocalisations, the number and type of measured acoustic variables (Parsons and Jones 2000), no significant difference between DFA and ANN was detected in our study. One could have expected better classification with ANN since the algorithm is based on the error-correction learning rule, however, for our studied vocalisations, both methods revealed similar results. This suggests that either one or the other method can be used to classify calls to individuals at least in walrus.

Playback tests on mothers suggest that walrus females were able to recognise their calf's voice. They reacted significantly more strongly to the calls of their own calf than to those from an unknown calf. These experiments confirmed the preliminary observations made in previous walrus studies (Fay 1982; Miller and Boness 1983; Miller 1985). We expected stronger females' reactions to the playback of calf' calls females would have been tested in the absence of their young. The responsiveness of females towards playback of pup's calls varies strongly between species. Indeed, even if in some species, females responded strongly in the presence of their young (1 captive California sea lion *Zalophus californianus*, Hanggi 1992; Northern elephant seal *Mirounga angustirostris*, Petrinovich 1974), for most other studied species, either females showed a weak responsiveness when tested in the presence of the young (in grey seals *Halicherus grypus*: McCulloch and Boness 2000; in Australian sea lions *Neophoca cinerea*: Pitcher, Harcourt and Charrier, unpublished data) or a strong behavioural reactions (i.e. approach and vocal response) when tested in absence of the offspring (fur seals: *Callorhinus ursinus*, Insley 2001; *Arctocephalus tropicalis*, Charrier et al. 2002). Another potential factor to explain a weak responsiveness in females could be the time spent between the playback test and the last suckling session. For instance, such motivational state has been shown to be of a particular importance for the responsiveness of pups to mother's calls (Charrier et al. 2004) but remains to be tested in females.

Unfortunately, walrus calves were not tested during this study, but we think that mother–calf vocal recognition is likely to be mutual since both protagonists have mutual benefits to recognise each other. Indeed, females give birth to a single calf every 2 or 3 years, so the maternal investment is very high in this species. Even if other group members show some protective behaviour towards barking calves, females will only nurse their own calf (Fay 1982; Nowak 2003). Separations occur frequently during group movements on unstable floating ice blocks, predator attacks or hunters, and group displacement during foraging trips. For all these reasons, mother–calf vocal recognition is essential for both protagonists.

Future playback experiments will determine if calves are also able to discriminate the calls of their mother from those of other females. Equally important is the determination of what acoustic parameters are used by mothers and calves to identify each other. This will involve modified or synthesized signals in which different parameters will be modified in order to bring to light the key parameters involved in individual recognition. Our own preliminary tests with one captive mother–calf pair seemed to indicate that the exact values of call frequencies and of the FM pattern could play a role in this identification process (Charrier, personal observation).

Reunions between walrus mother and calf occur on ice where the herd hauls out or in the water (both underwater and on surface) when the herd is moving or escaping from a danger. Our propagation tests gave interesting outcomes on the efficiency of mother–calf vocal recognition in their natural environments. According to our results, we can conclude that Atlantic walrus barks reliably transferred individual identity up to 128 m over water surface and up to 16–32 m over ice. Over water surface, vocal communication seems highly efficient at very long range. However, as far as it has been observed, mother and calf seem to remain always at close proximity and separations only occur during herd movements or due to predator intrusion. Over ice, the acoustic signals were much less efficient, but they still should allow a reliable individual vocal recognition at their natural distance range. Walrus hearing abilities in air have been shown to be efficient between 0.1 and 4 kHz (Kastelein et al. 1993, 1996), a frequency range corresponding to the natural range of their vocalisations. So even propagated barks can be detected and then individual identity decoded.

Lastly, if frequency spectrum and FM pattern are the key components of mother–calf vocal recognition, they have been found highly resistant to degradations through the two studied natural environments inhabited by walruses.

These propagation tests were made under optimal conditions: good weather, no-ice or sea movements, and no animals. So, under more common natural circumstances (wind, sea wave and vocalisations from conspecifics), mother–calf communication signals might not be as efficient as in our playback procedure.

The walrus is the sole species of the Odobenid family, and its natural behaviour has not been widely studied. In the present study, we showed that mothers and calves produced stereotyped vocalisations allowing individual identification, and that mothers can recognise their calf's vocalisations. In the light of our acoustic and propagation analyses, the mother–young individual recognition process is likely to rely on frequency modulation and frequency spectrum. Such an individual vocal recognition system seems quite similar to those previously found in some otariid species that show similar biological and ecological traits. Future investigations will determine if this individual vocal recognition is mutual, and if the individual acoustic signature is different between mothers and calves.

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