



Individuality in harp seal, *Phoca groenlandica*, pup vocalizations

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In gregarious breeders, parents often use individually stereotyped vocalizations as a cue to relocate offspring. Harp seals aggregate in large colonies on pack ice during the whelping season. During the 11-day lactation period, females alternate between periods at sea and attending their pup. If they use vocal cues in the relocation process, individual variation in pup vocalizations would be expected. We recorded vocalizations, sex and age class for 91 individuals at whelping patches in the Greenland Sea. Pups produced three call types: tonal, pulsed and a combination of the two. Only tonal vocalizations were used for analyses. To explore individual variation in measured vocal parameters, we used classification trees: 43% of 4075 vocalizations were classified correctly according to individual. The first split was driven by the third peak frequency, splitting male pups from females. For females total duration produced most further splits, whereas the maximum frequency of the lower harmonic, the maximum frequency of the second harmonic and total duration caused splits between males. We correctly identified 55% of 42 female pups and 8% of 49 male pups based on vocal parameters. Calls were misclassified according to individual but never according to sex. Repeated measures of eight individuals over several age classes showed that 82% of 869 calls were correctly classified regardless of age. Alongside vision and smell, acoustic cues appear to be important in relocating offspring. Differences in vocal variability between sexes may reflect different selection pressures working on males and females.

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In gregarious breeders, clear and consistent communication of individual identity is necessary to reduce confusion over reproductive investment (Halliday 1983). Female aggression towards nonfilial offspring when searching for their own, as well as the inability to relocate offspring, can lead to decreased offspring survival (Trillmich 1981; Phillips & Stirling 2000; Insley 2001; Charrier et al. 2002). Individually stereotyped calls, a prerequisite for vocal recognition, occur in numerous species, such as between mother and offspring evening bats, *Nycticeius humeralis* (Scherrer & Wilkinson 1993) and ancient murrelets, *Synthliboramphus antiquus* (Jones et al. 1987). Similarly, king penguins, *Aptenodytes patagonicus*, exclusively feed the chicks that are capable of identifying and responding to the parent's call (Aubin & Jouventin 2002).

In pinnipeds, the majority of species congregate to form large breeding concentrations during the pupping season.

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Typically, in otariid species females forage throughout lactation (e.g. Bowen 1991; Bowen et al. 2002), and lactation can last several months (e.g. Trillmich 1981; Kovacs & Lavigne 1992; Insley 2001). Vocal recognition is important because otariid mothers alternate between attendance periods ashore to nurse their pup and foraging periods at sea, during which the pup can be alone for 3–15 days (e.g. Trillmich 1996). Female and offspring are frequently both active participants in reunions (Trillmich 1981; Gisiner & Schusterman 1991; Insley 2001; Charrier et al. 2002; Dobson & Jouventin 2003), and in some species mother and pup are able to identify each other for up to 4 years (Insley 2000).

In phocids, breeding strategies are more variable, with some females remaining ashore whereas others spend periods at sea, throughout lactation. A number of phocid species have individually stereotyped calls (e.g. harbour seal, *Phoca vitulina*: Renouf 1984; Perry & Renouf 1988; northern elephant seal, *Mirounga angustirostris*: Insley 1992; Hawaiian monk seal, *Monachus schauinslandi*: Job et al. 1995; grey seal, *Halichoerus grypus*: McCulloch et al. 1999). Mothers tend to reject nonfilial pups, although allosuckling occurs in several species (northern elephant seals: Bartolomew & Collias 1962; Hawaiian monk

seals: Job et al. 1995; grey seals: Fogden 1971; McCulloch et al. 1999).

Ice-breeding phocids generally form more dispersed aggregations than species that breed on land. Mothers of several of the ice-breeding species forage to sustain lactation, and therefore spend some time at sea during the pupping season (Lydersen & Kovacs 1999). Although aggregations on ice are generally less dense than on land, hourly or daily movements of the ice, causing the pup to drift away from the rest of the herd, may complicate the relocation process. Hooded seal, *Cystophora cristata*, females appear to deal with this problem by remaining on the ice with their pup continuously throughout the lactation period and there is no evidence that the pair recognizes one another once separated (Ballard & Kovacs 1995). However, little is known about the processes influencing mother–infant reunions in other ice-breeding species.

Harp seal, *Phoca groenlandica*, females form large whelping aggregations on the Arctic pack ice, around late February to early March (e.g. Kovacs 1987; Lydersen & Kovacs 1999). Pupping is strongly synchronous, with most pups being born within 2 days, and suckling lasts around 10–12 days (e.g. Kovacs & Lavigne 1986; Lavigne & Kovacs 1988; Kovacs et al. 1991). During this period, females are believed to forage a few hours per day, leaving their pups alone on the ice (Lydersen & Kovacs 1993, 1999). During the nursing period, pups are relatively sedentary, rarely leaving their ice floe or entering the water (Kovacs 1987). This sedentary nature helps mothers to relocate their offspring after feeding bouts under the ice (Kovacs 1995). Although harp seals breed on pack ice, this habitat can differ widely in structure and form between areas and years (e.g. Pinet 1992; Estep et al. 1994). In consequence, the instability of the ice floes and varying weather conditions may not allow for spatial memory to be the sole factor involved in the relocation process.

Visual and acoustic cues provided by the pup are thought to facilitate initial relocation, whereas olfactory cues provide confirmation (Kovacs 1995). Harp seal pups start vocalizing soon after birth (Kovacs 1987). However, the function of this vocalizing behaviour remains unclear.

The structure of harp seal pup vocalizations is highly complex and variable (Miller & Murray 1995). Since adult harp seals produce a varied and complex vocal repertoire (e.g. Terhune et al. 1987; Terhune 1994; Serrano 2001), the complexity of pup vocalizations is thought to reflect the early use of the sounds that are later produced by adults (Miller & Murray 1995). Gradual changes in pup vocalizations caused by changes in their vocal apparatus might occur in pups of differing ages. In addition, their body weight triples and their size increases during the 12-day lactation period (Kovacs & Lavigne 1985). This may have consequences for acoustic aspects of pup vocalizations, because sender morphology can affect aspects of auditory signal form (Bradbury & Vehrencamp 1998).

Differences between the sexes might also influence the development of vocalization (Sayigh et al. 1995). Since adult harp seals have a large vocal repertoire in which there exists vocal sexual dimorphism (Serrano 2001), this variation may be present in juveniles as well.

Our aims in this study were to examine (1) whether individual variation is present in pups' vocalizations during the lactation period, (2) the effects of pup development on vocalization by comparing calls of suckling harp seal pups from five age classes, (3) the influence of sex on the acoustic structure of pup calls by comparing vocalizations of male and female pups.

METHODS

We carried out this study during the harp seal pupping season from 18 to 30 March 2002. No licences or permits were needed. Vocalizations of suckling individual harp seal pups were recorded in two whelping patches located within the West-ice region. The patches were situated in two pack ice areas between Greenland and Jan Mayen, in the Greenland Sea (Fig. 1; patch A: 72°14'N, 12°43'W; patch B: 72°10'N, 13°10'W).

Weather permitting, concentrations of mothers and pups (approximate estimate of the number of pups in patch A was 277 and in patch B 1416; Haug et al. 2002) were located using a helicopter and the ice-strengthened expedition vessel R/V 'Lance' as a base.

Within these concentrations, we chose clusters of pups in areas where the helicopter could land safely and ice conditions permitted access on foot to several pups. The helicopter landed within a few metres of the nearest mother–pup pair. We tried to make landings and lift offs as short as possible. Helicopter landings frequently caused the nearest pups to start vocalizing, while mothers sometimes left the ice. However, both mother and pup were usually reunited within minutes of the helicopter taking off.

All pups were caught and thereafter tagged with a Dalton rototag through the webbing of the right hind flipper. This tag has been developed for long-term identification of domestic sheep and goats. The tag (4 × 1 cm) was inserted into the right hind flipper of the seal pup with a custom-made rototag applicator. The tags are designed to be self-piercing and free swinging and are able to rotate a full 360° out of trouble. Studies on a variety of species have shown that piercing caused by the insertion of the rototags heals quickly, with no apparent detrimental effect on the behaviour of the individuals (e.g. Heupel et al. 1998). In harp seals, the wound caused by insertion of the rototag caused little to no bleeding and had healed cleanly in all pups that were revisited on subsequent days. During the tagging procedure, mothers left their pups and watched from a distance either from another floe or from the water. For all pups tagged during this study, reunion between mother and pup after the procedure was verified and happened within minutes after the observers left the pup. We determined each pup's sex, age class or 'stage' (the latter based on criteria developed by Stewart & Lavigne 1980; Table 1).

Recorded pups were marked with brightly coloured spray-paint to facilitate relocation for repeated recordings. The spray-paint stayed on the pups for a maximum of 3 days. No pups were affected adversely by this procedure and were repeatedly seen together with their mothers

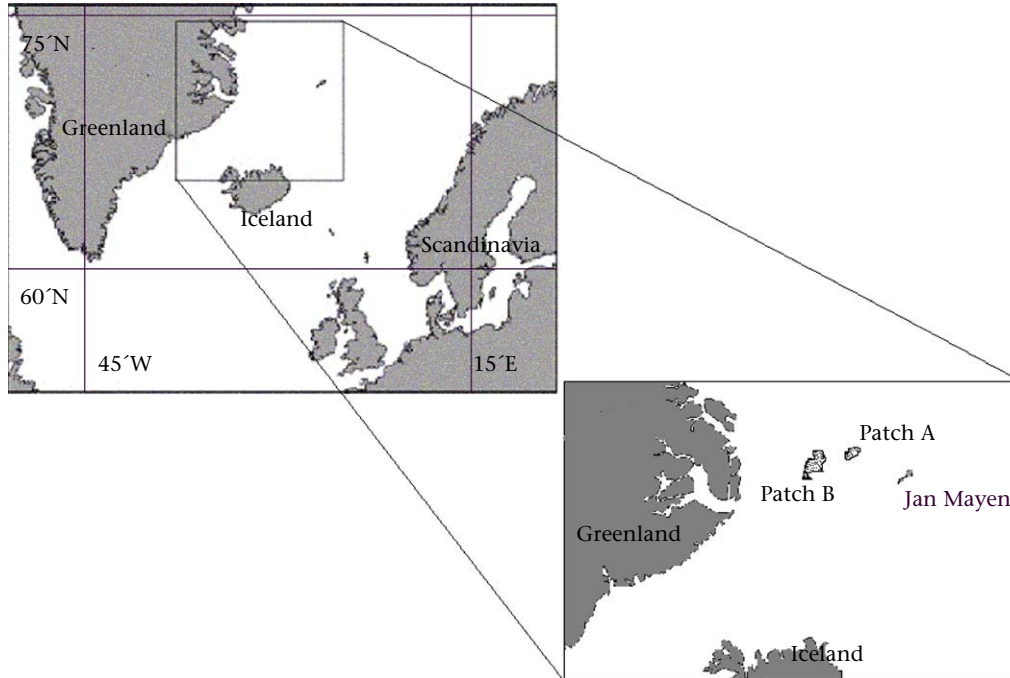


Figure 1. Map of area from which vocalizations of individual harp seal pups were recorded in two whelping patches, located in two pack ice areas (patches A and B).

afterwards. To relocate whelping patches, we used a VHF transmitter placed centrally on a brightly coloured ice floe. Systematic searching of areas with coloured pups allowed us to make repeated recordings from a number of individuals. We chose groups of pups haphazardly for recordings, giving priority to easily accessible and vocalizing individuals. We also made some recordings directly after tagging.

To record vocalizing pups, we used a Sennheiser microphone (MD 421-II: sensitivity 170 dB; frequency bandwidth 36 Hz–17 kHz \pm 3 dB) connected to a Sony digital audiotape recorder (TCD-D8: frequency response 5 Hz–22 kHz). Individuals showed varying responses to our presence, but overall showed little or no reaction when approached closely during recordings. We tried to minimize disturbance of the animals. We held the microphone 0.1–0.3 m from the vocalizing pup. For each pup

the mean duration of recording was 5 min, during which an average of 51 calls was recorded per individual. The recordings were played and then resampled (sampling frequency 22 kHz, dynamic range 170 dB). Spectrographic analyses were conducted with Batsound 2.0 (Pettersson Elektronik, Uppsala, Sweden) and Gram 4.1.2 (Horne 1998).

Signals were divided into three categories according to their spectrogram quality (Fast Fourier Transforms: dt: 10 ms; df: 102 Hz; FFT size: 512). Quality was defined as good (all variables were measurable), medium (one variable could not be measured) and poor (more than one variable could not be measured). Only good-quality calls were used for further analyses. Using overall call shape, we assigned each signal to a 'signal type' i.e. tonal call, pulsed call or a combination of the two (Fig. 2). Tonal calls typically exhibited harmonic structure. Pulsed calls

Table 1. Age classification according to Stewart & Lavigne (1980)

Age class/stage (number)	Age (days)	Description
Newborn (A)	0	Pup still wet, bright yellow colour often present. Often associated with placenta and blood-stained snow
Yellowcoat (B)	0–1	Pup dry, yellow amniotic stain still persistent on pelt. Pup is lean and moving awkwardly
Thin Whitecoat (C)	2–4	Amniotic stain faded, pup with visible neck and often conical in shape, pelage white
Fat Whitecoat (D)	5–9	Visibly fatter, neck not visible, cylindrical in shape, pelage still white
Graycoat (E)	10–15 (weaning)	Darker juvenile pelt begins to grow under the white lanugo giving a grey cast to the pelt, 'salt-and-pepper'-look in later age classes
Ragged-jacket (F)	16–24	Lanugo shed in patches, at least a handful from torso (nose, tail and flippers do not count)
Beater (G)	25–older	Fully moulted, weaned pups (a handful of lanugo may remain)

were characterized by a pulsed signal, lacking harmonic structure.

After quality selection, no pulsed call or combination vocalizations were present in the data set; we therefore used only tonal calls in these analyses. Individuals with fewer than 10 recorded vocalizations were excluded from analyses. Initially, 13 vocal parameters were measured for a subset of the data (10 randomly selected individuals: $N = 5$ males and 5 females). These were: (1) call duration (DURN), (2–4) three harmonics of greatest amplitude (PF1–3), (5) the number of harmonics (HARM), (6) the maximum frequency of the lower harmonic (SH1), (7) the maximum frequency of the second harmonic (EH1), (8–10) the amplitude of the three harmonics of greatest amplitude (AMPF1–3), (11) the duration of the ascending part of the call (DURASC), (12) the duration of the plateau part (DURPLAT) and (13) the duration of the descending part of the call (DURDESC) (Fig. 3a–c).

Tree-based methods offer a useful approach to exploring multivariate data (e.g. see chapter 10 in Venables & Ripley 1999; De'ath & Fabricius 2000). Call parameters were log transformed. Variation in vocal parameters across individuals was investigated with classification trees (CART). Analyses were carried out in R (Ihaka & Gentleman 1996), using the RPART library for classification trees. As opposed to other multivariate techniques such as discriminant analyses and principal component analyses, CART analyses provide a useful technique for exploring multivariate nonparametric data. Furthermore, CART analyses produce a result that is readily visually accessible.

Initially, a CART was carried out on the subsample (13 parameters measured for 10 individuals) to determine which parameters were important in driving the splits between individuals. In total, seven vocal parameters were highlighted as important (vocal parameters 1–7). These parameters were then used to analyse the complete data set. Individual variation in vocal parameters within and between pups was explored using CARTs. Table 2 lists descriptive statistics for females and males for the seven parameters used in the CARTs.

RESULTS

Recordings were made from 110 individuals distributed over the first five age classes. After quality selection, 4075 calls from 91 individuals were suitable for use in the main analyses. Of these, 49 were male (IDs A–AW) and 42 were female (IDs AX–CM). Repeated recordings of the same individual were made for eight pups: 475 calls for four females (IDs A, B, D, F) and 394 calls for four males (IDs C, E, H, G). Our data set was analysed in two stages: the complete data set and the repeated recordings.

Complete Data Set

An initial 27-node classification tree was pruned with cross-validation. Using the 1-SE rule (i.e. the smallest tree for which the cross-validated relative error rate is within one standard error of the minimum; De'ath & Fabricius

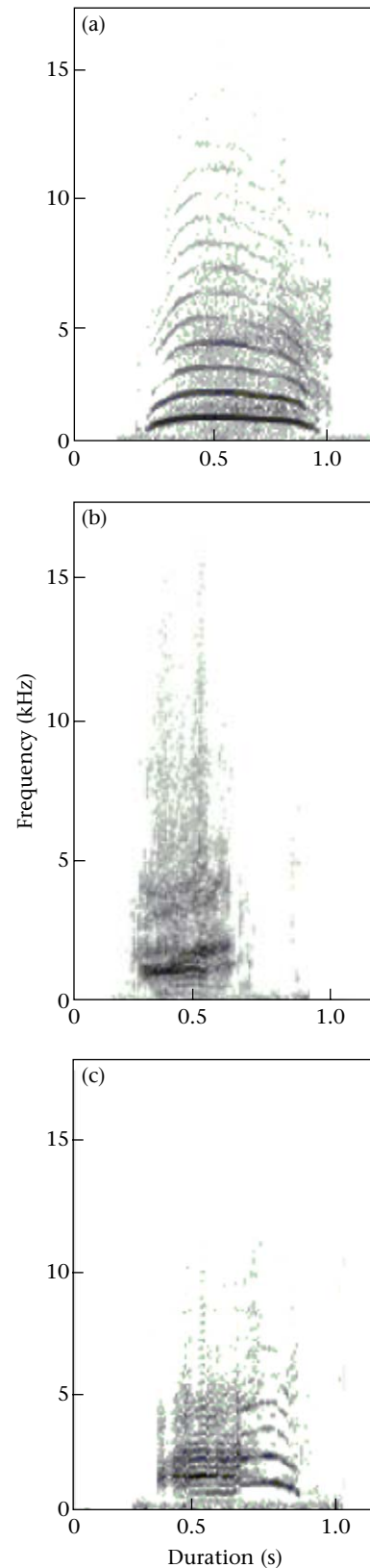


Figure 2. Visual representation of signal types grouped using overall call shape: (a) tonal call, (b) pulsed call and (c) combination of pulsed and tonal vocalization (frequency bandwidth 36 Hz–17 kHz \pm 3 dB).

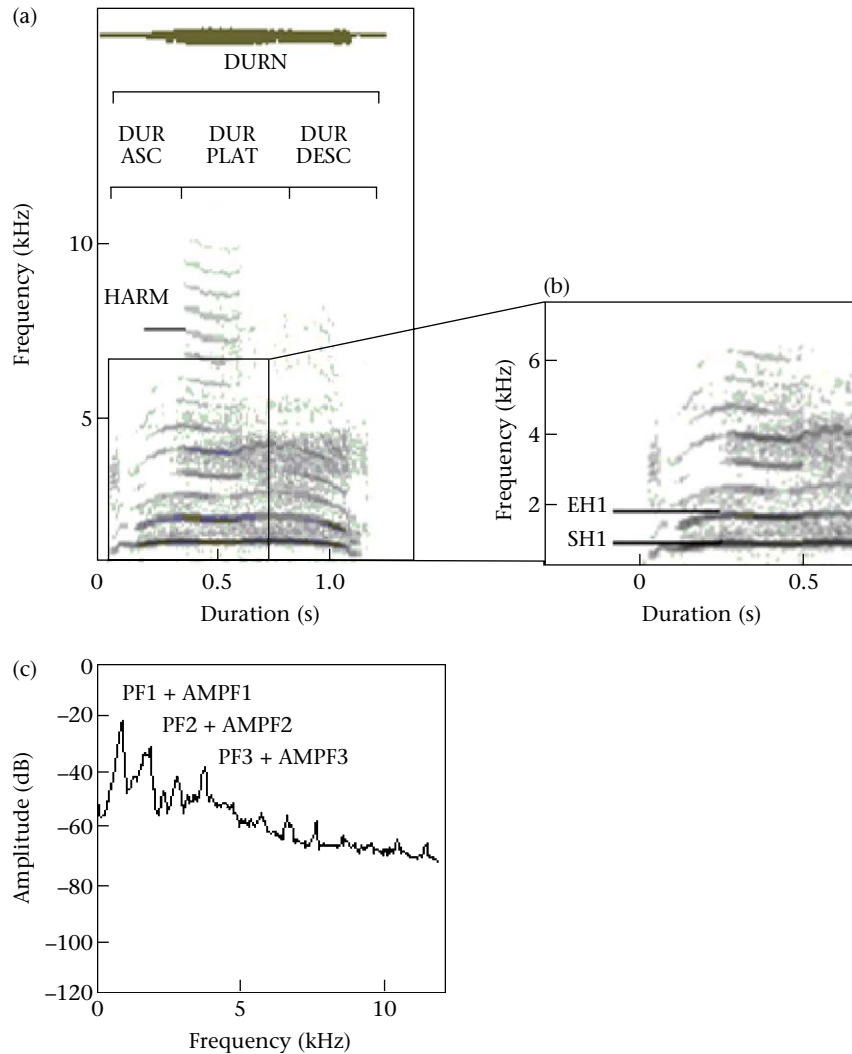


Figure 3. The 13 vocal parameters measured. (a) Spectrogram. Duration (DURN), duration of the ascending part of the signal (DURASC), duration of the plateau part of the signal (DURPLAT), duration of the descending part of the signal (DURDESC), number of harmonics (HARM). (b) Enlarged section of the spectrogram: maximum frequency of lower harmonic (SH1) and maximum frequency of second harmonic EH1. (c) Power spectrum: the three peak frequencies PF1, PF2, PF3 and accompanying amplitudes of the peak frequencies AMPF1, AMPF2 and AMPF3.

2000) suggested that the appropriate descriptive tree was one with 26 nodes (Fig. 4). The analysis correctly classified 43% of calls according to individual. In this CART, the first major split was based on PF3, causing male pups to split from females. For females, DURN was responsible for the next two splits, after which a number of parameters were responsible for the further splits; SH1, EH1 and DURN were responsible for splits that occurred between individual males. Of the 42 female pups, 55% were correctly identified based on their vocal parameters, whereas 8% of 49 male pups were correctly identified. Of 4075 calls, there were 2314 (57%) misclassifications; of these, 14% were female calls and 86% were male calls. Misclassified female calls were never found classified within male IDs, and vice versa. Therefore, although both female and male calls could be misclassified according to individual, they were never misclassified according to sex.

The percentage of correctly classified calls according to age class was 5% of calls correctly classified in stage A ($N = 108$), 15% in stage B ($N = 670$), 12%

in stage C ($N = 1454$), 6% in stage D ($N = 1637$) and 5% in stage E ($N = 206$). Misclassified calls fell predominantly within either stage B (37% of misclassified calls) or stage C (26% of misclassified calls).

Repeated Recordings

Of the eight pups repeatedly recorded over separate age classes, one was recorded during age classes 1 and 3, two over age classes 2 and 3, one over age classes 2 and 4 and three over age classes 3 and 4. One pup was recorded over age classes 2–4. The logistic difficulties in relocating individual pups repeatedly restricted our sampling regime.

CART analysis showed that 82% of calls were correctly classified according to individual, regardless of varying age classes (Fig. 5). The vocal parameters driving the splits were PF3 and DURN for females and PF3 and EH1 for male pups. Of the 12% of misclassified calls, 9.6% were attributed to males and 2.4% to females.

Table 2. Descriptive statistics of the vocalizations of male ($N = 49$) and female ($N = 42$) harp seal pups recorded in the Greenland Sea

Vocal parameters	Sex	N	$\bar{X} \pm SD$	(%)
DURN (ms)	F	1173	871.24 ± 276.15	31.69
DURN (ms)	M	1188	855.76 ± 595.72	69.61
PF1 (kHz)	F	1173	1.23 ± 0.39	31.71
PF1 (kHz)	M	1188	1.14 ± 0.37	32.46
PF2 (kHz)	F	1173	2.09 ± 0.64	30.62
PF2 (kHz)	M	1188	1.92 ± 0.77	40.10
PF3 (kHz)	F	1173	3.13 ± 0.72	23.00
PF3 (kHz)	M	1188	2.82 ± 1.10	39.01
HARM	F	1173	10.87 ± 6.05	55.66
HARM	M	1188	11.78 ± 7.03	59.68
SH1 (Hz)	F	1173	1042.67 ± 282.07	27.05
SH1 (Hz)	M	1188	1016.40 ± 274.56	27.01
EH1 (Hz)	F	1173	1675.54 ± 451.90	26.97
EH1 (Hz)	M	1188	1586.51 ± 454.48	28.65

DURN: duration; PF1–3: first, second and third peak frequency; HARM: number of harmonics; F: female; M: male; CV: coefficient of variation.

DISCUSSION

Little is known about mother–pup behaviour and aspects influencing reunion in ice-breeding phocids. In this study, we explored a broad range of acoustic parameters to examine vocal variability in harp seal pup vocalizations. The majority of the parameters that were used had been shown to be of importance in the recognition process between mother–pup pairs in other pinniped species (e.g.

Renouf 1984; Insley 1992; Job et al. 1995; Charrier et al. 2002). When the acoustic data were analysed as a whole, harp seal pup vocalizations showed a relatively low percentage of individual variation. However, confounding factors such as age and sex may influence this result. None the less, it is unlikely that acoustic cues form the sole recognition system for harp seal mothers and pups. Terhune et al. (1979) found that half of the harp seal pups observed vocalizing were rejected after naso–naso contact and more than half of the pups nursed had not vocalized. Olfaction and, depending on the ice situation, a limited reliance on spatial memory are also important cues for relocation and recognition of pups (Kovacs 1987, 1995).

In some species, vocalizations by mothers are important in reunions, for example in the California sealion, *Zalophus californianus*, and northern fur seal, *Callorhinus ursinus* (Trillmich 1981; Gisiner & Schusterman 1991; Insley 2001). We did not record vocalizations of mothers because harp seal females rarely vocalize to their offspring (Kovacs 1987). Although the function of these vocalizations remains unclear, it is unlikely that they play an active role in reunions.

No significant differences were found between vocalizations of harp seal pups in separate age classes. This result is similar to that reported for Hawaiian monk seal and South American fur seal, *Arctocephalus australis*, pups (Job et al. 1995; Phillips 1998). In these species, pup vocalizations did not differ significantly in the percentage of correctly classified calls when age classes were analysed

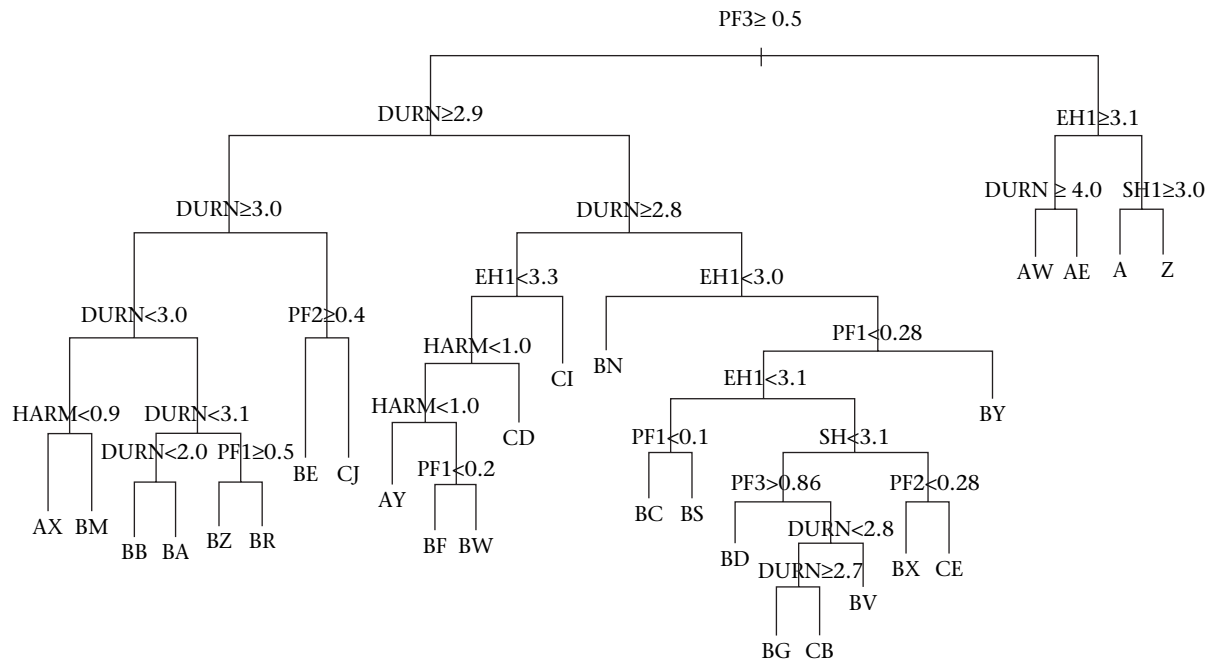


Figure 4. A 26-node classification tree showing how vocalizations from 91 individual harp seal pups split, based on log-transformed data of seven measured vocal parameters [call duration (DURN), three harmonics of greatest amplitude (PF1–3), the number of harmonics (HARM), the maximum frequency of the lower harmonic (SH1) and the maximum frequency of the second harmonic (EH1)]. Letters at the bottom of the tree represent individual pups. Of these pups, 49 were male (IDs A–AW) and 42 were female (IDs AX–CM). The vertical depth of each split explains the proportion of total variation explained by that split. Splits early in the tree (i.e. near the top of the page) account for more variability in the data than those lower down in the tree.

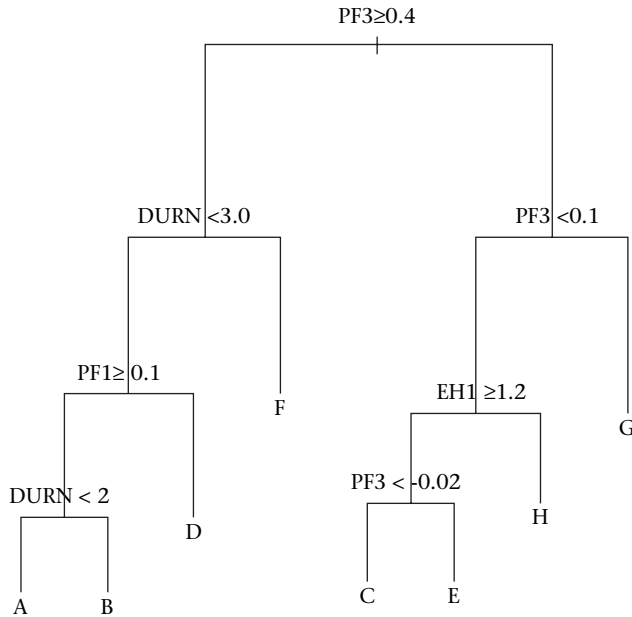


Figure 5. An eight-node classification tree showing how repeated recordings of vocalizations from eight harp seal pups over different age classes split, based on log-transformed data of seven measured vocal parameters [call duration (DURN), three harmonics of greatest amplitude (PF1–3), the number of harmonics (HARM), the maximum frequency of the lower harmonic (SH1) and the maximum frequency of the second harmonic (EH1)]. Letters at the bottom of the tree represent individual pups. Of these pups, four were female (IDs A, B, D, F) and four were male (IDs C, E, H, G). The vertical depth of each split explains the proportion of total variation explained by that split. Splits early in the tree (i.e. near the top of the page) account for more variability in the data than those lower down in the tree.

separately. However, when northern and sub-Antarctic fur seal pups were recorded over longer periods, their vocalizations were found to change gradually (northern fur seal: *Insley 2000*; sub-Antarctic fur seal, *Arctocephalus tropicalis*: *Charrier et al. 2003*). Although the length of the lactation period in these species is considerably longer and a direct comparison may not be appropriate, changes in harp seal pup vocalizations as a consequence of the developmental state of vocal anatomy might not have been detectable because of the short duration of our study.

When repeated recordings of individual harp seal pups were analysed, no significant differences were found between correctly classified proportions within individuals. Although the sample size of the repeated recordings was relatively small, this finding is in accordance with the fact that no significant differences were found between age classes. Changes in body mass during the early stages of development are therefore unlikely to affect vocal development.

Our analyses showed a significantly higher proportion of correctly classified vocalizations for female than for male pups. This result suggests that female vocalizations are more individually distinct than male vocalizations. If vocal individuality plays a key role in the recognition process between harp seal mothers and pups, mothers might experience more difficulty in recognizing male

offspring. In this case, misdirected maternal investment could have consequences for neonatal development, such as reduced male pup growth rates compared with those of females. However, mass at birth, mass at weaning and growth rates do not differ between the sexes in harp seal neonates (*Kovacs & Lavigne 1986*). None the less, all of the behavioural and physiological studies of harp seal mother–pup pairs to date have been restricted to the Gulf of St Lawrence and other Canadian populations, in which the stability of the breeding substrate differs substantially from that of the West-ice region in which our study was conducted (*Terhune et al. 1979*; *Kovacs & Lavigne 1986*; *Kovacs 1987, 1995*; *Lydersen & Kovacs 1993*). The Gulf of St Lawrence comprises large flats of ice, with breathing holes through which mothers return to their young (*Lavigne & Kovacs 1988*; *Kovacs 1995*). Mothers might be able to use spatial memory to relocate these holes as a means of reuniting with pups. In contrast, the West-ice is made up of small mobile ice floes, the location and size of which are heavily influenced by currents and weather conditions (e.g. *Pinet 1992*; *Estep et al. 1994*); thus mothers would not be able to use geographical cues such as the location of breathing holes to aid the relocation of pups. Behavioural and physiological data collected in the Canadian breeding grounds may therefore not be representative of harp seals breeding in the West-ice area. Studies of neonatal development could provide an answer to the question whether the difference in vocal variation between male and female pups has consequences for pup relocation by the mother and subsequently for pup development.

One explanation for the differences between the sexes found in this study may be the following. Adult harp seals have a large vocal repertoire in which vocal sexual dimorphism exists (*Serrano 2001*). Sex-specific vocalizations occur exclusively during the breeding season and are thought to be used in courtship as well in social interactions among males (*Serrano 2001*). Male phocids use vocal displays in male–male competition as well as in mate attraction during the breeding season (*Beier & Wartzok 1979*; *Hanggi & Schusterman 1994*; *Van Parijs et al. 1997*). In red deer, *Cervus elaphus*, calling rate is a selection criterion females use to assess quality of a mating partner (*McComb 1987, 1991*). Similarly, female harp seals could prefer males with specific vocal attributes. Therefore, reduced variability in male harp seal pups may be an important factor influencing their future vocal development as adults.

To our knowledge, evidence of sex differences in vocalizations of infant mammals is rare (e.g. *Ralls et al. 1985*; *Sousa-Lima et al. 2002*). In the Amazonian manatee, *Trichechus inunguis*, male and female calves use specific calls differently (*Sousa-Lima et al. 2002*), whereas captive male harbour seals are more likely to mimic sounds from their environment than female harbour seal pups (*Ralls et al. 1985*). In both studies, no differences in individual variation between the sexes were detected.

In free-ranging bottlenose dolphin, *Tursiops truncatus*, calves signature whistles differ between the sexes, (*Sayigh et al. 1995*): females are more likely than males to produce whistles that are distinct from those of their mothers.

Since female bottlenose dolphins remain in nearly constant association with their calves over several years, it seems likely that there would be selection pressure for distinctive whistles among matrilineally related females, facilitating mother–calf contact (Sayigh et al. 1995). Adult female harp seals also appear to exhibit a degree of site fidelity (Sergeant 1991; Perry et al. 2000). Similar selection pressures might therefore be working on female pup vocalizations to differ from those of their mothers, whereas fewer constraints may exist for male pup vocalizations.

Female vocal individuality already present in the juvenile phase could therefore serve its function during later developmental age classes. Ultimately, female vocal individuality could also be of importance in reproductive strategies. For species in which most of the reproductive activities take place underwater, vocal communication is frequently used to distinguish between the sexes (e.g. Beier & Wartzok 1979; Rogers et al. 1996). Unusually for aquatic-mating species, both female and male harp seals are vocally active during the breeding season. In several aquatic-mating species, individual variation in male vocalizations is important for both male–male competition and the maintenance of display areas (e.g. Hanggi & Schusterman 1994; Ballard & Kovacs 1995; Van Parijs et al. 2000). However, little is known about the relative importance of female vocalizations during the mating season. In leopard seals, *Hydrurga leptonyx*, females are known to use loud underwater broadcast calls (Rogers et al. 1996). Therefore, female vocalizations may serve an important role in the aquatic mating system of the harp seal. The vocal behaviour of harp seal neonates could reflect aspects of these differences in the vocal behaviour of adult males and females. Further studies on adults as well as juveniles are needed to explore individual, developmental and sex differences in harp seal vocal communication.

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References

- Aubin, T. & Jouventin, P. 2002. How to identify kin in a crowd: the penguin model. *Advances in the Study of Behaviour*, **31**, 243–277.

- Ballard, K. A. & Kovacs, K. M. 1995. The acoustic repertoire of hooded seals (*Cristophora cristata*). *Canadian Journal of Zoology*, **73**, 1362–1374.
- Bartolomew, G. A. & Collias, N. E. 1962. The role of vocalization in the social behaviour of the northern elephant seal. *Behaviour*, **10**, 1–14.
- Beier, J. C. & Wartzok, D. 1979. Mating behavior of captive spotted seals (*Phoca largha*). *Animal Behaviour*, **27**, 722–781.
- Bowen, W. D. 1991. Behavioural ecology of pinniped neonates. In: *The Behaviour of Pinnipeds* (Ed. by D. Renouf), pp. 66–127. London: Chapman & Hall.
- Bowen, W. D., Read, A. J. & Estes, J. A. 2002. Feeding ecology. In: *Marine Mammal Biology, an Evolutionary Approach* (Ed. by R. Hoelzel), pp. 217–246. Oxford: Blackwell.
- Bradbury, J. W. & Vehrencamp, S. L. 1998. Costs and constraints on signal evolution. In: *Principles of Animal Communication* (Ed. by J. W. Bradbury & S. L. Vehrencamp), pp. 537–570. Sunderland, Massachusetts: Sinauer.
- Charrier, I., Mathevon, N. & Jouventin, P. 2002. How does a fur seal mother recognize the voice of her pup? An experimental study of *Arctocephalus tropicalis*. *Journal of Experimental Biology*, **205**, 603–612.
- Charrier, I., Mathevon, N. & Jouventin, P. 2003. Fur seal mothers memorize subsequent versions of developing pups' calls: adaptation to long-term recognition or evolutionary by-product? *Biological Journal of the Linnean Society*, **80**, 305–312.
- De'ath, G. & Fabricius, K. E. 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. *Ecology*, **81**, 3178–3192.
- Dobson, F. S. & Jouventin, P. 2003. How mothers find their pups in a colony of Antarctic fur seals. *Behavioural Processes*, **61**, 77–85.
- Estep, K. W., MacIntyre, F., Noji, T. T., Stensholt, B. & Øritsland, T. 1994. Seal sizes and habitat conditions assessed from aerial photography and video analysis. *ICES Journal of Marine Science*, **51**, 253–261.
- Fogden, S. C. L. 1971. Mother–young behaviour at grey seal breeding beaches. *Journal of Zoology*, **164**, 61–92.
- Gisiner, R. & Schusterman, R. J. 1991. California sea lion pups play an active role in reunions with their mothers. *Animal Behaviour*, **41**, 364–366.
- Halliday, T. R. 1983. Information and communication. In: *Animal Behaviour: Communication Vol. 2* (Ed. by T. R. Halliday & P. J. B. Slater), pp. 43–81. Oxford: Blackwell Scientific.
- Hanggi, E. B. & Schusterman, R. J. 1994. Underwater acoustic displays and individual variation in male harbour seals, *Phoca vitulina*. *Animal Behaviour*, **48**, 1275–1283.
- Haug, T., Corkeron, P. J., Nilssen, K. T. & Stenson, G. B. 2002. Report from aerial surveys of ice-breeding seals in the Greenland Sea pack-ice during the 2002 whelping season. *Fiskeriforsknings Report*, **8**, 7–8.
- Heupel, M. R., Simpfendorfer, C. A. & Bennett, M. B. 1998. Analysis of tissue responses to fin tagging in Australian carcharhids. *Journal of Fish Biology*, **52**, 610–620.
- Horne, R. S. 1998. *Gram 4.1.2*. Stafford, Virginia: Visualization Software LLC.
- Ihaka, R. & Gentleman, R. 1996. R: a language for data analysis and graphics. *Journal of Computational and Graphical Statistics*, **5**, 299–314.
- Insley, S. J. 1992. Mother–offspring separation and acoustic stereotypy: a comparison of call morphology in two species of pinnipeds. *Behaviour*, **120**, 103–121.
- Insley, S. J. 2000. Long-term vocal recognition in the northern fur seal. *Nature*, **406**, 404–405.

- Innsley, S. J. 2001. Mother–offspring vocal recognition in northern fur seals is mutual but asymmetrical. *Animal Behaviour*, **61**, 129–137.
- Job, D. A., Boness, D. J. & Francis, J. M. 1995. Individual variation in nursing vocalizations of Hawaiian monk seal pups, *Monachus schauinslandi* (Phocidae, Piniipedia), and lack of maternal recognition. *Canadian Journal of Zoology*, **73**, 975–983.
- Jones, I. L., Falls, J. B. & Gaston, A. J. 1987. Vocal recognition between parents and young of ancient murrelets, *Synthliboramphus antiquus*. *Animal Behaviour*, **35**, 1405–1415.
- Kovacs, K. M. 1987. Maternal behaviour and early behavioural ontogeny of harp seals, *Phoca groenlandica*. *Animal Behaviour*, **35**, 844–855.
- Kovacs, K. M. 1995. Mother–pup reunions in harp seals, *Phoca groenlandica*: cues for the relocation of pups. *Canadian Journal of Zoology*, **73**, 843–849.
- Kovacs, K. M. & Lavigne, D. M. 1985. Neonatal growth and organ allometry of Northwest Atlantic harp seals (*Phoca groenlandica*). *Canadian Journal of Zoology*, **63**, 2793–2799.
- Kovacs, K. M. & Lavigne, D. M. 1986. Maternal investment and neonatal growth in phocid seals. *Journal of Animal Ecology*, **55**, 1035–1051.
- Kovacs, K. M. & Lavigne, D. M. 1992. Maternal investment in otariid seals and walruses. *Canadian Journal of Zoology*, **70**, 1953–1964.
- Kovacs, K. M., Lavigne, D. M. & Innes, S. 1991. Mass transfer efficiency between harp seal (*Phoca groenlandica*) mothers and their pups during lactation. *Journal of Zoology*, **223**, 213–221.
- Lavigne, D. M. & Kovacs, K. M. 1988. Life cycles. In: *Harps and Hoods* (Ed. by D. M. Lavigne & K. M. Kovacs), pp. 21–44. Waterloo: University of Waterloo Press.
- Lydersen, C. & Kovacs, K. M. 1993. Diving behaviour of lactating harp seal, *Phoca groenlandica*, females from the Gulf of St Lawrence, Canada. *Animal Behaviour*, **46**, 1213–1221.
- Lydersen, C. & Kovacs, K. M. 1999. Behaviour and energetics of ice-breeding, North Atlantic phocid seals during the lactation period. *Marine Ecology Progress Series*, **187**, 265–281.
- McComb, K. 1987. Roaring by deer stags advances the date of oestrus in hinds. *Nature*, **330**, 648–649.
- McComb, K. 1991. Female choice for high roaring rates in red deer, *Cervus elaphus*. *Animal Behaviour*, **41**, 79–88.
- McCulloch, S., Pomeroy, P. & Slater, P. J. B. 1999. Individually distinctive pup vocalizations fail to prevent allo-suckling in grey seals. *Canadian Journal of Zoology*, **77**, 716–723.
- Miller, E. H. & Murray, A. V. 1995. Structure, complexity and organization of vocalizations in harp seal (*Phoca groenlandica*) pups. In: *Sensory Systems of Aquatic Mammals* (Ed. by R. A. Kastelein, J. A. Thomas & P. E. Nachtigall), pp. 237–264. Woerden, The Netherlands: De Spil Publishers.
- Perry, E. A. & Renouf, D. 1988. Further studies of the role of harbour seal (*Phoca vitulina*) pup vocalizations in preventing separation of mother–pup pairs. *Canadian Journal of Zoology*, **66**, 934–938.
- Perry, E. A., Stenson, G. B., Bartlett, S. E., Davidson, W. S. & Carr, S. M. 2000. DNA sequence analysis identifies genetically distinguishable populations of harp seals (*Pagophilus groenlandicus*) in the northwest and northeast Atlantic. *Marine Biology*, **137**, 53–58.
- Phillips, A. V. 1998. Vocal communication and mother–pup interactions in the South American fur seal, *Arctocephalus australis*. M.Sc. thesis, University of Alberta.
- Phillips, A. V. & Stirling, I. 2000. Vocal individuality in mother and pup South American fur seals, *Arctocephalus australis*. *Marine Mammal Science*, **16**, 592–616.
- Pinet, P. R. 1992. The open ocean. In: *Oceanography* (Ed. by P. R. Pinet), pp. 493–503. St. Paul: West Publishing.
- Ralls, K., Fiorelli, P. & Gish, S. 1985. Vocalizations and vocal mimicry in captive harbor seals, *Phoca vitulina*. *Canadian Journal of Zoology*, **63**, 1050–1056.
- Renouf, D. 1984. The vocalization of the harbour seal pup (*Phoca vitulina*) and its role in the maintenance of contact with the mother. *Journal of Zoology*, **202**, 583–590.
- Rogers, T. L., Cato, D. H. & Bryden, M. M. 1996. Behavioural significance of underwater vocalizations of captive leopard seals, *Hydrurga leptonyx*. *Marine Mammal Science*, **12**, 414–427.
- Sayigh, L. S., Tyack, P. L., Wells, R. S., Scott, M. D. & Irvine, A. B. 1995. Sex difference in signature whistle production of free-ranging bottlenose dolphins, *Tursiops truncatus*. *Behavioral Ecology and Sociobiology*, **36**, 171–177.
- Scherrer, J. A. & Wilkinson, G. S. 1993. Evening bat isolation calls provide evidence for heritable signatures. *Animal Behaviour*, **46**, 847–860.
- Sergeant, D. E. 1991. Harp seals, man and ice. *Canadian Special Publication of Fisheries and Aquatic Sciences*, **114**, 1–153.
- Serrano, A. 2001. New underwater and aerial vocalizations of captive harp seals (*Pagophilus groenlandicus*). *Canadian Journal of Zoology*, **79**, 75–81.
- Sousa-Lima, R. S., Paglia, A. P. & Da Fonseca, G. A. B. 2002. Signature information and individual recognition in the isolation calls of Amazonian manatees, *Trichechus inunguis* (Mammalia: Sirenia). *Animal Behaviour*, **63**, 301–310.
- Stewart, R. E. A. & Lavigne, D. M. 1980. Neonatal growth in Northwest Atlantic harp seals, *Phagophilus groenlandicus*. *Journal of Mammalogy*, **61**, 670–680.
- Terhune, J. M. 1994. Geographical variation of harp seal underwater vocalizations. *Canadian Journal of Zoology*, **72**, 892–897.
- Terhune, J. M., Terhune, M. E. & Ronald, K. 1979. Location and recognition of pups by adult female harp seals. *Applied Animal Ethology*, **5**, 375–380.
- Terhune, J. M., MacGowan, G., Underhill, L. & Ronald, K. 1987. Repetitive rates of harp seal underwater vocalizations. *Canadian Journal of Zoology*, **65**, 2119–2120.
- Trillmich, F. 1981. Mutual mother–pup recognition in Galapagos fur seals and sea lions: cues used and functional significance. *Behaviour*, **78**, 21–42.
- Trillmich, F. 1996. Parental investment in pinnipeds. *Advances in the Study of Behaviour*, **25**, 533–577.
- Van Parijs, S. M., Thompson, P. M., Tollit, D. J. & Mackay, A. 1997. Distribution and activity of male harbour seals during the mating season. *Animal Behaviour*, **54**, 35–43.
- Van Parijs, S. M., Janik, V. M. & Thompson, P. M. 2000. Display-area size, tenure length, and site fidelity in the aquatically mating male harbour seal, *Phoca vitulina*. *Canadian Journal of Zoology*, **78**, 2209–2217.
- Venables, W. N. & Ripley, B. D. 1999. *Modern Applied Statistics with S-plus*. 3rd edn. New York: Springer Verlag.