Display-area size, tenure length, and site fidelity in the aquatically mating male harbour seal, *Phoca vitulina*

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Abstract: Previous studies of the distribution and activity of male harbour seals, *Phoca vitulina*, based on telemetric techniques have shown that males restrict their range at the onset of the mating season and perform vocal and dive displays. While these data illustrated broad changes in male behaviour and distribution, they were not precise enough to reveal the extent to which individual males repeatedly return to the same locations to display. In this study we used an acoustic array to localise male vocalisations. This technique provided small-scale information on male behaviour over 3 consecutive years. This study provides the first details concerning display-area size in an aquatically mating phocid. Male vocalisations were located in two discrete areas each covering between 40 and 135 m². Vocalisations were repeatedly located in these two areas over the 3-year period. Comparisons of four vocal parameters suggested that only one individual occupied each area throughout a mating season. Furthermore, comparative analysis suggested that males might return to the same two display areas in successive years. Although the number of males using the site was small, this study showed that acoustic localisation can be a valuable tool for detailed study of the underwater behaviour of aquatically mating pinnipeds.

Résumé : Des études antérieures de la répartition et de l'activité de Phoques communs, *Phoca vitulina*, mâles indiquent que les mâles restreignent leur aire d'activité au début de la saison de reproduction et se font remarquer par des manifestations vocales et des plongées. Bien que ces données illustrent bien les modifications importantes du comportement et de la répartition chez les mâles, elles ne sont pas suffisamment précises pour mettre en lumière l'importance des retours répétés aux mêmes terrains de parade. Dans cette étude, nous avons utilisé tout un réseau acoustique pour repérer l'origine des cris des mâles. Cette technique nous a permis d'obtenir des informations à petite échelle sur le comportement des mâles pendant une période de 3 années consécutives. Nous présentons ici des détails encore inédits sur les dimensions du terrain de parade chez un phocidé à accouplement aquatique. Les cris des phoques ont été repérés en deux zones discontinues de 40 à 135 m² de surface et ces deux zones ont été fréquentées à répétition pendant les 3 ans. La comparaison de quatre variables vocales semble indiquer qu'un seul individu occupe chaque zone pendant toute la saison des amours. De plus, les résultats d'une analyse comparative permettent de croire que les mâles réutilisent les deux mêmes terrains de parade au cours d'années consécutives. Malgré le petit nombre de mâles à chaque site, nos résultats démontrent que le repérage acoustique peut être un outil précieux lors d'études détaillées du comportement sous l'eau chez les pinnipèdes à accouplement aquatique.

[Traduit par la Rédaction]

Introduction

Pinnipeds are polygynous mammals that exhibit extreme variation in male reproductive success (Boness 1991; Le Boeuf 1991). In land-breeding pinnipeds, males defend territories and (or) resources (Trillmich 1986; Boness 1991). Territory size and tenure length vary among individuals, and

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males show a high degree of site fidelity, with individuals returning to the same sites both within and between years (Francis and Boness 1991).

Much less is known about the mating systems of pinnipeds that mate in the water (Boness 1991; Hanggi and Schusterman 1994; Sjare and Stirling 1996; Van Parijs et al. 1997). The paucity of information concerning the reproductive strategies of aquatically mating pinnipeds is primarily due to the logistical difficulties of studying species that mate at sea. Within the Phocidae, 15 out of the 18 species mate aquatically, and this represents 45% of all pinnipeds. The lack of data concerning the reproductive strategies of nearly half of all pinniped species represents a considerable gap in knowledge of the reproductive systems of marine mammals.

The use of a three-dimensional environment for mating by aquatically breeding species suggests that male reproductive strategies may be influenced by factors different from those that are important to land-breeding species. In the few aquatically breeding pinniped species that have been studied in some detail, most (e.g., the Weddell seal, *Leptonychotes*

weddellii (Bartsch et al. 1992), bearded seal, *Erignathus barbatus* (Cleator et al. 1989), and harbour seal, *Phoca vitulina* (Hanggi and Schusterman 1994; Van Parijs et al. 1997), use underwater vocalisations in male–male competition and (or) advertisement to females. Furthermore, both Juan Fernandez fur seals, *Arctocephalus philippii* (Francis and Boness 1991), and Weddell seals (Bartsch et al. 1992) appear to defend aquatic territories during the mating season, although little is known about the characteristics of these aquatic territories.

The harbour seal is one of several phocid species that mates aquatically (Sullivan 1981; Hanggi and Schusterman 1994; Bjørge et al. 1995; Coltman et al. 1997; Van Parijs et al. 1997). In most harbour seal breeding areas, parturition occurs in midsummer, with females coming into oestrus after a 3- to 4-week lactation period (Temte et al. 1991). Energetic constraints force females to forage during late lactation (Bowen et al. 1992; Boness et al. 1994). Therefore, females are widely dispersed at sea during the mating season, and it is thought unlikely that it is economic for males to monopolise females (Thompson et al. 1994). Males decrease their range during this period (Van Parijs et al. 1997) and produce stereotypic vocal and dive displays that are thought to serve in male–male competition or advertisement to females (Hanggi and Schusterman 1994; Bjørge et al. 1995; Coltman et al. 1997; Van Parijs et al. 1997, 2000). In Scotland, males display-dive throughout the females' range, around pupping sites, on female feeding grounds farther out at sea, and along transit routes between the two (Van Parijs et al. 1997, 1999, 2000). Males exhibit both individual and geographical variation in their vocalisations during the mating season (Van Parijs et al. 1999).

In previous studies of the distribution of individual phocids during the mating season, telemetric techniques have generally been used (e.g., Thompson et al. 1994; Van Parijs et al. 1997). While these data have illustrated broad changes in behaviour and distribution, such as changes in female distribution, male range size, and dive behaviour prior to and during the mating season, they have not been precise enough to provide information on a smaller scale. In contrast, acoustic-localisation techniques offer the potential for studying marine mammals at sea at much finer spatial scales (Clark et al. 1986; Møhl et al. 1990; Clark and Ellison 2000; Frankel et al. 1995; Janik 2000). In acoustic localisation the difference in the times of arrival of a signal at different transducers in a hydrophone array is used to locate a sound source.

In this study we acoustically located the stereotypic underwater vocalisations of male harbour seals (Hanggi and Schusterman 1994; Van Parijs et al. 1997, 2000) in order to record the fine-scale distribution of males during the mating season over 3 successive years. We show how acoustic-localisation techniques can be used to obtain detailed, fine-scale information on the reproductive strategies of aquatically mating pinnipeds.

Methods

This study was undertaken during July of 1995, 1996, and 1997 in the Kessock channel, a confined area covering approximately 500 × 1400 m that forms the entrance to Beauly Firth, Scotland (57°30′ N, 4°14′ W) (Fig. 1), where females haul out and give birth to their pups. Water depth in the middle of the Kessock channel

increases from 6 to 38 m from east to west, and the maximum tidal range is 5 m. The seafloor consists of mud and pebbles. As a study site, the Kessock channel offers two exceptional opportunities: it allows the possibility of monitoring the behaviour of male harbour seals on a long-term basis and it lies directly en route to the feeding grounds for females pupping in Beauly Firth.

Acoustic recordings of male harbour seal vocalisations were made in the Kessock channel using three HTI SSQ94 hydrophones installed in a triangle to form a two-dimensional array (for a detailed account of the array design and calibration see Janik et al. 2000). Two hydrophones were placed on the north shore and one on the south shore of the channel, with inter-hydrophone distances of 208, 513, and 560 m. The hydrophone cables were each connected to a Micron TX 101 VHF radio transmitter. The signal from each radio transmitter was received via a S5Y YAGI aerial and a YAESU FRG-9600 radio receiver and recorded onto a multitrack Tascam Porta II tape recorder. The frequency response of the Tascam recorder ranged from 40 Hz to 12.5 kHz ± 3 dB. The equipment was installed in an observation hut 30 m above sea level on the north shore of the channel. The array localisation error inside the array and within 500 m of the hydrophones ranging from 2.5 to 13 m, while the maximum localisation error for sounds farther outside the hydrophone array was 20.4 m (Janik et al. 2000). All recordings and visual observations were made in a sea state of Beaufort 1 or 2 and without rain.

Two different sampling protocols were used to make acoustic recordings with the array. First, recordings were made for 20 min in each hour over a tidal cycle on 3 separate days in July of 1996 and 1997. Secondly, every 3–4 days, 20-min recordings were made 4 h after low tide in July of 1995, 1996, and 1997. Recordings were made 4 h after low tide because this corresponded to the daily peak in male vocalisations (Van Parijs et al. 1999).

All recordings were analysed using the localisation software program within SIGNAL (Engineering Design, Belmont, Mass.) (Beeman 1996). In this program, localisation of a sound source is based on the difference in times of arrival of the same signal at the two hydrophones in each pair. We attempted to localise every vocalisation heard in each 20-min sample. However, in 40.1% (*n* = 875) of cases, locations could not be determined because vocalisations were of poor quality or low amplitude. These were not included in any analysis.

All locations were plotted on a 1:2500 scale map of the Kessock channel. These locations were then digitised into an ATLAS GIS mapping package for presentation. Locations fell into distinct clusters (see Results). To estimate the area of each of these clusters at different stages of the tidal cycle or season, we used all the locations from each time period and calculated the minimum convex polygons around each cluster using MCPAAL (National Zoological Park, Smithsonian Institution, Washington, D.C., U.S.A.).

Male harbour seal vocalisations consist of a loud and pulsed burst of sound, the amplitude of which fades in and out at the start and end of the call (Van Parijs et al. 1997). Initially, recorded vocalisations were separated into three different quality categories, poor, medium, and good, based on their spectrogram quality (a reflection of the quality of the recording and the amount of ambient noise present). Only medium- and good-quality signals, where all parameters of a spectral contour could be measured distinctly, were used for the following analyses. Individual variation in male vocalisations within and between distinct clusters was determined by measuring four standard vocal parameters (Van Parijs et al. 2000): lower frequency (MIN), frequency with the greatest energy (F_{maxE}), total duration (TOT), and pulse duration (PULSE) (Fig. 2). Lower frequency was defined as the highest frequency of either the start or end section of a vocalisation, while F_{maxE} was defined as the frequency with the greatest amplitude, indicated by the darkest colour on a spectrogram. To avoid errors in measuring these parameters,

Fig. 1. Map showing the location of the two-dimensional hydrophone array in the Kessock channel, which forms part of the inner Moray Firth, northeast Scotland (57°30′N, 4°14′W). Each hydrophone (H1, H2, H3) was fixed to the end of a pier in the channel.
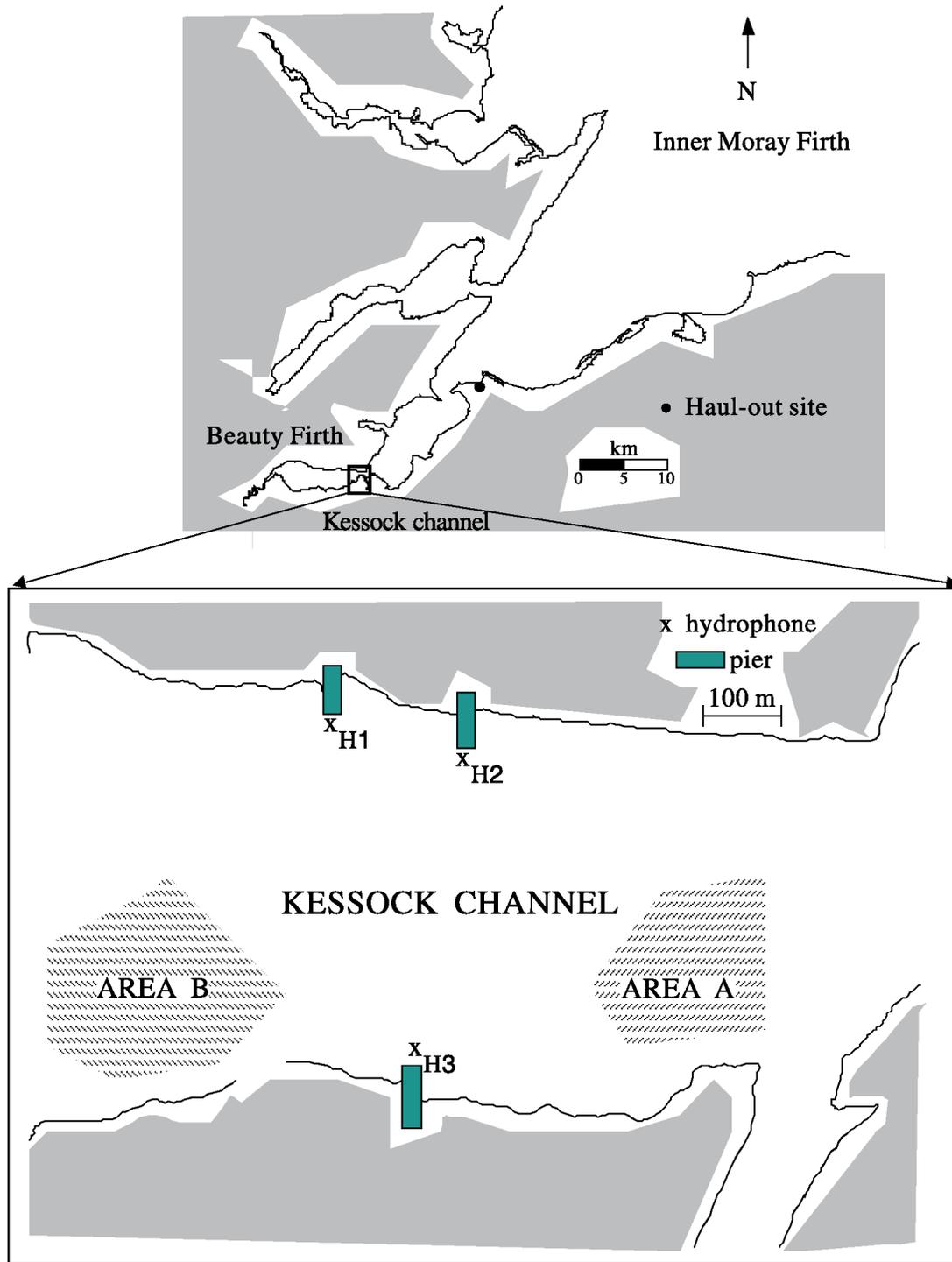

we ensured that the recording level and all spectrogram settings were the same for all recordings.

All vocalisations used during the localisation procedure were digitised at a sampling rate of 10 kHz ± 10 Hz over a time frame of 15 ± 0.0015 s and stored as spectrograms within SIGNAL. Spectrograms were calculated with 50% overlap (Fast Fourier Transforms (FFT), Δt = 10 ms, Δf = 102 Hz, FFT size = 512, effective filter bandwidth = 102 Hz, frame length = 10 ms). The four parameters were then measured on screen with a cursor for each stored

vocalisation. Repeated-measures one-way ANOVAs were used to determine whether there were significant differences in the vocal parameters between clusters in a single year and between years. We applied a Bonferroni procedure to all the data to avoid rejecting a null hypothesis as a result of double-testing the same data (Bakeman and Gottman 1986). This lowered the threshold significance level to $P < 0.01$.

Vocal variation within and between spatial clusters was further examined through discriminant analysis, which determined the

Fig. 2. Two spectrograms of male vocalisations, one each from areas A and B, in 1995, indicating the four parameters measured: total duration, pulse duration, frequency with the greatest energy (F_{maxE}), and lower frequency (kHz). Analysis settings were as follows: frequency resolution 31.5 Hz, sampling rate 10 000 Hz, spectrogram gain –33.0 dB, and spectrogram range 16.0 dB. Note the difference in the scales between the two spectrograms.
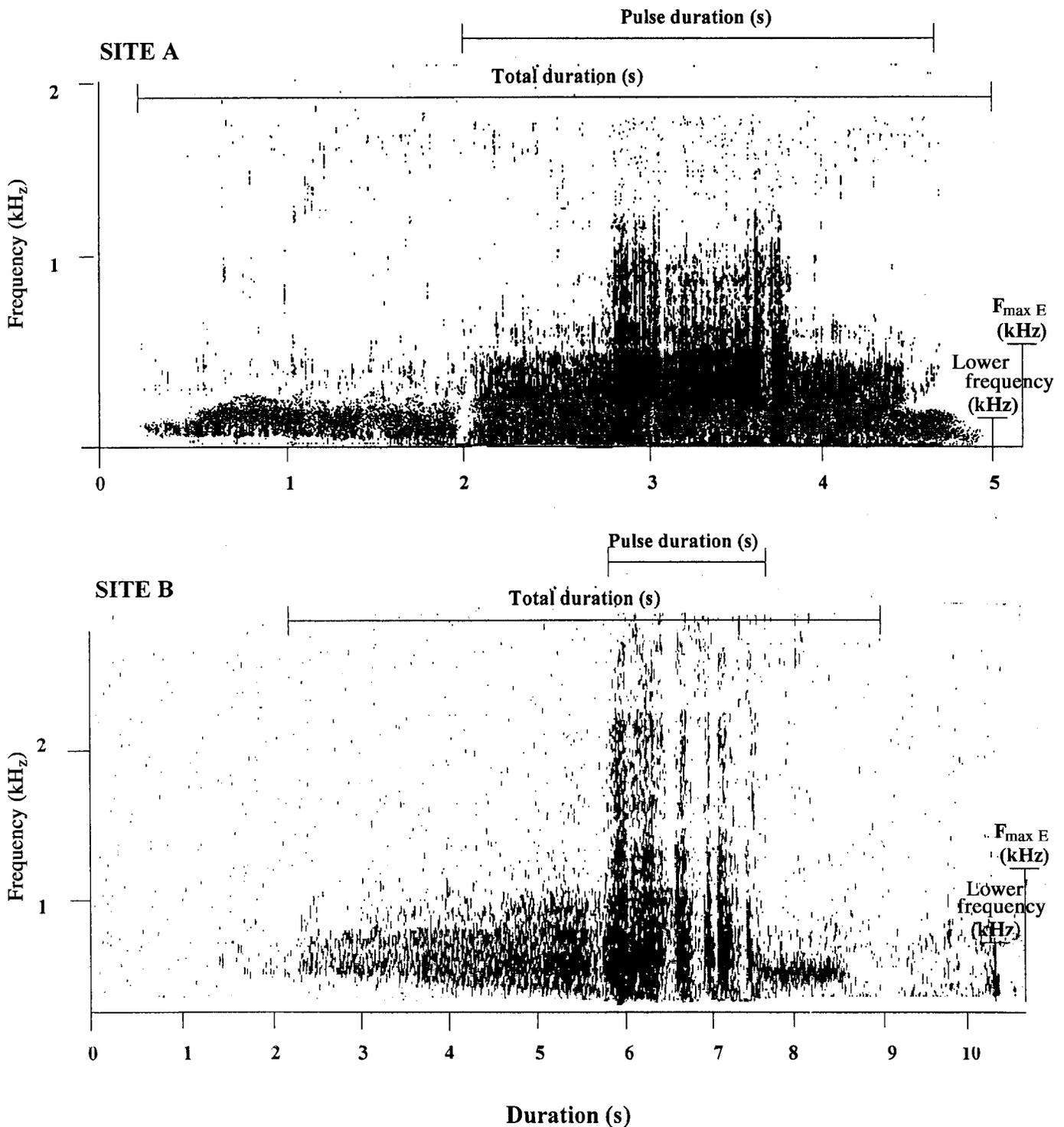
extent to which the measured vocalisations could be classified into distinct clusters. Discriminant analysis was used to perform a fully factorial multivariate ANOVA using all parameters (SPSS Inc. 1997). Canonical scores were determined for each parameter and the dependent variable canonical coefficients were used to produce discriminant scores. These coefficients were standardised by within-group standard deviations so that their magnitude could be compared across variables with different scales. The final classification predicted the percentage of cases that would be correctly classified and sorted all discriminant scores into two groups, function 1 and function 2. Lastly, the analyses calculated the mean posterior probabilities of vocalisations being classified correctly.

Fig. 3. Acoustic locations of all vocalisations recorded in the Kessock channel over three tidal cycles (polygons 1, 2, and 3; the numbers on the polygons indicate each tidal cycle and have no further significance) on separate days during July of 1996 and 1997 (see Table 1). Recordings were made on three hydrophones in the channel (H1, H2, and H3).
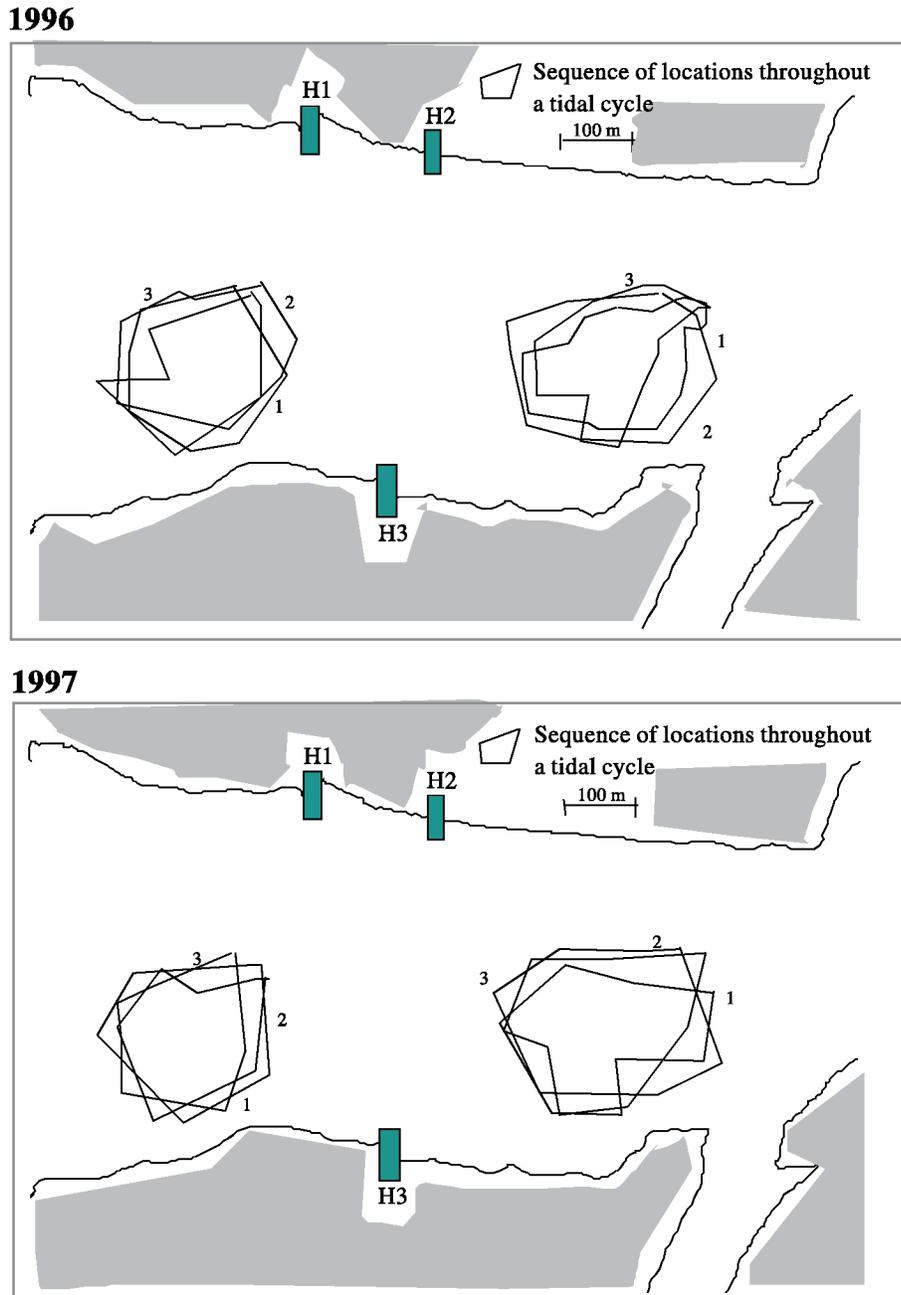

Results

Male vocalisations in the Kessock channel were consistently located within two distinct clusters: one cluster, to the east of hydrophone 3, was called area A, and the other, to the west of hydrophone 3, was called area B (Fig. 1). The vocalisations that could be localised ($n = 401$) were consistently located in these two areas throughout both the tidal cycle (Fig. 3) and peak-period recordings during the 3 recording years (Fig. 4). There was no overlap in locations between the two areas; instead, a minimum distance of about 200–250 m separated them at all times. The display areas were similar in size both within and between years (Table 1): area A ranged from 63.19 to 133.37 m^2 and area B from 41.59 to 115.34 m^2 (Figs. 3 and 4).

The results of five parametric ANOVAs comparing vocalisations showed significant variation in all vocal parameters between areas A and B (MIN: sum of squares = 529 157, $F_{[1,401]} = 89.5$, $P < 0.0001$; F_{maxE}: sum of squares = 292 551, $F_{[1,401]} = 5.6$, $P = 0.018$; TOT: sum of squares = 149, $F_{[1,401]} = 130.1$, $P < 0.0001$; PULSE: sum of squares = 396, $F_{[1,401]} = 39.2$, $P < 0.0001$). Furthermore, discriminant analyses determined that the measured vocalisations could be classified correctly according to their area with 100% (1995 and 1997)

Fig. 4. Acoustic locations of all male vocalisations recorded every 3–4 days in the Kessock channel during July of 1995, 1996, and 1997 (see Table 1). Recordings were made on three hydrophones in the channel (H1, H2, and H3).

1995

1996

1997
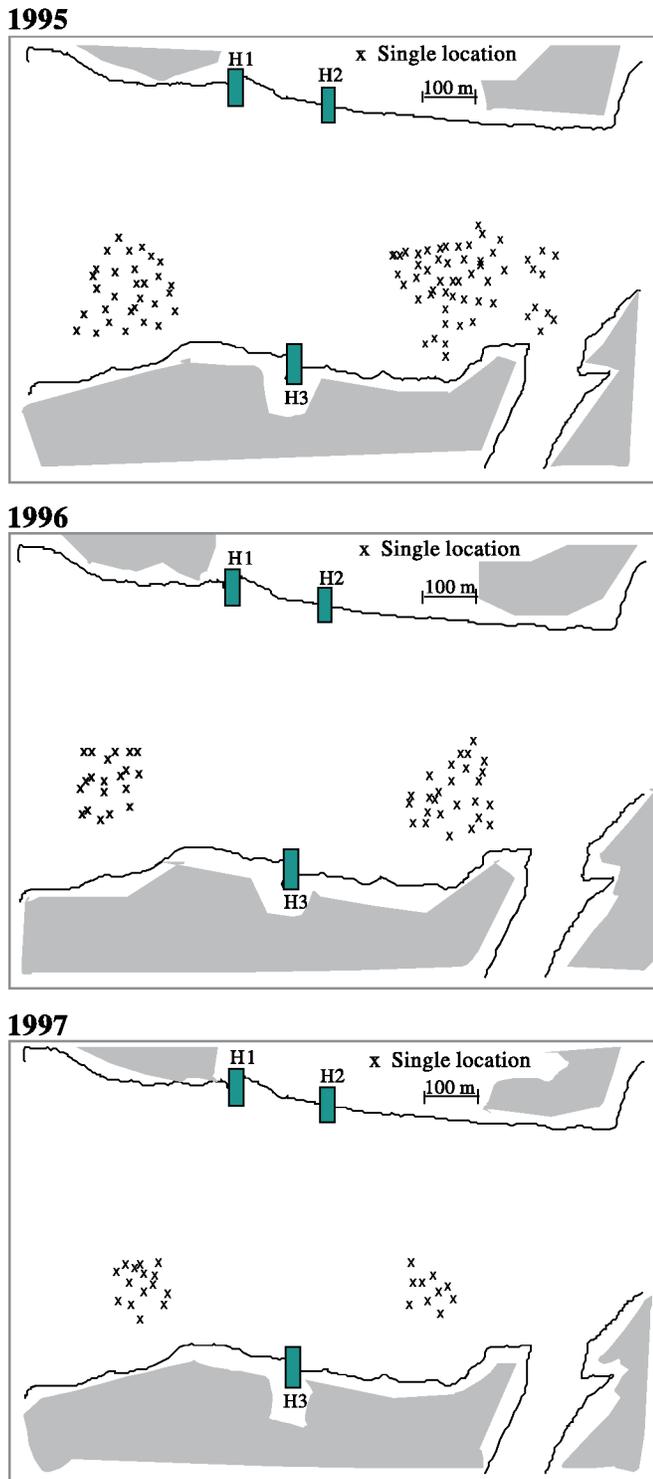
Table 1. The convex area polygons (m²) of all charted locations (*n*) in areas A and B for the three tidal cycles (1, 2, and 3) in July of 1996 and 1997 and during peak-period recordings made in July of 1995, 1996, and 1997 (see Figs. 3 and 4).

	Area A		Area B	
	Convex area polygon (m²)	*n*	Convex area polygon (m²)	*n*
Tidal cycles				
15 July 1996 (1)	81.1	25	52.8	24
22 July 1996 (2)	103.3	34	47.1	18
30 July 1996 (3)	65.4	20	64.7	35
17 July 1997 (1)	92.5	33	62.6	39
22 July 1997 (2)	67.6	30	77.8	35
26 July 1997 (3)	102.7	48	76.8	33
In July				
1995	91.2	56	68.6	30
1996	133.37	105	101.38	97
1997	132.0	121	115.4	122

Further ANOVAs determined that there was no significant difference between vocal parameters for area A among the 3 years of the study (Table 3). However, there was significant variation between vocal parameters for area B among the 3 years, with vocalisations from 1997 showing significant differences from those in both 1995 and 1996 (Tables 3 and 4). Table 5 provides mean values for each parameter and year for each area. All vocal parameters for area A had similar mean values over all 3 years, in contrast to area B, where the parameter values in 1997 were markedly different from those in 1995 and 1996.

Discussion

This study has shown that it is possible to use acoustic localisation to study fine-scale movements and behaviour of aquatically mating pinnipeds. Previous studies of male harbour seals based on telemetric techniques have shown large-scale changes in distribution (Van Parijs et al. 1997) and display behaviour (Hanggi and Schusterman 1994; Bjørge et al. 1995; Coltman et al. 1997; Van Parijs et al. 1997, 2000) during the mating season. However, in these studies the methods used to position an individual have not been sufficiently precise to determine the extent to which individual males return repeatedly to the same locations to display. Nor have these methods been refined enough to determine the more detailed behaviour of males in display areas.

In this study we used acoustic localisation of male vocalisations to provide small-scale spatial information on male reproductive strategies. The possibility that females also vocalise cannot be ruled out. However, despite considerable research on this species, both in the wild and in captivity, no female vocalisations have been identified, therefore we conclude that the vocalisations were from reproductively active males.

Our results constitute the first detailed account of the size of the display area of an aquatically mating phocid (Figs. 3 and 4, Table 1). The observed male harbour seals vocalised in small, distinctive areas covering around 40–135 m² (Table 1). Furthermore, the display areas at our study site were

and 96.6% (1996) accuracy (Table 2). Calculations of the mean posterior probability showed that the probability of classifying individuals according to their vocalisations was high in all years (Table 2).

Table 2. Discriminant analysis comparing all four measured vocal parameters from sites A and B for each year separately.

Year	Wilks' λ	χ^2	df	P	Percentage correctly classified	Posterior probability (%)[a]
1995	0.16	301.26	5,401	<0.0001	100	82±2
1996	0.24	479.7	5,401	<0.0001	96.6	91±1
1997	0.18	500.6	5,401	<0.0001	100	83±1

[a]Values are given as the mean ± SE.

Table 3. One-way ANOVAs of each of the four vocal parameters (minimum frequency (MIN), frequency with greatest energy (F_{maxE}), total duration (TOT), and pulse duration (PULSE)) measured within areas A and B between all 3 years (1995, 1996, and 1997).

	Sum of squares	df	F	P
Site A				
MIN (kHz)	2 808	2,401	1.05	0.35
F_{maxE} (kHz)	24 287	2,401	1.3	0.27
TOT (s)	1 002	2,401	1.9	0.1
PULSE (s)	1 093	2,401	2.5	0.082
Site B				
MIN (kHz)	3 105 984	2,401	584.2	<0.0001
F_{maxE} (kHz)	30 072 104	2,401	810.5	<0.0001
TOT (s)	2 658.1	2,401	180	<0.0001
PULSE (s)	18.3	2,401	12	<0.0001

Table 4. One-way ANOVAs comparing the four measured vocal parameters (minimum frequency (MIN), frequency with greatest energy (F_{maxE}), total duration (TOT), and pulse duration (PULSE)) for site B in 1995 and 1996 versus 1997.

Years	Sum of squares	df	F	P
1995 vs. 1996				
MIN	251.6	1,248	0.16	0.7
F_{maxE}	530	1,248	1.7	0.9
TOT	0.19	1,248	0.2	0.66
PULSE	2.5	1,248	0.6	0.1
1995 vs. 1997				
MIN	2 604 625	1,303	877.4	<0.0001
F_{maxE}	24 067 669	1,303	1118.6	<0.0001
TOT	2 259.7	1,303	246	<0.0001
PULSE	6.6	1,303	9.2	0.003
1996 vs. 1997				
MIN	1 847 119	1,223	540.7	<0.0001
F_{maxE}	19 391 062	1,223	699.1	<0.0001
TOT	1 544.1	1,223	128.2	<0.0001
PULSE	17.8	1,223	23.1	<0.0001

spatially discrete, being separated by 200–250 m (Figs. 3 and 4). Acoustic localisation consistently placed display locations in the same two areas of the study site throughout 3 consecutive years (Figs. 3 and 4). Both areas were located in water depths of 5–15 m just outside the deeper area of the channel, which is subject to strong tidal currents (20–40 m).

Analyses of the vocal parameters showed that there were significant differences among display areas (see Results and Table 2). These results suggest that only one individual may have been present in each display area throughout a mating season and over consecutive years. In Scotland, male harbour seals show individual variation in their vocalisations (Van Parijs et al. 2000). However, the probability that the measured vocal parameters would differentiate one individual from another varied greatly. The posterior probability that each of the 30 males in the previous study would be differentiated was highly variable, ranging from 21 to 99% (Van Parijs et al. 2000). In this study, the probability that the vocal parameters would separate males was high (Table 2). We suggest that, based on these results, it is likely that only one individual vocalised in each area during the mating season. Furthermore, the noticeably high probability that males from both display areas would be differentiated from one another suggests that males holding adjacent territories may exhibit a greater degree of variation in their vocalisations than males with display areas at greater distances. Further analyses in this study showed that vocalisation characteristics exhibited no significant variation within display areas A and B over 2 and 3 consecutive years, respectively (Tables 3, 4, and 5). These results suggest that the same individuals may

have returned to the same display areas over several years. However, these results should be interpreted with caution, as they do not rule out the possibility that male vocalisation characteristics change with time and potentially in relation to the location of their display area.

Studying the behaviour of male harbour seals throughout their range is logistically complex. This study covered a reasonably sized area of 500 × 1400 m, but only two males were found displaying in this area at any one time. Therefore, we are limited in the conclusions we can draw, owing to the small sample size. Male harbour seals are found vocalising throughout a females' range (Van Parijs et al. 1999), therefore male display behaviour may vary greatly among sites. Further research on small-scale behaviour throughout a female's range would greatly add to our understanding of male reproductive strategies.

A combination of techniques, including telemetry devices (Bjørge et al. 1995; Coltman et al. 1997; Van Parijs et al. 1997), genetics (Coltman et al. 1998, 1999), and a variety of acoustic techniques (Hanggi and Schusterman 1994; Van Parijs et al. 1997, 1999, 2000), is gradually enabling a picture to be built of the reproductive strategies used by aquatic mating pinnipeds. In harbour seals, males appear to adapt their reproductive strategies according to geographical area (Van Parijs et al. 2000). This suggests that aquatically mating pinnipeds may be useful species for further exploring the

Table 5. The four vocal parameters measured for each vocalisation recorded in areas A and B during July of 1995, 1996, and 1997.

Area and year	TOT (s)	PULSE (s)	F_{maxE} (Hz)	MIN (Hz)
Area A				
1995 ($n = 140$)	4.8±0.2	2.4±0.3	444±4.1	278±8.0
1996 ($n = 165$)	4.9±0.2	1.9±0.1	486±5.2	290±8.2
1997 ($n = 85$)	4.4±0.4	2±0.1	475±4.3	288±2.7
Area B				
1995 ($n = 145$)	6.9±0.3	2.7±0.1	698±8.9	290±3.9
1996 ($n = 170$)	7.2±0.4	3±0.2	712±2.8	302±6.3
1997 ($n = 85$)	10.8±0.5	5.2±0.1	1067±2.67	438±6.3

adaptations of mammalian mating strategies to different environments. We suggest that acoustic techniques, such as those used in this study, combined with telemetry techniques may be useful in further exploring the reproductive strategies of aquatic pinnipeds.

Acknowledgments

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