Geographic variation and acoustic structure of the underwater vocalization of harbor seal (*Phoca vitulina*) in Norway, Sweden and Scotland

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The male harbor seal (*Phoca vitulina*) produces broadband nonharmonic vocalizations underwater during the breeding season. In total, 120 vocalizations from six colonies were analyzed to provide a description of the acoustic structure and for the presence of geographic variation. The complex harbor seal vocalizations may be described by how the frequency bandwidth varies over time. An algorithm that identifies the boundaries between noise and signal from digital spectrograms was developed in order to extract a frequency bandwidth contour. The contours were used as inputs for multivariate analysis. The vocalizations' sound types (e.g., pulsed sound, whistle, and broadband nonharmonic sound) were determined by comparing the vocalizations' spectrographic representations with sound waves produced by known sound sources. Comparison between colonies revealed differences in the frequency contours, as well as some geographical variation in use of sound types. The vocal differences may reflect a limited exchange of individuals between the six colonies due to long distances and strong site fidelity. Geographically different vocal repertoires have potential for identifying discrete breeding colonies of harbor seals, but more information is needed on the nature and extent of early movements of young, the degree of learning, and the stability of the vocal repertoire. A characteristic feature of many vocalizations in this study was the presence of tonal-like introductory phrases that fit into the categories pulsed sound and whistles. The functions of these phrases are unknown but may be important in distance perception and localization of the sound source. The potential behavioral consequences of the observed variability may be indicative of adaptations to different environmental properties influencing determination of distance and direction and plausible different male mating tactics.
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I. INTRODUCTION

The harbor seal (*Phoca vitulina*) is an aquatic-mating phocid with a mating system generally considered to include serial monogamy and lek-type system (Fisher, 1954; Bigg, 1981; Boness, Coltman *et al.* 1997; 1991; Hanggi and Schusterman, 1994; Thompson *et al.*, 1994; Van Parijs *et al.*, 1997, 1999, 2000b). During the mating season, from July to late August, male harbor seals restrict their home range and start spending much of their time in the water at particular sites where they perform short stereotypic dives described as display activity (Bjørge, 1995; Van Parijs *et al.*, 1997, 1999, 2000a, 2000b; Hayes *et al.*, 2004). Favorable display sites are generally located in areas where female encounter rate is particular high (e.g., close to female haul-out and pupping sites), but males have been shown to display also over a wider area covering the whole of the female distribution (Van Parijs *et al.*, 1997, 1999, 2000a). The short, stereotypic dives may be repeated for periods up to 7 hours and males appear to show strong site fidelity towards display sites (Bjørge *et al.*, 1995; 2002; Van Parijs *et al.*, 2000b). During each dive, the male emits between one and five loud vocalizations (Hanggi and Schusterman, 1994; Bjørge *et al.*, 1995; Van Parijs *et al.*, 1997, 1999, 2000a; Hayes *et al.*, 2004; see Fig. 1). The best-known harbor seal vocalization is a broadband, nonharmonic roar with energy in the frequency range between 50 and 4000 Hz. The roar is the only harbor seal vocalization that is reported from all studied areas, i.e., USA (Hanggi and Schusterman, 1994; Hayes *et al.*, 2004), Norway (Bjørge *et al.*, 1995), Sweden (Wahlberg *et al.*, 2002), Scotland, U.K. (Van Parijs *et al.*, 1997, 2000a), and Canada (Van Parijs *et al.*, 2002; 2003). The function of the roar vocalization appears primarily to be advertising the presence of a male in breeding condition, and has therefore been suggested to be used in male–male competition and/or as reproductive advertisement display to attract females (Hanggi and Schusterman, 1994; Van Parijs *et al.*, 1997, 1999, 2000a, 2000b; Hayes *et al.*, 2004). Similar sexual display behavior is observed in other male pinnipeds such as walruses (*Odobenus rosmarus*) (Ray and Watkins, 1975; Stirling *et al.*, 1983, 1987), bearded seals (*Erignathus barbatus*) (Ray *et al.*, 1969; Cleator *et al.*, 1989), and Weddell seals (*Leptonychotes weddelli*) (Thomas and Kuechle, 1982; Thomas and Stirling, 1983) seals.

Recent research has shown that vocal variation in harbor

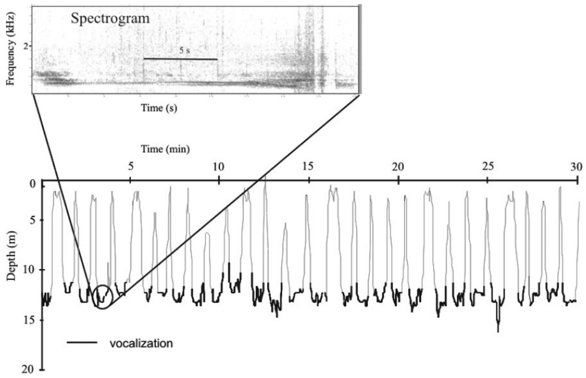

FIG. 1. Dive profiles and a spectrogram of an adult male harbor seal displaying and vocalizing, 23 July 1995 at Eynhallow, the Orkney Islands, Scotland, U.K.

seal roars occurs at the oceanic, regional, population, and subpopulation level (Van Parijs *et al.*, 1999, 2003), as well as individual variation in temporal (Van Parijs *et al.*, 2000a) and spectral features (Hanggi and Schusterman, 1994; Van Parijs *et al.*, 2000a). Factors that appear to have been important in the development of vocal geographic differences in harbor seals and other pinnipeds (Thomas and Stirling, 1983; Thomas *et al.*, 1988; Cleator *et al.*, 1989; Terhune, 1994; Van Parijs *et al.*, 2000a; 2003) includes: (1) long distances between recording sites; (2) a strong fidelity to specific breeding sites; (3) vocal learning; (4) a polygynous mating system; (5) different acoustic transmission properties; and (6) adoptions to various environmental challenges that influence male mating strategy.

To investigate individual and geographical differences, Hanggi and Schusterman (1994) and Van Parijs *et al.* (2000a) identified specific frequency boundaries within the frequency range of the roars. The boundaries (e.g., max and min values) were read off directly from spectrograms, by evaluating the darker and lighter shades that represent the intensity levels. Although the roar's frequency bandwidth may be reliable identified by individual researchers using this method, the technique is subjective and will probably generalize poorly across researchers. Moreover, computer-based spectrographic screen measurements are still manual and do not take advantage of the possibilities that digital spectrograms offer. Using a computer not only reduces human judgments but makes it less cumbersome to extract a large number of variables from each vocalization. Analytic techniques that utilize the underlying numerical intensity levels have recently been explored (Buck and Tyack, 1993; McCowan, 1995; Murray *et al.*, 1998). Buck and Tyack (1993) developed an algorithm that extracted the frequency component with the most energy to obtain a time-varying pitch contour of bottlenose (*Tursiops truncatus*) whistle. Similarly, McCowan (1995) and Murray *et al.* (1998) characterized bottlenose and false killer whale (*Pseudorca crassidens*) vocalizations by 20 and 30 measurements of the peak frequency, as well as changes in the duty cycle (Murray *et al.*, 1998). These techniques ensure an objective description of the vocalizations and make it easier to compare results from different studies. However, in nonperiodic signals, such as the harbor seal roar, dominant frequency measurements are not suitable because the peak frequency will vary randomly across the time axis (in accordance with the random nature of such signals). Clark *et al.* (1987) generated an algorithm that used the entire spectrogram of swamp sparrow (*Melospiza georgiana*) songs, rather than an extracted contour. Similarity between two songs was computed by cross correlating the numerical intensity levels along the time axis, and the resulting peak value of the correlation expressed the extent of how well the intensity levels in two songs overlap each other. This algorithm cannot describe the vocalizations themselves, only the differences between particular pairs of vocalizations.

A. Study objectives

The first aim of the present study was to investigate patterns of vocal geographical variation in six colonies in the Northeast Atlantic by means of an algorithm for extracting frequency bandwidth contours of harbor seal vocalizations. The second aim of this study was to provide a qualitative description of the detailed acoustic structure of the roar produced by harbor seals, and classify it into traditional sound-types categories such as nonharmonic sounds, pulsed sounds, and whistles.

II. DATA COLLECTION

Vocalizations were recorded at six harbor seal colonies in the Northeast Atlantic (Koster in Sweden; Eynhallow in Scotland; Sandøy, Froan, and Kongsfjord in Norway (Fig. 2) during the mating season of 1995 and 1996. Each study site holds the major seal colony of the respective area, and comprises coastal archipelagos with numerous intertidal rocks, small islets, and islands serving as haul-out sites during the breeding season. The diel and tidal cycle varies inversely from south to north. Koster (site 1, Fig. 2) has the smallest tidal amplitude (30 cm), and the sun is down for almost 5 h, while Kongsfjord (site 5, Fig. 2) has the largest tidal amplitude (200 cm) and 24-h daylight during summer. At Sandøy, and partly Nordmjelde (site 3 and 4, Fig. 2), haul-out sites are distributed over large areas, whereas in Eynhallow, and especially Kongsfjord (site 5 and 6; Fig. 2), the seals appear to prefer one or two haul-out sites, and are therefore less dispersed. Koster and Froan (site 1 and 3) may be considered as intermediate regarding the distribution of suitable haul-out sites (for more details on localities see Roen *et al.*, 1994 [Koster, Froan, and Kongsfjord], Bjørge *et al.*, 2002b [Sandøy], Bjørge *et al.*, 1995 [Froan], Wiig, 1988 [Nordmjelde], Henriksen and Haug, 1994 [Kongsfjord], and Van Parijs *et al.*, 1997 [Eynhallow]).

Recordings were made from small boats, either anchored or drifting close to calling animals. The hydrophone was fixed beneath a spar boy to reduce vertical motion, and lowered 1 to 3 m below the surface. A recording session started when we heard vocalizations of good quality (based on our subjective impression) and lasted from a few minutes to 4 h. In 1995, a custom-built hydrophone (frequency response 0.02 to 70.00 kHz) and amplifier (Sea Mammal Research Unit, University of St-Andrews, Scotland, UK) was used, and in 1996 a Brüel & Kjær 8104 hydrophone (frequency response 0.01–75.00 kHz ± 3.0 dB) was used. A

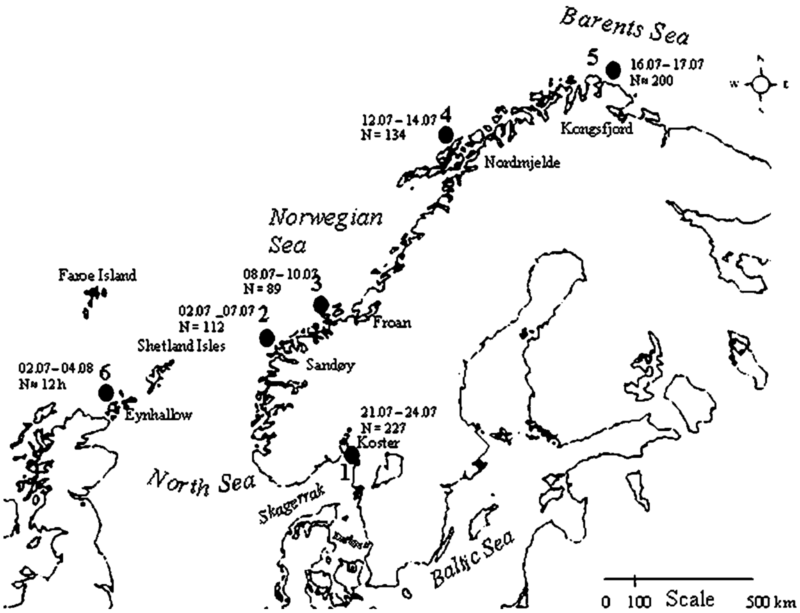

FIG. 2. Map showing the recording sites at six areas of the Northeast Atlantic: (1) Koster in Bohuslän County on the Swedish west coast; (2) Sandøy in Møre County on the Norwegian west coast; (3) Froan in Sør-Trøndelag County on the Norwegian west coast; (4) Nordmjelde in Nordland County in Northern Norway; (5) Kongsfjord in Finnmark County in Northern Norway; (6) Eynhallow in northwest Orkneys in northern Scotland, U.K. Numbers beside sites represent recording dates.

Sony digital audio tape recorder (DAT), TCD-D7, was used for all recordings. The frequency response of the recording equipment was limited by the tape recorder, which uses a sampling rate of 44.1 kHz, for a frequency bandwidth to 22 kHz. This bandwidth is well within the frequency range of harbor seal vocalizations (<5 kHz) reported by Hanggi and Schusterman (1994).

From each colony, 20 vocalizations with a high signal-to-noise ratio were chosen for analysis, yielding a data set of $6\times20=120$ vocalizations. To maximize the breadth of the sample at each site, recordings were made over a radius of at least 20 km at each colony (e.g., recorded 15–60 min and moving the boat to a new position several kilometers away). The recording positions were fixed with a GPS receiver (Garmin GPS 45), and if drifting, start- and endpoint, as well as intermediate readings were taken. The positions were plotted on boat sport charts (1:50.000 or 1:20.000) and clustered in discrete groups considering both space and time. Based on a ‘‘signal-to-noise character’’ (0–6), previously assigned to each vocalization by listening to the tapes, vocalizations with good quality (character 4–6) from at least five different groups were randomly chosen for analysis. Based on the evidence that males seem to display consistently within the same small discrete areas throughout the mating season (Bjørge *et al.*, 1995; Van Parijs *et al.*, 1997), this procedure should ensure that several individuals are analyzed from each colony. In addition, at several recording sites, several seals were obviously calling simultaneously within the audible distance of the hydrophone, increasing the likelihood of recording several individual males.

III. ANALYSIS

A. Frequency contour

In order to describe the harbor seal vocalizations, an algorithm was developed in an attempt to extract a time-varying contour of the vocalizations' frequency bandwidth. The selected 120 vocalizations were first normalized to the same peak amplitude and digitized (sampling rate $=22$ kHz and sampling size $=8$ bit) onto a Macintosh computer using the CANARY software package (Cornell Laboratory of Ornithology; Charif *et al.*, 1995). The digital spectrogram was computed using Hanning windows (Oppenheim and Schafer, 1998), 16 384-point FFTs, and overlap factor of 8. This yields a frequency-by-time matrix in which each column represents a sound spectrum derived over 743 ms. The frequency resolution of the spectrum is 5.4 Hz and the dynamic range is 48 dB. The start- and endpoint of the vocalizations were identified from the digitized waveform, and if obscure, combined with the spectrogram display [Figs. 3(a) and (b)].

The vocalization length (L) varied from 5.8 to 23.8 s. To ensure that corresponding variables in vocalizations with different durations reflect the same relative time sequence (e.g., variable 20 reflects the middle part in all calls), the bandwidth for each vocalization was estimated at regular intervals of $L/40$. With an overlap factor of 8, this procedure had a precision of minimum 46 ms. The use of 40 variables was chosen as a trade-off between adequately describing the shape of long vocalizations and avoiding too much redundant information in short vocalizations. Preliminary analysis showed that no vocalization contained energy above 2500 Hz. Thus, to increase computer speed, the overall bandwidth of the matrix was reduced from 11 500 to 2500 Hz so that before presentation to the ‘‘frequency bandwidth contour’’ algorithm each vocalization was represented with a 41×9800 matrix. The next step was to obtain a contour from the normalized matrix, where the contour was the value of the lower and upper frequency boundary of the bandwidth in each column (Fig. 3). We selected the average intensity of the matrix as reference value, and defined the upper and lower frequency boundaries of the bandwidth as the frequency coordinates where the intensity in ten vertical neighboring cells exceeded the overall average intensity level of the matrix by 12 dB [Fig. 3(c)]. This threshold value was arbitrary, but turned out to be sufficient to capture the general shape of the vocalizations and eliminate background noise. Repeating this approach for each column (spectrum) yielded

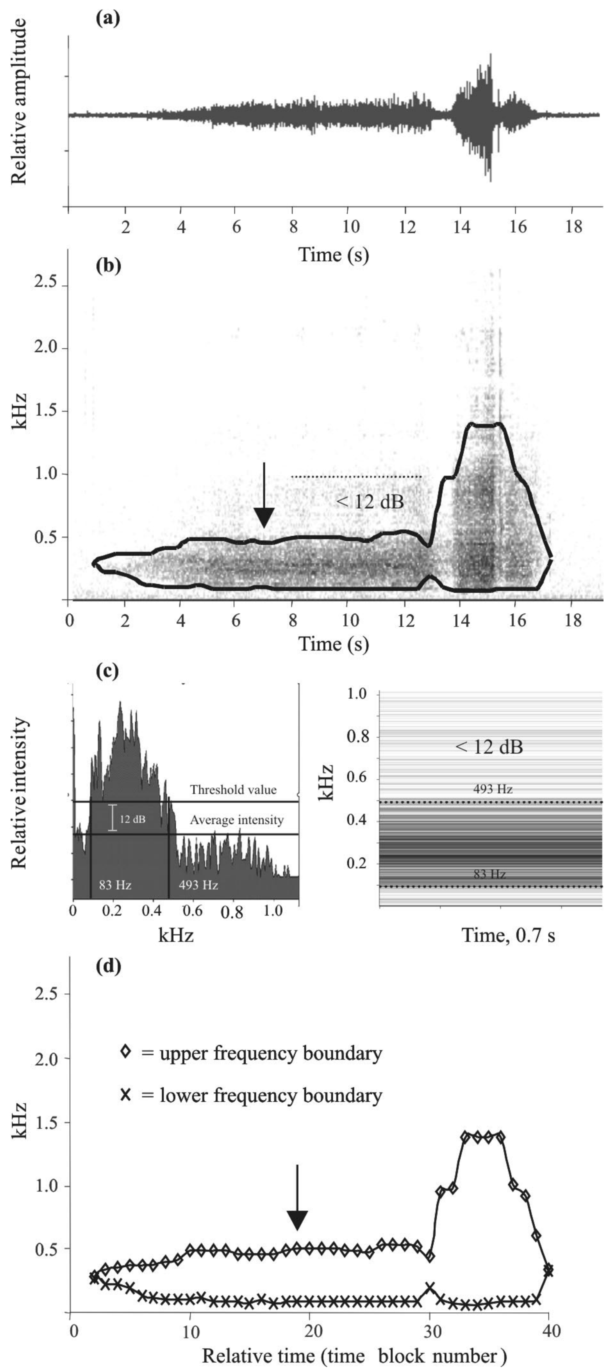

FIG. 3. Graphic illustration of how the frequency bandwidth was extracted from the harbor seal roars: (a) The waveform; (b) The spectrogram with superimposed contour. Analysis resolution = 43 Hz and 93 ms; (c) Spectrum and spectrogram illustrating schematically how the algorithm identifies and extracts the frequency coordinates. Analysis resolution = 5.4 Hz and 743 ms; (d) The frequency contour.

an estimate of the frequency bandwidth of each roar at 41 points in time [Fig. 3(d)]. Some vocalizations included noise (mainly from waves hitting the boat or vertical movements by the boat) in the analysis window with equal intensity as the signal of interest. To avoid that, spurious peaks such as these were registered as part of the vocalizations; the algorithm checked if the average intensity (for the same frequency interval) in either of the two next columns also exceeded the specific frequency boundary. If not, the algorithm assumed that the first value was an artifact and replaced the value of the cell with the average intensity in the matrix.

B. Geographic variation

PRIMER (Clarke and Warwick, 1994) was used as a statistical tool for exploring potential patterns within the data set. The frequency contours were converted to a triangular matrix of similarity between each pair of calls using a Bray–Curtis similarity coefficient (Bray and Curtis, 1957) and grouped by means of hierarchical agglomerative cluster analysis and finally ordinated with nonmetric multidimensional scaling (MDS; Kruskal and Wish, 1978). The results are presented as a dendrogram that clusters the contours in discrete groups, and as a two-dimensional ordination plot that visualizes the relationship between contours. One important feature of the multivariate analyses is that they in no way utilize any known structure among the contours of the colonies (Clarke and Warwick, 1994). The dendrogram and ordination were constructed only from the pairwise similarities among the 120 contours.

C. Traditional analysis

To determine the vocalizations' sound types, traditional analyses based on visual inspections of waveforms, spectra and spectrograms (Davies, 1964; Watkins, 1967) were performed on all vocalizations. Analysis resolution (filter bandwidth/frame length) was selected to emphasis acoustic structure of interest in either the time- or the frequency domain, i.e., both ''wide- and narrow-band'' spectrograms were produced. The time- and frequency range may be scaled to emphasize fine details of interest. Power spectra and waveform were available for any events in the signal.

IV. RESULTS

A. Patterns of geographic variation in the six harbor seals colonies

Based on the frequency contours, the six colonies were divided clearly into two major acoustic groups [Fig. 4(a)]. Group A consisted of Koster, Froan, Nordmjelde, and Kongsfjord, and group B contained Sandøy and Eynhallow [Fig. 4(a)]. Only 6 of the 120 vocalizations did not fit into this pattern (four from Kongsfjord and two from Sandøy). The two major groups could further be subdivided into several subgroups. At approximately 84% similarity threshold, 87% of the contours were grouped together with vocalizations from the same geographical area [Fig. 4(a)]. Thus, all subgroups are dominated by vocalizations from a single colony. The MDS plot (stress = 0.13) is in agreement with the dendrogram, although there is more disturbance between subgroup A5 and A6 [Fig. 4(b)]. The agreement between the two analysis methods suggests that the subgroups, and thus the frequency patterns, varied geographically. The analyses also indicated that seals in Koster and Nordmjelde used two vocalizations types. These types had different frequency patterns, e.g., the powerful roar ending the vocalizations constituted the greater part of the vocalizations in one type from Koster [Fig. 4(c)]. A nonparametric test, ANOSIM (Clarke

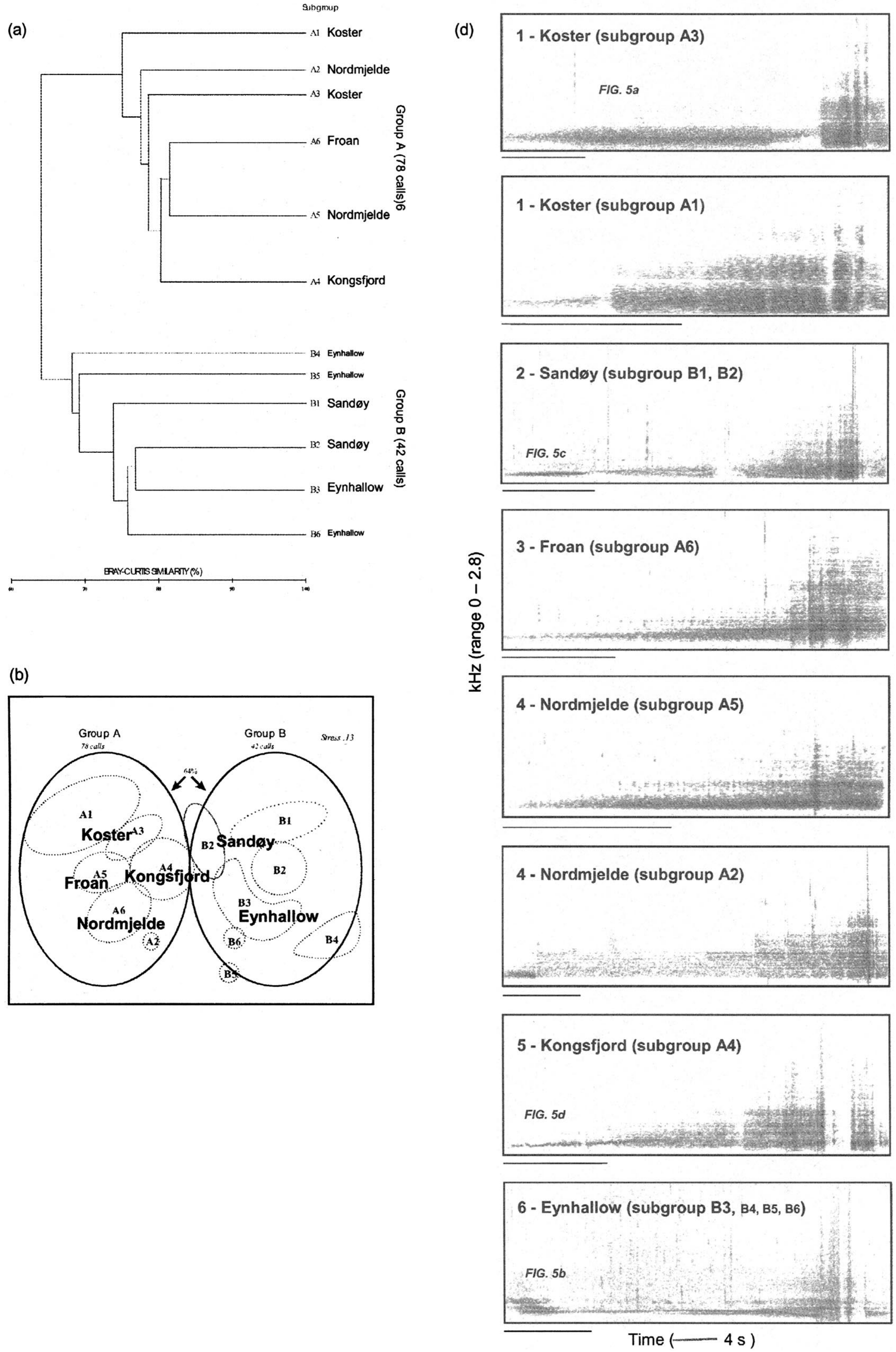

FIG. 4. Summary of acoustic relationship of six harbor seal colonies in the Northeast Atlantic: (a) The degree of acoustic similarity expressed as Bray–Curtis similarities, and displayed as a simplified dendrogram and a two-dimensional MDS plot with superimposed groups from the dendrogram; (b) Sample spectrogram of vocalizations from the colonies and subgroup in the similarity analysis. Note the two different vocalization types at Koster and Nordmjelde. Analysis resolution = 43 Hz and 93 ms. Segment shown in Fig. 5 is marked.

TABLE I. ANOSIM pairwise comparison of the frequency contours to the six seal colonies. The R values indicates the degree of separation, i.e., Sandøy and Froan/Nordmjele are best separated, while Froan and Nordmjele are least separated. Note: All colony pairs are significant different ($P<0.05$).

	Koster	Sandøy	Froan	Nordmjele	Kongsfjord
Sandøy	0.93	⋯	⋯	⋯	⋯
Froan	0.61	0.94	⋯	⋯	⋯
Nordmjele	0.37	0.94	0.29	⋯	⋯
Kongsfjord	0.48	0.67	0.57	0.48	⋯
Eynhallow	0.87	0.35	0.87	0.91	0.64

and Warwick, 1994), showed that differences between all colonies were significant ($P<0.005$; $R_{\text{global}}=0.63$; Table I).

B. Acoustical pattern

The harbor seals' vocalizations recorded in this study were broadband roars with most energy concentrated around 280 Hz (±74 Hz) but with intense bands (more than 12 dB above the background level) at intervals up to 2000 Hz (average = 1111 Hz, SD 346 Hz). Frequency range typically increased as the roar progressed, usually with a very abrupt increase in intensity and frequency bandwidth towards the end of the vocalization (highest frequency was located on average 82% ± 7% out in the call). Vocalization length varied between 5.8 and 23.9 s, with an average duration of 15.0 s (±4.0 s).

The majority of the vocalizations from Sandøy, Kongsfjord, and Eynhallow started with a characteristic short, tonal-like introductory phrase that was amplitude- and/or frequency modulated with high relative intensity (Table II). In contrast, the vocalizations from Koster, Froan, and Nordmjelde showed a relative intensity that was building up gradually during the call and was only composed of broadband, nonharmonic sound.

1. Broadband nonharmonic sound

a. "Spectrally structured sound." This was the dominating sound type in all vocalizations (Table II). The sound type is characterized by a broad frequency bandwidth with relatively intense spectral peaks [Fig. 5(a) and Fig. 6(a)] giving an aural impression of a continuous roar [Fig. 5(a)]. In 75% of the vocalizations from Nordmjelde [roars clustered in subgroup A5 in Fig. 4(a)] the roar had a rumbling quality due to much more marked time-varying spectral peaks, i.e., distinct pulses exhibiting broadband energy.

2. Tonal sound

b. "Warble." This sound type showed a combination of pulsed- and frequency-modulated structure [Fig. 5(b)]. The most striking feature was a rhythmic frequency-modulated carrier wave that varied between 240 and 300 Hz at a rate of 18 Hz. The pulsed component, indicated by the third peak in the 4096-point (21-Hz) spectrum [Fig. 6(b)], had a carrier frequency around 450 Hz and a pulse rate of 18 Hz. The large accompanying amplitude modulation was also visible by a close examination of the signal. This distinct sound type was only found in vocalizations from Eynhallow (90%, Table II), and was produced at the beginning of the vocalizations (2.7 ± 0.7 s). To the human ear, the signal had a rumbling quality with characteristic variations in the pitch.

c. "Tonal pulsed." This sound type was composed of a pure tone around 200 Hz with regular pulse length and interpulse intervals [Fig. 5(c)]. Short (3.2 ± 0.6 s) tonal pulsed introductory phrases were typical for vocalization from Sandøy (Table II). The signal had a growling quality, similar to a series of guttural (throaty) R's. Although characterisic for Sandøy, two vocalizations from Eynhallow also started with a similar but longer pulse train (6.5 ± 1.6 s). Moreover, less intense and marked pulses were identified after the "warble and whistle buzz" phrases in vocalizations from Eynhallow and Kongsfjord (Table II).

d. "Whistle-buzz." The whistle was similar to a simple, continuous sine wave but differed by having a small, irregular frequency modulation [Fig. 5(d)]. The carrier frequency (center frequency) was around 180 Hz and the maximum frequency magnitude variation was approximately 30 Hz. This sound type was only found in the start of vocalizations from Kongsfjord (Table II). The whistle was usually followed by a very short tonal-pulse train with interpulse intervals close to the lower limit of human perception, making it difficult to separate the pulses in time. To the human ear, the

TABLE II. Frequency of occurrence of sound-types in all six seal colonies.

		Occurrence of frequency %						
		Colony						
Category	Location in call	Koster	Sandøy	Froan	Nordmjelde	Kongsfjord	Eynhallow	Overall
Spectral structured	Whole call ex. the introductory phrase	16.7	16.7	16.7	16.7	16.7	16.7	100
Warble (FM+AM)	Introductory phrase	0.0	0.0	0.0	0.0	0.0	15.0	15.0
Tonal pulsed (AM)	Introductory phrase and part 1	0.0	16.7	0.0	4.2	15.0	16.7	52.5
Whistle (FM)	Introductory phrase	0.0	0.0	0.0	0.0	15.0	0.0	15.0

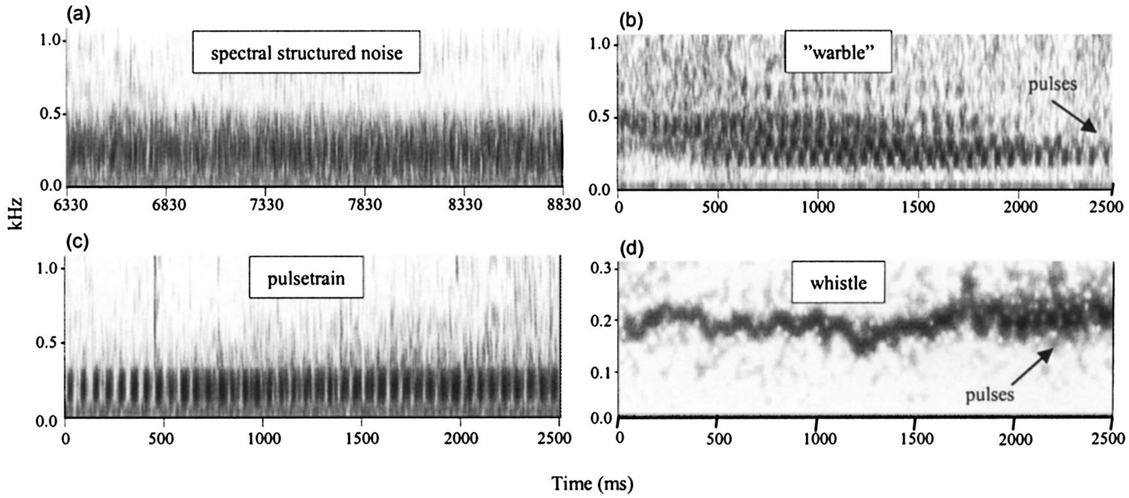

FIG. 5. Examples of four different sound types marked in Fig.4. (a) Spectral-structured sound; (b) Warble; (c) Pulse train; (d) Whistle. Analysis resolution $=342$ Hz and 12 ms for (a), (b), (c), and analysis resolution $=171$ Hz and 24 ms for (d).

whole phrase appeared virtually continuous and bore a strong resemblance to a buzzing bumblebee.

V. DISCUSSION

A. Methods

Since the harbor seal vocalization has a complex acoustic structure, it was important to develop a method that could objectively recognize the boundaries of the frequency bandwidth. The technique used in this study analyzes numerical values from digital spectrograms to extract a frequency bandwidth contour. There may be reason to question the reliability of bandwidth measurements in general. However, comparing the contour of the vocalizations (i.e., its "shape") rather than a few discrete measurements will probably reduce some of the effects of different recording conditions, such as different recording distances. As vocalizations from more colonies are compared, useful variables for exploring variability in harbor seal vocalizations may change. However, a time-varying contour will probably be more universal (but see Van Parijs *et al.*, 2003).

The technique used to "align" the contours in this study assumes a high level of temporal consistency, e.g., if vocalization length increases, the length of each part must increase correspondingly. This was the case for most of the harbor seal vocalizations. However, in two vocalizations from Kongsfjord, the powerful end constituted a considerably larger portion of the total vocalization. Other methods of aligning contours exist, e.g., "time warping," which was developed for the problems of speech recognition. This method has been used successfully to align the fundamental frequency contour of bottlenose dolphin whistle (Buck and Tyack, 1993). This is a more complex method, and one loses information about the percentage proportions that each part constitutes.

The threshold value of 12 dB was determined through experimentation and observation. The threshold value was set relative to the average intensity value of the normalized matrix, rather than the standard approach of measuring the distance (in Hz) at a predetermined point down (in dB) from the peak frequency. This made the algorithm vulnerable to intense background noise such as waves hitting the side of the boat. However, the alternative, using the peak frequency for each time block, means that the random peak frequency must be used as reference point. The critical ratio of harbor seal is around 19–27 dB (Turnbull and Terhune, 1990). Since the matrix was reduced to 2500 Hz, the roar constitutes a considerable part of the energy in the analysis window. Thus, it is likely that the contour portrays energy that the seals are able to hear.

B. Patterns of geographic variation

Comparison of harbor seals' vocalizations from six colonies in the Northeast Atlantic revealed geographic variation in the frequency contours and use of sound types. The distance between the six harbor seal colonies ranges from 200 km to more than 2000 km (Fig. 2). The lack of correlation between acoustic relationship (Fig. 4) and distance (Fig. 2) suggests that the main causal factor responsible for the ob-

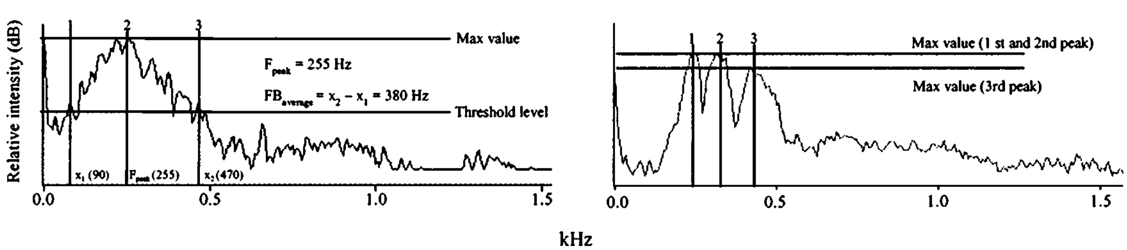

FIG. 6. Spectra of the (a) spectral-structured sound and (b) warble from Fig. 5. Analysis resolution $=21$ Hz.

served geographical differences in the repertoire may be geographic isolation. The harbor seal is regarded as stationary (Thompson and Miller, 1990), with only limited movement throughout the year (Bigg, 1981). Strong site fidelity probably results in sufficient isolation for the vocalizations to evolve independently in the colonies, leading to vocal divergence with time, and maintaining acoustic integrity of the colonies. Large distances, combined with a strong fidelity to specific breeding sites, were also thought to be the principal reason for geographic variation in the repertoire of Weddell seals (Thomas and Stirling, 1983; Thomas *et al.*, 1988), bearded seals (Cleator *et al.*, 1989), harp seals (Terhune, 1994), and harbor seals (Van Parijs *et al.*, 2003).

The large vocal difference between Sandøy and Froan (area 2 and 3; Fig. 2) shows that disjunct vocal variations also can occur over relatively small distances. Although the two colonies are only separated by only 200 km, the seals produced very different roars and were actually divided into different major acoustic groups (Fig. 4). Moreover, the two colonies had the largest R value of all colony pairs (ANOSIM=94%; Table I) and all Sandøy roars started with the characteristic pulse train which were not present in roars from Froan [Fig 5(c); Table II]. Local variations in repertoire have been described in a few pinnipeds. Cleator *et al.* (1989) and Van Parijs *et al.* (2000a, 2003) found distinct differences in bearded and harbor seal vocalizations between two colonies separated by only 150 km. If variation in underwater vocalizations reflects the degree of isolation between the colonies, these data suggest that the adult harbor seal is sedentary at a scale of less than 200 km. However, there are several other possible explanations for the observed vocal variation between the colonies. The harbor seal vocalizations are likely acquired through imitation and learning (Ralls *et al.*, 1985; Van Parijs *et al.*, 2003; see the review in Janik and Slater, 1997), and thus are primarily passed from generation to generation by cultural, rather than genetic, transmission (Ford, 1991). Once a transient seal is recruited to a colony, it may show enough social plasticity to learn the local roar. A motivation for changing the vocalization type may be a preference among resident females for site-specific roars and/or an increased aggression among resident males for unfamiliar roars. Another reason for changing or modifying the vocalizations may be different environmental acoustical transmission properties, ambient noise sources, predators, depth, or topographical differences, making it advantageous to communicate over various distances at the different colonies. Since it is not known when juvenile harbor seals learn the roar, another possible explanation of the observed differences between Sandøy and Froan is that the seal pups partly learn the roar in the breeding areas, but the vocalization is developed and improved further after the juvenile seals have been recruited to the new colony. Therefore, Froan and Sandøy may maintain their acoustic integrity even if a limited exchange of animals takes place between the two colonies.

In conclusion, the observed vocal differences between all six harbor seal colonies may be explained by functionless vocal divergence between groups that is isolated due to large distances and strong site fidelity to specific breeding areas. A possible limited exchange of animals may be present but may be masked by the harbor seals ability to learn new sounds by imitation, and by immigration of juvenile seal's that have not yet learned the adult repertoire (the roar vocalization).

C. Acoustical pattern

A particular feature of our dataset were the short introductory phrases that were amplitude- and frequency modulated (Fig. 5 and Fig. 6). These sound types have, to our knowledge, not been documented in other harbor seal colonies that have been fairly well studied (Hanggi and Schusterman 1994; Van Parijs *et al.*, 1999, 2000a, 2003; Hayes *et al.*, 2004). Tonal introductory phrases were characteristic for seals from Sandøy in Møre, Kongsfjord in Finnmark and Eynhallow at the Orkney Islands (Table II). Similar patterns and sound types are well known in other marine mammals, e.g., the "warble" [Fig. 5(b)] and "whistle buzz" [Fig. 5(d)] are found in harp seals (calls 4, 5, 8 and call 2 in Møhl *et al.*, 1975 and Terhune, 1994).

An important and crucial feature of an advertisement and territorial call is the possibility for receivers to (1) determine the location (i.e., direction and distance); (2) identity; and (3) the reproductive status and quality of the sender.

Tonal pulsed sound was identified in half of the vocalizations and may have functions in sound localization and distance perception. A possible mechanism for indicating the distance between a receiver and a source could be the number of pulses detected, because the number of detected pulses will increase with the improvement of signal-to-noise ratio as the distance between source and receiver decreases. Moreover, an investigation of the capability of harbor seals to localize a sound source showed that pulsed sounds yielded better results than continues tones (Terhune, 1974, 1988). Cleator *et al.*, (1989) suggested that the bearded seal might be able to judge the distance to the singer because various parts of the song travel differently through the water. Also, the humpback whale song may have characteristic spectral structures that may contain information of how far away the singer is located. (Mercardo and Frazer, 1999). Thus, producing vocalization with different sound types and especially pulsed tones may provide harbor seals a possible code for proximity.

Hanggi and Schusterman (1994) and Van Parijs *et al.* (2002) found individual variation within measured frequency bandwidth variables, as well as in temporal variables (Van Parijs *et al.*, 2002). As mentioned before, one of our concerns of using bandwidth measurements is the risk of degradation and/or masking of such signal over distance. A better candidate for such a call structure is a tonal vocalization with an emphasized and modulated carrier frequency (Dabelsteen *et al.*, 1993). If seals live in colonies with high ambient noise, complicated social structure (e.g., display area differences; see Van Parijs *et al.*, 2000a) the frequency bandwidth could become insufficient to assure individual recognition, and more specialized signals such as the introductory phrases may be necessary.

A lek mating system refers to two or more males displaying to females and to each other at traditional sites in which resources are not defended and the females visit only to mate (Höglund and Alatalo, 1995). Individual recognition and assessment of quality is prerequisite for the presence of lek and lek behavior in harbor seals. We consider that both these conditions are possible in the vocalizations we have recorded from harbor seals.

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