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Temporal and spatial variation in harbor seal (*Phoca vitulina* L.) roar calls from southern Scandinavia

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Male harbor seals gather around breeding sites for competitive mating displays. Here, they produce underwater vocalizations possibly to attract females and/or scare off other males. These calls offer prospects for passive acoustic monitoring. Acoustic monitoring requires a good understanding of natural variation in calling behavior both temporally and among geographically separate sites. Such variation in call structure and calling patterns were studied in harbor seal vocalizations recorded at three locations in Danish and Swedish waters. There was a strong seasonality in the calls from end of June to early August. Vocalizations at two locations followed a diel pattern, with an activity peak at night. Recordings from one location also showed a peak in call rate at high tide. Large geographic variations were obvious in the total duration of the so-called roar call, the duration of the most prominent part of the call (the roar burst), and of percentage of energy in roar burst. A similarly large variation was also found when comparing the recordings from two consecutive years at the same site. Thus, great care must be taken to separate variation attributable to recording conditions from genuine biological differences when comparing harbor seal roars among recording sites and between years. © 2017 Acoustical Society of America. [<http://dx.doi.org/10.1121/1.4977999>]

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I. INTRODUCTION

Male harbor seals (*Phoca vitulina*) vocalize extensively during their breeding season (e.g., Van Parijs *et al.*, 1999; Van Parijs *et al.*, 2003). Several types of underwater vocalizations have been identified, such as grunts, groans, creaks, bubbly growls, and roars (Hanggi and Schusterman, 1994). In addition, flipper slap sounds of high intensity are produced by seals slapping the water surface (Wahlberg *et al.*, 2002). The most prevalent and characteristic sound is the so-called roar (Van Parijs *et al.*, 2000a; Van Parijs *et al.*, 2000b; Bjørgesæter *et al.*, 2004). It is the only vocalization reported from all previously investigated study sites (Van Parijs *et al.*, 2000a; Van Parijs and Kovacs, 2002; Van Parijs *et al.*, 2003; Hayes *et al.*, 2004a). The roar is described as starting with low-frequency growling that builds up to a roar, a loud and pulsed burst with frequencies up to 2.5 kHz, followed by a decrease in frequency content towards the end. The amplitude gradually increases at the beginning of the call and fades out at the end (Van Parijs *et al.*, 1997; Bjørgesæter *et al.*, 2004).

The precise function of the roar, as well as other vocalizations, is unknown, although the coincidence of vocalizations with the breeding season suggests a role in mating behavior. The mating system of harbor seals is poorly described, but several observations are consistent with a lek-type mating system (Boness *et al.*, 2006). Such mating

systems are characterized by non-violent competition among males for females through ritualized displays (lekking), followed by female choice. Even though there are no clear observations of lekking displays by male harbor seals, several studies suggest that individual males defend small underwater territories, within which they repetitively produce underwater calls (Van Parijs *et al.*, 1997; Bjørgesæter *et al.*, 2004; Boness *et al.*, 2006). These calls could either play a role in maintaining the territory (Hayes *et al.*, 2004a) or in attracting females (possibly signaling strength or fitness of the male), or both (Van Parijs *et al.*, 2000b).

One way to establish the role of male harbor seal vocalizations during mating is to investigate what determines the rate of vocalizations. In some areas, there is a large increase in the prevalence of vocalizations during high tide (Van Parijs *et al.*, 1999), perhaps because more female seals are in the water during high than low tide, thus inciting males to vocalize more. In other areas, the vocalizations follow a diel pattern, with most roars in the morning and afternoon (Hayes *et al.*, 2004a) or at night (Van Parijs *et al.*, 1999). The reason for the diel pattern in vocalizations is unclear but most likely related to the foraging behavior of the females and thus expected to coincide with the peak presence of females swimming to or from the haul-outs (as suggested by Hayes *et al.*, 2004a).

Irrespective of mating system, the role of the underwater calls has some important implications for evolution of the signals. Mating signals, in order to serve their purpose, must propagate well through the environment and for them to function as honest signals of fitness they must also carry information about important features such as size and

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strength of the calling male, available for the female to base her choice on and/or for competing males to judge each other's strength. Both constraints (environment and signaling to conspecifics) can be predicted to vary among different populations of seals. Sound propagation conditions may differ between habitats. In addition, a simple geographic separation of populations can be expected to lead to behavioral differences even without a directional selection pressure, since stochastic processes, such as genetic drift or vocal learning, may change vocal signals over evolutionary time (Freeberg *et al.*, 2012). Ord and Garcia-Porta (2012) found that the best supported model for the evolution of communication complexity in four different taxonomic groups was through neutral evolutionary stochastic processes. Similar results were obtained by Irwin *et al.* (2008) who found that sound signal divergence in greenish warblers (*Phylloscopus trochiloides*) was correlated with both geographic distance and genetic divergence and from this inferred support for the importance of stochastic evolution of communication systems.

The regular occurrence of harbor seal calling in the mating season means that passive acoustic monitoring could be a powerful tool to monitor presence and behavior of this species. In order to interpret passive acoustic monitoring data, however, a thorough understanding of natural variation in call structure and calling behavior both among recording sites and with time of day and time of year is required. Pronounced variation between geographically separated recording sites has been demonstrated in recordings from harbor seals in Scotland, Swedish west coast, Norwegian west coast, Canadian east coast, and California (Van Parijs *et al.*, 2003), in line with observations from other phocid seals, such as the bearded seal, *Erignathus barbatus* (Risch *et al.*, 2007) and the harp seal, *Pagophilus groenlandicus* (Terhune, 1994; Perry and Terhune, 1999). The evolutionary drivers behind the variation seen in Van Parijs *et al.* (2003) were not identified, although comparisons of similarity among groups were performed. This analysis, however, produced results that were counter to normal understanding of biogeography and genetic relationships within harbor seal subspecies. The most extreme case was the underwater calls from Scottish harbor seals, which turned out to be most similar to the calls from Californian harbor seals, rather than to other Atlantic subpopulations and thus inconsistent with the biogeography of the species.

In order to test the hypothesis that larger geographic and/or genetic separation is reflected in increased dissimilarity in mating calls, the present study was designed to compare calls from three different subpopulations of harbor seals in Southern Scandinavia, more specifically one population from the Danish Wadden Sea, one population from the Danish estuary Limfjord and one in Kalmarsund in the Swedish Baltic. The seals from the Wadden Sea and the Limfjord are genetically distinct, yet closely related (Olsen *et al.*, 2014) and believed to originate from a common colonization event about 200 years ago (Härkönen *et al.*, 2005), whereas there is genetic and archaeological evidence that the population in Kalmarsund has been reproductively isolated for at least 8000 years (Goodman, 1998; Härkönen *et al.*, 2005). Thus, if

genetic and geographic separations are important factors explaining differences in mating calls, the Kalmarsund roars should be distinctly different from the Wadden Sea and Limfjord harbor seal roars. Our results show, however, that the variation in roar calls between recording years at the same site is as large as or larger than variation among calls recorded at different study sites. It is therefore not straight-forward to explain the observed variations in harbor seal roars mainly from genetic and geographic causes.

II. MATERIALS AND METHODS

A. Study sites

Recordings were made at three different field sites (Fig. 1). The Kalmarsund recording site in the Baltic Sea was located between the Swedish East coast and the island of Öland. Kalmarsund is home to a small isolated population of harbor seals, which breed and haul out on the rocky coast. About 800 harbor seals were counted in 2011 (Risinger, 2014). Besides harbor seals, a few grey seals may visit this area. However, the larger haul-out of Baltic grey seals is found several hundred kilometers further north (Harding *et al.*, 2007) and there are no indications of Kalmarsund being a major foraging site for this species (Sjöberg and Ball, 2000). There is no tidal variation in Kalmarsund, the water level being entirely determined by meteorological factors.

The Wadden Sea recordings were made in Juvre Dyb, a tidal stream north of the island Rømø and close to Pajsand, one of the largest breeding colonies of harbor seals in the Danish Wadden Sea. More than 700 harbor seals were counted in the Juvre Dyb tidal stream area during the annual aerial counts in August 2010 (Danish Centre for Environment and Energy, unpublished), out of a total population in the Wadden Sea of more than 20 000 harbor seals (Trilateral Seal Expert Group, 2010). In addition, there are important haul-out sites further to the west, towards deeper waters (Tougaard, 1989). Almost all seals in this area are harbor seals, but the outer banks may occasionally be visited by grey seals (*Halichoerus gryphus*). Average tidal amplitude is 1.5 m and the haul-out banks are usually completely covered by water during high tide.

The Limfjord recordings were made close to Blinderøn, a sand bar in the central part of Limfjorden, which is a brackish estuary open to both the North Sea and Kattegat. Harbor seals are the only seals in the estuary, with about 200 seals counted on Blinderøn in 2010, out of a total of about 1000 seals in the entire central Limfjord (Danish Centre for Environment and Energy, unpublished). The tidal amplitude at Blinderøn is very low, less than 10 cm.

B. Recording equipment

Recordings from the Wadden Sea in 2010 and from Limfjord in 2011 were made with autonomous data loggers (DSG-Ocean, Loggerhead instruments, Sarasota, Florida). One data logger was deployed between 7 July and 1 August, 2010 in Juvre Dyb about 1 km from the breeding site Pajsand (55°11.145' N, 8°36.253'E). Two data loggers were

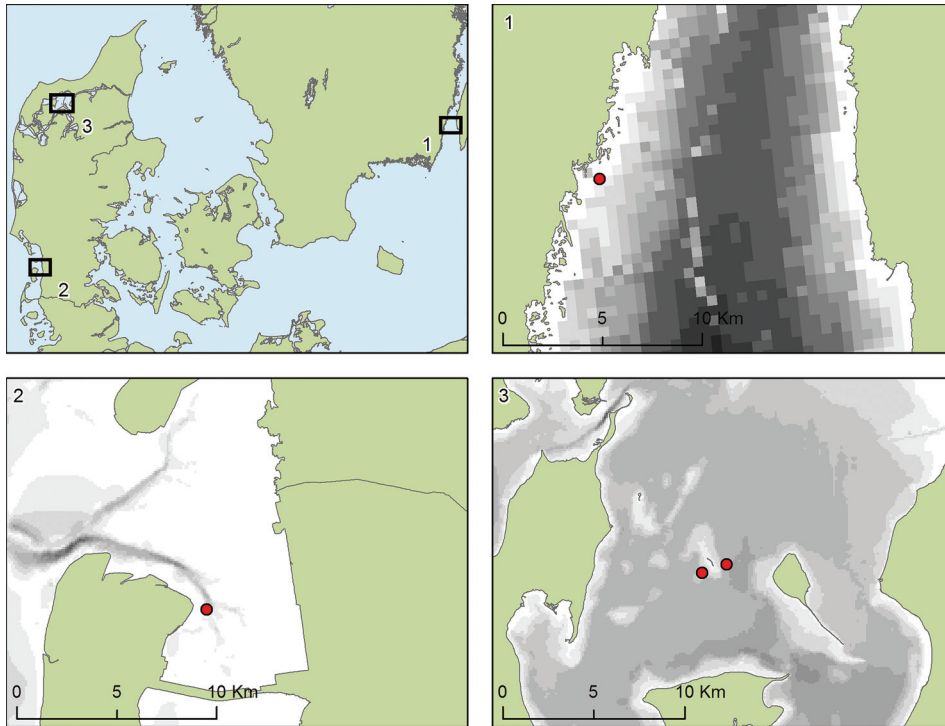


FIG. 1. Recording locations in Denmark and Southern Sweden. (1) Kalmarsund (Måsklippan), (2) Wadden Sea (Juvre Dyb), and (3) the Limfjord (Blinderøn), recordings on two sides of sand bar. Grey shading indicate bathymetry.

deployed in Limfjorden between 9 June and 7 July, 2011, one on either side of the breeding site Blinderøn ($56^{\circ}53.993' N$, $9^{\circ}1.601' E$ and $56^{\circ}53.736' N$, $9^{\circ}0.276' E$).

All three data-loggers were moored about 2 m above the sea bed, with a surface marker for retrieval. The sampling rate at Limfjord was 50 kHz (16 bit) and at Wadden Sea 20 kHz (16 bit). Loggers were equipped with HTI96 hydrophones (sensitivity of $-186 \text{ dB re } 1 \text{ V}/\mu\text{Pa}$ ($\pm 3 \text{ dB}$) in the frequency range 20 Hz to 25 kHz). Recording time was limited by memory capacity and therefore duty cycled: The Wadden Sea logger recorded for 30 min every 2nd hour (32 GB total capacity), whereas the Limfjord loggers recorded 4 min every hour (16 GB total capacity).

The recordings in Limfjord in 2010 and Kalmarsund in 2011 were made from a small boat with a hydrophone [TC 4032, Reson, Slangerup, Denmark, sensitivity of $-170 \text{ dB re } 1 \text{ V}/\mu\text{Pa}$ ($\pm 2 \text{ dB}$) in the range 15 Hz–40 kHz] and an Olympus LS-10 Linear PCM recorder, with sampling rate of 44 kHz (24 bit) and a 20 dB built-in amplification. Recordings in the Limfjord were made during 6 days between 2 July and 8 August 2010, close to Blinderøn, with a few additional recordings near another haul-out site on the SE corner of the island Livø, about 8 km from Blinderøn. Recordings in Kalmarsund were made between 2 and 5 July 2011.

C. Diel and tidal variation

Recordings were manually audited to identify calls. Several types were identified, but further analysis was performed only on the most common call type, the roar. Roars were counted in recordings from the data loggers to quantify diel and tidal variation. In the recordings from Limfjord in 2011 all recorded calls were counted in the 4 min recordings obtained every hour and in the recordings from the Wadden

Sea all calls were counted in 30 min recording periods for every second hour, resulting in hourly or bi-hourly estimates of call rates for the Limfjord and the Wadden Sea, respectively.

D. Selection of calls for individual analysis

Roars were selected so to reduce the risk of analyzing many vocalizations from the same animal (pseudoreplication). Only recordings with a high signal-to-noise-ratio were selected, in total about 100 calls from each recording set. The recordings from the Wadden Sea were between 20 and 30 min in duration and from each recording a maximum of three calls, all those with the highest SNR, were selected. From the 2011 Limfjord recordings, only one or two calls were picked out for analysis from each recording (4 min every hour) so that the analyzed calls were evenly distributed over time of the day.

Less data were available from the boat-based recordings in the Limfjord and in Kalmarsund, due to the relatively short recording time, and thus about 100 calls with the best signal-to-noise ratio were included from each site. The number of seals observed from the boat during recordings was noted. However, as vocalizations occurred under water, it was not possible to estimate the number of calling seals. Nevertheless, since recordings were made over several different days and with several seals around the boat, it is likely that recordings were obtained from a number of different seals at both locations, although some pseudoreplication seems unavoidable, especially for these data sets.

Numbers of roars selected for further analyses were: 91 from the Limfjord in 2011, 99 from the Limfjord in 2010 (including 15 calls recorded around Livø), 96 from the Wadden Sea in 2010, and 104 from Kalmarsund in 2011. The individual roars were analyzed in a randomized order,

rather than location by location, to reduce the risk of bias arising from a possible gradual change in classification criteria over the course of the analysis.

E. Analysis of calls

Further analysis of the individual roars was made by a custom script in MATLAB (Math Works Inc., version R2011b). Individual roars were cut from the primary recordings and saved individually. Each recording of a roar was down-sampled to 5 kHz, reduced to 16 bit resolution (for the 24 bit Olympus recordings), and high-pass filtered at 80 Hz (four-poled Butterworth). Roars were manually separated into four consecutive segments, assisted by a display of the waveform and the spectrogram (Fig. 2). The four segments were named “pulse train,” “start growl,” “roar burst,” and “end groan.” The “pulse train” segment was composed of a train of pulses with a low frequency tonal quality sounding like a deep guttural groan or growling. The “start growl” segment was a growling semi-broadband, low frequency build-up to the “roar burst.” The “start growl” never contained pulse trains, separating it from the “pulse train” segment. The “roar burst” segment was a broadband roar with frequencies from 100 Hz up to 2500 Hz. The last “end-groan” segment was a groan-like fade out of the call. Not all roars included all four segments, but as the roar burst was used to define a roar, this was present in all analyzed calls. A number of parameters were computed for the roar burst: duration (s), energy ($\mu\text{Pa}^2\text{s}$), L_{eq} (Pa), centroid frequency (Hz, *sensu* Au, 1993), peak frequency (Hz), root-mean-square (RMS) bandwidth (Hz, *sensu* Au, 1993), and -10 dB bandwidth (Hz). In addition, the total call duration (s) was measured.

Differences among the four sets of recordings were assessed by means of a canonical discriminant analysis with the parameters described above for the roar burst, as well as total call duration as input variables. Tidal and diel variation in the data logger recordings were assessed by derivation of the periodogram from the time series of the call rates. The periodogram was computed as the absolute value of the discrete Fourier transform (Bloomfield, 1976). The diel variation in the data from Limfjord 2011 was analyzed with Oriana software (version 4. Kovach Computing Services, Pentraeth, Wales, U.K.), using standard methods of circular statistics (Fisher, 1995).

III. RESULTS

The recordings revealed an extensive production of underwater vocalizations by the harbor seals. From the Wadden Sea recordings a total of 17 303 calls were identified during 112 h of recordings, yielding an average call rate of 2.6 calls per minute. In Limfjord, a total of 3036 calls were detected in the recordings made on both sides of the sand bar during 90 h of recordings in 2011; or, an average of 0.6 calls per minute. The call rates did not differ between the two sides of the sand bar: 1438 and 1598 calls were recorded from the East and West side, respectively (Wilcoxon paired test: $P=0.13$). In Kalmarsund, most of the calls (around 85%) were recorded South-East of the small island Måsgundet (Fig. 1); about 10% were recorded next to the two larger islands further north. The

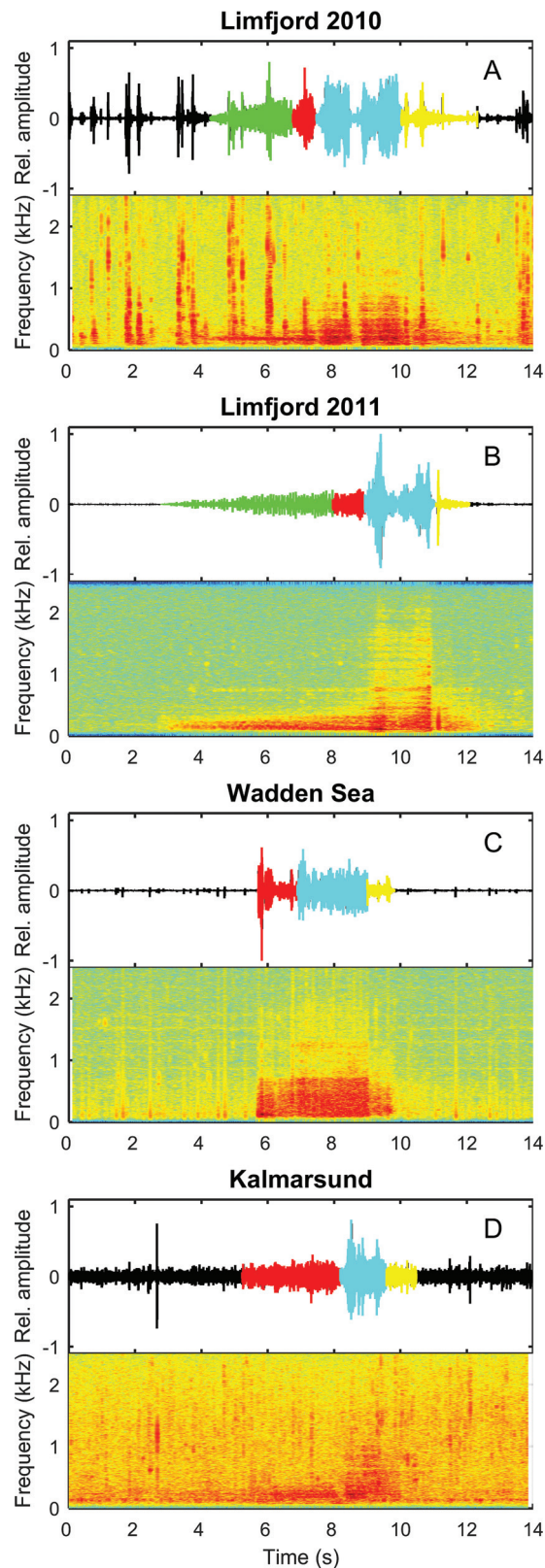


FIG. 2. Typical roars from the datasets, shown as waveforms and spectrograms. (A) Limfjord 2010, recorded from a boat. Broadband noise pulses are from waves hitting the boat. (B) Limfjord 2011, recorded by DSG-Ocean data logger, moored about 2 m above the bottom. (C) Wadden Sea 2010, also recorded by DSG-Ocean data logger, moored about 2 m above the bottom. (D) Kalmarsund 2011, recorded from a boat. The segments of each call are indicated by colors: green—“pulse train”; red—“start growl”; Blue—“roar burst,” yellow—“end groan.” Spectrogram settings: 1024 point FFT, Hann-weighted, 50% overlap. Signals were high-pass filtered at 80 Hz. Amplitudes were normalized and thus cannot be compared directly between recordings.

TABLE I. Harbor seal roar parameters (mean \pm 1 SE) for the four different recording sets. Recordings in the Wadden Sea and Limfjord 2011 were obtained by passive acoustic recorders, whereas recordings from Kalmarsund and Limfjord 2010 were obtained with a hydrophone from a boat. Number of calls analyzed per recording set: Wadden Sea ($n=96$), Kalmarsund ($n=104$); The Limfjord 2010 ($n=99$) and 2011 ($n=91$). In most cases the roar call contained more elements than just the roar burst. See text and Fig. 2 for explanation and illustration of individual call components. Roar burst energy expresses the acoustic energy in the roar burst relative to the total call energy.

| | Entire call Duration (s) | Roar burst | | | | |
|---------------|-----------------------------|---------------|---------------------|-------------------------------|---------------------------------|----------------|
| | | Duration (s) | Peak frequency (Hz) | Bandwidth _{rms} (Hz) | Bandwidth _{-10dB} (Hz) | Energy (%) |
| Limfjord 2010 | 9.5 \pm 0.3 | 3.1 \pm 0.1 | 208 \pm 8.9 | 104 \pm 7.3 | 430 \pm 30.8 | 61.8 \pm 2.3 |
| Limfjord 2011 | 12.9 \pm 0.4 | 2.7 \pm 0.1 | 155 \pm 5.7 | 59 \pm 2.3 | 274 \pm 9.5 | 64.8 \pm 2.5 |
| Wadden Sea | 8.1 \pm 0.4 | 4.6 \pm 0.3 | 160 \pm 4.7 | 69 \pm 3.0 | 341 \pm 15.3 | 94.1 \pm 0.8 |
| Kalmarsund | 4.2 \pm 0.3 | 2.2 \pm 0.1 | 190 \pm 5.5 | 99 \pm 8.7 | 305 \pm 30.3 | 78.7 \pm 2.2 |

last 5% were recorded north of Måsgrundet. Since the recordings in Kalmarsund and Limfjorden in 2010 were opportunistic, we could not quantify call rates for these recordings.

Several types of sounds were identified in the recordings: flipper slaps, bubble blowing, barks, tonal growls, and roars. These calls were identified according to the description of these call types in previous studies (Hanggi and Schusterman, 1994; Wahlberg *et al.*, 2002). Flipper slaps were heard at all sites. Bubble blowing was only recorded in Limfjord in 2010. Barks, resembling the sound of a dog’s bark, were short sounds, ranging from 0.2 ms to maximum 1 s, with no energy observed above 2 kHz and most energy between 100 Hz and 1 kHz. Tonal growls did not contain a roar, but were narrow-band, low frequency (around 100–150 Hz) tonal sounds with a growling or guttural quality. The duration of the tonal growl usually ranged between 2 and 7 s.

The roar was the most prevalent sound at all sites (76% of the data logger recordings from the Wadden Sea and the Limfjord 2011). The roars recorded in this study fit the descriptions of roars from earlier studies (Hanggi and Schusterman, 1994; Van Parijs *et al.*, 2003; Bjørgesæter *et al.*, 2004) and with comparable acoustic parameters (Table I). Differences in exact analysis methods among studies and lack of quantitative reporting prevent a direct comparison, however. Typical roars from the four data sets are shown in Fig. 2.

TABLE II. Presence/absence of the three call components across the four data sets. Bottom rows contain number of calls with the eight possible combinations of call components (P=pulse train, S=start growl, R=roar, E=end groan, _=absent). Roar component was always present, as this defined which calls to analyze.

| | Limfjord 2010 | Limfjord 2011 | Wadden Sea | Kalmarsund |
|-----------------------|------------------|------------------|---------------|------------|
| Total number of calls | 99 | 91 | 96 | 104 |
| % with “pulse train” | 58% | 95% | 10% | 9.6% |
| % with “start growl” | 77% | 85% | 68% | 59% |
| % with “end groan” | 63% | 93% | 50% | 23% |
| Call structure | Number of calls | | | |
| PSRE | 32 | 75 | 0 | 1 |
| PSR_ | 9 | 2 | 1 | 2 |
| P_RE | 14 | 8 | 0 | 1 |
| P_R_ | 2 | 1 | 0 | 6 |
| _SRE | 16 | 0 | 37 | 19 |
| _SR_ | 19 | 0 | 27 | 39 |
| __RE | 0 | 2 | 11 | 3 |
| __R_ | 7 | 3 | 20 | 33 |

A. Variation between recording sets

There were clear differences in calls between the four data sets, both in the structure of the calls and in the acoustic parameters of the individual segments of the calls. Table II shows the abundance of the different segments in calls from the different sets and also lists the combinations of call components and the frequency of occurrence in the four data sets. Differences in use of “pulse train” and the “end groan” were found, but not for “start growling.” The most pronounced difference was in the occurrence of “pulse train,” which was present in 94.5% of the calls from Limfjord but only in 9.4% and 1% from Kalmarsund and Wadden Sea, respectively. The roars recorded at Limfjord were most often associated with all the three other segments (“pulse train,” “start growling,” and “end groan”), unlike the roars from both the Wadden Sea and Kalmarsund, which often occurred alone, or in combination with only the “end groan.”

Because the roar burst was the defining criterion for roars, and therefore present in all calls, the measurements of this segment were chosen for a detailed comparisons of acoustical parameters: duration of roar burst, its peak frequency, RMS-bandwidth, and -10 dB bandwidth; and the percentage of energy in the roar burst compared to the total call energy. Furthermore, the measured total duration of the roar (including other call components than the roar burst) was used for comparison between sites. A MANOVA analysis indicated that means could not be aligned with less than four dimensions (P_1 , P_2 , and P_3 all <0.0001). Thus, three significant canonical discriminant functions were derived, which explained 46, 30, and 24% of the variation for the first, second, and third canonical, respectively (canonical loadings shown in Table III). The four data sets were significantly different (Wilk’s $\lambda=0.256$, $p < 0.001$, $df = 18/1078$,

TABLE III. Canonical loadings (canon.) for the input variables of the three canonical discriminant functions.

| | 1st canon. | 2nd canon. | 3rd canon. |
|------------------------------------|------------|------------|------------|
| Total call duration | 0.29 | -0.075 | -0.096 |
| Duration of roar burst | -0.19 | 0.48 | 0.504 |
| Peak frequency of roar burst | -0.0047 | -0.0045 | 0.0071 |
| RMS-bandwidth of roar burst | -0.011 | -0.013 | -0.0074 |
| -10 dB bandwidth of roar burst | 0.0027 | 0.0033 | 0.0029 |
| Roar burst energy re. total energy | 0.011 | 0.018 | -0.041 |
| % variance explained | 46% | 30% | 24% |

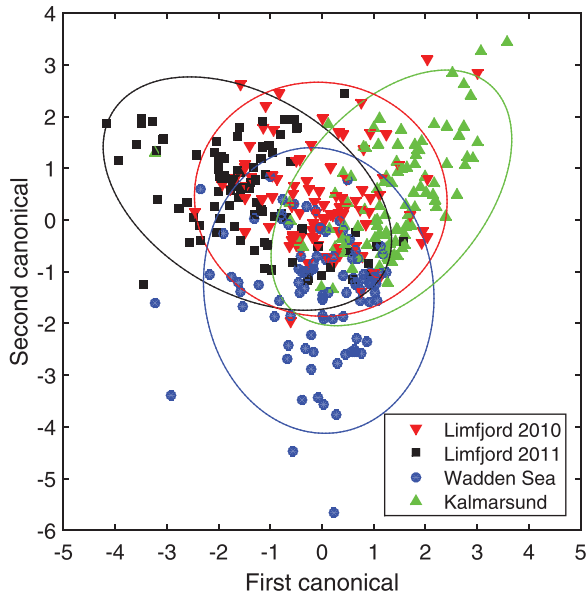


FIG. 3. All analyzed calls, separated according to recording set and plotted on first and second canonical axes (derived from canonical discriminant analysis of the roar burst parameters). Ellipses indicate 95% confidence limits.

$F = 37.09$; Bonferroni corrected Hotelling's $p < 0.001$ for all pairwise comparisons). All calls are shown in Fig. 3, plotted by their values of the first and second discriminant function. Classification based on the canonical discriminant functions could be accomplished with overall 74% of calls classified correctly. The Confusion matrix is shown in Table IV. Best separation was achieved between Limfjord in 2010 and Kalmarsund (3% and 5% classification errors) but this was only slightly better performance than the remaining pairs (between 7% and 14% errors).

The total call duration and duration of the roar burst carries most of the information used for separation of the four groups of calls, seen by the high canonical loadings (Table II). Limiting the canonical discriminant analysis to only total call duration and roar duration achieved 65% correct classification (Wilk's $\lambda = 0.393$, $F = 76.42$, $p < 0.001$), whereas an analysis with only the four remaining parameters achieved 60% correct classification (Wilk's $\lambda = 0.489$, $F = 26.24$, $p < 0.001$).

The call parameters correlated with each other to various degrees. Strongest correlation was found between RMS-bandwidth and -10 dB bandwidth (Pearson's $r^2 = 0.72$),

TABLE IV. Confusion matrix of classification of calls based on the canonical discriminant function. Total number of calls correctly classified was 74%. Number of calls per recording set: Wadden Sea ($n = 96$), Kalmarsund ($n = 104$); The Limfjord 2010 ($n = 99$) and 2011 ($n = 91$).

| Call origin | Call classified as coming from | | | |
|---------------|--------------------------------|---------------|------------|------------|
| | Limfjord 2010 | Limfjord 2011 | Wadden Sea | Kalmarsund |
| Wadden Sea | 11% | 5% | 72% | 5% |
| Kalmarsund | 3% | 11% | 9% | 78% |
| Limfjord 2010 | 71% | 7% | 9% | 5% |
| Limfjord 2011 | 14% | 77% | 9% | 12% |

whereas the remaining pairwise correlations were weak or non-significant (Pearson's $r^2 < 0.1$, except for % roar energy versus total duration and roar duration, where $r^2 = 0.16$ in both cases).

B. Seasonal and temporal patterns

In the Wadden Sea, vocalizations were detected during the entire data logger deployment in July 2010. There were fluctuations in daily call rates, perhaps due to weather, but start and end of the calling period was outside the recording period.

There was a pronounced seasonality in calling rates from the Limfjord data logger recordings in 2011. Almost no vocalizations were recorded in the beginning of June, then call rates increased throughout June peaking at or after beginning of July, when the data loggers were retrieved (Fig. 4). In 2010, when recordings were made from boat, the calling season had apparently ended earlier than 8 August, when no calls could be heard during a visit to the haul-out bank.

Variation in call rate with time of day was investigated in the data sets from the autonomous loggers only, as call rates could not be derived from the opportunistic boat-based recordings. In the Wadden Sea there was a strong coupling between call rate and tide, whereas this was not observed in the Limfjord, where the tidal amplitude is very low. Periodograms were generated from the time series of call rates (Fig. 5). Two pronounced peaks are visible in the periodogram from the data from the Wadden Sea: one corresponding to a period of 12.5 h (which is attributable to

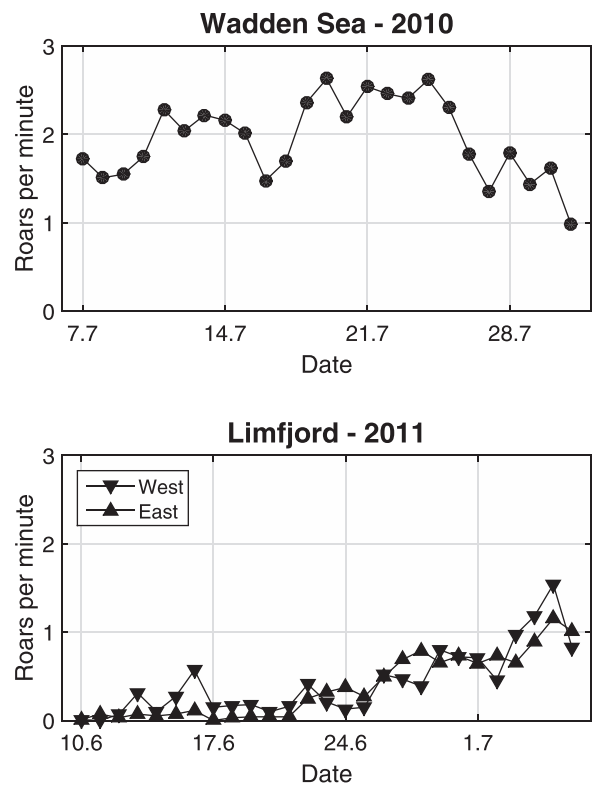


FIG. 4. Development of roar call rates with season in the Wadden Sea (2010) and Limfjord (2011). Call rates for the Limfjord shown for both recording stations, located on either side of the sand bar used by the seals for haul out.

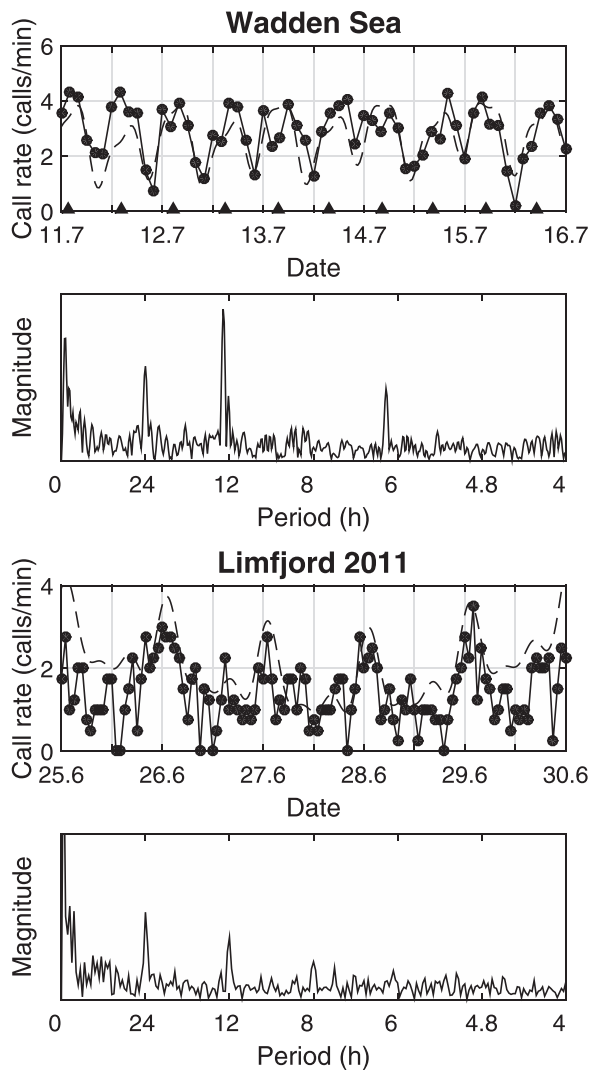


FIG. 5. A) Call rates (roars/min) in the Wadden Sea 2010, measured every second hour (upper panel), together with predictions of a simple model based on tide, time of day and a seasonal component. The prediction was generated by an inverse discrete Fourier transform of the peak values of the periodogram (shown in bottom panel). Triangles indicate time of high tide. The periodogram, generated as the absolute value of the discrete Fourier transform of the call rate time series, has pronounced peaks at 12.5 h (tide) and 24 h (light) and harmonic peaks at 12 h and 6.25 h. (B) Same as (A), but for Limfjord 2011. The periodogram only has a peak at 24 h, with harmonics and thus no tide component.

variation with tide), and one peak corresponding to a period of 24 h (attributable to diel variation). Two harmonics were also present with periods of 6.2 and 12 h, respectively. The presence of harmonics indicates that the fluctuations deviate from pure sine waves. Together this means that the fluctuations in the call rate in the Wadden Sea recordings can be very well described by the combined effect of two cyclic factors: a tidal cycle, peaking about 3 h after high tide and a diel cycle, peaking just after midnight (Fig. 5). Highest call rates were thus observed when high tide fell just after midnight and lowest calling rates when low tide coincided with noon.

In the data logger recordings from the Limfjord in 2011 a significantly increased call rate was seen from about 1 h before to about 3 h after midnight at both positions on either side of the sand bar (Fig. 5, Raleigh test $p < 0.0001$ in

both cases). The overall diel calling pattern differed between the east and west positions (χ^2 -test, $\chi^2 = 37.65$, $df = 23$ $p < 0.05$), but peak calling time (mean of the circular distribution) did not differ significantly between the two sites (Mardia-Watson-Wheeler test, $W = 0.183$, $p = 0.9$). Overall mean of the calling time distribution for the pooled data set was 00:42 h (00:07 h and 01:32 h for east and west, respectively). Sunrise was at around 3:30 and sunset at around 20:50 during the 28 days of deployment in 2011. This means that the seals' highest calling rates were reached during dark hours.

IV. DISCUSSION

A. Variation between data sets

In line with previous studies (Van Parijs *et al.*, 2003; Bjørgesæter *et al.*, 2004), we found considerable variation in harbor seal roars between geographical locations. The largest differences were observed in the prevalence of the “pulse train” component, which was present in most roars from Limfjord, but in very few roars from Wadden Sea and Kalmarsund. Similar differences between recording sites were also reported by Bjørgesæter *et al.* (2004), who compared roar vocalizations from five Norwegian colonies and one Orkney colony. They found different usage of the call types they termed “warble” (only recorded at Orkney), “whistle” (only recorded at Kongsfjord in Norway), and “tonal pulsed” (found at three Norwegian colonies as well as at Orkney).

The parameters of the roar and ‘roar burst’ also differed between recording sets. Especially the duration differed, evidenced by its high loadings on the first and second canonical discrimination functions (Table III). This was also found in previous studies (Van Parijs *et al.*, 2003). Total duration of the calls in the present study averaged 4.3–12.9 s, which is comparable to 5.8–23.8 s in Norwegian harbor seals. A reason for the apparently longer Norwegian roars could be that the tonal growl described here was not analyzed as a separate call by Bjørgesæter *et al.* (2004). We often heard the tonal growl without the roar and therefore treated it as a separate call. As the ratio of “roar burst” energy to the total energy of the call depends on the duration of the “roar burst,” it was not surprising that this parameter also was statistically different between Danish and Norwegian sites. The peak frequency found in our study, between 155 and 208 Hz, is lower than what is found in Norway and at Orkney Islands (280 Hz).

As the Kalmarsund population may have been isolated for 8000 years (Härkönen *et al.*, 2005) and has a unique DNA composition (Stanley *et al.*, 1996; Goodman, 1998), it was expected that the roar from these seals would differ greatly from the roar at other sites, which may only have been isolated from each other a few hundred years (Härkönen *et al.*, 2005). However, this was not the case. This suggests that other factors than genetic and geographical separation determines the structure of roars. One important factor could be differences between sound propagation properties between the three localities, which were indeed very different: The Wadden Sea is a shallow, high current

area with extremely high turbidity; the Limfjord is a relatively sheltered area with sandy/muddy bottom; and Kalmarsund is a rocky archipelago. These differences undoubtedly resulted in different sound propagating conditions for the calls and could very well be a major driving force for a selection towards optimizing communication distances and signal to noise ratio at the receiving animal.

A genuine surprise, however, was that the recordings of calls at the same location in Limfjord differed greatly between recording years: 2010 vs 2011. All analyzed signal parameters, except for the ratio of “roar burst” energy to total call energy, came out as significantly different. Several possible explanations can be envisioned. Perhaps the least probable explanation is an annual development in roars, as observed in calls from male humpback whales (Payne *et al.*, 1983; Payne and Payne, 1985). More likely, and also more worrisome, are the possibilities of pseudoreplication and effects of recording equipment. Even though the calls were carefully selected for analysis in a way to minimize the risk of pseudoreplication (only one or two calls were selected every hour in 2011; at least five seals were seen in the water during recordings in 2010), it is a real possibility that very few seals were producing vocalizations during the recordings, especially in 2010. Earlier studies have shown that individual vocalizations can differ between males from the same site (Van Parijs *et al.*, 2000b) and it remains a possibility that the true number of seals recorded was considerably lower than the about 100 calls analyzed from each year.

Another possible explanation offers itself readily, as the recording methods in Limfjord differed considerably between the two years. In 2010, calls were recorded with a hydrophone hanging from a small boat, whereas calls in 2011 were recorded by two autonomous data loggers close to the sea floor. Recording bandwidths were comparable between the two recordings and in any case sufficiently high to contain the calls within the flat part of the hydrophone frequency response curve and differences in the equipment *per se* is thus not expected to create substantial differences. More significant differences could be expected from different propagation paths in the two setups: one being a hydrophone suspended in open water, relatively close to the surface, while the others recorded closer to the bottom, possibly affected by the more reverberant environment. Also recording distances likely differed, although this could not be measured, which would lead to differences in reverberations and possibly high-pass filtering of the signals at longer ranges, due to the shallow waters (see, for example, Rogers and Cox, 1987), compared to the relatively long wavelengths of the signals (approximately 15 m at 100 Hz).

Other studies have in fact observed similar differences, for instance the two studies performed at Eynhallow, Orkney, with only few years in between. One study was conducted in 1998 (Van Parijs *et al.*, 2000a), and the other was conducted in the years 1995–1996 (Bjørgesæter *et al.*, 2004). The two studies used different recording equipment and measurements of some of the parameters gave different results between the years. Different methods were also used for extracting the parameters in different studies. Van Parijs *et al.* (2000a) visually measured on spectrograms, while

Bjørgesæter *et al.* (2004) used a MATLAB algorithm to extract the parameters automatically from the spectrograms. If the recording setup and analysis methods really do have significant influence on the measured parameters, this calls for great care whenever comparing different recordings. In particular, it may explain the otherwise puzzling results from Van Parijs *et al.* (2003), who compared harbor seal calls from ten different sites worldwide and used them as input for a similarity analysis. The most remarkable result of this analysis was that calls from Orkney and Moray Firth, Scotland were closer to calls from the Western Pacific, rather than to calls from the rest of the eastern Atlantic. When looking at the equipment in these recordings, six different types of hydrophones and eight different recorders were used across the ten sites investigated (Van Parijs *et al.*, 2003).

B. Seasonal and temporal variation

Harbor seals are very seasonal in their vocalizations, peaking in mid-summer (Van Parijs *et al.*, 1999) when mating takes place (Bjørge, 1992). In the Limfjord, calling started by the end of June and ceased in early August. The estimated duration of the vocalization season was 35–40 days. Recordings from the Wadden Sea did not cover the entire period, although there was a tendency to a decrease in calling rate by end of July. A temporary drop in calling rates was also seen between 15 and 17 July, most likely correlated with a gale in the area on 15 July, with strong winds also the following day. Given that the breeding bank may have been flooded, even at low tide, for several days, it is remarkable that the calling rate did not drop more than 30%–40% during the gale, which apparently affected the calling males very little.

A pronounced diel pattern was observed in the recordings from Limfjord and Wadden Sea, where most roars were recorded during the dark hours. As it was not possible to identify and separate calls from individuals, it is not possible to conclude whether the increase was due to increased recruitment of calling males, higher calling activity of individual males, or a combination of both. In the case of the Wadden Sea the correlation with tide was even more pronounced than the diel pattern, with the highest rates from 2 h before to 3 h after high tide. The peak at 3 h after high tide correlates with the time the breeding bank starts to dry up and seals return to the bank. In tidal areas such as the Wadden Sea tide is known to be the dominant factor determining haul-out behavior of seals (Nørgaard, 1996) and thus likely also their calling behavior. Additional data loggers, placed in the tidal deep, but at various distances to the breeding bank, would be helpful in elucidating the details in this behavior and whether the geographical center of vocalizations actually changes during the tidal cycle.

A pronounced peak in calling at night and at high tide was also found in Scottish harbor seals (Van Parijs *et al.*, 1999) whereas higher calling rates were found in Californian harbor seals at dawn and dusk, when females travelled through a slough to get back and forth from the haul-out site to the feeding grounds (Hayes *et al.*, 2004a). The movements of the females may thus have a large effect on the calling

behavior of the males. Several studies have also shown that foraging behavior of females in the breeding season differs from place to place. Some studies found that the females foraged during day time (Boness *et al.*, 1994; Thompson *et al.*, 1994; Chudzinska, 2009), whereas other studies found that they foraged during night-time (Coltman *et al.*, 1997; Hayes *et al.*, 2004a). Hayes *et al.* (2004a) also found that the lowest vocalization rate was reached when most seals were hauled-out.

C. Function of the roar call

The role of the roar calls remains to be established. The strong seasonality, centered on the time females are in estrus clearly suggests a role in reproductive behavior. Recent reports of off-season vocalizations of harbor seals on the Swedish west coast (Andersson *et al.*, 2015), however, suggest that seasonality may not be strong in all locations.

Several observations support that the roar is used as a communication signal during the breeding season. In a play-back experiment by Hayes *et al.* (2004b) it seemed that only males were reacting on the played back vocalizations, some of them even attacked the loudspeaker. No reaction was observed from females, which suggests that the vocalizations are used in male-male competitions (Hayes *et al.*, 2004b). On the other hand, this does not rule out that there is information for females embedded in the calls. The mating display of the males is expected to signal male strength during the mating season, as several studies found that males lose weight during the breeding period, because they spend much of the time displaying and not eating as much as in pre-breeding season (Walker and Bowen, 1993; Coltman *et al.*, 1998). It has been suggested that cues other than size (which is not a pronounced dimorphic trait in harbor seals) and dominance ranking (which has not been shown in harbor seals) could be used as indicators for male quality (Bradbury and Gibson, 1983). Another suggestion is the vigor in the display (Bradbury and Gibson, 1983). The combination of vocalization and flipper slaps could be a measure of male vigor and thereby a self-advertisement, which females could sample and compare to choose a possible mate. A study found that females were generally fertilized by males displaying further away from their normal pupping site than those displaying next to the site, which could imply that females are exercising a choice among males rather than going for the first one available (Boness *et al.*, 2006). This observation also speaks against mate guarding by the males.

From a communication point of view the roar at first appears as an ill-suited signal. There is very little structure to the call; especially the “roar burst” itself, which is noise-like in structure. The frequency band of the call is very low, in fact so low that the long wavelengths would be expected to reduce transmission distances in shallow waters, where the calling takes place. The long wavelengths also limit the maximum call intensity, as the size of the sound emitter (the seal’s mouth and/or throat region) is about two orders of magnitude smaller than the wavelength of the signal. One prominent feature of the roars is their very long duration. A longer signal is easier to detect for the conspecifics

(Kastelein *et al.*, 2010). A consideration here is the health state; this could possibly also be interpreted from the duration of the call. Seals are often infected with nematode lung worms, such as *Otostrongylus circumlitus* and *Parafilaroides gymnurus* (Ulrich *et al.*, 2016), which might lower the ability to hold their breath for longer time periods, and therefore shortening the vocalizations. Thus, longer signals might indicate a healthy male, able to stay submerged for a long time and with a larger functional lung volume.

Determining the precise role of the roar calls and the male-male and male-female interactions is complicated by the fact that this behavior occurs under water. A longer acoustic investigation, such as has been done on bearded seals (Van Parijs and Clark, 2006), could give more insights into how harbor seals use the areas around haul-out sites during the mating season and if the mating system differs between different haul-out sites, as suggested by previous studies (Boness *et al.*, 2006; Hayes *et al.*, 2006). Long-term studies could also reveal if individual males use the same mating system year after year, and if they can switch between different mating systems, such as in the male bearded seals, where some seals have been observed to switch from territory holders to roamers (Van Parijs and Clark, 2006). The ability to localize individual males, as observed by Van Parijs *et al.* (2000b), coupled with long term monitoring as in the present study, would provide valuable insights. Even more powerful studies could be performed if the passive acoustic monitoring was coupled to recordings from individual seals with on-board acoustic data loggers (such as the one described by Johnson *et al.*, 2009).

D. The prospects of passive acoustic monitoring

The study has demonstrated passive acoustic monitoring as a powerful and cost-effective technique to study mating behavior in harbor seals. More recordings of the vocalizations from harbor seals were obtained with the data loggers than from manned boat recordings. From the Limfjord there were 3036 calls recorded with the logger compared to 126 calls recorded from the boat. This difference is primarily a result of the much increased effort made possible by the data logger, assisted by the ability of the logger to record at night, concurrent with the peak in calling.

Passive acoustic monitoring is not without limits, of course. It can clearly be used to show positive evidence of presence of seals in an area, but the absence of seals cannot be concluded from a lack of recorded calls. As the calls are used in context of mating (see Andersen, 2015, however), they can nevertheless be very valuable as indicators for important mating areas. Harbor seals are protected under the European Habitats Directive (European Commission, 1992) and listed as an Annex 2 species. This means that EU member states are required to identify and protect habitats important for all aspects of the seals life. Currently, in most countries, the only protected areas are the haul-out sites. These are evidently critical to the species, but so are the mating areas and passive acoustic monitoring offers an effective and relatively inexpensive way of identifying these areas.

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