




Aquatic vocalization activity indicates the timing of the mating season of Saimaa ringed seals

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Abstract

Underwater vocalization is widely documented in phocids. In aquatic mating species, vocalization is typically associated with breeding, including intraspecific agonistic behavior and mate attraction. Ringed seal (*Pusa hispida*) produces a diverse range of aquatic vocalizations. However, the connection between these vocalizations and reproductive behavior is unclear. The Saimaa ringed seal (*P.h.saimensis*) also produces a variety of underwater vocalizations, with knocking calls especially suggested to be connected to the breeding season. In this study, we used four passive hydrophones during two successive winters, deployed in the breeding habitat of ringed seals in Lake Saimaa, to further explore vocalization behavior. A total of 13,197 vocalization events were identified in the recordings. Only a single vocalization type was recorded and classified as quick knocks. We identified a strong temporal pattern, with vocal activity peaking in April. This peak coincides with the end of the nursing period when mating is assumed to occur. Based on this and earlier studies, we propose that this specific call type is emitted for mate attraction or defense of underwater mating territory. This study pinpoints the timing of the mating season of Saimaa, the ringed seal and provides further insight into the behavior of this endangered subspecies.

KEYWORDS

behavior, breeding, Lake Saimaa, passive acoustic monitoring (PAM), pinniped, underwater vocalization

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1 | INTRODUCTION

Underwater vocalization is widespread in pinnipeds and has been observed especially in many aquatic mating phocids (Rogers, 2003; Van Parijs, 2003). This type of underwater vocalization is suggested to play a role in communication as it is closely linked to breeding behavior, including territory establishment, agonistic interactions, and mate attraction (Asselin et al., 1993; Hanggi & Schusterman, 1994; Hayes et al., 2004; Mizuguchi et al., 2016; Van Opzeeland et al., 2008; Van Opzeeland et al., 2010). While vocalizations associated with mating behavior have been known to be produced by females—such as in leopard seals (*Hydrurga leptonyx*), which vocalize to advertise their sexual receptivity (Rogers et al., 1996)—these vocalizations are typically produced by males (Hanggi & Schusterman, 1994; Van Opzeeland et al., 2008; Van Opzeeland et al., 2010). Aquatic vocalization is particularly advantageous in habitats with low visibility, allowing information to be transmitted without visual cues, in all directions and over large distances. The importance of this behavior is evident in the increase of vocal activity during or just prior to the beginning of the breeding season of species that mate underwater (Clark & Thomas, 2007; Prawirasasra et al., 2021; Rogers et al., 1996; Sills et al., 2021; Stirling, 1973; Stirling & Thomas, 2003; Van Parijs et al., 2001).

The ringed seal (*Pusa hispida*) is an aquatic-mating species, with an assumed polygynous mating system (Stirling, 1973; Stirling & Thomas, 2003; Yurkowski et al., 2011). The species was once believed to be one of the least vocal seal species due to predation pressure in the Arctic (Stirling, 1973, 1977; Stirling & Thomas, 2003). However, at least eight distinct types of aquatic calls including yelps, barks, chirps, clicks, growls, burst pulses, woofs, and knocks have since been identified (Hyvärinen, 1989; Kunnasranta et al., 1996; Mizuguchi et al., 2016; Rautio et al., 2009; Schevill et al., 1963; Stirling, 1973; Thomas & Stirling, 1983). Of these sound types, at least six (yelp, chirp, growl, click, burst pulse, and knock) have been documented in freshwater subspecies (Hyvärinen, 1989; Kunnasranta et al., 1996; Rautio et al., 2009). A previous study on captive ringed seals has shown that the occurrence of all call types increases during the breeding season, with knocks being the most frequently recorded call type (Mizuguchi et al., 2016). Vocalization behavior activity is therefore thought to indicate the timing of seal breeding seasons (Rogers, 2003; Van Parijs, 2003; Van Parijs et al., 1999, 2001).

The endangered Saimaa ringed seal (*Pusa hispida saimensis*) is a subspecies endemic to Lake Saimaa, in Eastern Finland. This small population of less than 500 individuals (Metsähallitus, 2024) is threatened by several human-induced risks such as by-catch mortality and climate change (Kovacs et al., 2012). In an attempt to conserve the population, extensive research has been conducted over the last several decades. As a result, the behavioral patterns of this subspecies are relatively well-studied (Kunnasranta et al., 2021). However, the mating behavior of this subspecies is not fully understood, and the exact timing of the mating remains uncertain. This study uses passive acoustic monitoring to assess seasonal and diel variations in vocalization behavior to uncover behavioral patterns that may serve as a rudimentary indicator of the timing of the Saimaa ringed seal mating.

2 | METHODS

2.1 | Data collection

This study was carried out in the central region of Lake Saimaa (61° 05' to 62° 36' N, 27° 15' to 30° 00' E), Eastern Finland. Approximately 180 km long and 140 km wide, this large labyrinthine lake comprises 10 distinct water basins, interconnected by narrow channels (Figure 1). Typically, lake ice-cover persists from late November until early May. In winter, Saimaa ringed seals dig lairs into snow drifts of island shoreline, for whelping (birth lairs) and resting (haul out lairs). A single pup is born in a subnivean lair in mid-February to mid-March and mating is suggested to occur toward the end of lactation (Sipilä, 1990). Audio recordings were obtained from the Haukivesi water basin—one of the main breeding areas of the Saimaa ringed seal—from January to early June in 2022 and 2023.

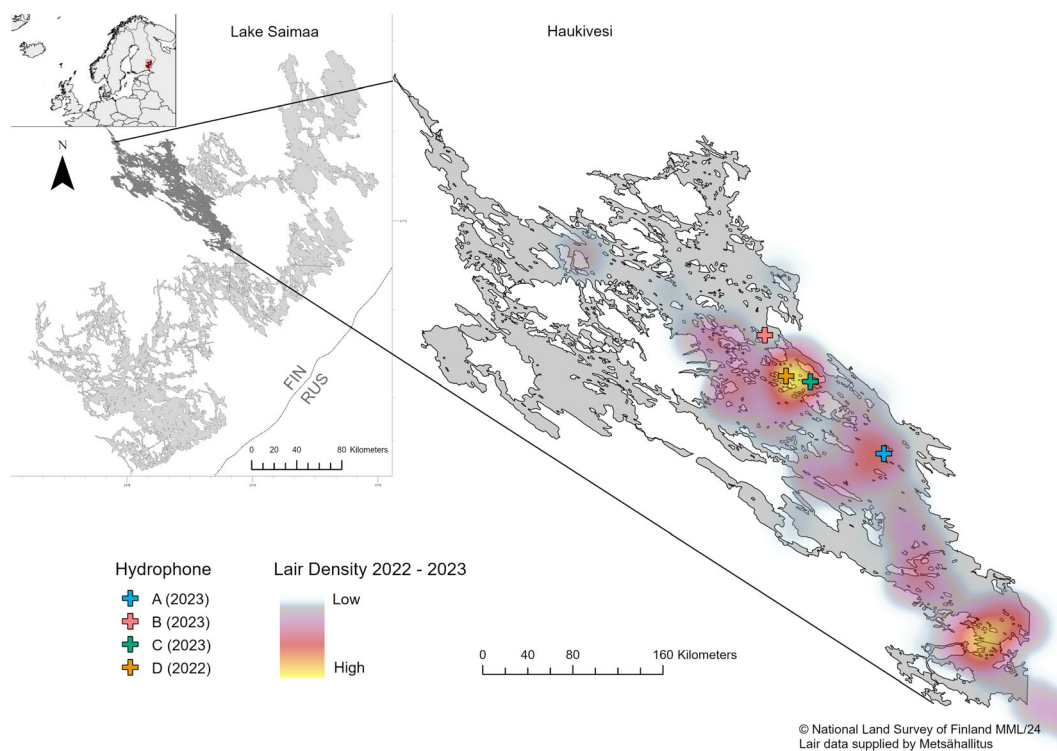


FIGURE 1 Map of Lake Saimaa, showing the focal water basin (Haukivesi) with hydrophone locations and a heat density map of ringed seal birth and haul-out lairs for 2022 and 2023.

TABLE 1 Deployment and recording parameters for each hydrophone for recording underwater sounds of Saimaa ringed seals.

| Hydrophone | Depth (m) | Recording start | Recording end | Hours of recording | Dates included in the analysis |
|------------|-----------|-----------------|---------------|--------------------|--------------------------------|
| A | 8.3 | 06/01/2023 | 01/06/2023 | 3519 | 06/02–31/05 (2856 h) |
| B | 6.8 | 05/01/2023 | 01/06/2023 | 3543 | None |
| C | 7.5 | 20/12/2022 | 18/05/2023 | 3563 | 01/02–18/05 (2544 h) |
| D | 10.2 | 28/01/2022 | 01/07/2022 | 3684 | 01/02–31/05 (2856 h) |

Note: Dates included in the analysis highlight data exclusion due to Hydrophone B detecting minimal vocalizations, and inconsistencies in the deployment dates.

Four passive acoustic hydrophones (SoundTrap 600 STD, Ocean Instruments, New Zealand) were deployed to record the underwater sounds. The instruments were programmed to record continuously with a sampling rate of 96 kHz with varying deployment periods (see Table 1). A single hydrophone was deployed during winter 2022 and three during winter 2023. Each hydrophone was positioned within different known breeding locations with a minimum direct distance of 13.8 km between two hydrophones. Based on average adult winter home ranges (Niemi et al., 2019), this was designed to avoid simultaneously detecting an individual's vocalizations on multiple hydrophones. The hydrophones were suspended 2 m from the water surface with a subsurface buoy and moored using approximately 12–20 kg weights. The average water depth of recording sites was 7.3 m. In addition to the hydrophones, data on the locations of birth and haul-out lairs were collected during the annual population censuses

conducted in late April (see Sipilä, 2003). The distance between a hydrophone and the nearest observed lair ranged from approximately 500 to 1000 m.

2.2 | Data processing

Audio files were decompressed using SoundTrap Host software (version 4.0.13) and converted into WAV format. Spectrograms of the recordings were then visually examined using Raven Pro software (version 1.6.4), and seal calls were aurally and visually confirmed. Calls were categorized based on the previous classification of ringed seal vocalization types (Kunnasranta et al., 1996; Mizuguchi et al., 2016; Rautio et al., 2009).

2.3 | Modeling temporal variation in vocalization behavior

To estimate the temporal variation in the vocal activity of Saimaa ringed seals, the number of call events (calls per hour) was modeled as a function of Julian day and hour of the day, separately for each hydrophone, using generalized additive models (GAM) (Wood, 2011, 2017). Although hydrophone B did detect some vocalizations, these occurred only at the beginning of the recording period and were minimal, and, while included in the call description, were removed from the statistical analysis. In addition, although a few vocalizations were recorded outside of the breeding period, observations from December, January, and June were removed from the analysis as not all hydrophones had been deployed during these months. Since the response was heavily zero-inflated (92% zeros), we ran hurdle models within a Bayesian framework using the *brms* package (Bürkner, 2017) in R (R Core Team, 2023). A hurdle model is a two-part model, typically consisting of a binary process to determine whether an observation is zero or positive, followed by a truncated count model for positive outcomes. The model comprised a logistic component to account for the binary response (zero and nonzero counts), and a negative binomial error distribution was used to account for the over-dispersed nonzero count component of the response variable. We used an interaction of penalized thin-plate and cyclic regression splines with shrinkage (Marra & Wood, 2011) to model the two-way relationship between the response and *Julian* and *Hour*, respectively. In addition, separate covariate smooths were fitted for each hydrophone via the “by” argument. We also investigated the possible effect of predictors on the hurdle process (probability of having a zero response) by comparing a set of candidate models with different combinations of predictors *Julian* and *Hydrophone* and a model without any predictors on the binary component ($hu \sim 1$) (see Table 2). All models were run with four independent chains and 4000 Markov Chain Monte Carlo (MCMC) iterations preceded by 1000 warm-up (burn-in) steps while sampling every 10th iteration. We used the default noninformative

TABLE 2 Comparison of candidate models for predicting the binary component (presence or absence) of Saimaa ringed seal calls, modeled using a generalized additive hurdle model.

| Model | ELPD-LOO difference | Standard error of difference | Predictors on binary component |
|-------|---------------------|------------------------------|---|
| fit3 | 0.0 | 0.0 | $s(\textit{Julian}, \textit{bs} = \textit{“ts”})$ |
| fit1 | −140.8 | 17.2 | None (intercept) |
| fit2 | −286.1 | 24.9 | $\textit{Hydrophone} + s(\textit{Julian}, \textit{bs} = \textit{“ts”})$ |

Note: Model comparison was done by leave-one-out (LOO) cross-validation, and the difference in ELPD (LOO estimate of the expected log pointwise predictive density) is given for each model along with its standard error. Models are ranked from top to bottom by highest predictive accuracy. $s(\textit{Julian})$ = smooth of Julian day, \textit{bs} = basis spline, “ts” = thin plate spline with shrinkage (Marra & Wood, 2011). Model comparison was done by leave-one-out (LOO) cross-validation, and the difference in ELPD (LOO estimate of the expected log pointwise predictive density) is given for each model along with its standard error. Models are ranked from top to bottom by highest predictive accuracy. $s(\textit{Julian})$ = smooth of Julian day, \textit{bs} = basis spline, “ts” = thin plate spline with shrinkage (Marra & Wood, 2011).

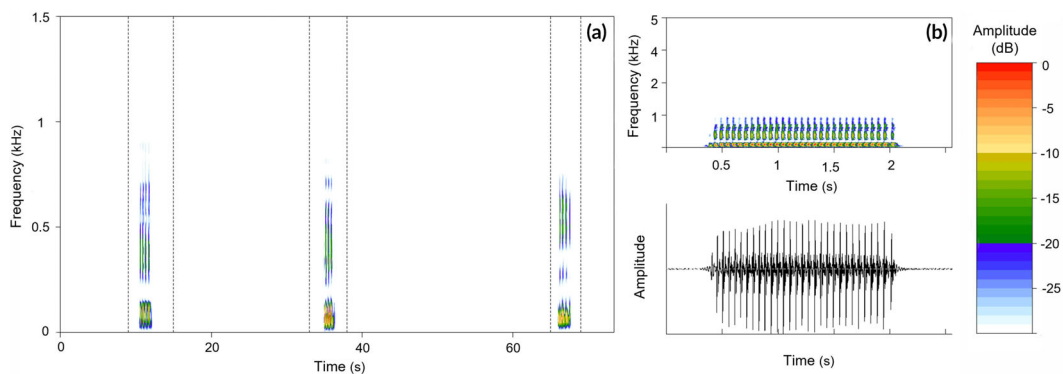


FIGURE 2 Waveform and spectrogram examples of Saimaa ringed seal Type B knocking vocalization. (a) Three vocal calls occurring in succession. (b) A single call consists of a series of rapid knocking elements. Spectrograms (Hamming window, FFT window size 4096 points, 90% overlap) were generated using the Seewave package (Sueur et al., 2008) in R (R Core Team, 2023).

priors for all variables. Convergence of chains was verified visually and based on the potential scale reduction factor on split chains (Rhat) values, and the independence of draws was determined based on the effective sample size (ESS) values. Posterior predictive checks verified model fit, and models were compared by leave-one-out (LOO) cross-validation (Vehtari et al., 2017, 2024). To test whether predicted vocalization frequencies at observed peak days and hours were significantly different, we extracted fitted values using the fitted() function from the brms package (Bürkner, 2017) and manually compared the estimated differences and their credible intervals.

3 | RESULTS

3.1 | Call detections

A total of 13,197 call sequences (hereby referred to as calls) were detected from altogether 14,309 h of audio recordings. Due to the consistently low ambient noise levels (likely as a result of ice cover and the characteristics of the lake environment), calls were easy to distinguish. The audio data were analyzed in entirety, and all vocalizations were annotated. Only one vocalization type was found in the recordings: Type B fast knocks (Rautio et al., 2009) (Figure 2). To build a characterization of the fundamental features of the vocalization type, a subset (10%) of the data was further analyzed. The data subset contained randomly selected vocal events ($n = 1341$) from the four hydrophones. Each call was then individually examined and the parameters of call duration, number of pulses (knocks) per call, and interknock interval were recorded. The mean and standard deviation of each parameter were also calculated.

3.2 | Description of vocalization

All vocalizations consisted of a series of rapid knocking sounds (comparable to the sound of a jackhammer), and their parameters are shown in Table 3. Each call consisted of an average of 26 individual knocks ($SD \pm 6.6$, range = 11–56), lasting, in total, an average of 1.33 s ($SD \pm 0.17$, range = 0.87–3.67 s). The average duration between each individual knock was 0.04 s ($SD \pm 0.01$, range = 0.02–0.09 s). Knocks were sometimes found as a single call but were most often produced in bouts. Calls were low in frequency, with the majority of the energy concentrated between 50 and 200 Hz.

TABLE 3 Descriptive statistics for Saimaa ringed seal quick knock calls.

| Hydrophone | <i>n</i> | Duration (s) ± SD | Number of knock pulses ± SD | Inter-pulse-interval (s) ± SD |
|----------------|----------|-------------------|-----------------------------|-------------------------------|
| A | 264 | 1.19 ± 0.18 | 21 ± 5.0 | 0.05 ± 0.01 |
| B | 29 | 1.39 ± 0.26 | 28 ± 9.0 | 0.04 ± 0.02 |
| C | 96 | 1.31 ± 0.18 | 30 ± 9.2 | 0.04 ± 0.02 |
| D | 952 | 1.38 ± 0.12 | 27 ± 5.6 | 0.04 ± 0.07 |
| Overall ranges | | 0.87–3.67 | 11–56 | 0.02–0.09 |
| Overall means | | 1.33 ± 0.17 | 26 ± 6.6 | 0.04 ± 0.01 |

TABLE 4 Saimaa ringed seal vocalization detections for each hydrophone, showing the dates of the first and last detection as well as the day on which the highest number of knocking events was recorded.

| Hydrophone | Number of calls | First detection | Last detection | Peak date |
|------------|-----------------|-----------------------------|-----------------------------|-----------------------------|
| A | 2639 | 14-01-2023 (Julian day 14) | 08-05-2023 (Julian day 128) | 12-04-2023 (Julian day 103) |
| B | 29 | 05-01-2023 (Julian day 5) | 08-05-2023 (Julian day 128) | N/A |
| C | 956 | 25-12-2022 (Julian day 359) | 18-05-2023 (Julian day 138) | 05-04-2023 (Julian day 95) |
| D | 9573 | 28-01-2022 (Julian day 28) | 30-06-2022 (Julian day 181) | 14-04-2022 (Julian day 105) |

3.3 | Temporal variation in vocalization behavior

Ringed seal vocalizations were detected on all hydrophones and occurred across the entirety of the recording periods (Table 4). The number of vocalizations varied between each hydrophone, with Hydrophone B detecting few. Knocks were detected within the first days of recording (December) and continued throughout the deployment until retrieved in July. The highest number of calls occurred in April, and the difference between the day with the highest and lowest number of recorded calls was significant with all hydrophones as evidenced by the nonoverlapping credible intervals. Although vocalizations were identified across the recording periods, the estimated number of calls per hour showed a clear pattern of seasonality (Figure 3). A gradual increase in the number of knocking events was witnessed from recording day 60 (February 17), with a sharp incline to peak on Julian day 115 (April 13). The number of events then progressively declined during May. Although the date of the first and last detection and the amount of vocalization activity varied across the hydrophones, the overall seasonal trend was evident for each location. The model with a smooth *Julian* as the predictor on the binary component and the number of calls in the GAM (model fit3) had the best fit to the data out of the candidate models (Table 2).

3.4 | Diel variation in vocalization behavior

In addition, analysis of vocalization patterns reveals a distinct diel variation across the recording period (Figure 4). In March and April, the highest knocking rate was observed between 10:00 and 15:00, with reduced activity occurring during the late evening (20:00–00:00). In May, however, a notable shift was observed, with increased vocal activity occurring between 20:00 and 00:00, with lower events recorded during the day. Statistical testing did not reveal a significant increase in vocalization frequency during these peak hours compared to other times (credible intervals included zero) for each month.

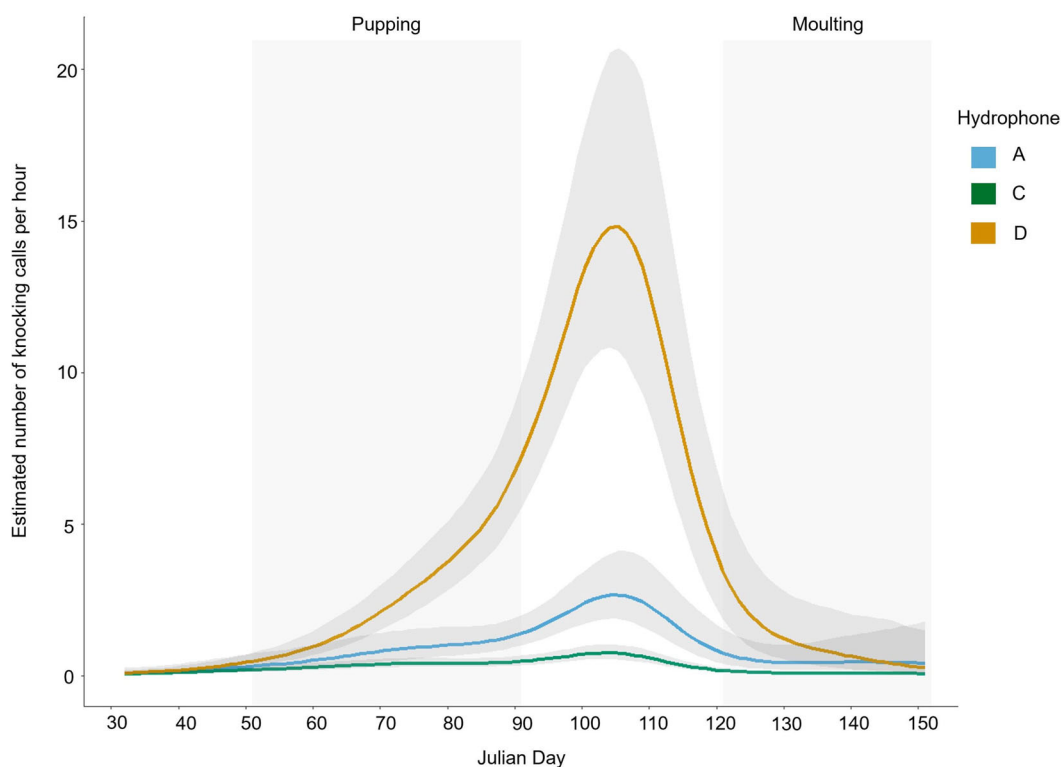


FIGURE 3 Conditional effects of Julian Day on the number of knocking calls per hour produced by Saimaa ringed seals plotted for each hydrophone. The solid lines depict the model-estimated mean and shaded areas show 95% credible intervals. The approximate dates of pupping and molting are highlighted in relation to this vocal activity.

4 | DISCUSSION

Our study represents the first long-term recording of Saimaa ringed seal underwater vocalization. From these recordings, we observed a single call type, characterized by a series of rapid knocking sounds. This finding supports observations made by Rautio et al. (2009), who first documented this vocalization type while studying the vocal repertoire of Saimaa ringed seals. Although this sound type has been previously described, the large size of our data allows for a more robust definition of this vocalization and its role in seal behavior. Interestingly, the presence of only a single call type in our recordings contrasts with other studies on ringed seals, which documented a much wider vocal repertoire (Barbosa et al., 2024; Jones et al., 2014; Kunnasranta et al., 1996; Mizuguchi et al., 2016; Prawirasasra et al., 2021; Rautio et al., 2009; Stirling, 1973).

This limited vocal diversity may be a reflection of the timing and positioning of recordings. It is possible that transmission loss, due to shallow water and background noise, impacted call detectability, particularly for quieter or lower-frequency calls. Furthermore, ringed seals are known to be territorial, physically defending underwater territories and breathing hole access (Stirling & Thomas, 2003). Therefore, the static positioning of hydrophones likely limited recordings to a small number of individuals. In particular, males are known to exhibit underwater territorial behavior during the breeding season, positioning themselves near the primary breathing holes of nursing females until they are receptive (Kelly et al., 2010; Stirling et al., 1983; Stirling & Thomas, 2003). During this time, vocalization serves an important role in reproductive behavior, which may explain the evident seasonality in calls. Based on this, we suggest that these fast, knocking calls are used as a function of mate attraction and/or territory defense.

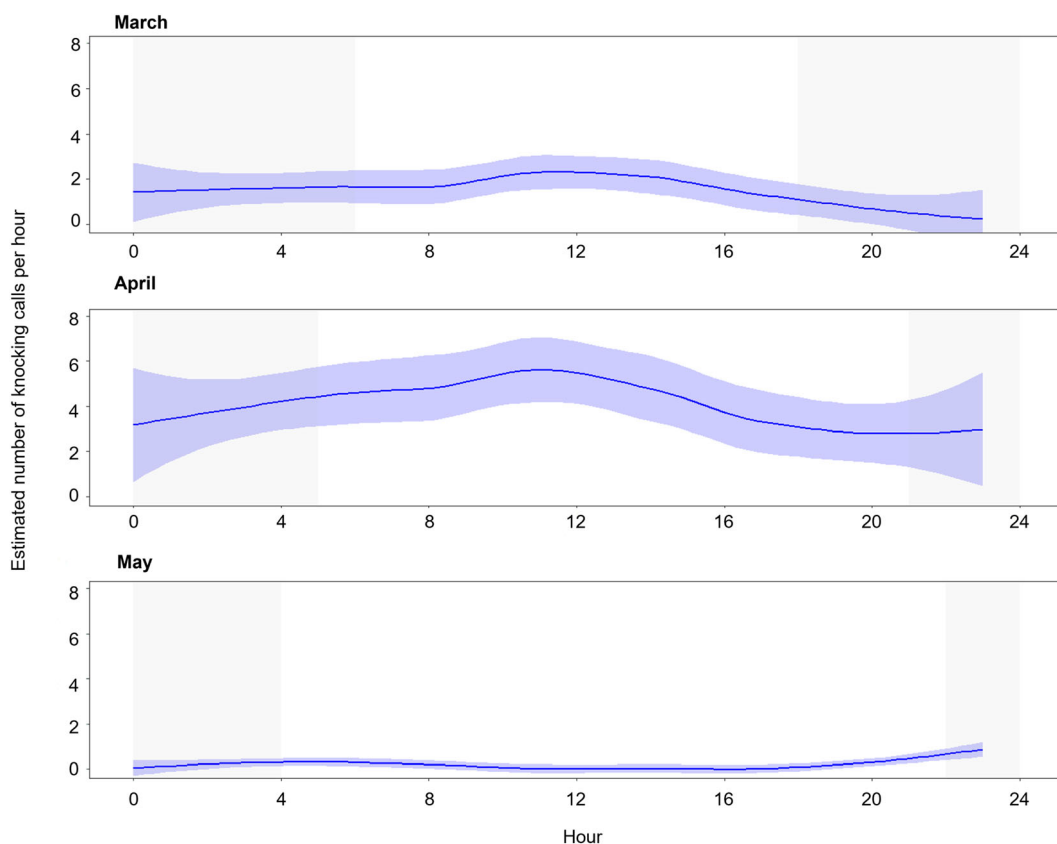


FIGURE 4 Conditional effects of *Hour* (of the day) on the number of knocking calls per hour produced by Saimaa ringed seals during March, April, and May. The solid lines depict the model-estimated mean and shaded areas show 95% credible intervals. Plots encompass data from Hydrophones A, C, and D. Shading represents photoperiod, with nighttime intervals shaded.

4.1 | Seasonal variation in vocalization behavior

Saimaa ringed seals were vocally present at all hydrophone locations during this study. There was variation in the number of vocalizations at each hydrophone, with hydrophone B detecting only a low number of calls. It is unknown whether this variation is linked to individual differences in seal behavior, or whether the proximity to birth and haul-out lairs may influence this result as the minimum distance between this hydrophone and a recorded lair was approximately 1000 m (see Figure 1).

Calls were observed across the entirety of the recording period (December–July), suggesting that ringed seals may produce these calls throughout the year. Previous studies on captive ringed seals (Mizuguchi et al., 2016) and Ladoga ringed seals (*P. h. ladogensis*) (Kunnasranta et al., 1996) observed calls also outside of the breeding season, supporting our findings. Despite this, our data revealed a clear pattern of seasonality, which may indicate the role that ringed seal vocalization has in reproductive behavior.

Vocalization activity was shown to increase toward the end of March, with a notable peak occurring in mid-April, and was synchronized across all hydrophone sites. The initial increase in vocal activity is consistent with the timing of the Saimaa ringed seal pupping season in mid-February to March, during which, females give birth to a single pup in subnivean lairs situated on the shoreline of islands or islets (Sipilä, 2003). Following this peak, there was a rapid decline in vocal activity which was minimal during May. This reduction in vocal activity coincides with the annual

molting period, where seals typically spend longer times hauled out (Niemi et al., 2023). This annual pattern in underwater vocalization matches that found in ringed seals in the high Arctic (Stirling et al., 1983), and is similar to that recorded in several other phocids, including Weddell seal (*Leptonychotes weddellii*), bearded seal (*Erignathus barbatus*), gray seal (*Halichoerus grypus*), harbor seal (*Phoca vitulina*), harp seal (*Pagophilus groenlandicus*), spotted seal (*Phoca largha*), leopard seal, and ribbon seal (*Histiophoca fasciata*) (Asselin et al., 1993; Green & Burton, 1988; Jones et al., 2011; Rogers et al., 1996; Serrano & Miller, 2000; Sills & Reichmuth, 2022; Van Parijs et al., 1999, 2001). Each of these studies found increased vocalization activity to be associated with reproductive behavior, including mate attraction (Matthews et al., 2018) and male–male agonistic interactions, particularly in territorial defense (Charrier et al., 2013).

In Lake Saimaa, peak vocalization activity corresponds with the collapse of the subnivean lairs due to warming temperatures in early spring. It is during this time that underwater mating is presumed to occur (Mclaren, 1958), supported by our results. While it remains unknown which environmental factors are significant in the onset of the mating period, our results showed an evident seasonal trend which suggests that similar to observations in harbor seals (Van Parijs et al., 1999) and bearded seals (Van Parijs et al., 2001), vocalizations of the Saimaa ringed seal could serve as an indicator for determining the precise timing and duration of the mating season.

4.2 | Diel variation in vocalization behavior

The number of knocking events showed a diel pattern, which varied depending on seasonality. During the lead-up to the mating season (March and April), seals were vocally active during the daytime and least active during the night hours. These vocalization patterns align with established behavioral patterns, showing increased activity during the day, corresponding with foraging behavior (Nykänen et al., 2024), and decreased vocal activity at night, when seals typically rest in lairs (Niemi et al., 2023). This diel variation likely reflects the time at which seals are in the water and, thus, able to vocalize. Similarly, Calvert and Stirling (1985) identified a diel cycle in ringed seal vocalization in the Barrow Strait, showing the highest call rate between 08:30 and 16:30. Interestingly, these findings differ from that of other seal species which show increased vocal activity during night hours (Boye et al., 2020; Nikolich et al., 2018; Serrano & Miller, 2000; Shabangu & Charif, 2021; Terhune & Ronald, 1976; Van Parijs et al., 2001.) This contrast likely reflects the behavior and ecology of the ringed seal, and may provide further clues about behavioral patterns.

5 | CONCLUSIONS

This research represents the first comprehensive long-term study on the underwater vocalization patterns of the Saimaa ringed seal. The data collected allow us to determine, for the first time, the timing of the mating period. Although it is unknown whether calls are produced by males or females, we suggest that this vocalization type is primarily used as a function of mate attraction and/or territory defense. Furthermore, this study has successfully detected underwater vocalizations of the Saimaa ringed seal using passive acoustic monitoring. This opens opportunities for future monitoring strategies using audio data, offering a nonintrusive and cost-effective approach for long-term monitoring.

AUTHOR CONTRIBUTIONS

Mairi Young: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; supervision; validation; visualization; writing – original draft; writing – review and editing. **Milaja Nykänen:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; supervision; validation; visualization; writing – original draft; writing – review and editing. **Marja Niemi:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; supervision; validation; visualization; writing – original draft; writing – review and editing. **Mika**

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DATA AVAILABILITY STATEMENT

Data generated and analyzed within the study are not publicly available due to laws protecting the location of Saimaa ringed seal haul-outs. Data may be available from the corresponding author upon reasonable request.

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