Are Icelandic harbor seals acoustically cryptic to avoid predation?

Rößler, Helen; Tougaard, Jakob; Sabinsky, Puk Faxe; Rasmussen, Marianne H.; Granquist, Sandra M.; Wahlberg, Magnus

Published in:
J A S A Express Letters

DOI:
10.1121/10.0003782

Publication date:
2021

Document version:
Final published version

Document license:
CC BY

Citation for published version (APA):
Rößler, H., Tougaard, J., Sabinsky, P. F., Rasmussen, M. H., Granquist, S. M., & Wahlberg, M. (2021). Are Icelandic harbor seals acoustically cryptic to avoid predation? J A S A Express Letters, 1(3), [031201-1]. https://doi.org/10.1121/10.0003782

Go to publication entry in University of Southern Denmark's Research Portal

Terms of use
This work is brought to you by the University of Southern Denmark. Unless otherwise specified it has been shared according to the terms for self-archiving. If no other license is stated, these terms apply:

• You may download this work for personal use only.
• You may not further distribute the material or use it for any profit-making activity or commercial gain
• You may freely distribute the URL identifying this open access version

If you believe that this document breaches copyright please contact us providing details and we will investigate your claim. Please direct all enquiries to puresupport@bib.sdu.dk

Download date: 15. Oct. 2023
Are Icelandic harbor seals acoustically cryptic to avoid predation?

Helen Rößler, Jakob Tougaard, Puk F. Sabinsky, et al.

ARTICLES YOU MAY BE INTERESTED IN

Connecting the grain-shearing, creep, and squirt flow models for wave propagation in the seabed
JASA Express Letters 1, 036003 (2021); https://doi.org/10.1121/10.0003783

How loud is the underwater noise from operating offshore wind turbines?
The Journal of the Acoustical Society of America 148, 2885 (2020); https://doi.org/10.1121/10.0002453

Long-term frequency changes of a potential baleen whale call from the central Indian Ocean during 2002–2019
JASA Express Letters 1, 021201 (2021); https://doi.org/10.1121/10.0003444
Are Icelandic harbor seals acoustically cryptic to avoid predation?

Helen Rößler,1,a) Jakob Tougaard,2,b) Puk F. Sabinsky,1 Marianne H. Rasmussen,3,c) Sandra M. Granquist,4,d) and Magnus Wahlberg1,e)

1Department of Biology, University of Southern Denmark, Campusvej 55, 5230 Odense M, Denmark
2Department for Bioscience, Aarhus University, Frederiksbergvej 399, 4000 Roskilde, Denmark
3University of Iceland Research Center in Husavik, Hafnarstætt 3, 640 Húsavik, Iceland
4Marine and Freshwater Research Institute, Fornubólum 5, 220 Hafnarfjörður, Iceland

helen.roessler@gmx.net, jat@bios.au.dk, pukfaxes@gmail.com, mhr@hi.is, sandra.magalena.granquist@hafogvatn.is, magnus@biology.sdu.dk

Abstract: Male harbor seals (Phoca vitulina) produce stereotypic underwater roars during the mating season. It remains unclear to what extent roar structures vary due to predation levels. Here, seal roars from waters with many (Iceland) and few (Denmark and Sweden) predators were compared. Most Icelandic roars included a long pulse train and a pause. Icelandic roars occurred less frequently, lasted longer (20.3 ± 6.5 s), and were recorded with lower received sound levels (98.3 ± 8.9 dB re 1 μPa root mean square) than roars from Denmark and Sweden. Local extrinsic factors may shape sound production in harbor seals more than previously reported.

© 2021 Author(s). All article content, except where otherwise noted, is licensed under a Creative Commons Attribution (CC BY) license (http://creativecommons.org/licenses/by/4.0/).

[Editor: Laura N. Kloepper] https://doi.org/10.1121/10.0003782

Received: 3 December 2020  Accepted: 23 February 2021  Published Online: 24 March 2021

1. Introduction

Harbor seals (Phoca vitulina) are distributed in temperate and polar coastal waters along the eastern and western North Pacific and North Atlantic coasts (Berta, 2009; Bowen et al., 2009; Stanley et al., 1996). Harbor seals mate underwater, but details of their mating behavior remain unclear (Hayes et al., 2006). Some evidence indicates a hotspot lek system, consisting of underwater display territories where males compete while being noticed by females (Boness et al., 2006; Hayes et al., 2004a; Hayes et al., 2004b). Males also appear to patrol along the coastline in a form of mate-guarding or scrambled competition (Van Parijs et al., 1997; Van Parijs et al., 1999).

During the mating season, after lactation and before molt (Thompson, 1988), underwater calls are produced, presumably by males. The most frequently produced harbor seal call is a broad-band roar with a frequency content below 4 kHz and shorter than 20 s (Hanggi and Schusterman, 1994; Van Parijs et al., 2000b; Bjørgesæter et al., 2004; Sabinsky et al., 2017). Their reported average source level is 144 dB root mean square (rms) re 1 μPa at 1 m recorded from wild harbor seals in Alaska (Matthews et al., 2017) and approximately 140 dB re 1 μPa at 1 m from one captive harbor seal in California (Casey et al., 2016).

Acoustic communication is impacted by a variety of factors, such as the time of year or the type of environment. It is also conceivable that higher predation risk from, e.g., orcas (Orcinus orca) (Deecke et al., 2002) and gray seals (Halichoerus grypus) (Brownlow et al., 2016) affect harbor seal underwater communication during mating. Harbor seals exposed to predators may face an exacerbated trade-off between reproduction and self-maintenance and are thus expected to adapt signal parameters to maximize their fitness.

Icelandic harbor seals are a suitable population to investigate the evolutionary influence of predator-prey interaction on call production. They are genetically distinct from other North Atlantic seals with little or no exchange with other populations (Stanley et al., 1996; Goodman, 1998). Orcas (Samarra et al., 2018) and gray seals (Granquist and Hauksson, 2019a) are present in Icelandic waters, making it likely that roars may be shaped to reduce predation risk. In this study, we recorded Icelandic harbor seals to understand how their calls differ from areas with little predation pressure in Danish
and Swedish waters. Some of the differences could potentially be attributed to the different predation pressures rather than to the large geographical distance between the different harbor seal populations.

2. Materials and methods

2.1 Study sites

Data collection took place at two study sites (Heggstaðanes and Illugastaðir, N 65.6°, W 20.9°) separated by approximately 20 km, on the Northwest coast of Iceland (supplementary Fig. 3), where 9% of the total Icelandic harbor seal population (approximately 9400 animals) occurs (Granquist and Hauksson, 2019b). At Heggstaðanes, seals haul out on six rocky sites [H1–H6, supplementary Fig. 3(c)]. At Illugastaðir, Vatnsnes peninsula, two parallel rocky skerries are located approximately 100 m apart. There are tidal variations at both study sites with an average tidal amplitude of 50 cm (Meteo365.com Ltd., 2018). Seabed structure at both study sites is rough sand, shells, or rocky with brown algae.

2.2 Acoustic recordings: Acoustic data logger deployments

Two self-contained underwater sound recorders were used (SoundTrap 300 HF, OceanInstruments, Auckland, New Zealand). Deployments were made in 3–15 m water depth. One recorder was deployed between the skerries at Illugastaðir from July 3 to September 5, 2017 [supplementary Figs. 4(A) and 5(c)] and recorded for 10 min every hour. The second recorder was deployed and recorded continuously 11 times at Heggstaðanes [supplementary Figs. 3, 4(B), and 5(c)] from July 4 until September 13. Both SoundTraps recorded WAV files with a sample rate of 48 kHz and 16-bit resolution.

The SoundTraps were calibrated before field work by the manufacturer and after field work by relative calibration, both in air and underwater. Details of system calibration can be found in the supplementary material.1

2.3 Analysis of seal calls

Recordings were screened using Adobe Audition, version 1.5 (Adobe, Inc., San Jose, CA). Seal calls were manually selected from the recordings and time stamped. We only selected calls with a signal-to-noise ratio better than 6 dB, measured as the difference between the rms intensity of the call and the ambient noise within the bandwidth of the call. Calls were analyzed with a custom-made script (Sabinsky et al., 2017) in MATLAB, version R2016b (MathWorks Inc., Natick, MA).

Each roar recording was down-sampled to 5 kHz and high-pass filtered at 80 Hz (four-pole Butterworth filter). The calls were manually divided into seven different color-coded consecutive sections. The measured parameters for every section were duration (s), energy ($\mu$Pa² s), rms (Pa), centroid frequency (Hertz), peak frequency (Hz), rms bandwidth (Hz), -10 dB bandwidth (Hz), and kurtosis (Southall et al., 2008). Mean, maximum, minimum, and standard deviation (SD) of each parameter were plotted. In addition, the total duration (s) of each call (including pauses) was measured. Received sound level (RL in $\mu$Pa rms over a duration of a 95% energy window) was calculated as described in Madsen and Wahlberg (2007) and expressed as dB re 1 $\mu$Pa rms.

All statistical tests were done in R for Windows, version 3.3.1 (R Foundation, Vienna, Austria) with R Studio (version 1.1.383). To find data-driven groups in the Icelandic data set, a k-means cluster analysis was applied on the roar burst parameters (see above), including the total call duration. Before this, the data were scaled, and $k$ was determined with $k = 3$ as best fit by the ratio of the sum of squares divided by the total sum of squares for each k-means model. All parameters of the roar burst were compared with a canonical linear discriminant analysis (CLDA) to harbor seal roar bursts from Blinderøn in Limfjord in 2010 and 2011 (Denmark), Juurre in the Wadden Sea (Denmark), and Kalmarsund (Sweden) (Sabinsky et al., 2017). Statistical differences of how the site (as descriptive variable) affected the factors of total call duration, energy, and roar burst duration were tested using three generalized linear models (GLMs).

3. Results

All detected calls were recorded at Heggstaðanes (Iceland) at the first haul-out site (H1) on July 4 from 9:40 a.m. until July 5 at 9:00 a.m. There was no apparent pattern in calling over the recording period, but calls could be heard at all times of the day and night.

In total, 76 calls fitting inclusion criteria were observed at H1. Average $\pm$ SD received sound level of the roar burst was 98.3 $\pm$ 8.9 dB re 1 $\mu$Pa rms. Mean total duration was 20.3 $\pm$ 6.5 s, and the fundamental frequency ($f_0$) was 75–100 Hz.

The analyzed calls had seven components labelled A, B, C, D, E, F, and G (Fig. 1) arranged in nine different sequences (Table 1). The highest number of calls had the combination AB- -FG, with components C, D, and E variously missing in the middle positions (Table 1). In 96% of the cases, there was a “first pause” (B) after the “first pulse train” (A). Each component’s duration was extracted from the oscillogram, which showed that the first pulse train (A) was the longest component (duration in seconds, Table 1).

Three different groupings could be identified within the calls. Clusters overlapped, but classification based on the $k$-means function could be accomplished with overall 51.6% of calls classified correctly ($k$-means, $n = 76$, $k = 3$).

For the comparison of the Icelandic roars with Danish and Swedish roars, roar burst parameters were extracted from all three sites (Table 2).
For the cluster analysis of Icelandic, Danish, and Swedish roar bursts, the following roar burst parameters were included: duration, centroid frequency, rms-bandwidth, –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 call was used for comparison between sites. Four significant linear discriminant functions were derived, of which the first two explained 91% of the total variance.

Fig. 1. Examples of oscillograms and spectrograms of a complete “ABCDEFG” call (top) and an “AB---FG” call (bottom). Background noise is shown in blue, “first pulse train” (A) is green, “first pause” (B) is black, “second pulse train” (C) is pink, “second pause” (D) is black, “start of growling” (E) is red, “roar burst” (F) is cyan, and “end groan” (G) is yellow. The top call had a signal-to-noise ratio of 12 dB, and the bottom call had a signal-to-noise ratio of 11 dB. Signals were resampled at 5 kHz, and the spectrogram had a fast Fourier transform size of 512 points, Hann window, and 25% overlap.

Table 1. Call types with the encountered combinations of call components (A–G) and number of calls of that call type (A = first pulse train, B = first pause, C = second pulse train, D = second pause, E = start of growling, F = roar burst, and G = end groan) and duration of each of the seven components (mean ± SD). Roar burst component (F) was always present, as this defined which calls to analyze as roars.

| Call type | Call components | Number of calls | Duration ± SD (s) |
|-----------|-----------------|-----------------|------------------|
| I         | A B C D E F G   | 12              | 9.1 ± 2.5        |
| II        | A B C D F G     | 11              | 9.6 ± 2.5        |
| III       | A B C E F G     | 2               | 9.0 ± 2.5        |
| IV        | A B C E F G     | 5               | 9.3 ± 2.5        |
| V         | A B C E F G     | 18              | 9.1 ± 2.5        |
| VI        | A B C E F G     | 25              | 9.0 ± 2.5        |
| VII       | A C D E F G     | 1               | 9.0 ± 2.5        |
| VIII      | A C D E F G     | 1               | 9.0 ± 2.5        |
| IX        | F G             | 1               | 9.0 ± 2.5        |
| Calls     | 75 73 32 25 33 76 76 |                | 9.0 ± 2.5        |
| %         | 99 96 42 33 43 100 100 |               | 9.0 ± 2.5        |

The data indicates that the roar burst parameters are effective in distinguishing between call types, and the discriminant functions provide a robust method for analyzing the acoustic characteristics of roar bursts across different species.
fewer animals, and themselves emit very low source levels. The size of the investigated Icelandic haul-out sites was 46–59 animals (supplementations recorded in Denmark and Sweden, these vocalizing individuals would have to be several kilometers from the haul-out colonies (Sabinsky et al., 2017). See Sabinsky et al. (2017) for details about the Danish and Swedish recordings.

The most parsimonious explanation for the very low received levels in our recordings is therefore that seals themselves emit very low source levels. The size of the investigated Icelandic haul-out sites was 46–59 animals (supplementary Fig. 6),1 which is much fewer individuals than many of the Danish and Swedish recording sites. Fewer animals, and therefore possibly fewer males, at each local site could have been a reason for reduced acoustic activity and low emitted source levels. It was unknown during this study if several individuals were vocalizing during the recording period. The carried energy in the roar burst was significantly lower in Heggstaðanes (Iceland) than at any other location (GLM, \( p < 0.001 \); Fig. 2).

4. Discussion

Underwater mating roars from Icelandic harbor seals differed in duration and received energy level from the roars produced by Danish and Swedish harbor seals. All Icelandic roars were recorded around one haul-out site, and roars were only heard early in the recorded season. In Denmark, calls are heard throughout the mating season and at many sites around the haul-out colonies (Sabinsky et al., 2017). Also, studies from Scotland (Van Parijs et al., 1997; Van Parijs et al., 1999) and east and west coasts of North America (Van Parijs and Kovacs, 2002; Hayes et al., 2004a; Boness et al., 2006; Nikolich, 2016; Matthews et al., 2017) indicate that harbor seal vocal displays are usually easy to detect and recognize during the breeding season. Icelandic harbor seals thus appear to be more silent during the mating period than other populations.

The timing of mating in Icelandic harbor seals is largely unknown. Our recordings indicate that mating was ongoing in early July, even though it may have started earlier. Gentry (1998) argued that higher latitudes, with harsh weather and strong but predictable seasonality, seem to favor short lactation periods in seals. This could indicate a possible earlier ending of the lactation period in Iceland than in Danish and Swedish populations. However, even though there were no calls recorded throughout most of July, mating-related displays were observed in Iceland in this time period, when calls are ubiquitous in Danish and Swedish waters. Therefore, mating in Iceland could have continued throughout July, but without vocalizations (Sullivan, 1981; Bishop, 1967) or with a change of location [such as suggested by Van Parijs et al. (2000a)]. It is also possible that the observed mating-related displays were from younger animals not involved in mating (Thompson, 1989; Perry, 1993; Nicholson, 2000).

The low received levels of the Icelandic calls could either be caused by a large propagation loss (i.e., seals being far away from the data logger) or by the seals emitting low intensity signals. It would be surprising if the transmission loss could affect recordings to the extent observed here, especially given the high number of seals observed close to the hydrophone during recordings. If the low received levels were due to seals calling at a distance with the same intensity as vocalizations recorded in Denmark and Sweden, these vocalizing individuals would have to be several kilometers from the haul-out sites, which is highly unusual for harbor seals (Van Parijs et al., 2003; Sabinsky et al., 2017).

The low source levels could also be explained by an adaptive strategy to avoid predation. Predators, such as gray seals or orcas, are much more prevalent in Icelandic waters (Deecke et al., 2002; van Neer et al., 2015) than, for example, in Danish waters. Orcas may indeed use passive listening to detect and locate marine mammal prey as a specialized hunting strategy, instead of relying on echolocation (Deecke et al., 2005). Orca hearing is most sensitive at 15–20 kHz [at 35 and 36 dB re 1 \( \mu \text{Pa} \), respectively;
Szymanski et al. (1999)] and with a hearing cutoff at 600 Hz (>100 dB re µPa; Branstetter et al. (2017)]. With the harbor seal vocalization frequency mainly below 500 Hz (Van Parijs et al., 2000a), a reduction in source level from Icelandic seals would reduce the distance of audible calls for orcas considerably. By lowering the source level of their calls, the Icelandic seals may be able to pursue their underwater acoustic displays without revealing themselves to predatory orcas.

Fig. 2. Total call duration (A), roar burst duration (B), and energy % (C) of calls plotted (minimum, first quartile, median, third quartile, and maximum) against sites in Denmark (Blinderøn in Limfjord, n = 190; Juvre in the Wadden Sea, n = 96), Iceland (Heggstaðanes, n = 76), and Sweden (Kalmarsund, n = 104). GLM, statistically significant codes: highly significant (***, p < 0.001; NS, not significant.)

Szymanski et al. (1999)] and with a hearing cutoff at 600 Hz (>100 dB re µPa; Branstetter et al. (2017)]. With the harbor seal vocalization frequency mainly below 500 Hz (Van Parijs et al., 2000a), a reduction in source level from Icelandic seals would reduce the distance of audible calls for orcas considerably. By lowering the source level of their calls, the Icelandic seals may be able to pursue their underwater acoustic displays without revealing themselves to predatory orcas.
While this strategy may reduce predation risk from eavesdropping orcas, it also decreases the likelihood of the call reaching its intended recipient. Harbor seals may use different strategies to resolve this dilemma. In Alaska, harbor seals use much higher source intensities than what we presume is the case in Iceland, despite being in an area frequented by orcas (Matthews et al., 2020). This may help the males to maintain their competitive edge during mating, with the risk, however, of being consumed by orcas. Thus, lowering the frequency emphasis rather than the source level may be the way out of this dilemma for Alaskan harbor seals (Matthews et al., 2017). The prolonged calls in Iceland, with less intensity, may constitute another way to keep the signals attractive and honest during mating activities, while at the same time decreasing predation risk.

Acknowledgments

We thank Eðvald Daniélsson and Sölvi Ósvoldsson from Seal Watching, Hvammstangi; Guðmundur Jónsson and Gunnar Sveinsson at Illugastaðir, Sigurður Línald Bórisson and Eric dos Santos for help in the field, for communication support, and local assistance. Funds were provided through the University of Southern Denmark for travel and equipment. Ursula Siebert, Joseph Schnitzler, and Johannes Baltzer of the Institute for Terrestrial and Aquatic Wildlife Research (ITAW) provided equipment.

References and links

1See supplementary material at https://www.scitation.org/doi/suppl/10.1121/10.0003782 for more site and setup details and visual behavior observation details including figures.

Berta, A. (2009). “Pinniped evolution,” in Encyclopedia of Marine Mammals, 2nd ed., edited by W. F. Perrin, B. Würsig, and J. G. M. Thewissen (Academic, London), pp. 861–868.

Bishop, R. H. (1967). “Reproduction, age determination, and behavior of the harbor seal, Phoca vitulina L., in the Gulf of Alaska,” M.S. thesis, University of Alaska, Anchorage, AK.

Bjørgeøstet, A., Uglund, K. I., and Bjørge, A. (2004). “Geographic variation and acoustic structure of the underwater vocalization of harbor seal (Phoca vitulina) in Norway, Sweden and Scotland,” J. Acoust. Soc. Am. 116, 2459–2468.

Boness, D. J., Bowen, W. D., Bühleler, B. M., and Marshall, G. J. (2006). “Mating tactics and mating system of an aquatic-mating pinniped: The harbor seal, Phoca vitulina,” Behav. Ecol. Sociobiol. 61, 119–130.

Bowen, W. D., Beck, C. A., and Austin, D. A. (2009). “Pinniped ecology,” in Encyclopedia of Marine Mammals, 2nd ed., edited by W. F. Perrin, B. Würsig, and J. G. M. Thewissen (Academic, London), pp. 852–861.

Branstetter, B. K., Leger, J. S., Acton, D., Stewart, J., Houser, D., Finneran, J. J., and Jenkins, K. (2017). “Killer whale (Orcinus Orca) behavioral audiograms,” J. Acoust. Soc. Am. 141, 2387–2398.

Brownlow, A., Onoufriou, J., Bishop, A., Davison, N., and Thompson, D. (2016). “Corkscrew seals: Grey seal (Halichoerus Grypus) infanticide and cannibalism may indicate the cause of spiral lacerations in seals,” PLoS One 11, e0156464.

Casey, C., Sills, J., and Reichmuth, C. (2016). “Source level measurements for harbor seals and implications for estimating communication space,” Proc. Mtgs. Acoust. 27, 01034.

Deecke, V. B., Ford, J. K. B., and Slater, P. J. B. (2005). “The vocal behaviour of mammal-eating killer whales: Communicating with costly calls,” Anim. Behav. 69, 395–405.

Deecke, V. B., Slater, P. J. B., and Ford, J. K. B. (2002). “Selective habitation shapes acoustic predator recognition in harbour seals,” Nature 420, 171–173.

Gentry, R. L. (1998). Behavior and Ecology of the Northern Fur Seal (Princeton University, Princeton, NJ).

Goodman, S. J. (1998). “Patterns of extensive genetic differentiation and variation among European harbor seals (Phoca vitulina vitulina) revealed using microsatellite DNA polymorphisms,” Mol. Biol. Evol. 15, 104–118.

Granquist, S., and Hauksson, E. (2019a). “Aerial census of the Icelandic grey seal (Halichoerus Grypus) population in 2017: Pup production, population estimate, trends and current status,” Report HV 2019-02, Hafnraðskónstafnun, Reykjavík, Iceland.

Granquist, S., and Hauksson, E. (2019b). “Population estimate, trends and current status of the Icelandic harbour seal (Phoca vitulina) population in 2018/Landssetalning 2018: Stofnsetærharm, sveilur og ástönd stofnir,” Report HV 2019-36, Hafnraðskónstafnun, Reykjavík, Iceland.

Hanggi, E. B., and Schusterman, R. J. (1994). “Underwater acoustic displays and individual variation in male harbour seals, Phoca vitulina,” Anim. Behav. 48, 1275–1283.

Hayes, S. A., Costa, D. P., Harvey, J. T., and Le Boeuf, B. J. (2004a). “Acoustic mating strategies of the male Pacific harbor seal (Phoca vitulina richardi): Are males defending the hotspot?” Mar. Mamm. Sci. 20, 639–656.

Hayes, S. A., Kumar, A., Costa, D. P., Mellinger, D. K., Harvey, J. T., Southall, B. L., and Le Boeuf, B. J. (2004b). “Evaluating the function of the male harbour seal, Phoca vitulina, roar through playback experiments,” Anim. Behav. 67, 1133–1139.

Hayes, S. A., Pearse, D. E., Costa, D. P., Harvey, J. T., Le Boeuf, B. J., and Garza, J. C. (2006). “Mating system and reproductive success in eastern Pacific harbor seals: Reproductive success in harbour seals,” Mol. Ecol. 15, 3023–3034.

Madsen, P. T., and Wahlberg, M. (2007). “Recording and quantification of ultrasonic echolocation clicks from free-ranging toothed whales,” Deep-Sea Res. 54(8), 1421–1444.

Matthews, L. P., Fournet, M. E. H., Gabriere, C., Klinck, H., and Parks, S. E. (2020). “Acoustically advertising male harbour seals in southeast Alaska do not make biologically relevant acoustic adjustments in the presence of vessel noise,” Biol. Lett. 16, 20190795.
Meteo365.com Ltd. (2018). Tide Times and Tide Chart for Hrutafjordur, https://www.tide-forecast.com/locations/Hrutafjordur-Iceland/tides/latest (Last viewed 29 May 2018).

Nicholson, T. E. (2000). “Social structure and underwater behavior of harbor seals in Southern Monterey Bay,” M.S. thesis, San Francisco State University, San Francisco, CA.

Nikolich, K. (2016). “Quantitative classification of harbor seal breeding calls in Georgia Strait, Canada,” J. Acoust. Soc. Am. 140, 1300–1308.

Perry, E. A. (1993). “Aquatic territory defence by male harbour seals (Phoca vitulina) at miquelon—Relationship between active defence and male reproductive success,” Ph.D. thesis, Memorial University of Newfoundland, St. John’s, Newfoundland, Canada.

Sabinsky, P. F., Larsen, O. N., Wahlberg, M., and Tougaard, J. (2017). “Temporal and spatial variation in harbor seal (Phoca vitulina L.) roar calls from southern Scandinavia,” J. Acoust. Soc. Am. 141, 1824.

Samarra, F. I. P., Bassoi, M., Béésu, J., Eliasdóttir, M. Ó., Gunnarsson, K., Mruszok, M.-T., Rasmussen, M., Rempel, J. N., Thorvaldsson, B., and Vikingson, G. A. (2018). “Prey of killer whales (Orcinus orca) in Iceland,” PLoS One 13, e0207287.

Southall, B., Bowles, A., Ellison, J., Gentry, R., Greene, C. Jr., Kastak, D., Ketten, D., Miller, J., Nachigall, P., Richardson, W., Thomas, J., and Tyack, P. (2008). “Marine mammal noise exposure criteria: Initial scientific recommendations,” Aqu. Mamm. 33(4), 1–121.

Stanley, H. F., Casey, S., Carnahan, J. M., Goodman, S., Harwood, J., and Wayne, R. K. (1996). “Worldwide patterns of mitochondrial DNA differentiation in the harbor seal (Phoca vitulina),” Mol. Biol. Evol. 13, 368–382.

Sullivan, R. M. (1981). “Aquatic displays and interactions in harbor seals, Phoca vitulina, with comments on mating systems,” J. Mammal. 62, 823–831.

Szymanski, M. D., Bain, D. E., Kiehl, K., Pennington, S., Wong, S., and Henry, K. R. (1999). “Killer whale (Orcinus orca) hearing: Auditory brainstem response and behavioral audiograms,” J. Acoust. Soc. Am. 106, 1134–1141.

Thompson, P. (1988). “Timing of mating in the Common Seal (Phoca vitulina),” Mamm. Rev. 18, 105–112.

Thompson, P. M. (1989). “Seasonal changes in the distribution and composition of common seal (Phoca vitulina) haul-out groups,” J. Zool. 217, 281–294.

van Neer, A., Jensen, L. F., and Siebert, U. (2015). “Grey seal (Halichoerus grypus) predation on harbour seals (Phoca vitulina) on the island of Helgoland, Germany,” J. Sea Res. 97, 1–4.

Van Parijs, S. M., Corkeron, P. J., Harvey, J., Hayes, S. A., Mellinger, D. K., Rouget, P. A., Thompson, P. M., and Kovacs, K. M. (2003). “Patterns in the vocalizations of male harbor seals,” J. Acoust. Soc. Am. 113, 3403–3410.

Van Parijs, S. M., Hastie, G. D., and Thompson, P. M. (1999). “Geographical variation in temporal and spatial vocalization patterns of male harbour seals in the mating season,” Anim. Behav. 58, 1231–1239.

Van Parijs, S. M., Hastie, G. D., and Thompson, P. M. (2000a). “Individual and geographical variation in display behaviour of male harbour seals in Scotland,” Anim. Behav. 59, 559–568.

Van Parijs, S. M., Janik, V. M., and Thompson, P. M. (2000b). “Display-area size, tenure length, and site fidelity in the aquatically mating male harbour seal, Phoca vitulina,” Can. J. Zool. 78, 2209–2217.

Van Parijs, S. M., and Kovacs, K. M. (2002). “In-air and underwater vocalizations of eastern Canadian harbour seals, Phoca vitulina,” Can. J. Zool. 80, 1173–1179.

Van Parijs, S. M., Thompson, P. M., Tollit, D. J., and Mackay, A. (1997). “Distribution and activity of male harbour seals during the mating season,” Anim. Behav. 54, 35–43.