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ARTICLE

Underwater vocalizations in foraging female Antarctic fur seals (*Arctocephalus gazella*) in the Kerguelen Islands

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Abstract

In the marine environment, many animals use sound to interact and communicate with their conspecifics or other species. Over the last decades, the development of sound recording systems has allowed a significant advance in our knowledge of sound production in marine animals. We deployed miniature sound and movement tags on Antarctic fur seals (AFS), a small otariid foraging on mesopelagic fish, to uncover potential underwater vocalizations in this species. Tags recorded underwater sounds synchronously with high-resolution AFS movements and diving behavior, allowing us to investigate the behavioral context of vocalizations in the natural environment. We provide evidence of underwater vocalizations in foraging female AFS in a context of foraging at sea. AFS produced stereotyped calls made of low-frequency pulses produced in series, exclusively during foraging dives. We hypothesized that these acoustic pulse series could be used as an acoustic lure to confuse or attract fish prey, however, a larger sample size is needed to study the adaptive significance of these underwater vocalizations.

KEYWORDS

Antarctic fur seals, *Arctocephalus gazella*, foraging behavior, vocalizations

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1 | INTRODUCTION

In water, sound is omnipresent and is one of the main sources of information used by marine animals. As sound travels faster and over longer distances in the marine environment than in air, many marine animals, ranging from small invertebrates to large marine mammals, use sound to interact and communicate with their conspecifics or other species (see Duarte et al., 2021 for review). Over the last decades, the development of sound recording systems has allowed a significant advance in our knowledge of sound production in marine animals (Erbe & Thomas, 2022). Newly developed devices that can be deployed on marine animals and record their sound production synchronously with their behavior allow researchers to explore the behavioral context of vocalizations, providing insights into the function of these vocalizations (Akamatsu et al., 2005; Burgess et al., 1998; Johnson & Tyack, 2003).

In cetaceans, vocalizations are well documented, and deployments of animal-borne digital acoustic recorders have provided a wide range of insights into their vocal behavior (Johnson et al., 2009). Underwater vocal behavior is well described for many phocid seal species, especially polar ones (e.g., Klinck et al., 2010 on crabeater seals, *Lobodon carcinophaga*; Rogers et al., 1996 on leopard seals, *Hydrurga leptonyx*; Mizuguchi et al., 2016 on ringed seals, *Pusa hispida*; Pahl et al., 1997 on Weddell seals, *Leptonychotes weddellii*; Frouin-Mouy & Hammill, 2021 on hooded seals, *Cystophora cristata*), but only anecdotal recordings have been made for otariid species (Charrier, 2021). For phocids, underwater vocalizations are thought to be used for conspecific communication, and territorial or courtship signaling (Van Opzeeland et al., 2008). The few studies on underwater sound production of otariids (Erbe et al., 2017) either recorded sounds from captive animals (Schusterman & Baillet, 1969 on California sea lions, *Zalophus californianus*; Schusterman et al., 1970 on Steller sea lions, *Eumetopias jubatus*) or used hydrophones suspended below boats (Norris & Watkins, 1971 on Juan Fernandez fur seals, *Arctocephalus philippii*), which allows describing the characteristics of the calls but not identifying the behavioral context of the vocalizations.

Antarctic fur seals (*Arctocephalus gazella*; AFS hereafter) are small otariids breeding on sub-Antarctic islands. They alternate between foraging periods at sea and periods on land for breeding and molting. During reproduction, they gather in large colonies that can reach several thousand individuals. Colonies consist of harems with a dominant male, several females and their single pup each (Kuzin, 2011; Martin et al., 2021; Riedman, 1990). On land, they are highly vocal and produce barks and guttural calls that play key roles in social interactions, such as threats, or pup/mother interactions (Aubin et al., 2015; Erbe et al., 2017; Page et al., 2002). However, to our knowledge, underwater vocal production and their behavioral context have never been investigated in AFS (Erbe et al., 2017).

To understand potential underwater vocalizations and their behavioral context in their natural environment, we deployed miniature sound and movement tags (Johnson & Tyack, 2003) on female AFS during their at-sea foraging trips. Tags recorded underwater sounds synchronously with high-resolution AFS movements and diving behavior, allowing us to investigate simultaneously fine-scale movements of AFS and possible underwater vocal production. The objectives of this study were (1) to assess the occurrence of underwater vocalizations, and if produced, (2) to describe their characteristics, and (3) to assess their behavioral context. We discuss if underwater vocalizations could be used to startle prey or as an acoustic lure to attract or confuse prey (Marten et al., 2001; Norris & Møhl, 1983).

2 | METHODS

2.1 | Device deployments and data collection

Data were collected on three lactating female AFS in January 2023 at Pointe Suzanne, Kerguelen Islands (49°26'S, 70°26'E, Southern Ocean) under the ethical regulation approval of the French Ethical Committee for Animal Experimentations (#37480-2022052514544991 V7) and the Committee for Polar Environment (A2021-48). Females were captured with a hoop net, anesthetized with isoflurane gas, respectively measured and weighted to the nearest centimeter and 100 g. They were equipped with a head-mounted DTAG-4 mini sound tag (68.0 × 31.0 × 20.7 mm,

58 g in air) programmed to sample GPS position up to every minute, tri-axial acceleration (250 Hz), tri-axial magnetometer (50 Hz), pressure (50 Hz), and audio data (96 kHz, 200 Hz to 48 kHz bandwidth). Tags were set to record only during night hours (from 6 p.m. to 6 a.m. local time, i.e., foraging periods of AFS (Boyd & Croxall, 1992; Jeanniard-du-Dot, Trites, et al., 2017) to save battery. Tags were glued to the hair using quick-setting epoxy glue (Araldite AW 2101, Ciba) and recovered after a single foraging trip at sea (6–8 days) using the same capture and sedation methods.

2.2 | Data analyses

Data recovered from tags were analyzed using custom-written codes and functions from <https://www.animaltags.org> in MATLAB (version 2022b; <https://www.mathworks.com/>). Statistical analyses were conducted in R (R Core Team, 2018).

2.2.1 | Detection of vocalizations and spectrogram analyses

Occurrences of vocalization were detected from recorded spectrograms in 10% of randomly selected dives per individual. This number of dives was chosen by plotting the proportion of dives with vocalizations against the number of analyzed dives, which reached a plateau when 6%–8% of dives per individuals were analyzed (Figure S1).

Vocalizations were analyzed using Raven Lite software (version 2.0.5; <https://www.birds.cornell.edu/ccb/raven-pro/>) and MATLAB. Vocalizations consisted of series of repeated pulses. We measured the pulse duration (milliseconds) on the waveform, and the minimum, maximum, and dominant frequency (frequency of the maximum amplitude) of pulses (Hertz) were measured on the frequency spectrum on a randomly selected subsample of pulses. The number of pulses per series and the series duration (seconds) were measured on a randomly-selected subsample of series. The number of analyzed pulses or series was determined by the change in the means of each of the parameters (mean series duration, number of pulses per series, pulse duration, pulse frequency) as we increased the analyzed sample size, and we stopped the analysis when the means did not continue to change with increased samples.

2.2.2 | Metrics describing AFS behavior

Dive identification

Dives were identified from the pressure data recorded by tags. A dive was defined as animals diving deeper than 3 m for more than 4 s (Jeanniard-du-Dot, Guinet, et al., 2017). The bottom phase was defined as the period of time when depth is above 75% of the maximum dive depth.

Prey capture attempts

Prey capture attempts (PrCAs hereafter) were detected from the 250 Hz tri-axial acceleration data recorded by tags, by computing the norm of the differential of the tri-axial acceleration (norm-jerk hereafter), as described in (Chevallay et al., 2023). Spikes in the norm-jerk signal higher than $3,000 \text{ m/s}^2$ were classified as prey strikes (Chevallay et al., 2023). As prey may be encountered in patches or may elude capture, leading to a bout structure in prey strikes, strikes occurring less than 15 s from the previous strike were grouped in the same PrCA bout according to the distribution of interstrike intervals (Chevallay et al., 2023). Dives where at least one strike was detected were classified as hunting dives.

TABLE 1 Summary of field deployments: individual length and weight, deployment and retrieval date, number of days of recordings, and hours of audio recordings for three female AFS equipped with sound tags in the Kerguelen Islands (austral summer 2023) during a single foraging trip at sea.

	Individual ID		
	1 (ag22_365b)	2 (ag22_365c)	3 (ag22_365d)
Weight (kg)	30	31	33
Length (cm)	110	111	119
Deployment date	December 31, 2022	December 31, 2022	December 31, 2022
Retrieval date	January 8, 2023	January 6, 2023	January 7, 2023
Number of days of recordings	8	6	7
Hours of audio recordings	101	112	118

Swimming activity

High-resolution tri-axial accelerometer data allow for the identification of flipper strokes and can thus be used to describe the AFS swimming activity. Flipper strokes were detected from the dynamic acceleration of both the heave and the surge axes (Jeanniard-du-Dot et al., 2016) by applying a high-pass filter with a cut-off frequency of 1.6 Hz, i.e., 70% of dominant stroke frequency, on both axes. Absolute values of the dynamic heave and surge accelerations were then summed to obtain the swimming effort, a proxy for AFS swimming activity (Aoki et al., 2012; Maresh et al., 2014).

3 | RESULTS

3.1 | Summary of field deployments

Tags recorded data during 8, 6, and 7 days for ind. 1 (ag22_365b), ind.2 (ag22_365c), and ind. 3 (ag22_365d), respectively (Table 1), for a total of 331 hr of audio data (Table 1).

3.2 | Acoustic characteristics of underwater vocalizations

Vocalizations were only found for ind. 1 and ind. 2, but not for ind. 3. For ind. 1 and ind. 2, underwater vocalizations consisted of series lasting 2.4 ± 0.6 s (Q1–Q3: 1.9–2.8 s) and 3.2 ± 1.0 s (Q1–Q3: 2.3–5.6 s), made of 33 ± 7 (Q1–Q3: 28–36) and 35 ± 14 pulses (Q1–Q3: 24–45), with a pulse rate of 14 ± 2 Hz (Q1–Q3: 13–15 Hz) and 11 ± 3 Hz (Q1–Q3: 9–13 Hz), respectively (Figure 1). Series were repeated over a mean duration of 56.3 ± 28.1 s for ind. 1 and 13.8 ± 14.2 s for ind. 2. While the recording quality was sufficient to detect pulse series in ind. 2, the water flow noises prevented us from extracting detailed characteristics of the pulses produced. Therefore, we only measured pulse frequency and duration for ind. 1. Pulses lasted 31 ± 5 ms, they had a dominant frequency of 435 ± 89 Hz, a minimum frequency of 55 ± 20 Hz and a maximum frequency of 1006 ± 105 Hz (Table 2, Figure 1C and E). Between series of pulses, AFS consistently produced another type of sound (Table 2, Figure 1A and B), that lasted 95 ± 19 ms, and had dominant, minimum and maximum frequencies of 386 ± 156 Hz, 75 ± 30 Hz, and 941 ± 165 Hz, respectively (Table 2, Figure 1D and F).

3.3 | Context of underwater vocalizations

Vocalizations were recorded in 80% of dives for ind. 1, 30% of dives for ind. 2, and in 0% of dives for ind. 3. Vocalizations were only recorded in deeper and longer dives with longer time spent in the bottom of the dive (Figure 2,

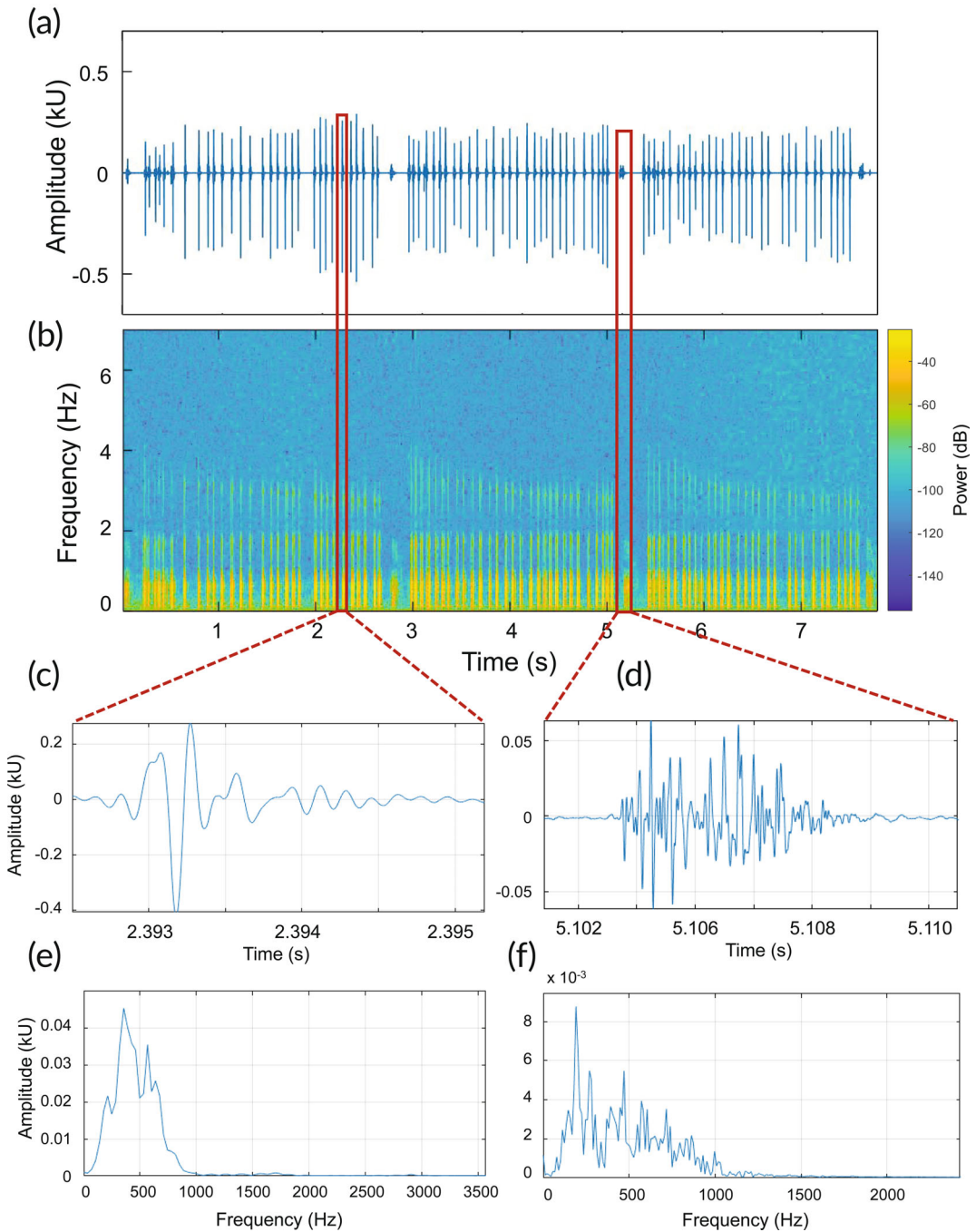


FIGURE 1 Underwater vocalizations performed by ind. 1, an AFS female equipped with a miniature sound tag in the Kerguelen Islands in January 2023: waveform (A) and spectrogram (B), showing a sequence of three series of ~ 30 very short pulses between which an inter-series sound was consistently produced. (C) and (D): waveform of a single pulse or inter-series sound. (E) and (F): Frequency spectrum of a single pulse or inter-series sound.

Wilcoxon test, $p < .001$), typical of foraging dives, i.e., long and deep dives, and were never recorded in transit dives, i.e., short and shallow dives. For ind. 1, 93% of hunting dives, i.e., dives with at least one strike, were associated with vocalizations. For ind. 2, vocalizations were recorded in 43% of hunting dives.

TABLE 2 Characteristics of two underwater sounds produced by a female AFS from the Kerguelen Islands equipped with a sound tag during a single foraging trip at sea (austral summer 2023): sound duration, dominant, minimum, and maximum frequencies. Pulses were produced in series, between which a second type of sound was consistently produced, referred as interseries sound.

	Pulse	Interseries sound
Duration (ms)	31 ± 5 [28–35]	95 ± 19 [85–106]
Dominant frequency (Hz)	435 ± 89 [354–543]	386 ± 156 [247–525]
Minimum frequency (Hz)	55 ± 20 [41–67]	75 ± 30 [49–95]
Maximum frequency (Hz)	1,006 ± 105 [923–1,066]	941 ± 165 [857–1,007]

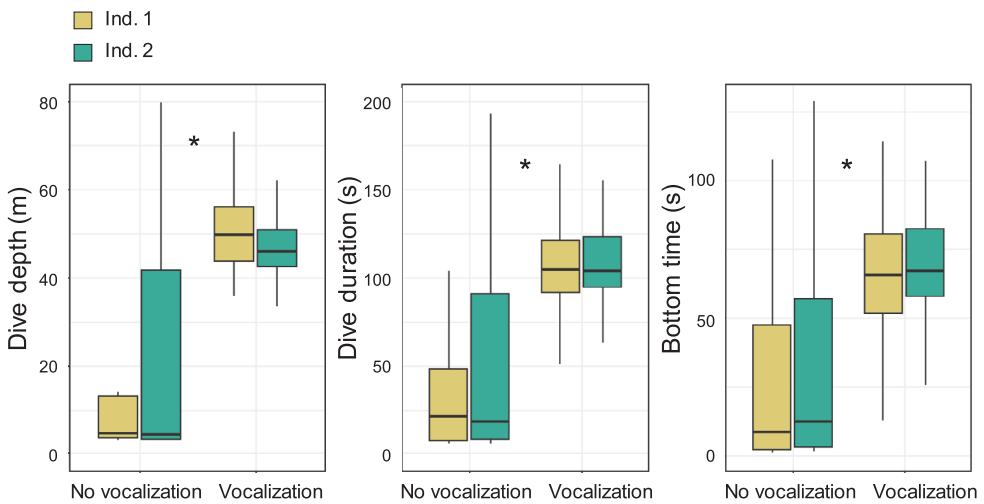


FIGURE 2 Comparison of dives parameters (dive depth, dive duration and bottom time) for dives with vocalizations and dives without vocalizations, for the two female AFS equipped with sound tags in the Kerguelen Islands in January 2023. Asterisks represent significant differences in dive parameters between dives with vocalizations and dives without (Wilcoxon test, $p < 0.05$).

All vocalizations were emitted during the bottom phase of the dive (Figure 3). For ind. 1, vocalizations consistently followed the same behavioral pattern: the individual starts its descent by swimming actively without vocalizing, and then sharply reduces the number of flipper strokes once it reaches the bottom phase. Between 2 and 4 s (Q1–Q3) after reaching the bottom phase, the individual starts vocalizing until the start of the ascent, stopping temporarily vocalizing during PrCAs (Figure 3).

3.4 | Foraging behavior and vocalizations

PrCA bouts performed by ind. 1, which vocalized in 93% of hunting dives, were significantly shorter than PrCA bouts performed by ind. 2, which vocalized in 43% of hunting dives, and by ind. 3, which never vocalized (Figure 4, ANOVA, $p < .001$). Ind. 1 also displayed significantly lower swimming efforts during PrCA bouts compared to ind. 2 and 3 (Figure 4, ANOVA, $p < .001$).

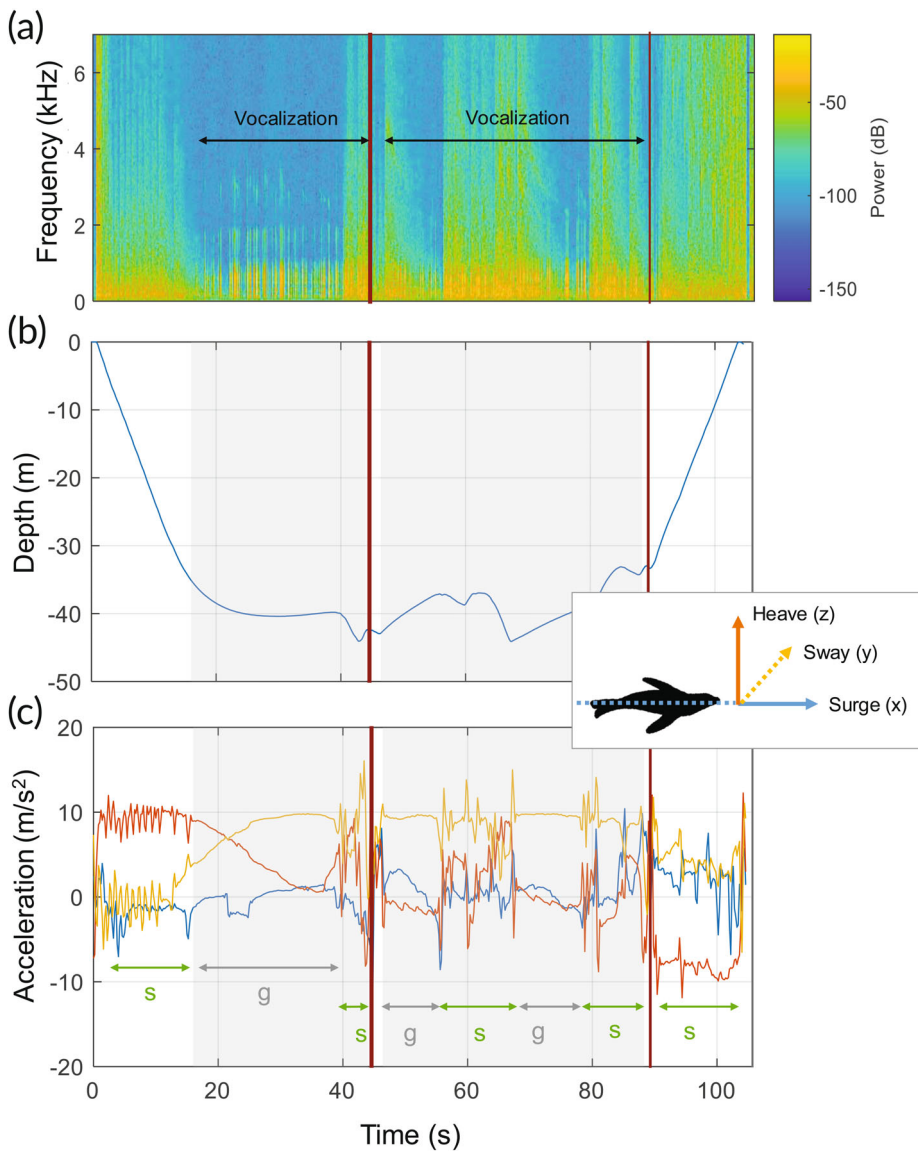


FIGURE 3 Example of a dive of ind. 1, an AFS female equipped with a sound tag in January 2023. (A) Spectrogram of sound recordings during the dive. Black arrows define the periods where vocalizations were produced. (B) Dive profile recorded during a single dive. (C) Tri-axial accelerometer data recorded at a 250 Hz sampling rate during the dive. The insert represents the three axes of the accelerometer: longitudinal (surge, x), left-right (sway, y), dorso-ventral (heave, z). Letters s and g refer respectively to stroking and gliding periods. The red rectangles indicate PrCA bouts, and the gray shaded regions correspond to the periods where underwater vocalizations were produced by the individual.

For ind. 2 which only vocalized in 43% of hunting dives, no difference in swimming effort was found between PrCA bouts preceded by vocalizations and PrCA bouts without (Figure 4) (Wilcoxon test, $p = .9026$). Duration of PrCA bouts that were preceded by vocalizations and PrCA bouts that were not preceded by vocalizations was similar (Figure 4, Wilcoxon test, $p = .6411$).

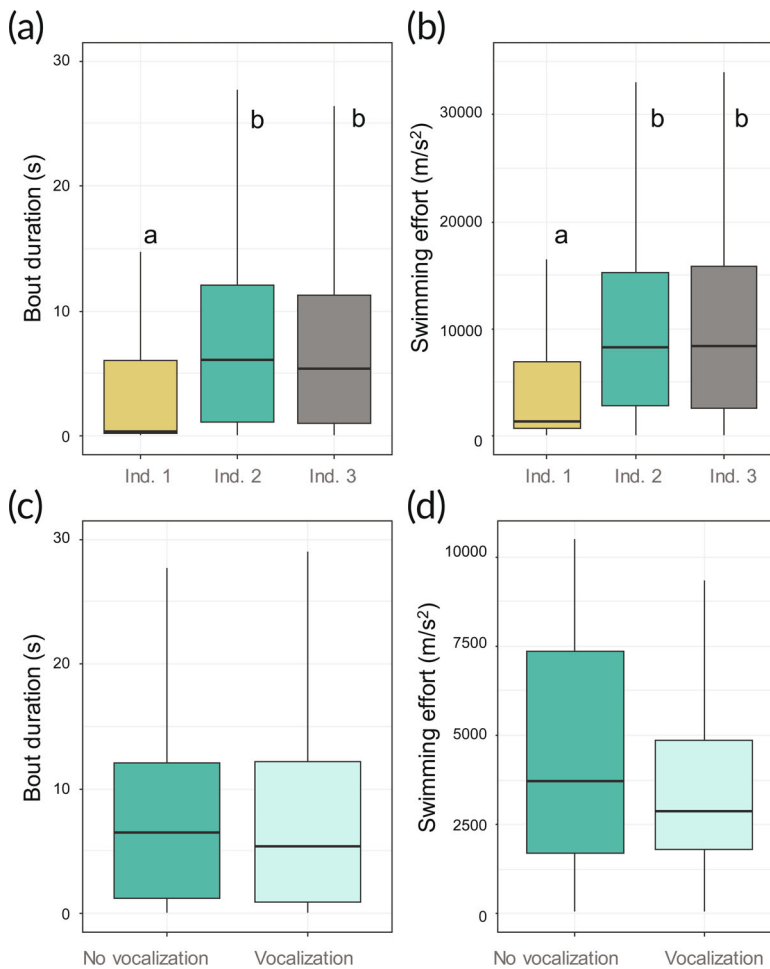


FIGURE 4 (A) and (B): PrCA bout durations and swimming efforts during PrCA bouts of the three female AFS equipped with sound tags in the Kerguelen Islands (austral summer 2023). Letters indicate significant differences between individuals (ANOVA, $p < .05$). (C) and (D): Comparison of bout durations and swimming efforts during PrCA bouts preceded by vocalizations and PrCA bouts that were not preceded by vocalizations for ind. 2, for which vocalizations were recorded in 43% of hunting dives.

4 | DISCUSSION

We provide the first evidence of underwater vocalizations in free-ranging female AFS in a context of foraging at sea. Miniature sound recorders deployed on females allowed us to identify stereotyped calls made of low-frequency pulses produced in series during foraging dives. These calls resembled those recorded on Juan Fernandez fur seals (Norris & Watkins, 1971), California sea lions (Poulter, 1963; Schevill et al., 1963), and Steller sea lions (Schusterman et al., 1970), which are also known to produce series of pulses. In particular, Juan Fernandez fur seals produce series of 17–43 pulses lasting 50–110 ms each and with a dominant frequency of 150–200 Hz (Norris & Watkins, 1971). Similarly, tagged AFS produced series of 28–45 pulses lasting 28–35 ms with a dominant frequency of 350–540 Hz. As these pulse calls have been recorded in different genera of otariids, they are likely widespread among otariid species; however, few studies have investigated their underwater vocal behavior so their prevalence among otariids remains to be explored. Most underwater vocalizations recorded so far in otariids are barks produced from males

and during the breeding season, and thus are likely barks that males produce also in air while defending their territories and harems (Charrier, 2021). The series of pulses recorded in this study seem different from typical bark series and were produced in a context of foraging at-sea.

By deploying movement and sound tags on AFS, we were able to study the behavioral context of vocalizations and to hypothesize on their possible roles. Although otariids such as AFS are very vocal on land and produce various calls to communicate in colonies (Aubin et al., 2015; Page et al., 2002), AFS are known to be solitary foragers that disperse during their foraging trips (Jeanniard-du-Dot & Guinet, 2021). Therefore, it is unlikely that vocalizations are used for communication with conspecifics during foraging. However, there is no visual evidence that AFS always forage solitary, so the use of vocalizations for communication cannot be excluded. However, we did not detect vocalizations produced by other AFS at close vicinity in our study.

For the two females in which vocalizations were detected, they were exclusively recorded during foraging dives. We noticed a strong consistency in call production patterns: calls were typically produced during the bottom phase of the dive, with a start of the call at the end of the descent and a stop of the call just before the ascent. The bottom phase of the dive is the phase in which most of prey capture events occur (Viviant et al., 2016), which suggests that these vocalizations have a foraging function.

It has been hypothesized that penguins produce underwater calls just before prey capture to startle their prey and immobilize it (Thiebault et al., 2019), as suggested in other marine predators such as common bottlenose dolphins (*Tursiops truncatus*) or killer whales (*Orcinus orca*) (Marten et al., 2001; Norris & Møhl, 1983). AFS mostly forage on myctophids, for which no hearing range information is available. Most fish species can hear sounds between 50 and 3,000 Hz (Popper & Schilt, 2008), which includes calls produced by our tagged AFS. This suggests that the fish prey of AFS can hear AFS calls. However, unlike dolphins that produce loud impulsive “bangs” and penguins that emit short calls just before prey capture, AFS emit calls almost continuously during the bottom phase, so it is unlikely that these continuous sounds can startle prey.

One could hypothesize that these acoustic pulse series are used as an acoustic lure. Indeed, calls produced by AFS are quite similar to fish choruses (McCauley & Cato, 2016; Parsons et al., 2016), leading us to suggest that calls could be used to confuse or attract fish prey. So far, no acoustic pulses produced independently to those from the equipped fur seals were detected. Indeed, the received level of pulses is stable while if another organism produced the sound, the received level would vary according to the distance between the equipped AFS and the organism. While we cannot test this hypothesis, we were able to study the fine-scale hunting behavior of AFS to infer information on prey behavior. In particular, a previous study using sonar and movement tags showed that evasive prey were associated with higher swimming efforts and longer prey capture events (Chevallay et al., 2023). Here we compared these two behavioral parameters between the female that consistently produced calls (ind. 1), the female that only vocalized in 43% of dives (ind. 2), and the female that never produced calls (ind. 3). Overall, we found that ind. 1 displayed lower swimming efforts while hunting than ind. 2 and 3. Prey capture bouts were also significantly shorter for ind. 1. This might suggest that prey were easier to capture for the female which vocalized most. This result supports the acoustic lure hypothesis; however, this must be interpreted cautiously due to our small sample size and the lack of direct information on prey behavior.

To further test this hypothesis, we focused on the female that only vocalized in 43% of hunting dives. We compared its hunting behavior during dives with vocalizations and dives without vocalizations. Our hypothesis was that if vocalizations are used as an acoustic lure, PrCA bouts preceded by vocalizations should show lower swimming efforts than PrCA bouts not preceded by vocalizations. We did not find any statistical difference in swimming efforts during PrCA bouts that were preceded by vocalizations and those that were not preceded by vocalizations. For this female (ind. 2), vocalizations were significantly shorter than for ind. 1 (only lasting 10–15 s vs. 50–60 s for ind. 1). These differences raise questions about the function of these vocalizations and should be explored more deeply by performing multiple tag deployments that include miniature video cameras on the same individuals. A larger sample size is needed to study the prevalence of underwater vocalizations among the AFS population and their benefits for foraging success.

Our limited sample size prevented us from making strong inferences about this behavior or determining the prevalence of this vocal behavior among the AFS population. However, the fact that two out of three AFS performed vocalizations suggests that it might be a widespread behavior in the population. This study provides the basis for using sound and movement tags to investigate further the adaptive significance of these underwater vocalizations of AFS.

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AUTHOR CONTRIBUTIONS

Mathilde Chevallay: Conceptualization; formal analysis; investigation; methodology; writing – original draft. **Christophe Guinet:** Conceptualization; funding acquisition; methodology; resources; supervision; validation; writing – review and editing. **Tiphaine Jeanniard du Dot:** Conceptualization; funding acquisition; investigation; methodology; resources; supervision; validation; writing – review and editing.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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