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Passive acoustics suggest two different feeding mechanisms in the Atlantic walrus (*Odobenus rosmarus rosmarus*)

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Abstract :

The vocal repertoire of walruses has been widely described in the bioacoustic literature. These marine mammals produce several distinct types of vocalizations for intraspecific communication during the breeding season. In this study, we provide the first evidence of walrus-generated sounds during foraging dives when they feed on bivalves. We recorded two types of sounds that we associated to different feeding mechanisms. The first sound type was brief and low in frequency that we relate to the suction of soft parts from the bivalves' shells through the use of walrus powerful tongues, which is the common feeding behavior reported in the walrus literature. We also recorded a second sound type composed of multiple broadband pulse trains. We hypothesize the latter were associated with bivalve shell cracking by walruses, which would represent a new feeding mechanism in the walrus literature. This new feeding mechanism is either related to bivalves' ecology or to walruses removing the sediment when searching for food. During this study, we observed bivalves lying on the seafloor instead of being buried in the sediment in walrus feeding areas while scuba diving. As a result, walruses cannot use suction to feed on soft body part of bivalves and have to use another strategy, mastication. Our findings provide a first step towards using passive acoustics to quantify walrus behavior and feeding ecology.

Keywords : Bioacoustics, Bivalves, Feeding behavior, Marine mammal, Young Sound fjord

INTRODUCTION

Walruses are large pinnipeds inhabiting continental shelf waters mainly north of the Arctic Circle (Stewart et al. 2014). Walruses are benthic feeders that mainly consume bivalve mollusks during the open-water season (Vibe 1950; Fay et al. 1997; Gordon 1984). Ray et al. (2006) estimated that Pacific walruses annually consume approx. 3 million metric tons of benthic biomass in the Bering and Chukchi seas.

Through their foraging behavior, walruses play an important ecological role by redistributing sediments in the water column (Ray et al. 2006). In addition, extensive and rapid losses of sea ice in the Arctic have raised conservation concerns for benthic assemblages in their diversity and biomass (Piepenburg 2005). Indeed, sea ice acts on the infauna diversity and biomass, thus impacting the walruses' feeding habits, diet or behaviour and their distribution (Born et al. 2003). Hence, studying bivalve distribution and biomass, as well as walrus feeding behavior will be crucial to predict walrus adaptations and distribution in arctic coastal areas impacted by global change (Garde et al. 2018).

Visual observations of feeding behaviors both in captivity and *in-situ* and analysis of stomach contents revealed that suction is the major mechanism of food ingestion (Fay 1982; Levermann et al. 2003; Dehn et al. 2007). Walruses place the whole burrowed mollusc between their lips, remove the soft tissues (foot and/or siphon) of bivalves by using their powerful jaw, and then expulse shells (Gordon 1984). However, such a behavior is difficult to confirm underwater through visual observations (Vibe 1950; Born et al. 2003), and other techniques should be developed to quantify these underwater feeding mechanisms.

Interestingly, walruses produce a wide variety of airborne and waterborne sounds to communicate between individuals. Their underwater vocalizations, including grunting, bell-like and knock sounds, have been well documented in the bioacoustic literature (e.g., Schevill et al. 1966; Stirling et al. 1987; Mouy et al. 2012). To date, no study has yet determined the acoustic behavior of walruses during foraging dives.

In this study, we used passive acoustics to identify and record sounds generated underwater by free-living Atlantic walruses while foraging in northeastern Greenland (Young Sound fjord). To our knowledge this is the first report of walrus feeding sounds. It provides new insights into foraging techniques and highlights the potential of passive acoustics as a tool to study underwater animal behaviors in general and more specifically in this study, walrus feeding ecology.

MATERIALS AND METHODS

Study site

'Sand Island', a small island (1 km long and 0.3 km wide), is located at the mouth of the Young Sound fjord (North East, Greenland). It is made of sandy beaches reaching a height of only 2.5 ms above sea level at high tide and it is one of the few known terrestrial walrus haul-out sites in Greenland (up to 37 animals observed in summer 2007, 45 animals in 2008; Egevang et al. 2007). Sand Island is surrounded by sandy bottom on a wide strip of shallow water. The Young Sound walrus population takes advantage of this shallow area Characterized by a high density and diversity of mollusks, with bivalves (primarily *Mya truncata L.*, *Hiatella arctica L.* and *Astarte spp.*; Sejr et al. 2000) dominating the macro zoobenthos community at 10–40 m depth with biomasses reaching up to 200 g wet weight/m^2 (Born et al. 2003).

Data collection

Sound recordings were conducted on the 6th and 9th of August 2015 close to Sand Island walrus by using a RTSYS EA-SDA14 autonomous acoustic recorder (gain of 15 dB, sampling frequency of 156 kHz) equipped with a wideband omnidirectional and calibrated HTI-92 hydrophone (High-Tech Inc., flat frequency response over the 10 Hz to 24 kHz range and sensitivity of -163 dB re. 1 µPa.V^{-1}).

The recording device was deployed on a drifting mooring from a 6 m long inflatable boat at less than 100 m of surfacing walruses. The engine was shut off as soon as the acoustic buoy was deployed to avoid noise contamination of the recordings and disturbance of the walrus. A total of 6 recordings were made at a range varying from 50 m to 100 m from walrus surfacing (see Online Resource 1). We also recorded the underwater ambient noise without the presence of walruses at the same site (44 min and 52 min on the 6th and 9th, respectively). Visual observations from the boat were performed during the whole acoustic recording sessions. All walruses exhibited typical surface behaviors such as back-up postures by diving head first that are related to typical foraging dives (Born and Knutsen 1997; Garde et al. 2018). During foraging behavior, walruses continuously dive at the same spot (Miller and Kochnev 2021). Hence after sound recordings, when walruses left the feeding area (up to ca. 1 h delay), pictures from the bottom were taken by two scuba divers to confirm the presence of bivalve species (e.g., Online Resource 2).

In addition, a supplementary controlled experiment was run in Kongsfjorden (Svalbard archipelago, 78°55'44.0" N, 11°56'02.0" E, water depth: 8 meters) in May 2020. Two scuba divers dug up individual bivalves (*Hiatella arctica L.*) and cracked their shells in the vicinity of the recording device described above, first using a clamp, and then by chewing them (i.e. human mastication). Sounds were recorded at 50 cm from the hydrophone which was positioned 50 cm above the bottom. The recorded sounds were then compared with those recorded during walrus foraging dives.

Acoustic analysis

All the acoustic recordings were cut into 10-s snapshots. Spectrograms were computed for each 10-s snapshot with a 32 Hz frequency resolution and 640 time-bins per snapshot (Hann window, 1024-point fast Fourier transform, 50% overlap). The acoustic recordings and corresponding spectrograms were listened to and manually inspected to identify walrus vocalizations as well as feeding sounds. Detailed power spectra (obtained by time-averaging the spectrograms) and spectrograms were built for each identified sound.

RESULTS AND DISCUSSION

We manually labeled a total of 128 walrus-generated sounds from the recordings performed on the 6th and 9th August 2015. The identified sound sequences were missing during ambient noise recordings when walruses were not present at the recording site. Table 1 summarizes the temporal and spectral characteristics of the four types of walruses-generated sounds identified in the dataset.

We recorded two different vocalization types similar to what can be found in the walrus bioacoustic literature. *Walrus grunts* were brief and low in frequency (Figure 1; Stirling et al. 1983; Miller 1985; Mouy et al. 2012; Charrier 2021). In contrast, *bell calls* are long and made of a single frequency (Schevill et al. 1966; Stirling et al. 1987; Sjare et al. 2003; Miller and Kochnev 2021). These two types of calls were recorded at the same time during walrus dives (Figure 1). These vocalizations are mostly displayed by male walruses during the breeding season (From December to March), but also occur throughout the year (Sjare et al. 2003; Mouy et al. 2012).

Interestingly, we also recorded two other sound sequences that were not associated with classical walrus vocalizations, suggesting that they may be related to other behaviors performed during foraging dives. In marked contrast with vocalizations, because these two sound sequences were never recorded during the same walrus dive (and recording sequence), we associated them to two different feeding mechanisms. To our knowledge, these sounds have never been reported in the walrus bioacoustic literature.

We recorded low frequency (below 1 kHz) and brief sounds similar to those produced when opening a wine bottle (see Online Resource 4). Manual inspection of spectrograms coupled with listening of the sounds allowed us to identify five different sequences, such as the one presented in Figure 2A. Theses sequences displayed a rhythmic structure, with the delay between two sounds varying between 1 and 2 s (Table 1). This sound could be interpreted as a byproduct of the common feeding behavior described for walruses, i.e. using their powerful tongues to suck the soft tissues (siphon and/or foot) from buried bivalves in sand (Gordon 1984; Kasteleim and Mosterd 1989; Kasteleim et al. 1994).

We also isolated two original recording sequences, each of ~30 s long displaying a rhythmic structure, with the delay between two sounds inside a sequence varying between 0.4 and 0.6 s (~ 20 sounds per sequence; Figure 2B; Online Resource 5). These sounds were described as broadband pulse trains, composed of 4 to 11 pulses per sound (mean: 6.3 ± 1.7) and were transient (mean: 118 ± 40 ms; Table 1). The intensity was distributed over a wide frequency band (up to 25 kHz), but with the highest intensity occurring in the low frequency (< 1 kHz; Table 1, Figure 2B). These sounds resembled the underwater recordings of manually cracked bivalves by scuba divers (see Online Resource 3). Interestingly, these pulse train sounds are similar to other taxa also feeding on bivalves by crushing their shells, such as in fish (Ajemian et al. 2021) and crustaceans (Meyer-Rochow and Penrose 1976; Jézéquel et al. 2018). We thus hypothesized that the recorded sounds could be related to shell cracking by walruses during foraging dives.

To our knowledge, this new potential behavior has never been described in the walrus literature. Indeed, previous studies have demonstrated they only use suction to feed on bivalves' soft tissues while leaving the shells intact (Fay 1982; Born et al. 2003; Jones et al. 2013). This new behavior could be directly linked to bivalves emerged from the sand, lying down on the seafloor. As a result, walruses cannot use suction mechanism because they are unable of employing their fins to manually move their preys to their mouths (Fay 1982; Levermann et al. 2003; Dehn et al. 2007). The emergence of the bivalves on the bottom was observed via scuba divers during this study (Online Resource 2). Indeed, some bivalve species living in the study site, such as *Hiatella arctica L.*, tend to naturally live on the seafloor because of their high densities (Sejr et al. 2000). Another explanation could be related to walruses removing sediments with their heads, leaving non-eaten bivalves on the seafloor (Born et al. 2003). This potential feeding behavior has never been documented before, but since walruses feed on a variety of benthic species they are likely to be adaptable in order to forage as optimally as possible. Although visual underwater confirmation is needed, our results provide the first indices suggesting a feeding mechanism not previously described in walrus that may be related to bivalve behaviours.

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DECLARATIONS

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Conflicts of interest/Competing interests

The authors declare no potential competing or conflict of interest

Availability of data and material

Sound files may be requested by email to the corresponding author

Code availability

MATLAB scripts may be requested by email to the corresponding author

BIBLIOGRAPHY

1. Ajemian MJ, Lamboy C, Ibrahim A, DeGroot BC, Bassos-Hull K, Mann DA, Chérubin L (2021) Capturing shell-crushing by large mobile predators using passive acoustics technology. J Exp Mar Bio Ecol 535:151497. https://doi.org/10.1016/j.jembe.2020.151497
2. Born EW, Knutsen LØ (1997) Haul-out and diving activity of male Atlantic walruses (*Odobenus rosmarus rosmarus*) in NE Greenland. J Zool 243:381-396. https://doi.org/10.1111/j.1469-7998.1997.tb02789.x
3. Born EW, Rysgaard S, Ehlmé G, Sejr MK, Acquarone M, Levermann N (2003) Underwater observations of foraging free-living Atlantic walruses (*Odobenus rosmarus rosmarus*) and estimates of their food consumption. Polar Biol 26:348-357. https://doi.org/10.1007/s00300-003-0486-z
4. Charrier I (2021) Vocal Communication in Otariids and Odobenids. In: Campagna C, Harcourt R (eds) Ethology and Behavioral Ecology of Otariids and the Odobenid, Springer Nature, Switzerland, pp. 265-289
5. Dehn LA, Sheffield GG, Follmann EH, Duffy LK, Thomas DL, O'Hara TM (2007) Feeding ecology of phocid seals and some walrus in the Alaskan and Canadian Arctic as determined by stomach contents and stable isotope analysis. Polar Biol 30:167-181. https://doi.org/10.1007/s00300-006-0171-0
6. Egevang C, Stenhouse IJ, Rasmussen LM, Willemoes M, Ugarte F (2007) Field Report from Sand Island, Northeast Greenland–2008. Nuuk: Grønlands Naturinstitut.
7. Fay FH (1982) Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens Illiger*. N Am Fauna 74:1-279. https://doi.org/10.3996/nafa.74.0001
8. Fay FH, Eberhardt LL, Kelly BP, Burns JJ, Quakenbush LT (1997) Status of the Pacific walrus population, 1950–1989. Mar Mamm Sci 13:537-565. https://doi.org/10.1111/j.1748-7692.1997.tb00083.x
9. Garde E, Jung-Madsen S, Ditlevsen S, Hansen RG, Zinglersen KB, Heide-Jørgensen MP (2018) Diving behavior of the Atlantic walrus in high Arctic Greenland and Canada. J Exp Mar Bio Ecol 500:89-99. https://doi.org/10.1016/j.jembe.2017.12.009
10. Gordon KR (1984) Models of tongue movement in the walrus (*Odobenus rosmarus*). J Morphol 182:179-196. https://doi.org/10.1002/jmor.1051820206
11. Jézéquel Y, Bonnel J, Coston-Guarini J, Guarini JM Chauvaud L (2018) Sound characterization of the European lobster *Homarus gammarus* in tanks. Aquat Biol 27:13-23. https://doi.org/10.3354/ab00692
12. Jones KE, Ruff CB, Goswami A (2013) Morphology and biomechanics of the pinniped jaw: mandibular evolution without mastication. Anat Rec 296:1049-1063. https://doi.org/10.1002/ar.22710
13. Kastelein RA, Mosterd P (1989) The excavation technique for molluscs of Pacific walruses (*Odobenus rosmarus divergens*) under controlled conditions. Aquat Mamm 15:3-5.
14. Kastelein RA, Muller M, Terlouw A (1994) Oral suction of a Pacific walrus (*Odobenus rosmarus divergens*) in air and under water. Z Saugetierkd 59:105-115.
15. Levermann N, Galatius A, Ehlme G, Rysgaard S, Born EW (2003) Feeding behavior of free-ranging walruses with notes on apparent dextrality of flipper use. BMC Ecol 3:1-13. https://doi.org/10.1186/1472-6785-3-9

16. Meyer-Rochow VB, Penrose JD (1976) Sound production by the western rock lobster *Panulirus longipes* (Milne Edwards). J Exp Mar Bio Ecol 23:191-209. https://doi.org/10.1016/0022-0981(76)90141-6
17. Miller EH (1985) Airborne acoustic communication in the Walrus *Odobenus rosmarus*. Natl Geogr Res 1:124-145.
18. Miller EH, Kochnev AA (2021) Ethology and behavioral ecology of the walrus (*Odobenus rosmarus*), with emphasis on communication and social behavior. In: Campagna C, Harcourt R (eds) Ethology and Behavioral Ecology of Otariids and the Odobenid, Springer Nature, Switzerland, pp. 437-488.
19. Mouy X, Hannay D, Zykov M, Martin B (2012) Tracking of Pacific walruses in the Chukchi Sea using a single hydrophone. J Acoust Soc Am 131:1349-1358. https://doi.org/10.1121/1.3675008
20. Piepenburg D (2005) Recent research on Arctic benthos: common notions need to be revised. Polar Biol 28:733-755. https://doi.org/10.1007/s00300-005-0013-5
21. Ray GC, McCormick-Ray J, Berg P, Epstein HE (2006) Pacific walrus: benthic bioturbator of Beringia. J Exp Mar Bio Ecol 330:403-419. https://doi.org/10.1016/j.jembe.2005.12.043
22. Schevill WE, Watkins WA, Ray C (1966) Analysis of underwater Odobenus calls with remarks on development and function of pharyngeal pouches. Zoologica (NY) 51:103-106. https://doi.org/10.5962/p.203287
23. Sejr MK, Jensen KT, Rysgaard S (2000) Macrozoobenthic community structure in a high-arctic East Greenland fjord. Polar Biol 23:792-801. https://doi.org/10.1007/s003000000154
24. Sjare B, Stirling I, Spencer C (2003) Structural variation in the songs of Atlantic walruses breeding in the Canadian High Arctic. Aquat Mamm 29:297-318.
25. Stewart RE, Kovacs KM, Acquarone M (2014) Introduction: walrus of the North Atlantic. NAMMCO Scient Pub 9:7-12.
26. Stirling I, Calvert W, Cleator H (1983) Underwater vocalizations as a tool for studying the distribution and relative abundance of wintering pinnipeds in the High Arctic. Arctic 36:262-274. https://doi.org/10.14430/arctic2275
27. Stirling I, Calvert W, Spencer C (1987) Evidence of stereotyped underwater vocalizations of male Atlantic walruses (*Odobenus rosmarus rosmarus*). Can J Zool 65:2311-2321. https://doi.org/10.1139/z87-348
28. Vibe C (1950) The marine mammals and the marine fauna in the Thule District (northwest Greenland) with observations on ice conditions in 1939-41. Medd Groenl 150:93-97.

TABLE CAPTION

Table 1: Temporal and spectral characteristics of walrus grunts, bell calls, feeding sound types 1 and 2. Sound features are presented in mean (sd). NA: not applicable for this type of sound.

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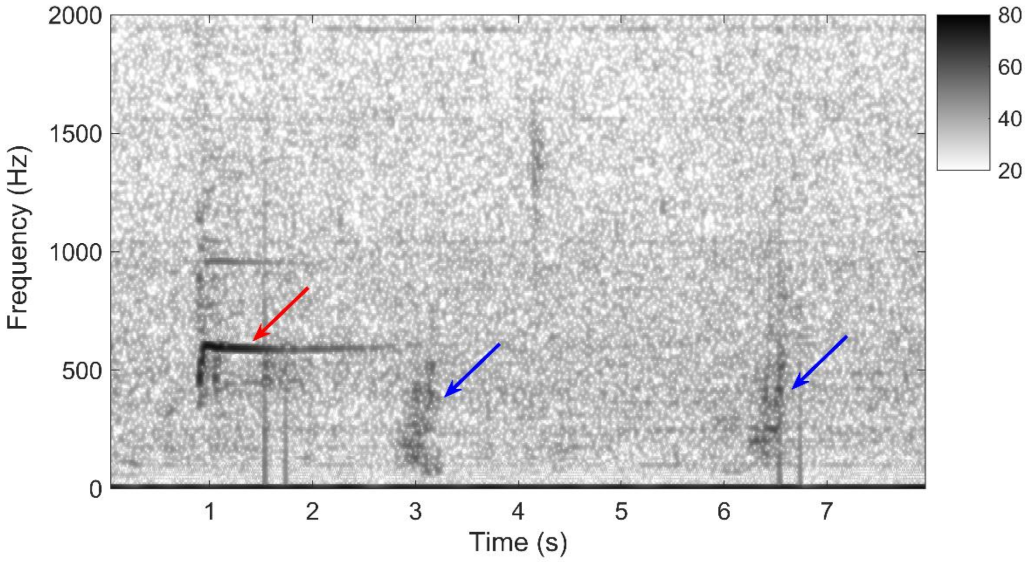
Type of walrus sound	*Number of detections*	*Sound duration (ms)*	*Rhythmic Structure*	*Peak frequency (Hz)*	*bandwidth (Hz)*	*Spectral shape*
Grunts	54	297 (51)	~ 3 s between each grunt	337 (91)	733 (220)	Low frequency pulse
Bell calls	7	1219 (435)	None	607 (58)	NA	Long ones
Feeding sound type 1	28	100-200	1-2 s between sounds, up to 8 sounds in a row	480 (86)	NA	Short tones
Feeding sound type 2	39	118 (40)	Up to 2 sounds per second, up to 20 sounds in a row	523 (260)	13113 (4058)	Broadband pulse train

FIGURE CAPTION

Figure 1: Spectrogram of typical underwater low frequency vocalizations of the Atlantic Walrus, representing a bell call (red arrow) followed by two grunts (blue arrow). The greyscale bar is in dB re 1µPa².Hz^{-1}.

Figure 2: Spectrograms showing the two different sound types recorded during walrus foraging dives. A: two low frequency sounds that we associated to suction behavior (red arrows). B: a sequence of 11 broadband pulse sounds that we associated to bivalve shell cracking. The greyscale bars are in dB re 1µPa².Hz^{-1}.



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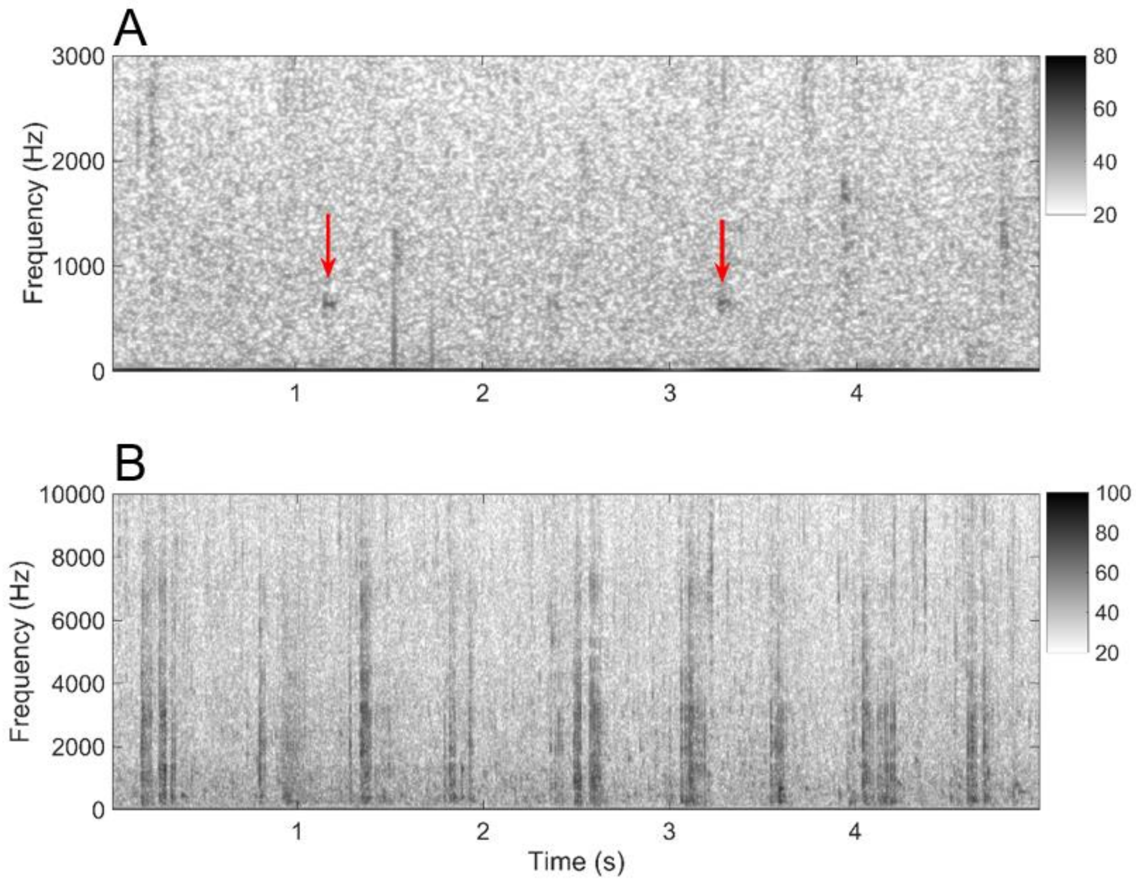

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