

Prey Selection by Walrus (*Odobenus rosmarus rosmarus*) in the Dutch Wadden Sea, the Netherlands

Sophie Brasseur,^{1,2} Jeroen Hoekendijk,^{1,2}
Judith D. L. van Bleijswijk,³ and Lise Klunder⁴

¹Wageningen University & Research, WMR, Ankerpark 23, Den Helder, 1791 AK, The Netherlands

E-mail: sophie.brasseur@wur.nl

^{2,3,4}Royal Netherlands Institute for Sea Research, Departments of COS,² MMB,³ and OCS,⁴
Landsdiep 4, 1797 SZ 't Horntje, Den Hoorn, Texel, The Netherlands

Abstract

Between February 2021 and April 2022, a female walrus (*Odobenus rosmarus rosmarus*) was observed multiple times along the North Sea and Norwegian coasts. Scat samples from the walrus were collected on two occasions when it visited the Dutch Wadden Sea between September and November 2021. It was assumed that the walrus fed locally, so to determine the animal's diet, scat samples were analyzed using molecular methods. In both scats, only the Atlantic razor (jackknife) clam (*Ensis leei*, M. Huber, 1843), a mollusk species invasive to the region, was found; this species had invaded the area relatively recently and is very abundant. The walrus did not seem to suffer from the warm water temperature, which reached more than 20°C in summer. We hypothesize that the temperature is not the reason for the walrus's distribution being restricted in the Arctic, but, instead, it was potentially overhunting and ongoing disturbance. The concurrence of the recovering walrus population in the Northeast Atlantic and global warming causing loss of sea-ice for haul out and augmenting human pressure in the Arctic might drive an increase in walrus visits at lower latitudes in the future. We therefore suggest adequate management plans be drawn up to anticipate this.

Key Words: walrus, diet, *Ensis leei*, prey, faecal DNA, metabarcoding, vagrant

Introduction

A young female Atlantic walrus (*Odobenus rosmarus rosmarus*) was observed several times along the coast of the Dutch Wadden Sea between September and November 2021. The animal was first observed in December 2019 in northern Norway. In spring 2021, she was seen in Denmark before returning to

northern Norway in the summer of that year. Instead of continuing north, the walrus returned south as if for a round trip, visiting Denmark, Germany, the Netherlands, and England in the autumn of 2021, and Scotland by the end of that year. She was then seen in the Shetlands in January 2022 before crossing back to Denmark, Sweden, and finally spending spring and summer of that year in southern Norway (Figure 1; Aae, 2022; Chiacchio & Aae, 2024). On 14 August 2022, the animal was killed in Norway due to authorities' concerns about her welfare and the public's safety.

Most likely, this female belongs to the Svalbard and Franz Josef Land walrus stock (Chiacchio & Aae, 2024), which has been protected since 1952 after centuries of severe overhunting. Abundance is not often monitored, and the latest estimate was 3,886 individuals in 2012 (confidence interval 3,553 to 4,262), which represented an exponential increase of about 8% per year between 2006 and 2012, potentially expanding back into their former range (Kovacs et al., 2014). Extralimital occurrences of the Atlantic walrus during the past century have been described in several sources (van Deinse, 1964; Born, 1988, 1992; Gjertz et al., 1993; van Bree, 1997; Brasseur & Evans, 2022), though few in such detail as was described for this animal (Chiacchio & Aae, 2024). Most often, (young) males were seen.

Throughout her travels, the walrus was observed to have wounds on her fore flippers (Figure 2C); however, she was otherwise characterized as healthy, leading to the conclusion that she must have fed regularly. While the observations show that the walrus returned to northern Norway in late June 2021, approximately 18 mo after she was first observed there, it seems impossible that the animal only fed in these northerly waters during her travels south. This holds true especially between September and November 2021 and in 2022 when she was often observed daily along

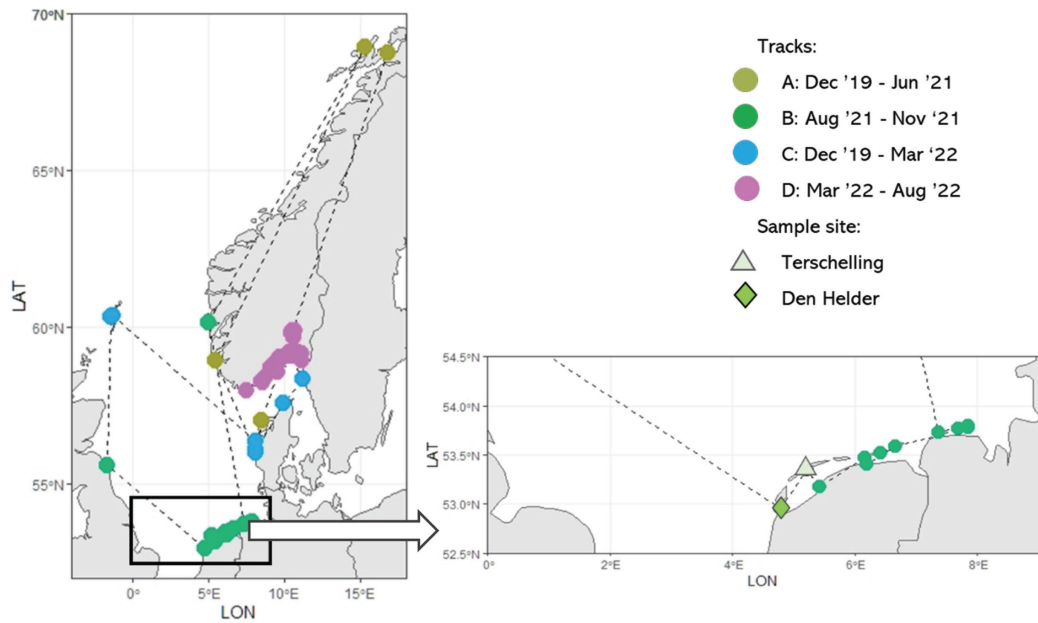


Figure 1. Locations of walrus (*Odobenus rosmarus rosmarus*) observations



Figure 2. (A) Walrus hauled out on a concrete pier in the harbour of Harlingen (6 October 2021); (B) walrus laying on a submarine in the Navy harbour of Den Helder (27 October 2021); (C) wounds on a walrus's fore flippers; and (D) walrus observed from the coast near Den Helder.

the Dutch coasts, with a maximum absence of 2 wks.

Though there are several studies on the diet of the Atlantic walrus (Vibe, 1950; Gjertz & Wiig, 1992; Fisher & Stewart, 1997), to our knowledge, the diet of this species in this more southern region is unknown. Many bivalves occur in the North Sea, sometimes in high densities, including the preferred prey of the walrus in northern regions, blunt gaper or truncate softshell (*Mya truncata*; Born & Wiig, 2021), and a related species, the soft-shell clam (*Mya arenaria*), which suggests walrus could forage in the North Sea. To examine this, we analyzed two walrus scats collected in the Netherlands.

Methods

Sample Collection

The walrus typically rested on land for several hours and then went out to sea before either coming back to the same site or moving off to the next. On multiple occasions, the walrus was observed to

have defecated. On only two occasions was it possible to collect a scat sample: one from the Island of Terschelling where the walrus had hauled out on the grass (13 October 2021; Figure 2A) and one from a walrus resting on a submarine in the Navy harbour of Den Helder (27 October 2021; Figure 2B). The samples were collected after the walrus left the site, placed in a plastic bag or container, and frozen at -20°C within 1 to 3 h after collection, pending further treatment.

For the analysis, the scat samples were thawed and then dissolved in phosphate-buffered saline (PBS; pH = 7.4) in a ratio of 1:1 (Palomares et al., 2002). As the sample collected in Den Helder was large (~1,000 ml) and divided in two containers, subsamples of ~100 ml each were taken after mixing in the original container. The dilution in PBS was done in two separate batches. For every sample, the PBS-scat mixture was stirred thoroughly, and four subsamples (~1.5 ml) of the dissolved matter of each sample were taken and placed in cryovials (Table 1). To exclude contamination, a container with only PBS was stirred, and

Table 1. Overview of scat samples, including weight, DNA concentration, and analysis performed in this study

Location	Code	Weight (g)	DNA (ng/μl)	Results – Bivalves	
				PCR	Metabarcoding
Terschelling, 13-10-21	1	1.6	1.6	<i>Ensis</i>	<i>Ensis</i>
	2	1.2	0.6	--	--
	3	1.5	< 0.5	--	Not tested
	4	1.4	0.94	<i>Ensis</i>	<i>Ensis</i>
Den Helder, 27-10-21	5	1.3	13	<i>Ensis</i>	Not tested
	6	1.2	26.4	<i>Ensis</i>	<i>Ensis</i>
	7	1.1	2.0	--	Not tested
	8	1.1	31.6	<i>Ensis</i>	<i>Ensis</i>
Den Helder, 27-10-21	9	1.4	16.7	<i>Ensis</i>	<i>Ensis</i>
	10	1.4	2.8	<i>Ensis</i>	Not tested
	11	1.1	21.7	--	--
	12	1.1	25.5	<i>Ensis</i>	Not tested
Control PBS	1	1.3	< 0.5	--	--
	2	1.4	< 0.5	--	Not tested
	3	1.5	< 0.5	--	Not tested
	4	1.2	< 0.5	--	Not tested
Negative control				--	--
				--	Not tested
Positive control					<i>Ensis</i> , <i>Mytilus</i> , <i>Mya</i>

four control samples were collected and placed in 2 ml cryovials. The cryovials and the remaining material were placed in separate plastic containers and frozen at -80°C for possible future studies.

DNA Extraction and Diagnostic PCR

For all 16 subsamples, total DNA was extracted from the pre-treated scat samples using the QIAamp Fast DNA Stool Mini Kit (Qiagen, Hilden, Germany), largely following the manufacturer's protocol for "Isolation of DNA from Stool for Human DNA Analysis." After the addition of lysis buffer, we centrifuged samples again at full speed for an additional 2 min to make sure all particles were pelleted (step 3 of the protocol; 3 min total). Extracted DNA was eluted in 200 µL (instead of 500 µL as written in the protocol) elution buffer and stored at -20°C. DNA concentration was measured with a Qubit fluorometer (Invitrogen, Thermo Fisher Scientific, Waltham, MA, USA).

Species-specific primer pairs developed to identify bivalve species common in the Wadden Sea and Dutch coastal area were readily available (Philippart et al., 2012, 2014). These species-specific primers were for *Cerastoderma edule*, *Ensis leei*, *Mya arenaria*, *Mytilus edulis*, *Macoma balthica*, and *Crassostrea gigas* (cockle, Atlantic razor clam, soft-shell clams, blue mussel, Baltic tellin, and Pacific oyster, respectively) and were ideal for procuring a first impression of the walrus's diet. Diagnostic PCRs were performed according to Philippart et al. (2014), with each 25 µL PCR mixture comprising 2.5 µL BioTherm™ PCR Buffer (15 mM MgCl₂), 2.5 µL dNTPs (Bioline, 2.5 mM), 0.25 µL of each primer (50 µM), 0.5 µL BSA (20 mg ml⁻¹), 0.125 µL BioThermPlus™ Taq (5 units µl⁻¹), 15.875 µL PCR H₂O, and 3 µL DNA template. Denaturation steps of the PCR program were 94°C for 2 min, followed by 35 cycles at 94°C for 30 s, annealing at 52.5°C for 30 s (for *Crassostrea gigas*) or at 50°C for 30 s (remaining five species); a final extension step at 72°C for 7 min; and a quick cooling to 4°C. The occurrence of a target species was scored from bands on 2% agarose gels after loading 5 µL of the PCR product.

Metabarcoding

Based on the results of the Qubit fluorometer and the diagnostic PCRs, seven samples were selected for further analysis (Table 1). These samples, together with one PBS control, a negative extraction control, a negative PCR control, and a positive control (a mock community) were used as a template for amplification in triplicate. The positive control included three common bivalves from the Wadden Sea: (1) the Atlantic razor clam,

(2) the soft-shell clam, and (3) the blue mussel. Library preparation was identical to Klunder et al. (2022). In summary, a 450 base pair (bp) part of the 18S rRNA gene, the nuclear small ribosomal subunit, was amplified using the primer pair F04 and R22mod from Sinniger et al. (2016). The forward and reverse primers were extended with unique 12nt barcodes. PCR products were purified and pooled in equimolar quantities. The pooled sample was submitted to Macrogen and sequenced on an Illumina MiSeq platform using the 2 × 300 bp TrueSeq V3 kit.

The Illumina reads were processed using the NIOZ in-house amplicon sequence analysis pipeline 'Cascabel' (Abdala Asbun et al., 2020). Forward and reverse reads were merged using *PEAR*, Version 0.9.10 (Zhang et al., 2014), with a minimum overlap of 10 bp. Samples were demultiplexed based on the 12nt unique barcodes using the QIIME scripts *extract_barcode.py* and *split_libraries.py* (Caporaso et al., 2010). Amplicon sequence variants (ASVs) were identified using *DADA2*, Version 1.24.0 (Callahan et al., 2016). ASVs were taxonomically assigned using the RDP classifier (Wang et al., 2007), with a minimum confidence threshold of 0.5. The SILVA 18S rRNA database (release 132.1; Pruesse et al., 2007) and our custom reference database (Klunder et al., 2022; Genbank Accession Numbers MZ709983-MZ710042) were used as reference. ASVs which were assigned as metazoan but had no match in the SILVA database (3 ASVs) were checked against the NCBI nucleotide database using *Blastn*. Raw Illumina sequences were deposited in the European Nucleotide Archive (ENA Accession Number PRJEB81887).

Results

Diagnostic PCR

The DNA concentration measured with a Qubit fluorometer (Invitrogen) varied among samples (Table 1). In the diagnostic PCR test results, only the Atlantic razor (jackknife) clam (*Ensis leei*, M. Huber, 1843) was detected; none of the other five mollusks were discerned. Eight out of 12 subsamples show a band for the razor clam at the expected amplicon size of 279 bp (Figure 3).

Metabarcoding

Based on the results of the diagnostic PCR, seven samples were selected for further metabarcoding analysis. The metabarcoding analysis resulted on average in 25,781 reads per sample (Table 2) of which only 8% belonged to metazoan taxa. The most dominant taxa are non-metazoan: fungi and Archaeplastida (i.e., algae). The control samples

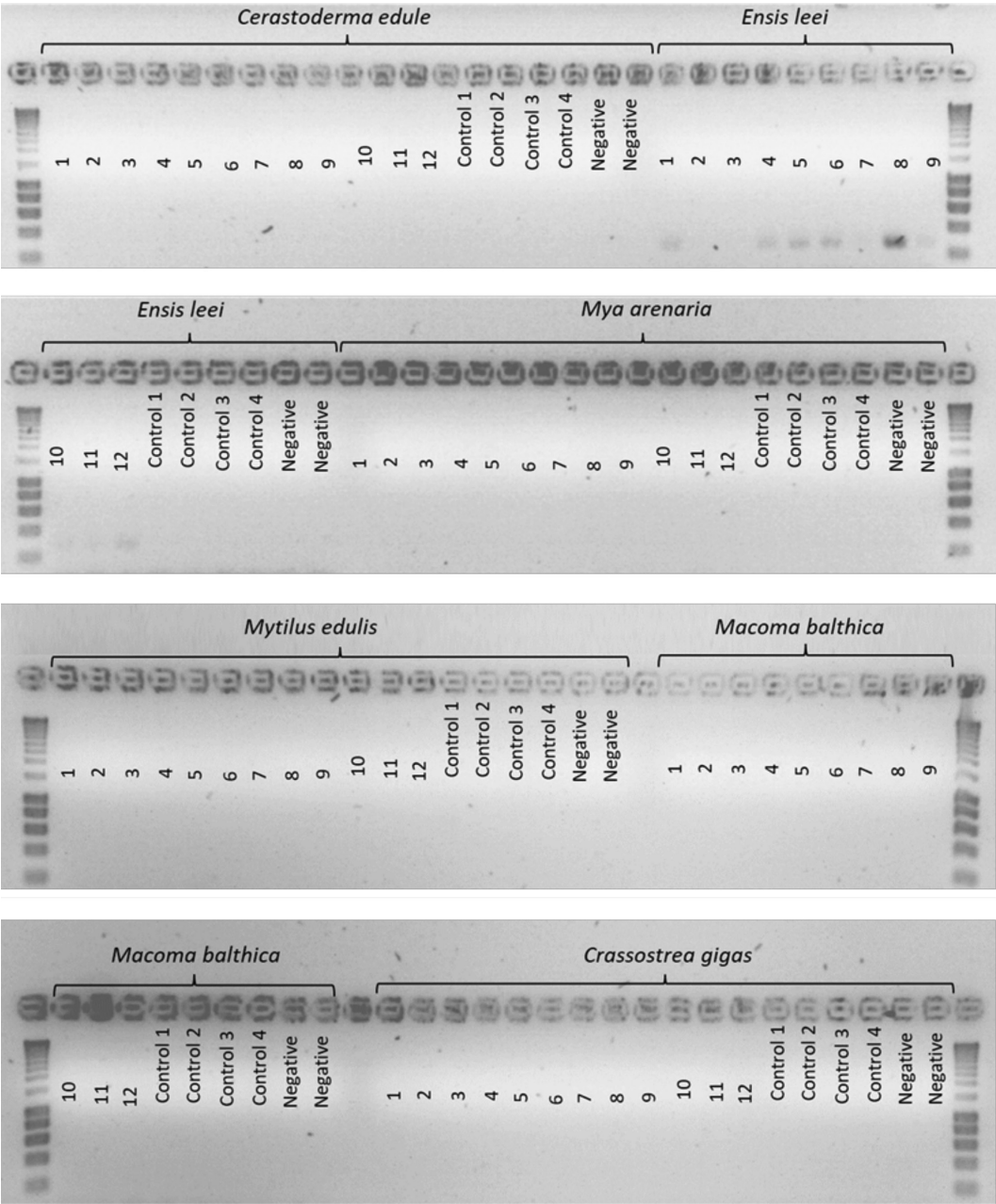


Figure 3. Results of the diagnostic PCR on gel. Numbers refer to the subsamples of the scats. “Controls” are PBS extraction controls, and “Negatives” are PCR negatives. Note that only bands for the razor clam (*Ensis leei*) are obtained.

had much lower read numbers—973 on average. The PBS control and extraction control both had reads assigned to metazoan taxonomic groups, whereas only non-metazoan taxa were found in the PCR control. Sequencing of the positive control containing the three bivalve species nicely

detected these three species, indicating a correct functioning of the test.

Focusing on metazoan taxa only, we found seven different phyla in the walrus scat samples (Table 2). Again, the razor clam was the only mollusk found in the metabarcoding analysis matched

Table 2. Metazoan community composition of scat samples in percentages of metazoan reads (phylum/family/genus)

Taxonomic group		Terschelling			Den Helder				Control		
Phylum	Family/Genus	1	2	4	6	8	9	11	PBS	Ext.	PCR
Total reads		13,475	47,248	23,961	43,138	38,932	9,226	4,993	1,952	383	584
Metazoan reads		268	204	1,135	1,173	5,088	6,495	343	525	343	0
		(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)
Annelida	Arenicolidae	0	0	0	0	5	0	0	0	0	0
	Cirratulidae	0	0	21	0	0	0	0	0	0	0
	Lumbrineridae	0	0	0	0	3	0	0	9	0	0
	Oligochaeta	0	0	0	0	0	0	0	32	0	0
	Orbiniidae	0	0	0	0	0.5	0.5	0	28	0	0
	Spionida	0	0	0	13	0	0	0	0	0	0
Arachnida		7	100	28	0	28	0	0	0	0	0
Arthropoda	Copepoda	0	0	0	10	2	88	0	0	1	0
	Crangon	23	0	0	0	0	0	0	0	0	0
Cnidaria		0	0	0	5	0	0	0	0	0	0
Echniodermata	Ophiurida	0	0	0	0	0	0	0	31	0	0
Nematoda		34	0	20	10	0	0	0	0	0	0
Mollusca	<i>Ensis</i>	36	0	31	62	62	12	1	0	0	0

with the diagnostic PCR. It was found in all scat subsamples except for sample 2. This sample also had the lowest number of metazoan reads and no visible band in the diagnostic PCR. On average, over the seven scat samples analyzed, razor clam accounted for 29% of the metazoan reads. Other metazoan taxa found in multiple samples were nematodes, copepods, and arachnida.

Discussion

In the walrus fecal samples collected in the Netherlands, only the Atlantic razor clam was identified as potential prey. To our knowledge, this is the first time this species was found in the walrus diet. Furthermore, on one occasion, the animal was observed from the coast near Den Helder diving and spitting out empty razor clam shells as she surfaced (“Rare Sighting of Walrus . . .,” 2021 [YouTube video]; Figure 2D; see the supplemental video for this article in the “Supplemental Material” section of the *Aquatic Mammals* website). The scat samples were collected with an interval of 14 d. Given the lack of variation in the

results, it is likely that these generally represent the diet of this walrus in this area.

The razor clam, native to the Northwest Atlantic coasts, recently invaded the Eastern Atlantic, with the first confirmed record from the German Bight in 1979 (Von Cosel et al., 1982). In some areas, including the Dutch coastal waters, this relatively large bivalve has grown to be the most abundant bivalve species occurring in dense aggregations of occasionally over 1,000 individuals/m² (Witbaard et al., 2015). The total stock in Dutch coastal waters may vary annually. In 2020, it was estimated at $5,654 \times 10^6$ kg (Troost et al., 2021), and few commercial ships exploit the stock commercially. It is, therefore, not surprising that the walrus would target such an abundant species.

Sequencing also showed other organisms such as nematodes, spiders, copepods, or microbial species to be present in the scat. It is unlikely, however, given their small size, that these were specifically targeted as prey by the walrus. We assume that these were either accidentally consumed during foraging or ingested by the razor

clams (i.e., secondary prey), or they may even have been on the scat when it was collected.

During her stay in the North Sea, the walrus not only managed to feed herself but also seemed quite tolerant of the relatively high sea surface temperatures. Both in 2021 (when the walrus was in the Wadden Sea) and in 2022 (when it was in southern Norway), sea surface temperatures reached over 20°C (www.bsh.de). This could imply, as suggested in Born et al. (2021), that walruses are actually quite tolerant to higher temperatures and that their known distribution in the Arctic is potentially determined by other factors such as human exploitation and ongoing disturbance (Bosscha Erdbrink & van Bree, 1986).

The observations of walruses in the North Sea and in other more temperate Atlantic waters might not be indicative of aberrant behaviour but could, instead, be indicative of the species expanding back into their former range as suggested in Kovacs et al. (2014). We hypothesize that as the Svalbard and Franz Josef Land walrus stock recovers, visits such as that of this young female walrus might become more frequent. Moreover, the ongoing melting of the Arctic sea-ice alters the walrus's habitat, affecting food accessibility and giving rise to an increased anthropogenic use of the Polar region. Therefore, more animals might be displaced southwards. The ample food availability as a result of the fortuitous invasion of the razor clam might even give rise to walruses being attracted to the area and to return after a first visit. It would therefore be wise, as suggested by Levin & Vincent (2023), to draw up adequate management plans to avoid situations where the shooting of a visiting walrus is deemed the only option.

Note: The supplemental video for this short note is available in the “Supplemental Material” section of the *Aquatic Mammals* website: <https://www.aquatic-mammalsjournal.org/supplemental-material>.

Acknowledgments

We would like to thank quite a few people who helped us in this study. First of all, for the search and collecting of the scats, Tini Tichelaar, Nils Greskewitz, and Annemarie van den Berg in Harlingen; Wouter Jan Strietman and Ies Akkerdaas on Terschelling; and Commander Jeroen van Zanten in Den Helder. Cor Sonneveld kindly helped with the transportation; Annalisa Delre performed the DNA extractions and diagnostic PCRs; and Harry Witte and Wietse Reitsma performed parts of the bioinformatic analyses. Finally, thanks to Eric Hercules for providing a clean space to extract the samples; Loran Kleine Schaars for helping us with

logistics; Sander Holthuijsen and Rob Witbaard for their advice on shellfish; and Jessica Schop and Geert Aarts for helping with the map and general support.

Literature Cited

- Aae, R. (2022). *Freja the 2019-2022 young female walrus* [sic]. Google My Maps.
- Abdala Asbun, A., Besseling, M. A., Balzano, S., van Bleijswijk, J. D. L., Witte, H. J., Villanueva, L., & Engelmann, J. C. (2020). Cascabel: A scalable and versatile amplicon sequence data analysis pipeline delivering reproducible and documented results. *Frontiers in Genetics*, 11, 489357. <https://doi.org/10.3389/fgene.2020.489357>
- Born, E. (1988). Hvalrosstrefere i Europa [Walrus stragglers in Europe]. *Flora og Fauna*, 94, 9-14.
- Born, E. W. (1992). *Odobenus rosmarus* Linnaeus, 1758 – Walross [*Odobenus rosmarus* Linnaeus, 1758 – Walrus]. In R. Duguay & D. Robineau (Eds.), *Handbuch der saugeriere Europar: Band 6: Meersauger, Teil 11: Robben – Pinnipedia* [Handbook of European mammals: Vol. 6. Sea mammals, Part 11: Seals – Pinnipedia] (pp. 268-299). AULA-Verlag, Wiesbaden.
- Born, E. W., & Wiig, Ø. (2021). Chapter 3: Ecology and behavior of Atlantic walruses. In X. Keighley, M. T. Olsen, P. Jordan, & S. Desjardins (Eds.), *The Atlantic walrus* (pp. 39-76). Academic Press. <https://doi.org/10.1016/B978-0-12-817430-2.00001-7>
- Born, E. W., Wiig, Ø., & Olsen, M. T. (2021). Chapter 13: The future of Atlantic walrus in a rapidly warming Arctic. In X. Keighley, M. T. Olsen, P. Jordan, & S. Desjardins (Eds.), *The Atlantic walrus* (pp. 309-332). Academic Press. <https://doi.org/10.1016/B978-0-12-817430-2.00012-1>
- Bosscha Erdbrink, D., & van Bree, P. (1986). Fossil *Odobenidae* in some Dutch collections (Mammalia, Carnivora). *Beaufortia*, 36(2), 13-33.
- Brasseur, S., & Evans, P. (2022). Working Group on Marine Mammal Ecology (WGME), 4(61).
- Callahan, B. J., McMurdie, P. J., Rosen, M. J., Han, A. W., Johnson, A. J. A., & Holmes, S. P. (2016). DADA2: High-resolution sample inference from Illumina amplicon data. *Nature Methods*, 13(7), 581-583. <https://doi.org/10.1038/nmeth.3869>
- Caporaso, J. G., Kuczynski, J., Stombaugh, J., Bittinger, K., Bushman, F. D., Costello, E. K., Fierer, N., Peña, A. G., Goodrich, J. K., & Gordon, J. I. (2010). QIIME allows analysis of high-throughput community sequencing data. *Nature Methods*, 7(5), 335-336. <https://doi.org/10.1038/nmeth.f.303>
- Chiacchio, M., & Aae, R. (2024). 3000 leagues under the sea: The voyages of vagrant walruses (*Odobenus rosmarus*) in temperate Europe. *Polar Biology*, 47, 179-185. <https://doi.org/10.1007/s00300-023-03218-5>
- Fisher, K. I., & Stewart, R. E. A. (1997). Summer foods of Atlantic walrus, *Odobenus rosmarus rosmarus*, in north-

- ern Foxe Basin, Northwest Territories. *Canadian Journal of Zoology*, 75(7), 1166-1175. <https://doi.org/10.1139/z97-139>
- Gjertz, I., & Wiig, Ø. (1992). Feeding of walrus *Odobenus rosmarus* in Svalbard. *Polar Record*, 28(164), 57-59. <https://doi.org/10.1017/S0032247400020283>
- Gjertz, I., Henriksen, G., Øritsland, T., & Wiig, Ø. (1993). Observations of walruses along the Norwegian coast 1967-1992. *Polar Research*, 12(1), 27-31. <https://doi.org/10.3402/polar.v12i1.6700>
- Klunder, L., van Bleijswijk, J. D. L., Kleine Schaars, L., van der Veer, H. W., Luttkhuizen, P. C., & Bijleveld, A. I. (2022). Quantification of marine benthic communities with metabarcoding. *Molecular Ecology Resources*, 22(3), 1043-1054. <https://doi.org/10.1111/1755-0998.13536>
- Kovacs, K. M., Aars, J., & Lydersen, C. (2014). Walruses recovering after 60+ years of protection in Svalbard, Norway. *Polar Research*, 33. <https://doi.org/10.3402/polar.v33.26034>
- Levin, A., & Vincent, S. (2023). The life and death of Freya the walrus: Human and wild animal interactions in the Anthropocene era. *Animals*, 13(17), 2788. <https://www.mdpi.com/2076-2615/13/17/2788>; <https://doi.org/10.3390/ani13172788>
- Palomares, F., Godoy, J. A., Páriz, A., O'Brien, S. J., & Johnson, W. E. (2002). Faecal genetic analysis to determine the presence and distribution of elusive carnivores: Design and feasibility for the Iberian lynx. *Molecular Ecology*, 11(10), 2171-2182. <https://doi.org/10.1046/j.1365-294X.2002.01608.x>
- Philippart, C. J. M., van Bleijswijk, J. D. L., Kromkamp, J. C., Zuur, A. F., & Herman, P. M. J. (2014). Reproductive phenology of coastal marine bivalves in a seasonal environment. *Journal of Plankton Research*, 36(6), 1512-1527. <https://doi.org/10.1093/plankt/fbu073>
- Philippart, C. J. M., Amaral, A., Asmus, R., van Bleijswijk, J., Bremner, J., Buchholz, F., Cabanellas-Reboredo, M., Catarino, D., Cattijisse, A., Charles, F., Comtet, T., Cunha, A., Deudero, S., Duchêne, J.-C., Fraschetti, S., Gentil, F., Gittenberger, A., Guizien, K., Gonçalves, J. M., Guarnieri, G., . . . Zuur, A. F. (2012). Spatial synchronies in the seasonal occurrence of larvae of oysters (*Crassostrea gigas*) and mussels (*Mytilus edulis galloprovincialis*) in European coastal waters. *Estuarine, Coastal and Shelf Science*, 108, 52-63. <https://doi.org/10.1016/j.ecss.2012.05.014>
- Pruesse, E., Quast, C., Knittel, K., Fuchs, B. M., Ludwig, W., Peplies, J., & Glöckner, F. O. (2007). SILVA: A comprehensive online resource for quality checked and aligned ribosomal RNA sequence data compatible with ARB. *Nucleic Acids Research*, 35(21), 7188-7196. <https://doi.org/10.1093/nar/gkm864>
- Rare sighting of walrus off Den Helder (the Netherlands). (2021). *YouTube* [video]. <https://www.youtube.com/watch?v=MuzsEfRD0M>
- Sinniger, F., Pawlowski, J., Harii, S., Gooday, A. J., Yamamoto, H., Chevaldonné, P., Cedhagen, T., Carvalho, G., & Creer, S. (2016). Worldwide analysis of sedimentary DNA reveals major gaps in taxonomic knowledge of deep-sea benthos. *Frontiers in Marine Science*, 3, 92. <https://doi.org/10.3389/fmars.2016.00092>
- Troost, K., Van Asch, M., Brummelhuis, E., Van den Ende, D., Van Es, Y., Perdon, K., Van der Pool, J., van Zweeden, C., & Van Zwol, J. (2021). *Schelpdierbestanden in de Nederlandse kustzone, Waddenzee en zoute deltawateren in 2020* [Shellfish in the Dutch coastal zone, Waddenzee and delta waters in 2020]. Centrum voor Visserijonderzoek (CVO). 98 pp.
- van Bree, P. J. H. (1997). On extralimital records of hooded seals, *Cystophora cristata* (Erxleben, 1777), on the western European continental coast. *Zeitschrift für Säugetierkunde*, 62, 182-186.
- van Deinse, A. B. (1964). De fossiele en recente walrussen van Nederland [The recent fossils of walruses from the Netherlands]. *Zoologische Mededelingen*, 39, 187-206.
- Vibe, C. (1950). The marine mammals and the marine fauna in the Thule district (northwest Greenland) with observations on ice conditions in 1939-41: Trichinosis in Arctic mammals. *Meddelelser om Grønland*, 150(6), 93-97.
- Von Cosel, R., Dörjes, J., & Mühlenhardt-Siegel, U. (1982). Die amerikanische Schwertmuschel *Ensis directus* (Conrad) in der Deutschen Bucht: I. Zoogeographie und Taxonomie im Vergleich mit den einheimischen Schwertmuschel-Arten [The American jackknife clam *Ensis directus* (Conrad) in the German Bight: I. Zoogeography and taxonomy in comparison with the native jackknife and razor clams]. *Senckenbergiana Maritima: Wissenschaftliche Mitteilungen der Senckenbergischen naturforschenden Gesellschaft*, 14(3-4), 147-173.
- Wang, Q., Garrity, G. M., Tiedje, J. M., & Cole, J. R. (2007). Naive Bayesian classifier for rapid assignment of rRNA sequences into the new bacterial taxonomy. *Applied and Environmental Microbiology*, 73(16), 5261-5267. <https://doi.org/10.1128/AEM.00062-07>
- Witbaard, R., Duineveld, G. C. A., Bergman, M. J. N., Witte, H. I. J., Groot, L., & Rozemeijer, M. J. C. (2015). The growth and dynamics of *Ensis directus* in the near-shore Dutch coastal zone of the North Sea. *Journal of Sea Research*, 95, 95-105. <https://doi.org/10.1016/j.seares.2014.09.008>
- Zhang, J., Kobert, K., Flouri, T., & Stamatakis, A. (2014). PEAR: A fast and accurate Illumina Paired-End reAd mergeR. *Bioinformatics*, 30(5), 614-620. <https://doi.org/10.1093/bioinformatics/btt593>