A vagrant walrus (Odobenus rosmarus) in Finland

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In July 2022, a vagrant female Atlantic walrus (*Odobenus rosmarus rosmarus*) was seen on the south coast of Finland. The same individual, which was called 'Stena' in the international press, had previously been observed in the waters of several other European countries along the North and Baltic Seas. By the time the animal reached Finnish waters it was in poor condition and did not survive a rescue attempt. Post-mortem investigation revealed that the animal was malnourished and its digestive tract was almost empty, but trace amounts of DNA from bivalves and other aquatic invertebrates could be recovered. However, apart from minor age-related ailment and superficial skin wounds, the walrus showed no obvious signs of illness or injuries. Dental wear suggested that the animal was at least 20 years old. Its body and cranial measurements, including tusk length, were well above the average size for a female Atlantic walrus. Mitochondrial DNA supported its origin in the eastern Barents Sea populations. The specimen was mounted and put on display in the Natural History Museum, Helsinki. This is the first confirmed free-ranging walrus observation in the northern part of the Baltic Sea and Finland.

Introduction

The walrus (*Odobenus rosmarus* Linnaeus, 1758) is one of the largest pinnipeds. It has a circumpolar Arctic distribution and the species is divided into two subspecies with geographically distinct ranges: the Atlantic (*O. r. rosmarus*) and

the Pacific (*O. r. divergens* Illiger, 1815) walruses (Fay 1985, Kastelein 2009). The Laptev Sea walrus population, sometimes treated as another subspecies, is now considered to be part of the Pacific taxon on the basis of genetic evidence (Lindqvist et al. 2009, 2016). The Pacific walrus is on average larger than the Atlantic, but there is considerable overlap in body size (Wiig & Gjertz 1996, Garlich-Miller & Stewart 1998). The Pacific population is currently estimated to comprise more than 200,000 individuals (Beatty et al. 2022), whereas the Atlantic population is 35,000-40,000 walruses, largely because of historical persecution by humans. Atlantic walruses have disappeared from many parts of their former range, such as Canada's Maritime Provinces and Iceland (McLeod et al. 2014, Higdon & Stewart 2018, Keighley et al. 2019, 2022, Garde & Hansen 2021). However, thanks to conservation measures, in recent years walruses have increased in some parts of their distribution area, such as Svalbard (Lydersen et al. 2008, Kovacs et al. 2014). Today, populations of Atlantic walrus are found in north-eastern Canada, Greenland, Svalbard, and the western Russian Arctic including Franz Josef Land and Novaya Zemlya (Wiig et al. 2014, Garde & Hansen 2021).

Vagrant walruses are sometimes seen far south of the species' usual distribution range. In Europe, such sightings are relatively frequent off Norway (Lund 1954, Bruun et al. 1968, Born 1988, Gjertz et al. 1993, Kubny 2022), and in the British Isles (Ritchie 1921, Anonymous 1926, Venables & Venables 1955, Hardy 1959, Cotton 2007, Findlay 2018, Hager 2021, Mullard 2022, Osborne 2023, Wong 2023, Chiacchio & Aae 2024). The southernmost European walrus observations are from southern France and northern Spain (Duguy 1986, Nores & Pérez 1988, Bryant 2021). Other records are from Belgium, the Netherlands, Germany, Denmark, and Sweden (Jensen 1927a, b, Lönnberg 1927, 1940, Redeke 1927, Mohr 1940, Hanström 1943, van Bree 1977, Joensen 1977, Cadée et al. 1982, Reijnders 1982, Mathiasson 1983, Born 1988, Wendehög & Berdenius 2003, Born et al. 2014, Chiacchio & Aae 2024). Because walruses are easy to recognise, conspicuous, and often relatively unbothered by human observers, vagrant individuals attract lots of attention from media and the public, allowing detailed documentation of their movements. Vagrant walruses often also receive affectionate nicknames and cases include 'Wally', who between March and September 2021 visited Ireland, the UK, France, Spain, and Iceland (Bryant 2021, Hager 2021, Mullard 2022); 'Freya', who between October 2021 and August 2022 visited the Netherlands, Germany, the UK, Denmark, Sweden, and Norway (Fogh-Andersen 2022, Witten 2022b); and 'Thor', who between November 2022 and February 2023 visited the Netherlands, France, the UK, and Iceland (Osborne 2023, Wong 2023).

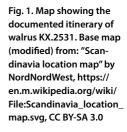
Initial observations and the walrus' itinerary

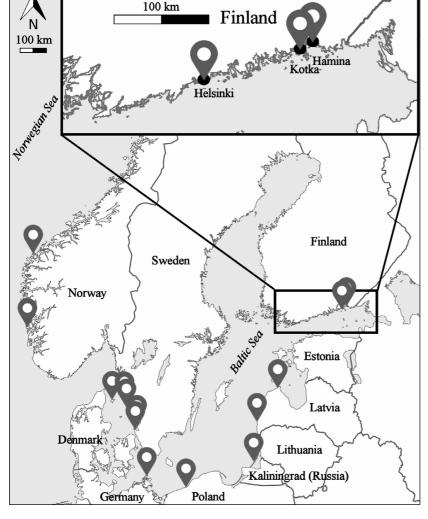
On 14 March 2022, an adult walrus was seen on the island of Vigra in Giske, Norway (Google Maps 2022). It received the name 'Stena' by the media in Norway, and although the animal later received other names in other countries, the one given to it originally became the internationally best known. 'Stena's' visit to European waters partially overlapped in time with that of 'Freya', mentioned above. However, these walruses could be identified as different individuals based on unique size and shape of tusks (Witten 2022a). 'Stena' stayed on the Norwegian coast for several weeks, gradually moving southwards (Fig. 1). It was seen in Denmark on 16 May, and on the south-western coast of Sweden on 4 June. On 16 June, the walrus had entered the Baltic Sea, where it was seen off Rügen, Germany. At this stage, the animal appeared to be in good health (Anonymous 2022). The walrus followed the Baltic Sea's eastern coastline and was seen in Poland on 23 June, in Kaliningrad, Russia, on 30 June, and then in Latvia on two occasions. In Latvia, it was first spotted on 3 July on a beach off the city of Liepāja (Pilāts 2022). It was next seen on 7 July, further north in Slītere National Park, where it stayed circa 12 hours lying on the beach. National park rangers observed that the walrus had a fresh small wound of unknown origin in the skin of the lower back.

On 15 July, the walrus came on land by a small boat harbour in Hamina, a town on the southern coast of Finland. The walrus became the object of an extraordinary amount of public interest. The animal's movements were followed closely in the Finnish media, and many news reports and articles were written about it (Valtanen 2023). The walrus remained ashore intermittently in Hamina for almost two days before it returned to the sea and swam away. It next came ashore in the town of Kotka, circa 18 km west of Hamina, after having briefly become entangled in a fyke net and capsizing a fisherman's boat. In the morning on 19 July, the walrus was found to have travelled from the top of a narrow bay circa 1.5 km inland along a small watercourse, and then about 50 m by land across suburban backyards, finally ending up in a small patch of forest near a house on private property, where it remained (Karvinen 2022).

Rescue attempt

The walrus was mostly sleeping, and only occasionally adjusted its body position or raised its head to observe the surroundings (Fig. 2a). It was not observed to defecate. On its ventral side, the animal's skin had several small superficial wounds, which attracted flies. These wounds probably resulted from its long crawl across dry land, over sharp rocks and various metal objects lying on the ground. At this point, the police had cordoned off the area and only rescue personnel and veterinarians were allowed to approach the animal. An attempt was made to rescue the walrus and transport it to Korkeasaari Zoo in Helsinki. This required anaesthetizing the animal to enable its safe handling and transport. In marine mammals, anaesthetics can trigger a dive reflex that causes life-threatening bradycardia and apnoea (Brunson 2014, Mulcahy & Fravel 2018). In the





present case, the animal was also in a poor physical condition, which increased the risk of anaesthesia-related complications. The animal was lying in a depression in a forest patch and it was estimated that the rescue operation would take hours. Hence, drugs that are suitable for short anaesthesia were not considered (Ølberg et al. 2017).

The animal's size presented an additional challenge. Although the walrus was emaciated, its body mass was still considerable and estimated to be circa 700 kg. The animal was initially sedated with a combination of Zoletil Forte Vet (1:1 tiletamine as hydrochloride and zolazepam as hydrochloride) 1 mg/kg, ketamine (Ketador, Richter Pharma AG, Austria) 2 mg/kg, medetomidine HCl (Medetomidine HCl 30 mg/ml, extem-

poraneously compounded by Yliopiston apteekki, Finland) 0.01 mg/kg, and atropine sulphate (Atropin 1 mg/ml, Takeda Austria GmbH, Austria) 0.03 mg/kg. This combination was a modification of walrus anaesthesia described in Brunson (2014). Drugs were administered intramuscularly into the upper hindquarter with two 20 ml plastic dart syringes with 2 × 60 mm plain needles, which were darted with a CO₂ injection pistol. After the initial dose, the animal got severe apnoea and 300 mg doxapram was hand-injected. This stimulated respiration but also affected the anaesthesia level, making it more superficial. An additional 6.3 mg medetomidine, 500 mg ketamine, and 150 mg Zoletil were hand-injected to secure the safety of the people handling the ani-



Fig. 2. The walrus in Kotka, Finland, on 19 July. a) The animal resting/sleeping in a forest patch near a suburban house before it was sedated. b) The eyes of the walrus were covered to keep it calm in case it would awake too soon from anaesthesia. Note the animal's emaciated condition.

Photos: Maiju Lanki.

mal. The whole procedure from the first dart to the injection of antidote took approximately 2.5 hours. With the help of a tractor, the animal was lifted with load straps onto a rug; next, it was carried to a transport crate in a lorry (Fig. 2b). Then, 15 mg of atipamezole HCl (Revertor, CP-Pharma Handelsges. mbH, Germany) was hand-injected before the transport to Helsinki started. The walrus however died during transport, shortly after midnight on 20 July.

Post-mortem examination and necropsy

The carcass was taken to the facilities of the Finnish Food Authority in Helsinki for post-mortem analysis. After initial external inspection, it was weighed, measured, and skinned. Next, a necropsy was performed, which included dissection and the taking of samples from all major internal organs. These tissue samples were processed and histologically examined in a routine manner. Bacteriological, virological, parasitological, and faecal DNA samples were taken. In addition to the skin, the bones of the walrus were removed for preservation. The animal's cranium was sawed open during the necropsy to extract the brain.

The necropsy confirmed that the female walrus was starving and in poor body condition. Its subcutaneous blubber layer was very thin and the fat reserves around internal organs and in bone marrow were virtually absent. Although the body dimensions were large (see below), at the time of its death it weighed only 597 kilograms. In addition to fresh small wounds obtained during the animal's recent overland travels, the skin contained a few old scars. Several specimens of the walrus-specific louse Antarctophthirus trichechi, both adults and 3rd instar nymphs (see Scherf 1963, and Leonardi & Palma 2013 for identification), were collected from the skin (Fig. 3). A tick (Ixodes ricinus) had also attached itself to the skin while the walrus was ashore. The walrus' lungs were heavily congested and oedematous. The gastrointestinal tract was almost empty, and no macroscopic food material was present in the stomach. Small gastric ulcers were observed in the stomach: these were most likely stress-related. One endoparasitic nematode, the seal worm or cod worm Pseudoterranova decipiens, was found in the stomach. In addition, an acute bacterial haemorrhagic cystitis caused by uropathogenic Escherichia coli was detected in the urinary bladder. The uterus and ovaries were normal for an old, non-pregnant female mammal. The existence of a corpus albicans but no corpus luteum indicates that the animal had ovulated, and might have been pregnant and given birth during previous reproductive cycles, but not during the current cycle (Garlich-Miller & Stewart 1999). Many organs showed signs of minor agerelated ailments, including small benign tumours and unspecific degeneration. Tests for Avian Influenza and SARS-CoV2 virus were negative. No evidence of Brucella, Campylobacter, Salmonella, Yersinia or Leptospira bacterial infections were detected. Parasitological and coprological examinations for Toxoplasma gondii, Trichinella sp. and gastrointestinal parasites yielded negative



Fig. 3. A female walrus louse Antarctophthirus trichechi collected during necropsy. Scale bar 1 mm. Photo: Jaakko Pohjoismäki.

results. Based on necropsy, the cause of death of the walrus was acute cardiac failure, contributed to by emaciated body condition and stress, and most likely triggered by anaesthesia.

NGS analysis of faecal DNA

For information on the diet and on the intestinal microbiome of the walrus specimen, metabarcoding analysis of faecal DNA was performed on two samples, one collected pre-mortem in Latvia, and another collected post-mortem in Finland. The Latvian sample was collected from a beach in Slītere National Park on 8 July, several hours after the animal had left the locality, whereas the Finnish sample was collected from the intestine. The analyses were carried out by Bioname (www. bioname.fi). DNA was extracted by using two optional apporaches: with Zymo Research Zymo Quick-DNA Fecal/Soil Microbe Miniprep kit (cat nr: D6010, USA) without toxic beta-mercaptoethanol, and with Macherey-Nagel Nucleo-Spin Stool Kit (ref 740472.250, Germany). The walrus faecal DNA was amplified by using three complementary primer pairs targeting the metazoan mitochondrial COI gene: ANML' LCO1490+CO1-CFMRa (Folmer et al. 1994, Jusino et al. 2019), 'fwh' fwhF2+fwhR2n (Vamos et al. 2017), and 'Leray' mlCOIintF+jgHCO2198 (Leray et al. 2013, Geller et al. 2013), one primer pair specifically targeting fish mitochondrial 12S rRNA gene (Teleo-12S-F+Teleo-12S-R; Martínez-Abraín et al. 2020), and one primer pair targeting bacterial 16S sRNA gene (515FB; Parada et al. (2016), modified from Walters et al. (2016); 806RB; Apprill et al. (2015), modified from Caporaso et al. (2011)). Locus-specific PCR setup followed Kankaanpää et al. (2020) and library preparation followed Vesterinen et al. (2016). Next-Generation Sequencing (NGS) was done on partial Illumina NovaSeq6000 SP Flowcell 2x250bp (Illumina Inc., USA) run by the Turku Centre for Biotechnology, Finland. Our bioinformatics pipeline followed Kaunisto et al. (2020).

Only few metazoan taxa were found in the faecal samples in the comprehensive NGS analysis (Table 1). We converted the absolute number of reads in each sample to relative read abundances (RRA; Deagle et al. 2019). In the Latvian sam-

ple, the most abundant taxa were a copepod *Acartia bifilosa* (97 % of all the reads), and two marine bivalves, *Kurtiella bidentata* (17.6 % of fwh) and the soft-shell clam *Mya arenaria* (1.9 % of fwh). The sample collected in Latvia also included traces of dipteran insects, presumably a result of contamination from the environment prior to the sampling. The Finnish sample contained traces of a planktonic freshwater cladoceran *Leptodora kindtii* (100 % of the filtered reads for ANML and Leray primer sets, and 96 % for fwh) and a freshwater bivalve, the duck mussel *Anodonta anatina* (3.4 % of the reads). No traces of fish were found in either sample.

The most common bacterial taxa in the Latvian sample were *Lactobacillales* (22 % of the reads), *Psychrobacter* (21 %), *Ignatzschineria* (19 %), *Peptacetobacter* (17 %), and *Glutamicibacter* (9 %). The Finnish sample was less diverse and was dominated by *Peptacetobacter* (67 % of the reads) and *Collinsella* (~5.5 %); other microbiont taxa were present with a smaller than 5 % proportion of the reads (Fig. 4).

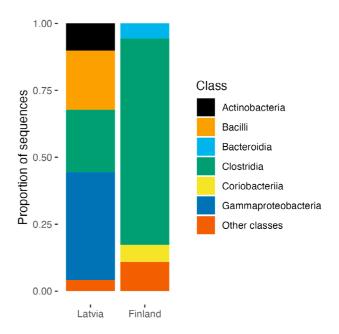


Fig. 4. Comparison of the bacterial composition in faecal samples collected from KX.2531 in Latvia and Finland. Bacterial classes were identified by molecular 16S rRNA analysis. Classes that made up less than 0.05 % of the total proportion are pooled ("Other classes"). ZOTU or genus-wise listing of results is available from author EJV on request.

Table 1. Metabarcoding results of walrus faecal DNA. Metazoan taxa identified in the Latvian and Finnish samples from KX.2531 separately for each of the three primer pairs. 'Count' refers to the number of filtered final sequences assigned to each taxa. 'RRA' refers to relative read abundance, that is, the proportion of sequences assigned to the taxa from the total number of sequences in the sample.

Sample	Phylum	Class	Order	Family	Species	Count	RRA			
ANML: LCO1490+CO1-CFMRa										
Latvia	Arthropoda	Copepoda	Calanoida	Acartiidae	Acartia bifilosa	40272	0.97			
Latvia	Arthropoda	Insecta	Diptera	Anthomyiidae	Fucellia griseola	677	0.02			
Latvia	Arthropoda	Insecta	Diptera	Tipulidae	Nephrotoma lundbecki	551	0.01			
Latvia	Arthropoda	Copepoda	Calanoida	Acartiidae	Acartia tonsa	86	<0.01			
Finland	Arthropoda	Branchiopoda	Haplopoda	Leptodoridae	Leptodora kindtii	6631	1.00			
Leray: mlCOlintF+jgHCO2198										
Latvia	Arthropoda	Copepoda	Calanoida	Acartiidae	Acartia bifilosa	14014	0.81			
Latvia	Mollusca	Bivalvia	Galeommatida	Lasaeidae	Kurtiella bidentata	3053	0.18			
Latvia	Mollusca	Bivalvia	Myida	Myidae	Mya arenaria	326	0.02			
Finland	Arthropoda	Branchiopoda	Haplopoda	Leptodoridae	Leptodora kindtii	13921	1.00			
fwh: fwhF2+fwhR2n										
Latvia	Arthropoda	Insecta	Diptera	Anthomyiidae	Fucellia griseola	186	0.60			
Latvia	Arthropoda	Collembola	Symphypleona	Dicyrtomidae	Dicyrtoma fusca	123	0.40			
Finland	Arthropoda	Branchiopoda	Haplopoda	Leptodoridae	Leptodora kindtii	56008	0.97			
Finland	Mollusca	Bivalvia	Unionida	Unionidae	Anodonta anatina	2000	0.03			

Walrus mitochondrial DNA and specimen origins

To verify the identity and phylogeographic affinities of the walrus specimen, two marker fragments of its mitochondrial genome were sequenced from DNA extracted from muscle tissue: the *COI* gene barcode region (622 bp), and 407 bp of the hypervariable control region (CR), for which extensive reference material is available in public databases (Lindqvist et al. 2008, Andersen et al. 2017). The sequences were deposited in GenBank with the accession numbers OR883405, OR886458, and aligned with available reference data.

The general features of global walrus mtDNA variation include a basic subdivision between the Atlantic and Pacific subspecies, and further subdivision of the Atlantic walrus into an exclusively NW Atlantic clade, and an amphi-Atlantic clade (Lindqvist et al. 2008, Ruiz-Puerta et al. 2023). The *COI* data attributes this walrus specimen to the latter lineage, but allows for no further resolution. The CR marker is more polymorphic, with 40 different haplotypes in the data of 212 NE Atlantic individuals in Andersen et al. (2017). There are three current subpopulations of the NE Atlantic walrus, those of East Greenland, Svalbard-Franz Josef Land, and the Pechora Sea (including the Kara Sea and Novaya Zemlya), respectively (Garde & Hansen 2021). Of these, the East Greenland subpopulation has a characteristic dominant haplogroup, which is rare elsewhere (haplogroup overlap circa 11 %). This specimen falls within the remaining, predominantly European or Eastern Barents Sea diversity (Fig. 5). It represents haplotype Atl 22, which has previously been recorded both from Franz Josef Land and Pechora Sea walrus specimens (Andersen et al. 2017). Whereas genetic differences between the Svalbard-Franz Josef Land populations and the Pechora Sea populations can be seen when using a larger set of markers, the mitochondrial marker alone cannot separate those provenances.

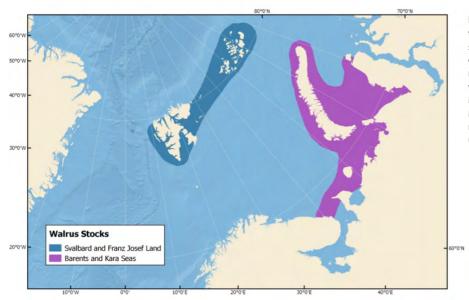


Fig. 5. Distribution of the Svalbard–Franz Josef Land and the Southern Barents Sea (Pechora Sea) and Kara Sea walrus populations. Map by North Atlantic Marine Mammal Commission (NAMMCO); used with permission.

Body and skull measurements

The dorsal curvilinear head-body length of the walrus was 328 cm. The 'standard length' (Scheffer 1967), i.e. the straight-line distance from snout to tip of tail, with the animal lying on its back, was not measured. However, according to Mansfield (1958:107), walrus standard length corresponds to 90 % of the dorsal curvilinear length measurement, and the estimated standard length of the specimen would then be 295 cm. This means that its head-body length was large for a female Atlantic walrus (Table 2). Tail length was not measured from the fresh carcass; however, according to data by Loughrey (1959), tail length in eight female Atlantic walruses was circa 2.67 % of head-body standard length. Thus, the specimen's estimated tail length was circa 7.9 cm.

Several measurements of the skull were taken and compared with measurements published in the literature (Table 2; for definitions of the measurements, see Loughrey 1959, Scheffer 1967, and McLeod et al. 2014). The cranial measurements confirmed that the specimen was large for a female Atlantic walrus. There were no visible injuries in the cranium, but the molariform teeth were heavily worn (Fig. 6). The tusks were long for a female walrus (Fig. 7). Their exposed curvilinear lengths, i.e. measured from the edge of the tooth socket along the length of the outer curve but excluding the root (the "clinical crown" of Table 2. Body and cranial measurements of the walrus KX.2531 compared with data on female Atlantic walrus from the literature. Weight is in kilograms (kg), other measurements are in centimetres (cm). Tusk length refers to the curvilinear length of the exposed crown. Note that the head-body length and tail length of KX.2531 are estimates; see text for details. Sources: a = Allen 1880; b = Pedersen 1936; c = Mansfield 1958; d = Loughrey 1959; e = Born 1992; f = Knutsen & Born 1994; g = Heptner et al. 1996; h = Garlich-Miller & Stewart 1998.

	KX.2531	range	mean	sources
weight	597	484-808	611	d, f, h
head-body length	295	229-305	267	c, d, e, f, h
tail length	7.90	5.00-9.00	6.10	d
condylobasal length	33.0	23.8-37.3	30.6	a, d, g
zygomatic width	22.3	16.1–25.7	20.4	a, d, g
mastoid width	24.7	19.8–26.2	23.2	a, d
interorbital width	6.89	5.42-7.05	6.06	a, d
rostrum width	15.8	10.0–15.8	13.9	a, d
mandible width	22.8	17.5–23.8	20.9	a, d
tusk length	52.0	8.40-45.0	24.6	a, b, c, d, e, g
upper tooth row	7.42	4.97–7.85	6.26	a, d
lower tooth row	6.55	N/A	N/A	N/A



Fig. 6. Mandible and maxilla of KX.2531, showing molariform tooth rows. Photo: Janne Granroth.



Fig. 7. Lateral view of the skull of KX.2531. Length of metal ruler 30 cm. Photo: Janne Granroth.

Fay 1982:116), were 52.0 cm for the left tusk and 51.5 cm for the right tusk. The total curvilinear lengths of the tusks including the root were 63.6 cm and 62.9 cm, respectively. The tusks showed

relatively little wear, and converged at their tips, which were nearly touching each other; such tusk convergence is typical of female walruses (Allen 1880). No attempt was made to estimate the animal's age based on annual growth layer counts in teeth (Garlich-Miller et al. 1993).

Preservation of the specimen

The Finnish Museum of Natural History decided to preserve the walrus's remains and put the mounted skin on display, whereas the skeleton was to be kept separately in the research collection. The first incision of the skin was made on the right-hand lateral side of the body, as this side would be positioned against the wall and invisible from the viewing side of the mounted animal. To preserve the skin, it was salted, and all muscle and fat tissue were removed. The skin was scoured to remove blood and soluble proteins, shaved to a thickness of circa 1-3 mm, and pickled to acidify it and prevent it from decaying. It was then tanned with Novaltan AL (Zschimmer & Schwarz Chemie GmbH, Germany), and insect-proofed with Eulan SPA 01 (Tanatex Chemicals BV, Netherlands). During the handling of the skin, tatters of epidermis fell off; this was indicative of the fact that the animal had died during the moulting period, which in walruses takes place in the summer (Fay 1985, Kastelein 2009). The enzymatic maceration of the bones with papain (Bauer Handels, Switzerland) followed the protocol in Niederklopfer and Troxler (2001). Bone Maceration Unit MU 1360-2 (Medis Medical Technology GmbH, Germany) was used to carry out the maceration. The bones were degreased with methylene chloride in a Bone Degreasing Unit BDU 1370-100 (Medis Medical Technology GmbH, Germany).

The artificial body, the manikin, was sculpted from polyurethane (Fig. 8a). The soft tissues of the head were modelled onto the skull with oilbased modelling clay (Roma Plastilina, Chavant Clay, USA), and cast in rigid polyurethane foam. The model was fitted with custom-made glass eyes (KL-Glasaugen, Germany) (Fig. 8b). The original tusks were replaced with casts made of PGD polyurethane resin (Creartec Trend-design GmbH, Germany). The skin was fitted onto the manikin and was let dry for three weeks. Patches of skin that had become discoloured during the process were restored by paintbrush with dry acrylic paint. Finally, the 436 whiskers, which had been removed before the processing of the skin began, were each individually re-attached to their original positions (Puolakoski 2024).

The mount with skin (Fig. 9), the skeleton including tusks, frozen muscle tissue samples, as well as DNA extractions thereof, are deposited as preparations in the collections of the Finnish Museum of Natural History, under the stable specimen identifier http://id.luomus.fi/KX.2531 from which their data are openly accessible.

Discussion

Walrus fossils are known from late Pleistocene deposits on the North Sea coast in Denmark and the Netherlands (Møhl 1974, 1985, Post 2005), but there are no known remains of walruses from the northern Baltic Sea region (Ukkonen 2002, Kangas 2018). Prior to 2022, the only well-document-ed record from recent times of a vagrant walrus in the Baltic Sea was an adult that visited the coast of north-eastern Germany in April 1939 (Mohr 1940, Hanström 1943). Interestingly, the female that visited Finland in 2022 ('KX.2531' from here on) is strictly speaking not the first walrus ever seen within the present geographical borders of this country. In 1939, a juvenile walrus, originally captured in Greenland, was kept in Helsinki Zoo

for circa three months. In December, this walrus, named 'Turso', managed to escape into the sea off Helsinki. The inexperienced animal presumably perished quickly, possibly by getting lost under the sea ice and drowning; its remains were never found (Lehtonen 1951, Kettunen 2022). Even if it had not escaped, it is unlikely that 'Turso' would have survived very long, as few European zoos were successful in keeping walruses in the early twentieth century (Svanberg 2010).

As noted, KX.2531 was a very large individual. Its estimated head-body length of circa 295 cm approaches the upper limit of published measurements of female Atlantic walruses. While Heptner et al. (1996:32) provided a markedly higher "maximum body length" of 338 cm for female Atlantic walruses, they did not specify whether they referred to curvilinear or standard length (sensu Scheffer 1967). Assuming that it was the curvilinear measurement, using the correction suggested by Mansfield (1958), i.e. 90 %, would result in a maximum standard length of 304.2 cm, which is closer to the estimate for KX.2531. Pedersen (1936) stated that female Greenland walruses reach head-body lengths of "circa 300 cm", similar to the dimension of KX.2531. Unfortunately, Pedersen (1936) specified neither his method of body length measurement nor the number of individuals his data were based on. In contrast, Mansfield (1958), Loughrey (1959), Born (1992), and Knutsen and Born (1994) all measured standard lengths. Mansfield's data set included 29 female Atlantic walruses, Loughrey's 12, Born's 16, and Knutsen and Born's 34. Of these 75 animals, the largest, an individual from Thule, Greenland, in Born's data set, reached 305 cm. The mean female head-body lengths given by these authors are, respectively, 254 cm, 260 cm, 267 cm, and 269 cm. The large size of KX.2531 is also demonstrated by its cranial measurements. In fact, they all exceed the mean values of published measurements (Table 2). However, the sample sizes for published cranial measurements are smaller than for the head-body measurements.

The curvilinear length of the exposed tusks of KX.2531, circa 52 cm, is also notable. In fact, it is longer than all published comparable tusk length measurements of female Atlantic walruses that we know of. Pedersen (1936) provided a tusk length range of 30–35 cm, and Heptner et al.



Fig. 8. Preparation of the mounted specimen. a) Full-body view of the polyurethane manikin. b) Close-up of the head, with the glass eyes in place. Photos: Ari Puolakoski.



(1996) 27–33 cm. A maximum tusk length of 41.8 cm was reported by Allen (1880) (N = 4), 35.6 cm (N = 27) by Mansfield (1958), 31.4 cm (N = 12) by Loughrey (1959), and 45.0 cm (N = 22) by Born (1992). The tusks of female Pacific walruses are longer. In Fay's (1982) study, the lengths of exposed tusks ("lengths of clinical crown") typically varied between 35 and 55 cm, with a maximum of 68 cm, and the total tusk length was suggested to reach a maximum of 80 cm. Thus, the tusks of KX.2531 were fairly long even by Pacific walrus standards. As the tusks grow through

out the lifetime, their length also testifies that KX.2531 represented the oldest part of the population, plausibly of 20 years or more; walruses can reach an age of up to 40 years in nature (Taylor et al. 2018, Robeck et al. 2022).

The only measurement which was not unusually large was body weight, undoubtedly due to the emaciated state of the specimen. In Loughrey's (1959) data set of five female Atlantic walruses the maximum body weight was 674 kg and the mean 569 kg, which is slightly less than the weight of KX.2531. Likewise, Knutsen and Born (1994) estimated weights of eight females, with a maximum of 808 kg and a mean of 653 kg. From these data it is clear that at the time of its death, KX.2531 was underweight for its size.

Insights to the reasons for the animal's weight loss may be sought by considering the potential food basis during the journey and evidence about actual diet remains in the metabarcoding of faecal and intestinal samples. Walrus feed primarily on bivalve molluscs and on other benthic macroinvertebrates, of which they may consume tens of kilograms per day (Garda et al. 2018). The bivalve mollusc diversity and available biomass in the brackish Baltic Sea is a fraction of that in marine environments, and the prospects for proper sustenance for the walrus seemed grim at the outset. The first faecal sample from Latvia contained DNA traces of two bivalves. *Mya arenaria* is the largest of the marine bivalves in the Baltic (> 5

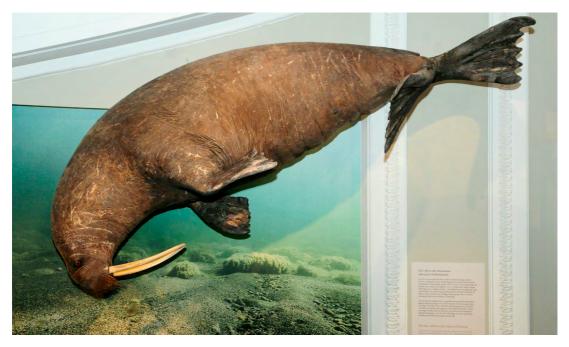


Fig. 9. The finished mounted specimen, prepared by Chief Taxidermist Ari Puolakoski, on display in the Natural History Museum, Helsinki. Photo: Janne Granroth.

cm) and perhaps the most likely prey item there. *Kurtiella bidentata* (= *Mysella bidentata*) however is a tiny clam (< 1 cm) and an unlikely prey item. Also, its distribution does not extend to the inner Baltic (e.g. Morys et al. 2017); if the walrus actually proceeded consistently east and north, it hardly could have ingested *Kurtiella* within two-three weeks before it was seen in Latvia.

The benthic biomass in the Eastern Gulf of Finland where the walrus was last encountered, with salinity < 5, is very low, c. 20 g/m² (Gogina et al. 2016). In the offshore zone, which might resemble the walrus' normal feeding habitat, the Baltic clam Macoma balthica, of a size 1-2 cm, is practically the only available bivalve, characterizing the macrozoobenthos along with Marenzelleria polychaetes. On the other hand, distributions of many freshwater species extend to the lowest-salinity nearshore waters of the Baltic. One of these species is the unionid mussel Anodonta anatina, which is of a proper prey size, up to 10 cm length, and accounts for a specific habitat type in river mouths, inlets and inshore lagoons, "benthic habitats characterized by Unionidae" ("suursimpukkapohjat"; Kotilainen et al. 2020). The two landing places of the walrus were

in the immediate vicinity of documented unionid habitats (Velmu 2024; Ari Laine, personal communication), in the very innermost bays, each several kilometres long and isolated by narrow straits at their entrance. It initially seemed possible that these inshore explorations were affected by cues of mollusc prey in the unfamiliar environment. With the first stranding in Hamina, the walrus defecated prominently, suggesting it still had foraged on the way. Three days later its intestinal tract was empty of food remains, but a trace of *Anodonta* DNA was recovered, indicating that it at least had attempted to feed on the freshwater mussel.

The differences between the bacterial composition of the Latvian and Finnish faecal samples suggest that the animal's gut microbial diversity had become diminished over time. This is likely due to the walrus' poor diet during its travel in the Baltic Sea.

The failure of the attempted rescue operation of the walrus was tragic but not unexpected. Because of their size and potential aggressiveness, walruses are difficult to handle and transport. To our knowledge, there has been only one successful rescue and release operation of a vagrant walrus in European waters. An approximately fiveyear old male walrus of circa 400 kg was captured with a net, without the use of anaesthesia, in the Netherlands in 1981; it was first transported by truck and ferry to a temporary holding site for observation, and later released into the North Sea (Reijnders 1982). This walrus was not only younger and smaller but also apparently in better physical condition than KX.2531.

From its place of origin in the eastern Barents Sea, KX.2531 must have travelled at least 3.000 km to reach the southern coast of Finland. Generally, young animals are more likely to travel long distances in search of a new territory or a mate than older animals are. In most marine mammals, males typically disperse longer distances than females, and this also holds for the walrus (Li & Kokko 2019; Mesnik & Ralls 2009). Tagging experiments have shown that male walruses may undertake movements of up to 1,500 km to reach new haul-out sites (Semenova et al. 2019). With such behaviour young males would also be more likely to become lost and end up far from their natural range. Several of the vagrant walruses in Europe have indeed been young males (e.g. Joensen 1977, Reijnders 1982, Bryant 2021, Mullard 2022). However, KX.2531 was a mature female that may have been past its reproductive prime.

Possible explanations for vagrant walruses may be sought in a combination of increased population size and environmental change. In the eastern parts of the Atlantic range, including the Russian Arctic, walruses have been legally protected since the 1950s, which has led to population recovery (Gjertz et al. 1998, Lydersen et al. 2012, Kovacs et al. 2014, Wiig et al. 2014, Semenova et al. 2019, Norwegian Polar Institute 2022). Population growth and ensuing increased competition for space and other resources could induce unusually long individual dispersal distances (Born 1988, Born et al. 2014, 2021). While hunting pressure has ceased, walruses have simultaneously had to contend with environmental change. The recent climatic changes are having an especially strong effect in Arctic regions by reducing the sea ice cover (Rantanen et al. 2022). The observed and projected sea ice loss is particularly extensive in the Barents Sea (Rieke et al. 2023). Sea ice is important for walruses, which must leave the water during periods of resting, moulting, and reproduction (Kovacs et al. 2015, Born et al. 2021). Sea ice reduction may also affect walrus foraging. Walruses feed mainly on benthic invertebrates, and their foraging is thus limited by water depth. Although walruses are capable of diving deeper, their daily foraging dives are typically concentrated to depths of less than 100 metres (Garde et al. 2018). Thus, foraging walruses tend to remain in coastal waters, within distances of 40–100 km from their haul-out sites (Garde & Hansen 2021). As a haul-out substrate, sea ice allows walruses to reach foraging areas further away from the coast. Although walruses can utilise both dry land and ice as haul-out substrates, a decrease of sea ice cover may lead to a net loss of suitable haul-out sites (Jay et al. 2012). It has been suggested that Atlantic walruses may be less vulnerable to such effects than Pacific walruses, as the current population size of the Atlantic subspecies is lower relative to its carrying capacity, and because the continental shelf is narrower in the Atlantic distribution area and feeding habitat is thus accessible also from land-based haul-outs (Born et al. 2021).

However, although there has been a general decreasing trend in sea ice cover in the Barents Sea in the period 1979-2023, it should be noted that the winter of 2021-2022 was not especially mild. In January and February 2022, the months immediately preceding the first observations of KX.2531 off the coast of Norway, the extent of ice cover in the Barents Sea was larger than it has been in many recent years (Norwegian Ice Service 2023). On the other hand, historical records suggest that long before the onset of anthropogenic climate change, vagrant walruses have been observed off the coasts of Europe and the Atlantic coast of North America (e.g. Ritchie 1921, Allen 1930, Löwegren 1944, Kiparsky 1952, Lund 1954, Manville & Favour 1960, Cotton 2007, Monaghan 2017, Mullard 2022, Chiacchio & Aae 2024). Thus, the scientific evidence for environmental change as a driver of Atlantic walrus extralimital movements is not clear-cut, and it cannot be stated with any certainty that the occurrence of KX.2531 in the Baltic Sea is related to climate change in general. The ultimate causes behind this individual's unusual visit to Finland remain unknown.

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References

- Allen, G.M. 1930: The walrus in New England. Journal of Mammalogy 11: 139–145.
- Allen, J.J. 1880: History of North American pinnipeds: a monograph of the walruses, sea-lions, sea-bears and seals of North America. – Miscellaneous Publications No. 12, p. 1–785. Department of the Interior, U. S. Geological and Geographical Survey of the Territories, Washington, D.C.
- Andersen, L.W., Jacobsen, M.W., Lydersen, C., Semenova, V., Boltunov, A., Born, E.W. Wiig, Ø. & Kovacs, K.M. 2017: Walruses (Odobenus rosmarus rosmarus) in the Pechora Sea in the context of contemporary population structure of Northeast Atlantic walruses. – Biological Journal of the Linnean Society 122: 897–915.
- Anonymous 1926: Walrus in Shetland. The Scottish Naturalist 1926: 140.
- Anonymous 2022: Walrus makes rare stop on German beach to delight of locals. – DPA/The Local, 17 June 2022. thelocal.de/20220617/walrus-makes-rare-stop-on-german-beach-to-delight-of-locals (accessed 19 Dec 2023)
- Apprill, A., McNally, S., Parsons, R. & Weber, L. 2015: Minor revision to V4 region SSU rRNA 806R gene primer greatly increases detection of SAR11 bacterioplankton. – Aquatic Microbial Ecology 75: 129–137.
- Beatty, W.S., Lemons, P.R., Everett, J.P., Lewis, C.J., Taylor, R.L., Lynn, R.J., Sethi, S.A., Quakenbush, L., Citta, J.J., Kissling, M. L., Kryukova, N. & Wenburg, J. 2022: Estimating Pacific walrus abundance and survival with multievent mark–recapture models. – Marine Ecology Progress Series 697: 167–182.
- Born, E.W. 1988: Hvalrosstrejfere i Europa. Flora og Fauna 94: 9-14.
- Born, E.W. 1992: Odobenus rosmarus Linnaeus, 1758 Walroß. In: Duguy, R. & Robineau, D. (eds.), Handbuch der Säugetiere Europas. Band 6: Meeressäuger. Teil II: Robben – Pinnipedia, p. 269– 299. Aula-Verlag, Wiesbaden.
- Born, E.W., Stefansson, E., Mikkelsen, B., Laidre, K.L., Andersen, L. W., Rigét, F.F., Villum Jensen, M. & Bloch, D. 2014: A note on a walrus' European odyssey. – NAMMCO Scientific Publications 9: 75–91.

- Born, E.W., Wiig, Ø. & Olsen, M.T. 2021: The future of Atlantic walrus in a rapidly warming Arctic. – In: Keighley, X., Olsen, M.T., Jordan, P. & Desjardins, S. (eds.), The Atlantic Walrus, p. 309– 332. Academic Press.
- van Bree, P.J.H. 1977: Over de recente zwerftocht van een walrus, Odobenus rosmarus (Linnaeus, 1758), langs de Nederlandse en Belgische kust. – De Levende Natuur 80: 58–63.
- Brunson, D.B. 2014: Walrus. In: West, G., Heard, D. & Caulkett, N. (eds.), Zoo and Wildlife Immobilization and Anesthesia. 2nd edition, p. 673–678. John Wiley & Sons.
- Bruun, E., Lid, G. & Lund, H.M.-K. 1968: Hvalross, Odobenus rosmarus, på norskekysten. – Fauna 21: 7–20.
- Bryant, M. 2021: 'He's so majestic': Wally the walrus hits Iceland on tour of Europe. – The Guardian, 1 October 2021. theguardian.com/ world/2021/oct/01/hes-so-majestic-wally-the-walrus-hits-iceland-ontour-of-europe (accessed 9 Nov 2023)
- Cadée, G.C., Cadée, M. & Cadée, N. 1982: Weer een walrus op Texel. – De Levende Natuur 84: 145–146.
- Caporaso, J.G., Lauber, C.L., Walters, W.A., Berg-Lyons, D., Lozupone, C.A., Turnbaugh, P.J., Fierer, N. & Knight, R. 2011: Global patterns of 16S rRNA diversity at a depth of millions of sequences per sample. – Proceedings of the National Academy of Sciences 108 (Suppl. 1): 4516–4522, doi.org/10.1073/pnas.1000080107 (accessed 21 Dec 2023)
- 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.
- Cotton, D.C.F. 2007: A critical review of Irish records of walrus Odobenus rosmarus (L.) with some unpublished observations from Cos Donegal, Sligo, Mayo and Galway. – The Irish Naturalists' Journal 28: 349–355.
- Deagle, B.E., Thomas, A.C., McInnes, J.C., Clarke, L.J., Vesterinen, E.J., Clare, E.L., Kartzinel, T.R. & Eveson, J.P. 2019: Counting with DNA in metabarcoding studies: how should we convert sequence reads to dietary data? – Molecular Ecology 28: 391–406. onlinelibrary.wiley.com/doi/full/10.1111/mec.14734 (accessed 18 December 2023)
- Duguy, R. 1986: Observation d'un morse (Odobenus rosmarus) sur la côte de Gironde, France. – Mammalia 50: 563–564.
- Fay, F.H. 1982: Ecology and biology of the Pacific walrus, Odobenus rosmarus divergens Illiger. – North American Fauna, Number 7, p. 1–279. United States Department of the Interior Fish and Wildlife Service, Washington, D.C.
- Fay, F.H. 1985: Odobenus rosmarus. Mammalian Species 238: 1-7.
- Findlay, S. 2018: Walrus spotted on the Scottish mainland for the first time in decades. – The Press and Journal, 20 March 2018. pressandjournal.co.uk/fp/news/highlands-islands/1437863/walrus-spottedon-the-scottish-mainland-for-the-first-time-in-decades/ (accessed 9 November 2023)
- Fogh-Andersen, J. 2022: Hvalros stranded ved mole i Nordjylland. Nordjyske, 17 February 2022. nordjyske.dk/nyheder/thisted/hvalros-strandet-ved-mole-i-nordjylland/a426daf5-497b-4268-a752-7daf-9691ff04 (accessed 19 Dec 2023)
- Folmer, O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R. 1994: DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. – Molecular Marine Biology and Biotechnology 3: 294–299.
- Garde, E. & Hansen, R.G. 2021: Stocks, distribution and abundance. In: Keighley, X., Olsen, M. T., Jordan, P. & Desjardins, S. (eds.), The Atlantic Walrus, p. 77–95. Academic Press.

- Garde, E., Jung-Madsen, S., Ditlevsen, S., Hansen, R.G., Zinglersen, K.B. & Heide-Jørgensen, M.P. 2018: Diving behavior of the Atlantic walrus in high Arctic Greenland and Canada. – Journal of Experimental Marine Biology and Ecology 500: 89–99.
- Garlich-Miller, J.L. & Stewart, R.E.A. 1998: Growth and sexual dimorphism of Atlantic walruses (Odobenus rosmarus rosmarus) in Foxe Basin, Northwest Territories, Canada. – Marine Mammal Science 14: 803–818.
- Garlich-Miller, J.L. & Stewart, R.E.A. 1999: Female reproductive patterns and fetal growth of Atlantic walruses (Odobenus rosmarus rosmarus) in Foxe Basin, Northwest Territories, Canada. – Marine Mammal Science 15: 179–191.
- Garlich-Miller, J.L., Stewart, R.E.A., Stewart, R.E. & Hiltz, E.A. 1993: Comparison of mandibular with cemental growth-layer counts for ageing Atlantic walruses (Odobenus rosmarus rosmarus). – Canadian Journal of Zoology 71: 163–167.
- Geller, J., Meyer, C., Parker, M. & Hawk, H. 2013: Redesign of PCR primers for mitochondrial cytochrome c oxidase subunit I for marine invertebrates and application in all-taxa biotic surveys. – Molecular Ecology Resources 13: 851–861. doi.org/10.1111/1755-0998.12138 (accessed 18 Dec 2023)
- Gjertz, I., Henriksen, G., Øritsland, T. & Wiig, Ø. 1993: Observations of walruses along the Norwegian coast 1967–1992. – Polar Research 12: 27–31.
- Gjertz, I., Wiig, Ø. & Øritsland, T. 1998: Backcalculation of original population size for walruses Odobenus rosmarus in Franz Josef Land. – Wildlife Biology 4: 223–230.
- Gogina, M., Nygård, H., Blomqvist, M., Daunys, D., Josefson, A.B., Kotta, J., Maximov, A., Warzocha, J., Yermakov, V., Gräwe, U. & Zettler, M.L. 2016: The Baltic Sea scale inventory of benthic faunal communities. – ICES Journal of Marine Science 73: 1196– 1213.
- Google Maps 2022: Stena, the 2022 old female walrus. Created by Rune Aae, 17 October 2022. – google.com/maps/d/viewer?mid= 1qtDSuGC20B3k5ST_h-NlihY4j4CAwRC2&hl=no&ll=56.75281477882717 %2C30.83458448872374&z=4 (accessed 20 Dec 2022)
- Hager, J. 2021: Walruses and leopard seals going astray. Polarjournal, 28 September 2021. polarjournal.ch/en/2021/09/28/walruses-andleopard-seals-going-astray/ (accessed 9 Nov 2023)
- Hanström, B. 1943: Skånes första valross. Skånes Natur Årsbok 30: 9–15.
- Hardy, A. 1959: The Open Sea: Its Natural History. Part II: Fish & Fisheries. Collins, London.
- Heptner, V.G., Chapskii, K.K., Arsen'ev, V.A. & Sokolov, V.E. (eds.) 1996: Mammals of the Soviet Union. Volume II, Part 3: Pinnipeds and Toothed Whales. – Smithsonian Institution Libraries / The National Science Foundation, Washington, D.C.
- Higdon, J.W. & Stewart, D.B. 2018: State of circumpolar walrus (Odobenus rosmarus) populations. – 100 p. Higdon Wildlife Consulting and Arctic Biological Consultants, Winnipeg, MB for WWF Arctic Programme, Ottawa, Canada.
- Jay, C.V., Fischbach, A.S. & Kochnev, A. 2012: Walrus areas of use in the Chukchi Sea during sparse sea ice cover. – Marine Ecology Progress Series 468: 1–13.
- Jensen, A.S. 1927a: Hvalrossen ved Skagen og dens vandringsveje. Naturens Verden 1927: 266–270.
- Jensen, A.S. 1927b: On a walrus (Trichechus rosmarus L.) which has visited Denmark and probably four other European countries. – Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening 84: 189–193.

- Joensen, A.H. 1977: Hvalros på afveje. Dansk Vildtforskning 1976– 1977: 46–47.
- Jusino, M.A., Banik, M.T., Palmer, J.M., Wray, A.K., Xiao, L., Pelton, E., Barber, J.R., Kawahara, A.Y., Gratton, C., Peery, M.Z. & Lindner, D.L. 2019: An improved method for utilizing highthroughput amplicon sequencing to determine the diets of insectivorous animals. – Molecular Ecology Resources 19: 176–190. doi.org/10.1111/1755-0998.12951 (accessed 19 Dec 2023)
- Kangas, N. 2018: Mursun ja ihmisen tarinaa pohjoisilta merialueilta. Elonkehä (4): 48–57.
- Kankaanpää, T., Vesterinen, E.J., Hardwick, B., Schmidt, N.M., Andersson, T., et al. 2020: Parasitoids indicate major climate-induced shifts in arctic communities. – Global Change Biology 26: 6276–6295. onlinelibrary.wiley.com/doi/10.1111/gcb.15297 (accessed 18 Dec 2023)
- Karvinen, E. 2022: Tällainen oli Stena-mursun matka: vietti pääsiäistä Norjassa ja juhannusta Puolassa. – Iltalehti, 20 July 2022. iltalehti.fi/kotimaa/a/2a0ad081-bc09-484b-a07d-8bb5dd685b68 (accessed 9 Nov 2023)
- Kastelein, R.A. 2009: Walrus (Odobenus rosmarus). In: Perrin, W.F., Würsig, B. & Thewissen, J. G. M. (eds.), Encyclopedia of Marine Mammals. II ed, p. 1212–1217. Academic Press.
- Kaunisto, K.M. Roslin, T., Forbes, M.R., Morrill, A., Sääksjärvi, I.E., Puisto, A.I.E., Lilley, T.M. & Vesterinen, E.J. 2020: Threats from the air: damselfly predation on diverse prey taxa. – Journal of Animal Ecology 89: 1365–1374. besjournals.onlinelibrary.wiley.com/doi/ full/10.1111/1365-2656.13184 (accessed 18 Dec 2023)
- Keighley, X., Olsen, M.T. & Jordan, P. 2022: Integrating cultural and biological perspectives on long-term human – walrus (Odobenus rosmarus rosmarus) interactions across the North Atlantic. – Quaternary Research 108: 5–25.
- Keighley, X., Pálsson, S., Einarsson, B.F., Petersen, A., Fernández-Coll, M., Jordan, P., Olsen, M.T. & Malmquist, H.J. 2019: Disappearance of Icelandic walruses coincided with Norse settlement. – Molecular Biology and Evolution 36: 2656–2667.
- Kettunen, N. 2022: Unohdettu mursumme. Helsingin Sanomat, 25 July 2022, B9.
- Kiparsky, V. 1952: L'histoire du morse. Annales Academiæ Scientiarum Fennicæ Series B 73(3): 1–53.
- Knutsen, L.Ø. & Born, E.W. 1994: Body growth in Atlantic walruses (Odobenus rosmarus rosmarus) from Greenland. – Journal of Zoology, London 234: 371–385.
- Kotilainen, A., Kiviluoto, S., Kurvinen, L., Sahla, M., Ehrnsten, E. et al. 2020: Threatened habitat types in Finland 2018: the Baltic Sea. Red List of habitats. Part II: Descriptions of habitat types. – The Finnish Environment 23, Finnish Environment Institute and Ministry of the Environment, Helsinki. http://urn.fi/ URN:ISBN:978-952-361-256-3 (accessed 24 Jan 2024)
- Kovacs, K.M., Aars, J. & Lydersen, C. 2014: Walruses recovering after 60+ years of protection in Svalbard, Norway. – Polar Research 33: 26034. doi.org/10.3402/polar.v33.26034 (accessed 9 Nov 2023)
- Kovacs, K.M., Lemons, P., MacCracken, J.G. & Lydersen, C. 2015: Walruses in a Time of Climate Change. – National Oceanic and Atmospheric Administration (NOAA). Arctic Report Card 2015. arctic.noaa.gov/report-card/report-card-2015/walruses-in-a-time-of-climate-change/ (accessed 9 Nov 2023)
- Kubny, H. 2022: Walruses going astray. Polarjournal, 23 July 2022. polarjournal.ch/en/2022/07/23/walruses-going-astray/ (accessed 9 Nov 2023)
- Lehtonen, V. 1951: Korkeasaaren kirja. Otava, Helsinki.

- Leonardi, M.S. & Palma, R.L. 2013: Review of the systematics, biology and ecology of lice from pinnipeds and river otters (Insecta: Phthiraptera: Anoplura: Echinophthiriidae). – Zootaxa 3630: 445–466.
- Leray, M. Yang, J.Y., Meyer, C.P., Mills, S.C., Agudelo, N., Ranwez, V., Boehm, J.T. & Machida, R.J. 2013: A new versatile primer set targeting a short fragment of the mitochondrial COI region for metabarcoding metazoan diversity: application for characterizing coral reef fish gut contents. – Frontiers in Zoology 10: 34. doi. orq/10.1186/1742-9994-10-34 (accessed 19 Dec 2023)
- Li, Y.-Y. & Kokko, H. 2019: Sex-biased dispersal: a review of the theory. – Biological Reviews 94: 721–736.
- Lindqvist, C., Bachmann, L., Andersen, L., Born, E.W., Árnason, Ú., Kovacs, K.M., Lydersen, C., Abramov, A.V. & Wiig, Ø. 2009: The Laptev Sea walrus Odobenus rosmarus laptevi: an enigma revisited. – Zoologica Scripta 38: 113–127.
- Lindqvist, C., Roy, T., Lydersen, C., Kovacs, K.M., Aars, J., Wiig, Ø. & Bachmann, L. 2016: Genetic diversity of historical Atlantic walruses (Odobenus rosmarus rosmarus) from Bjørnøya and Håøya (Tusenøyane), Svalbard, Norway. – BMC Research Notes 9: 112. doi.org/10.1186/s13104-016-1907-8 (accessed 25 Nov 2023)
- Lönnberg, E. 1927: En valross skjuten i Bohuslän. Fauna och Flora 22: 43–44.
- Lönnberg, E. 1940: En valross på villovägar. Fauna och Flora 35: 18–22.
- Loughrey, A.G. 1959: Preliminary investigation of the Atlantic walrus Odobenus rosmarus rosmarus (Linnaeus). – Wildlife Management Bulletin Series 1(14): 1–123.
- Löwegren, I. 1944: Valrossfångst i Bohuslän 1749. Fauna och Flora 39: 91.
- Lund, H. M.-K. 1954: The walrus (Odobenus rosmarus (L.)) off the coast of Norway in the past and after the year 1900, together with some observations on its migrations and "cruising speed". – Astarte 8: 1–12.
- Lydersen, C., Aars, J. & Kovacs, K.M. 2008: Estimating the number of walruses in Svalbard from aerial surveys and behavioural data from satellite telemetry. – Arctic 61: 118–128.
- Lydersen, C., Chernook, V.I., Glazov, D.M., Trukhanova, I.S. & Kovacs, K.M. 2012: Aerial survey of Atlantic walruses (Odobenus rosmarus rosmarus) in the Pechora Sea, August 2011. – Polar Biology 35: 1555–1562.
- Mansfield, A.W. 1958: The biology of the Atlantic walrus Odobenus rosmarus rosmarus (Linnaeus) in the Canadian Arctic. – PhD thesis, McGill University.
- Manville, R.H. & Favour, P.G. 1960: Southern distribution of the Atlantic walrus. – Journal of Mammalogy 41: 499–503.
- Martínez-Abraín, A., Marí-Mena, N., Vizcaíno, A., Vierna, J., Veloy, C., Amboage, M., Guitián-Caamaño, A., Key, C. & Vila, M. 2020: Determinants of Eurasian otter (Lutra lutra) diet in a seasonally changing reservoir. – Hydrobiologia 847: 1803–1816. doi. org/10.1007/s10750-020-04208-y (accessed 21 Dec 2023)
- Mathiasson, S. 1983: Valrossen sällsynt, kulturhistoriskt intressant arktisk gäst vid Västkusten. – Fauna och Flora 78: 253–261.
- McLeod, B.A., Frasier, T.R. & Lucas, Z. 2014: Assessment of the extirpated Maritimes walrus using morphological and ancient DNA analysis. – PLoS ONE 9(6): e99569. doi.org/10.1371/journal. pone.0099569 (accessed 9 Nov 2023)
- Mesnik, S.L. & Ralls, K. 2009: Mating systems. In: Perrin, W.F., Würsig, B. & Thewissen, J.G.M. (eds.), Encyclopedia of Marine Mammals. II ed, p. 712–719. Academic Press.

- Møhl, U. 1974: Subfossil finds of walrus from Denmark. Bulletin of the Geological Society of Denmark 23: 303–310.
- Møhl, U. 1985: The walrus, Odobenus rosmarus (L.), as a "Danish" faunal element during the Weichsel Ice Age. – Bulletin of the Geological Society of Denmark 34: 83–85.
- Mohr, E. 1940: Walrosse als Irrgäste in den europäischen Gewässern. Zoologischer Anzeiger 130: 253–255.
- Monaghan, N.T. 2017: Historic walrus tusk from Co. Wexford. Irish Naturalists' Journal 35: 151–153.
- Morys, C., Powilleit, M. & Forster, S. 2017: Bioturbation in relation to the depth distribution of macrozoobenthos in the southwestern Baltic Sea. – Marine Ecology Progress Series 579: 19–36. doi. org/10.3354/meps12236
- Mulcahy, D.M. & Fravel, V. 2018: Walrus medicine. In: Gulland, F. M.D., Dierauf, L.A. & Whitman, K.L. 2018: CRC Handbook of Marine Mammal Medicine. 3 edition, p. 591–595. CRC Press, New York.
- Mullard, J. 2022: The wandering walrus and other arctic vagrants. British Wildlife 33: 235–243.
- Niederklopfer, P. & Troxler, M. 2001: Knochenpräparation: Handbuch für Praktiker. – Romei AG, Rothenbrunnen.
- Nores, C. & Pérez, C. 1988: The occurrence of walrus (Odobenus rosmarus) in southern Europe. – Journal of Zoology, London 216: 593–596.
- Norwegian Ice Service 2023: Sea ice index Barents Sea. Cryo, Norwegian Meteorological Institute. cryo.met.no/en/sea-ice-indexbar (accessed 12 Dec 2023)
- Norwegian Polar Institute 2022: Walrus population in Svalbard. Environmental Monitoring of Svalbard and Jan Mayen (MOSJ). mosj.no/en/indikator/fauna/marine-fauna/walrus/ (accessed 9 Nov 2023)
- Ølberg, R.-A., Kovacs, K.M., Bertelsen, M.F., Semenova, V. & Lydersen, C. 2017: Short duration immobilization of Atlantic walrus (Odobenus rosmarus rosmarus) with etorphine and reversal with naltrexone. – Journal of Zoo and Wildlife Medicine 48: 972–978.
- Osborne, M. 2023: The unusual European journey of Thor the walrus. – Smithsonian Magazine / Smart News, 6 March 2023.
- Parada, A.E., Needham, D.M. & Fuhrman, J.A. 2016: Every base matters: assessing small subunit rRNA primers for marine microbiomes with mock communities, time series and global field samples. – Environmental Microbiology 18: 1403–1414. doi. org/10.1111/1462-2920.13023 (accessed 21 Dec 2023)
- Pedersen, A. 1936: Polardjur. Åhlén & Söners Förlag, Stockholm.
- Pilāts, V. 2022: Valzirgs jauna zvēru suga Latvijas faunā! Dabasdati.lv, 8 August 2022. dabasdati.lv/lv/article/valzirgs-ndash-jauna-zverusuga-latvijas-fauna/2022/ (accessed 29 Jan 2024)
- Post, K. 2005: A Weichselian marine mammal assemblage from the southern North Sea. – DEINSEA 11: 21–27.
- Puolakoski, A. 2024: Epäonnisen mursun tarina. Toppari 148: 15-20.
- Rantanen, M., Karpechko, A.Y., Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja, K., Vihma, T. & Laaksonen, A. 2022: The Arctic has warmed nearly four times faster than the globe since 1979. – Communications Earth & Environment 3: 168. doi. org/10.1038/s43247-022-00498-3 (accessed 29 Nov 2023)
- Redeke, H. C. 1927: Ein Walroß in der südlichen Nordsee. Zoologischer Anzeiger 74: 89–90.
- Reijnders, P.J.H. 1982: Observation, catch and release of a walrus, Odobenus rosmarus, on the Isle of Ameland, Dutch Wadden Sea. – Zoologischer Anzeiger 209: 88–90.

- Rieke, O., Årthun, M. & Dörr, J.S. 2023: Rapid sea ice changes in the future Barents Sea. – The Cryosphere 17: 1445–1456. doi. org/10.5194/tc-17-1445-2023 (accessed 29 Nov 2023)
- Ritchie, J. 1921: The walrus in British waters. The Scottish Naturalist 1921: 5–9, 77–86.
- Robeck, T., Katsumata, E., Arai, K., Montano, G., Schmitt, T., DiRocco, S. & Steinman, K.J. 2022: Growth, maturity, reproduction, and life expectancy in ex-situ Pacific walruses (Odobenus rosmarus divergens). – BMC Zoology 7: 57. doi.org/10.1186/s40850-022-00158-1 (accessed 29 Jan 2024)
- Ruiz-Puerta, E.J., Keighley, X., Desjardins, S.P.A., Gotfredsen, A.B., Pan, S.E., Star, B., Boessenkool, B., Barrett, J.H., McCarthy, M.L., Andersen, L.W., Born, E.W., Howse, L R., Szpak, P., Pálsson, S., Malmquist, H.J., Rufolo, R., Jordan, P.D. & Olsen, M.T. 2023: Holocene deglaciation drove rapid genetic diversification of Atlantic walrus. – Proceedings of the Royal Society B 290: 20231349. doi.org/10.1098/rspb.2023.1349 (accessed 25 Nov 2023)
- Scheffer, V.B. 1967: Standard measurements of seals. Journal of Mammalogy 48: 459–462.
- Scherf, H. 1963: Ein Beitrag zur Kenntnis zweier Pinnipedierläuse (Antractophthirus trichechi Boheman und Echinophthirius horridus Olfers). – Zeitschrift für Parasitenkunde 23: 16–44.
- Semenova, V., Boltunov, A. & Nikiforov, V. 2019: Key habitats and movement patterns of Pechora Sea walruses studied using satellite telemetry. – Polar Biology 42: 1763–1774.
- Svanberg, I. 2010: Walruses (Odobenus rosmarus) in captivity. Svenska Linnésällskapets Årsskrift 2010: 119–136.
- Taylor, R.L., Udevitz, M.S., Jay, C.V., Citta, J.J., Quakenbush, L.T., Lemons, P.R. & Snyder, J.A. 2018: Demography of the Pacific walrus (Odobenus rosmarus divergens) in a changing Arctic. – Marine Mammal Science 34: 54–86.
- Ukkonen, P. 2002: The early history of seals in the northern Baltic. Annales Zoologici Fennici 39: 187–207.
- Valtanen, M. 2023: Julkinen eläin. Suomen Kuvalehti 2023(37): 28– 35.
- Vamos, E., Elbrecht, V. & Leese, F. 2017: Short COI markers for freshwater macroinvertebrate metabarcoding. – Metabarcoding and Metagenomics 1: e14625. doi.org/10.3897/mbmg.1.14625 (accessed 19 Dec 2023)

- Velmu 2024: Velmu. Vedenalaisen meriluonnon karttapalvelu. velmu. syke.fi/ [search: pikkujärvisimpukka] (accessed 23 Jan 2024)
- Venables, L.S.V. & Venables, U.M. 1955: Birds and Mammals of Shetland. – Oliver and Boyd, Edinburgh, London.
- Vesterinen, E.J., Ruokolainen, L., Wahlberg, N., Peña, C., Roslin, T., Laine, V.N., Vasko, V., Sääksjärvi, I.E., Norrdahl, K. & Lilley, T.M. 2016: What you need is what you eat? Prey selection by the bat Myotis daubentonii. – Molecular Ecology 25: 1581–1594. onlinelibrary.wiley.com/doi/10.1111/mec.13564 (accessed 18 Dec 2023)
- Walters, W.A., Hyde, E.R., Berg-Kyons, D., Ackermann, G., Humphrey, G., Parada, A.E., Gilbert, J.A., Jansson, J.K., Caporaso, J.G., Fuhrman, J.A., Apprill, A. & Knight, R. 2016: Improved bacterial 16S rRNA gene (V4 and V4-5) and fungal internal transcribed spacer marker gene primers for microbial community surveys. – mSystems 1: e00009-15. doi.org/10.1128/msystems.00009-15
- Wendehög, M. & Berdenius, S.O. 2003: Oväntat valrossbesök på Tjörn. – Sveriges Radio, 23 August 2003. sverigesradio.se/artikel/278690 (accessed 9 Nov 2023)
- Wiig, Ø., Born, E.W. & Stewart, R.E. 2014: Management of Atlantic walrus (Odobenus rosmarus rosmarus) in the arctic Atlantic. – NAMMCO Scientific Publications 9: 315–341.
- Wiig, Ø. & Gjertz, I. 1996: Body size of male Atlantic walruses (Odobenus rosmarus rosmarus) from Svalbard. – Journal of Zoology, London 240: 495–499.
- Witten, P. 2022a: Derfor må du ikke nærme dig hvalrossen på Læsø. – Nordjyske, 17 May 2022. nordjyske.dk/nyheder/frederikshavn/ hvalros-er-gaaet-i-land-paa-laesoe-men-pas-paa/2919976 (accessed 19 Dec 2023)
- Witten, P. 2022b: Hvalros fra Hirtshals opfører sig som bølle i denne havn. – Nordjyske, 5 August 2022. nordjyske.dk/nyheder/frederikshavn/tumult-i-naboland-nordjyske-hvalrosser-paa-vilde-langture/3347421 (accessed 19 Dec 2023)
- Wong, C. 2023: Thor the walrus spotted on Iceland coast following visit to the UK. – New Scientist, 27 February 2023. newscientist.com/ article/2361548-thor-the-walrus-spotted-on-iceland-coast-following-visit-to-the-uk/ (accessed 9 Nov 2023)