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ARTICLE

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The movement patterns and foraging resources of Atlantic walruses (*Odobenus rosmarus rosmarus*) in Franz Josef Land archipelago and connectivity with the Kara-Barents Sea population

Maria Solovyova[1] | **Anna Gebruk**[2] | **Svetlana Artemyeva**[1] | **Viatcheslav V. Rozhnov**[1] | **Artyom Isachenko**[3] | **Renata Lazareva**[3] | **Pavel Chukmasov**[1] | **Dmitry Glazov**[1] | **Yulia Ermilova**[4] | **Alexander Kokorin**[4] | **Maria Mardashova**[4] | **Nikolay Shabalin**[4]

[1]A.N. Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences, Moscow, Russia

[2]School of GeoSciences, University of Edinburgh, Edinburgh, UK

[3]Arctic Research Center, Moscow, Russia

[4]Lomonosov Moscow State University Marine Research Centre, Moscow, Russia

Correspondence
Anna Gebruk, Changing Oceans Research Group, School of GeoSciences, Grant Institute | James Hutton Road, King's Buildings, Edinburgh, EH9 3FE, UK.
Email: anna.gebruk@ed.ac.uk

Abstract

The Franz Josef Land population of the Atlantic walrus (*Odobenus rosmarus rosmarus*) remains one of the least studied. Here, 26 walruses were tagged with satellite-linked radio transmitters in Franz Josef Land archipelago and Victoria Island in summer-autumn 2020 and 2021 to assess movements patterns and area utilization. In addition, 65 grab samples were taken to evaluate macrobenthic foraging resources. The mean duration of data records was 53 ± 27 days. The walruses traveled on average 29 ± 13.5 km/day with a mean speed of 1.2 ± 0.6 km/hr. The travel speed and distance were statistically different for male, female, and immature walruses. The individuals tagged on Victoria Island remained in the vicinity of the island, while walruses tagged within the Franz Josef Land archipelago moved between the islands, utilizing the entire area for foraging trips. One walrus migrated from Franz Josef Land to Novaya Zemlya in late November, providing evidence of connectivity with the Kara-Barents Sea population.

The area was characterized by high average biomass of macrobenthos. Bivalve mollusks, *Hiatella arctica*, were dominating macrobenthic biomass, likely being the main foraging resource for the walruses. Further observations are needed to better understand winter behaviors of Franz Josef Land walruses and possible impacts of climate change on movement patterns.

KEYWORDS

Atlantic walrus, foraging, Franz Josef Land, macrobenthos, *Odobenus rosmarus rosmarus*, satellite telemetry

1 | INTRODUCTION

The Atlantic walrus (*Odobenus rosmarus rosmarus*) is the largest pinniped in the Northern Hemisphere, commonly occurring in the Arctic and sub-Arctic waters from Eastern Canada to the Kara Sea (Wiig et al., 2014). The Atlantic walrus is listed as Near Threatened by the International Union for Conservation of Nature (Kovacs, 2016) and included as a focal ecosystem component crucial to the functioning and integrity of the Arctic marine ecosystems in the Circumpolar Biodiversity Monitoring Programme (CAFF, 2017). In the Barents Sea, Atlantic walruses are commonly recorded in the waters surrounding Svalbard, Franz Josef Land, Novaya Zemlya archipelago, and the Pechora Sea (Gebruk et al., 2021; Semenova et al., 2019; Wiig et al., 1996, 2014).

The Franz Josef Land population of the Atlantic walrus is one of the least studied due to the remoteness of the area. The relationship between the populations of walruses in Franz Josef Land and other walruses in the Barents Sea remains uncertain although a substantial body of evidence suggests summer and autumn migrations of walruses between Franz Josef Land and Svalbard, and the population is sometimes referred to as Svalbard-Franz Josef Land stock (Freitas et al., 2009; Lydersen & Kovacs, 2014; Wiig et al., 1996). The relationship with the walruses on Novaya Zemlya archipelago, however, is a subject of debate—some genetic studies suggest a potential overlap of the populations between Franz Josef Land and Novaya Zemlya archipelago (Shitova et al., 2015), while other studies declare that the Svalbard-Franz Josef Land population is a separate stock, genetically distinct from the Novaya Zemlya Archipelago—Eastern Barents–Pechora–White Sea population (Andersen et al., 2017). The population size of the Svalbard–Franz Josef Land group of walruses had been estimated as 2,000 individuals (Born et al., 1995), but there is a lack of recent survey data. In summer, walruses use the island as haul-out sites and there have been reports of over 1,000 individuals on a single haul-out (Gavrilo, 2010).

Walruses occupy a relatively narrow ecological niche and require suitable haul-out sites as well as sufficient foraging grounds with enough macrobenthic biomass within the accessible depth range to sustain their energy needs (Wiig et al., 2014). As an apex predator, walruses are often referred to as an indicator of the health of Arctic marine ecosystems, which has important implications for monitoring and management in the Arctic region (Boltunov et al., 2015).

Atlantic walruses are benthic predators that predominantly feed on bivalve mollusks (Born et al., 2003). The estimate of daily consumption by an individual adult walrus varies in literature from 35–50 kg of feeding biomass of macrobenthos corresponding to gross energy intake of 200 kJ/kg of body mass (Born et al., 2003), to a more conservative recent estimate of 23.6 kg of feeding resources, corresponding to 2% of body mass (Skern-Mauritzen et al., 2022). Most studies agree that the bulk of the diet of Atlantic walrus is formed by bottom-dwelling bivalve mollusks, however, their diet can also include benthic crustaceans, gastropods, and other invertebrates, as well as demersal fish and more rarely, marine mammals and birds (Born et al., 1995, 2003; Fox et al., 2010; Gebruk et al., 2021).

Understanding the habitat use, movement patterns, and feeding resources of this iconic Arctic species is particularly important as the increasing anthropogenic pressures in the region (such as shipping and offshore development), together with ongoing climate change continue to pose multiple stressors on the populations of Atlantic walruses (Gebruk et al., 2021; Semenova et al., 2019). Satellite-linked tags can provide valuable information on movement patterns and habitat use of the walruses, however, there are numerous challenges in the deployment of the tags and the limited satellite telemetry studies on Atlantic walruses often have data records that are short in duration and are limited to the summer season only (Freitas et al., 2009; Semenova et al., 2019; Wiig et al., 1996).

The purpose of this study was to (1) reveal the individual movement patterns and speed of movement of walruses, tagged in the waters of Franz Josef Land archipelago and Victoria Island in Autumn and compare between the different age and sex groups; (2) identify the areas of high probability of use by walruses to gain insight into seasonal range, migratory routes, and possible feeding grounds; (3) characterize foraging resources available for the walruses in the area in terms of biomass, species composition, and distribution of macrozoobenthos; and (4) assess the overlap between areas of high walrus use and high benthic biomass.

2 | METHODS

2.1 | Satellite tagging

Twenty-six walruses were tagged with satellite-linked radio transmitters (platform terminal transmitters, PTT) on the islands of the Franz Josef Land archipelago, Victoria, and Oranskiye Islands in August–September 2020 and 2021. This included 12 adult males, 7 females, and 5 immatures. Three types of transmitters were used: Pulsar transmitters designed by Ltd Es-Pas (Moscow, Russia), and SPOT and SPLASH transmitters designed by Wildlife Computers (Redmond, WA; Table 1). All transmitters provided position data received through the Advanced Research and Global Observation Satellite (ARGOS) system on a duty cycle of 6 hr “on” and 6 hr “off.”

PTTs were mounted on the walruses through the skin with stainless-steel harpoons using a wooden pole (Figure 1). No sedation methods were used.

The sex and age of each animal were visually estimated based on common morphological features: body size, length of tusks relative to the width and depth of the snout, and presence of lumps (nodules) on the neck and shoulders (following Citta et al., 2014).

2.2 | Foraging biomass assessment

To assess foraging resources available for the walruses in the area, samples of macrobenthos were collected from aboard R/V *Ivan Petrov* during field campaigns to the Franz Josef Land in summer-autumn 2020 and 2021. The sampling stations were chosen in proximity to the walrus haul-out sites where animals were tagged, with a few reference sites in the open-water and in-between the islands. The research area covered most of the Franz Josef Land archipelago as well as marine areas near Victoria Island to the west of the archipelago, three open-water control sites to the north of the archipelago, and two sites north of Novaya Zemlya archipelago (a total of 65 stations; Figure 2). Samples were taken with Van-Veen or Okean-0.1 benthic grabs with a capture area of 0.1 m^2 in three repeats for each station.

The samples were washed over a 0.5-mm nylon mesh and preserved on-board with 4% formaldehyde solution before transporting to the laboratory. In the laboratory, the samples were transferred into 70% ethanol solution.

In this study, the samples were assessed for overall macrobenthic biomass (wet biomass, g/m^2) and contributions of the key foraging items to overall biomass—morphospecies that contributed >1% to overall macrobenthic biomass

TABLE 1 The list of the platform terminal transmitters (PTTs) used in this study with PTT number and type, the date and location of tagging and key characteristics of the tagged walruses (sex and age group).

PTT number	Walrus sex	Walrus age	Tagging date	Tagging location	PTT type
2020					
206156	–	4–5	August 29	Jackson Island	Pulsar
206157	♀	10+	September 6	Northbrook Island	Pulsar
206158	♀	15+	September 6	Northbrook Island	Pulsar
206159	–	2	August 31	Dead seal Island	Pulsar
206161	♂	6–9	August 26	Eva-Liv Island	Pulsar
206162	♀	10	September 6	Northbrook Island	Pulsar
206163	♂	6–9	August 26	Eva-Liv Island	Pulsar
206166	♂	6–9	August 25	Geddes Island	Pulsar
206168	♂	15+	August 23	Hochstetter Island	Pulsar
206169	♂	10–15	August 25	Apolonov Island	Pulsar
2021					
209012	–	3	September 1	Apolonov Island	SPOT
209013	♀	6–9	August 25	Matilda Island	SPLASH
209014	–	3	August 29	Harley Island	SPLASH
209015	–	3	August 31	Three-ray Island	SPLASH
209016	♀	15+	August 25	Matilda Island	SPLASH
224150	♂	10–15	August 22	Victoria Island	Pulsar
224151	♂	10–15	August 22	Victoria Island	Pulsar
224152	♂	10–15	August 22	Victoria Island	Pulsar
224153	♀	15+	August 26	No-name island	Pulsar
224154	♂	10–15	August 25	Heiss Island	Pulsar
224155	♂	6–9	August 20	Victoria Island	Pulsar
224156	♂	6–9	August 22	Victoria Island	Pulsar
224157	♀	6–9	August 29	Harley Island	Pulsar
224158	♂	6–9	August 20	Wilczek Island	Pulsar
224159	♂	6–9	August 29	Harley Island	Pulsar
224160	♂	10–15	August 30	Eva-Liv Island	Pulsar

were identified to species level using local taxonomic keys, standardized using the World Register of Marine Species (WoRMS; https://www.marinespecies.org/). All specimens have been weighed with reported accuracy to 0.01 g. Bivalve mollusks and gastropods were weighed in shells. To assess significance of differences between groups of stations, a one-way pairwise analysis of similarities (ANOSIM) analysis was used ($p < .05$). The more detailed assessment of macrobenthic abundance, diversity, and community structure is a subject of a separate publication in preparation (Kokorin et al., unpublished data).

2.3 | Satellite telemetry data analysis

Satellite telemetry data were filtered in R Studio version 2022.07.1 + 554 using the Speed-Distance-Angle-filter (SDA-filter) of the "argosfilter" package (Freitas et al., 2008). The following configurations were used: the

FIGURE 1 A platform terminal transmitter (SPLASH) on a harpoon (left); tagged walrus (Pulsar transmitter) in water (right).

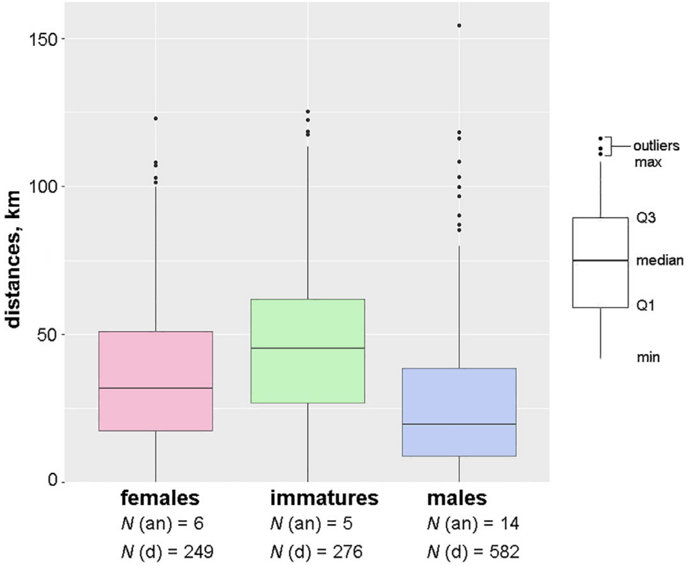

FIGURE 2 Box plot of daily distances, km traveled by different groups of walruses (females, immatures, males), *N* (an) is the number of animals in the group, *N* (d) shows the recorded number of days.

maximum speed of walrus movement was set to 2.8 m/s (10 km/hr; Dietz et al., 2014; Semenova et al., 2019); the maximum angle between the two sections of the path longer than 2.5 km was 15°, and 25° for the sections longer than 5 km (Freitas et al., 2008). The fixed contour method or the kernel method (Citta et al., 2012; Worton, 1989) was used to estimate areas of key habitat use (50% kernel) by the walruses (Wege et al., 2021). H-values were selected using the ad hoc method (Silverman, 1986). The result of the analysis is a set of polygons with different percentages of inclusion of the analyzed locations (10% of all locations are contained within the 10% contour, and almost all locations are within the 95% contour). The density of points (activity of using area by animals) is inversely related: a 10% contour polygon contains points with the highest density, and a 95% contour contains both high- and low-density points. A Kruskal–Wallis test (one-way ANOVA on ranks) was used to identify the difference between the movement speed of male, female, and immature walruses ($p < .05$). Bathymetric data for the Barents Sea were obtained through GebcoMaps (http://www.gebco.net) with reported accuracy of 1 m and spatial resolution 30 arcseconds (at a latitude of FJL [80°N], the length is approximately 9.7 km). Maps were generated using ArcMap v10.4.1. by the standard geoprocessing tools with the reference coordinate system UTM/WGS84 Zone 40 N.

3 | RESULTS

3.1 | Satellite telemetry

3.1.1 | Movement parameters

One (#206157) of the 26 installed PTT transmitted only two locations and was excluded from the analysis. The rest of the PTTs received data with a mean duration of tracking of 53 ± 27 days (ranging from 1 to 112 days; Table 2).

The animals traveled a mean distance of 29 ± 13.5 km daily, but the speed of movement differed between the sex and age groups. Immature walruses traveled the longest distances on average (42.2 ± 10.6 km/day). Females moved less (mean 32.2 ± 11.9 km/day). Males covered the smallest distances, 22.9 ± 11.2 km/day on average. Comparisons of the movement speed between immatures, adult males, and adult females showed statistically significant differences for each pair (Kruskal–Wallis test, $\chi^2 = 150.99$, $df = 2$, $p < 2.2e{-}16$; Figure 2).

The mean hourly speed for all animals was 1.2 ± 0.6 km/hr (1.8 ± 0.4 km/hr for immatures, 1.3 ± 0.5 km/hr for adult females, and 1.0 ± 0.5 km/hr for adult males).

3.1.2 | Habitat use

Walruses tagged on the islands of the Franz Josef Land archipelago mainly moved within the archipelago. Only one walrus (male #206163) swam over 350 km between November 16 and November 22 in 2020 to the northern tip of Novaya Zemlya, where it remained until the end of the PTT recording on December 16. Five walruses tagged on Victoria Island remained in the nearby waters at least until October 17 in 2021, when the last PTT #224156 stopped (Figure 3).

Twenty walruses were tagged in the waters of Franz Josef Land archipelago. Seventeen individuals used the whole marine area of the archipelago, moved between the islands, stopping at different haul-out sites, and making more local movements (Figure 4). Two PTTs (#206162 and #206169) did not provide a full picture of the movement patterns as they only transmitted for 6 and 7 days, respectively. The one remaining PTT was on an immature walrus (#206159), which generally remained in the same area for all 65 days of tracking.

Walruses tagged on Victoria Island remained in the vicinity of the island, while most of the animals tagged on various islands of the Franz Joseph Land archipelago utilized the entire archipelago during the summer-autumn movements.

Kernel analysis showed several areas of key habitat use by the walruses (50% kernel probability). The most actively used by the walruses were the waters near Hochstetter Island and the marine areas between Harley and Jackson Islands. Both areas were visited by six walruses during the tracking period. Other important areas were identified south of Freden Island (four walruses visited), near Wilczek Island (three walruses), south of Rudolf Island (three walruses), and between Bruce and Northbrook islands (three walruses). Walruses tagged on Victoria Island had a separate key area around the island (Figure 4). The kernel contours on Figure 4 show the probability of area use by the walruses, while the density of points is inversely related—contours with a lower probability value (in %) correspond to the areas of high probability of use by the walruses.

Almost all movements of walruses took place in the shallow waters: 95.9% of all locations for male walruses were recorded within the 200 m isobath and 80.0% of all locations were within the 100 m isobath. Similarly, for

TABLE 2 The tracking log for each PTT, the sex and age of the tagged animal, date of the first and last received transmission, total duration of the tracking in days and track length in km, number of locations, mean travel distance per day (km), and mean movement speed of walrus (km/hr) are presented.

PTT number	Sex	Age	Date of the first location	End date	Total days	Track length (km)	Number of locations[a]	Mean distance per day (km)	Mean movement speed (km/hr)
2020									
206156	–	4–5	August 29	October 21	54	1,802	473	33.4	1.4
206157	♀	10+	September 6	September 6	1	–	2	–	–
206158	♀	15+	September 6	November 28	83	3,245	1,752	38.6	1.6
206159	–	2	August 31	September 26	27	799	395	29.6	1.2
206161	♂	6–9	August 27	October 29	64	1,601	1,007	25.0	1.0
206162	♀	10	September 6	September 11	6	248	96	41.3	1.7
206163	♂	6–9	August 26	December 16	113	3,456	2,531	30.6	1.3
206166	♂	6–9	August 25	September 26	33	277	237	8.4	0.3
206168	♂	15+	August 23	September 28	37	543	472	14.7	0.6
206169	♂	10–15	August 26	August 31	6	181	39	30.1	1.3
2021									
209012	–	3	September 2	September 12	99	4,520	2,285	45.7	1.9
209013	♀	6–9	August 25	September 17	24	622	305	25.9	1.1
209014	–	3	August 29	November 19	83	3,879	2,441	46.7	1.9
209015	–	3	August 31	October 12	43	2,384	1,229	55.4	2.3
209016	♀	15+	August 25	November 6	74	3,478	2,073	47.0	2.0
224150	♂	10–15	August 22	October 6	46	1,858	823	40.4	1.7
224151	♂	10–15	August 22	October 13	53	2,377	702	44.9	1.9
224152	♂	10–15	August 24	September 29	37	898	462	24.3	1.0
224153	♀	15+	August 26	October 3	39	600	740	15.4	0.6
224154	♂	10–15	August 25	November 1	69	1,061	265	15.4	0.6
224155	♂	6–9	August 20	October 12	54	624	594	11.6	0.5

(Continues)

TABLE 2 (Continued)

PTT number	Sex	Age	Date of the first location	End date	Total days	Track length (km)	Number of locations[a]	Mean distance per day (km)	Mean movement speed (km/hr)
224156	♂	6–9	August 22	October 17	57	447	1,378	7.8	0.3
224157	♀	6–9	August 29	October 12	45	1,135	595	25.2	1.1
224158	♂	6–9	August 20	October 24	66	1,430	2,002	21.7	0.9
224159	♂	6–9	August 30	October 26	58	784	365	13.5	0.6
224160	♂	10–15	August 31	September 9	10	320	81	32.0	1.3

[a] After filtering.

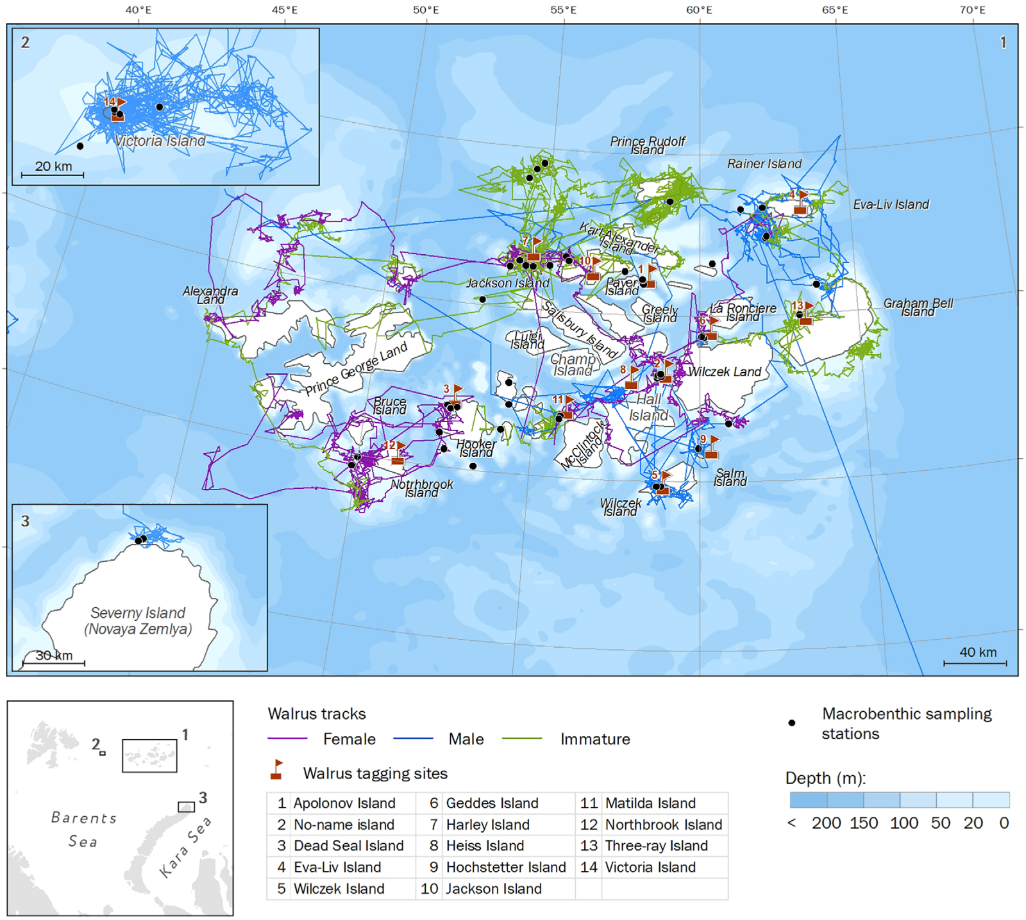

FIGURE 3 Movements of walruses in August–December 2020–2021. *N* females = 6, *N* males = 14, *N* immatures = 5. The insets show the movements of animals tagged on Victoria Island and part.

females, 93.0% of locations were within 200 m and 80.2% within 100 m, and for immature animals: 89.8% (>200 m) and 65.1% (>100 m), respectively (Figure 5).

3.2 | Macrobenthic biomass assessment

A total of 65 benthic grab stations were assessed for biomass of macrozoobenthos. Mean wet biomass of macrobenthos in the research area was 420 ± 14 g/m^2, ranging from 3 ± 0.1 g/m^2 at station 21_11, to 3,994 ± 151 g/m^2 at station 21_27 (Figure 6). All stations with maximum values were located within the Franz Josef Land archipelago, while the stations near Victoria Island and Novaya Zemlya islands had noticeably lower biomass values (Figure 6). Furthermore, macrobenthic biomass from Victoria Island was statistically different from Franz Josef Land ($p = .001$; $R^2 = 0.5$), but Novaya Zemlya stations were not found to differ from either Franz Josef Land ($p = .32$) or Victoria Island stations ($p = .52$), which could be influenced by the paucity of data from Novaya Zemlya (two stations only).

The bulk of the foraging biomass was clearly formed by only a handful of species (Figure 7). The main contribution to overall biomass of macrobenthos was formed by bivalve mollusk *Hiatella arctica* (36%), with additional contributions from sea urchin, *Strongylocentrotus* spp. (12%), barnacle, *Balanus balanus* (10%), and polychaeta, *Artacama proboscidea* (7%).

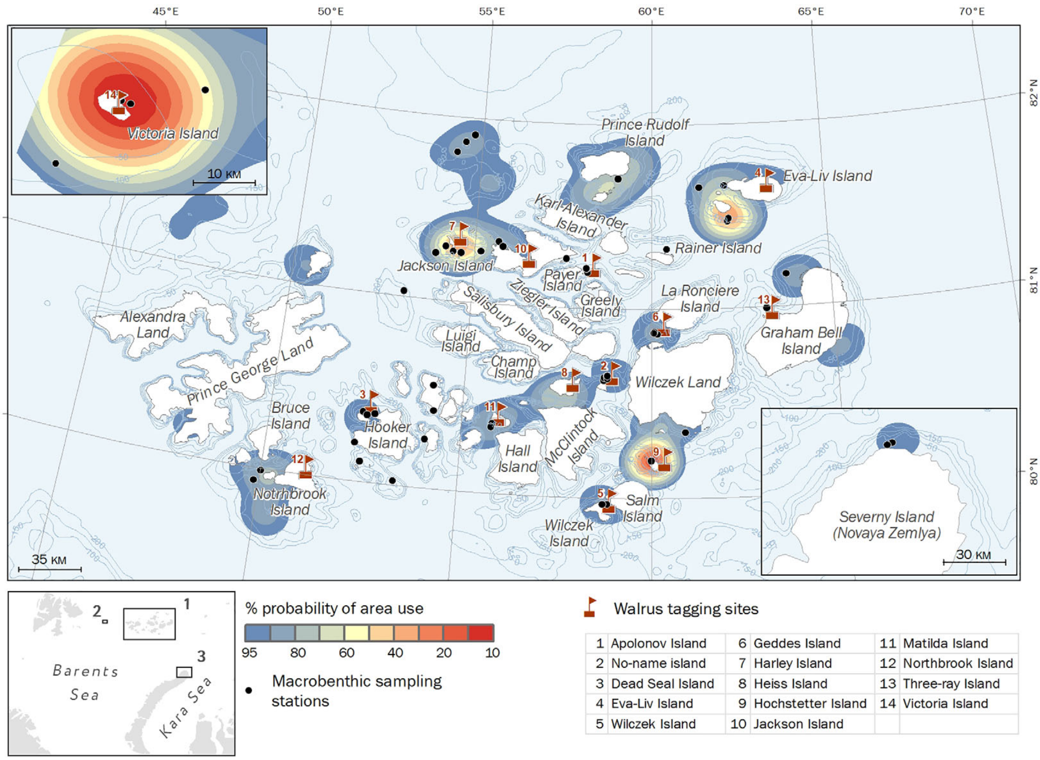

FIGURE 4 Kernel contours showing probability of area use (%) by walruses in August–December 2020–2021. *N* females = 6, *N* males = 14, *N* immatures = 5. The density of points (activity of using area by animals) is inversely related: a 10% contour polygon contains points with the highest density, and a 95% contour contains both high- and low-density points.

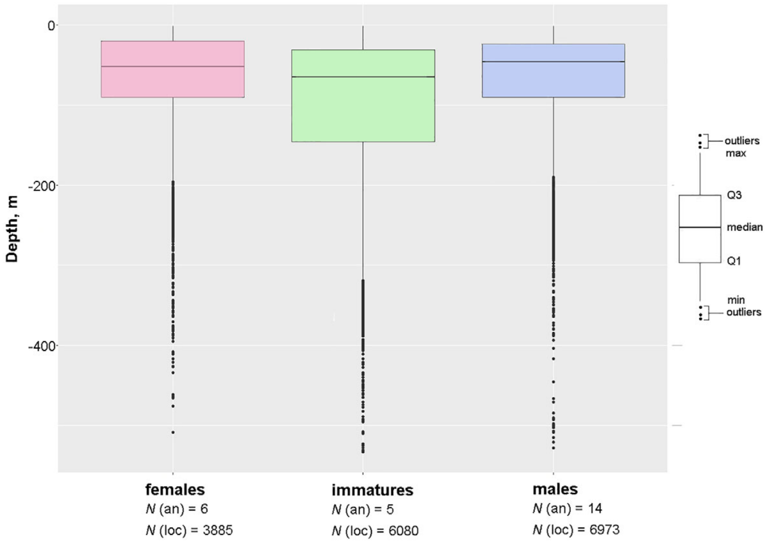

FIGURE 5 Box plot showing recorded locations of the three groups of walruses: females, immatures, males; *N* (an) denotes the number of animals in the group, *N* (loc) the number of locations, against depth (m).

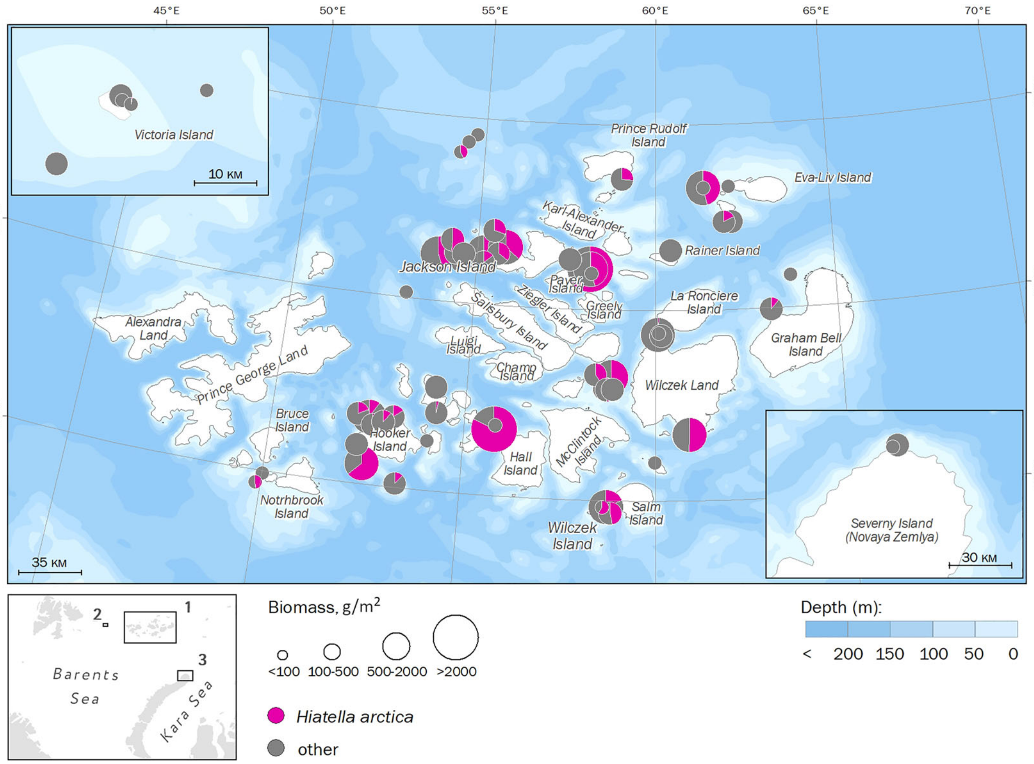

FIGURE 6 Macrobenthic invertebrate biomass variation in waters of the Franz Josef Land archipelago, Victoria Island, and Novaya Zemlya in the Barents and Kara Seas measured in August–November 2020–2021. The size of the pie chart corresponds to available wet biomass (g/m^2) and the proportion of the pie chart highlighted in pink indicates the proportional biomass of the bivalve mollusk, *Hiatella arctica*, a key food resource of Atlantic walruses.

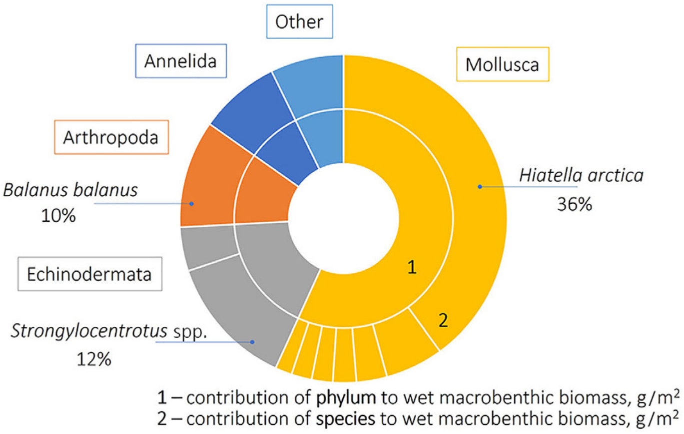

FIGURE 7 Contributions of different phyla and species of macrobenthic invertebrates to overall.

Macrobenthic samples were collected in a depth range from 11 to 176 m. Peak biomass was observed at about 62 m (Station 21_27, 3,994 g/m^2), however, the highest density of stations with high values of biomass was at approximately 15–30 m (Figure 8).

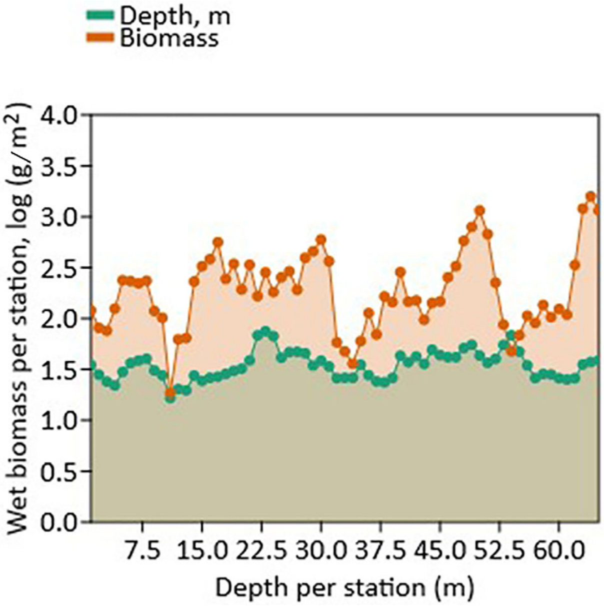

FIGURE 8 Distribution of wet macrobenthic biomass (log g/m^2) per sampling station plotted against depth (m). Points correspond to sampling sites. Biomass values are log-transformed. Missing values and one outlier station at 176 m are disregarded.

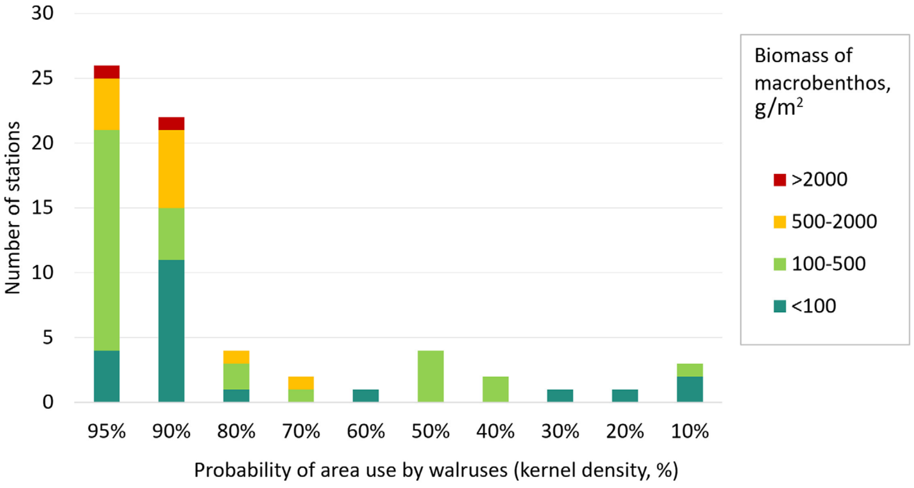

FIGURE 9 The walrus habitat use compared to macrobenthic resource availability: *x*-axis shows the kernel probability of area use (%) by walruses; *y*-axis is the number of stations corresponding to each category and the box plot shows the biomass of macrobenthos (wet mass, g/m^2).

Overlap between kernel density categories and biomass measurements was estimated (Figure 9). The stations with the highest macrobenthic biomass (>2,000 g/m^2) correspond to the 90%–95% kernel density areas, while most of the stations corresponding to key habitat use (10%–50% kernel) had lower biomass values (between 100 and 500 g/m^2; Figure 9).

4 | DISCUSSION

4.1 | Movement parameters

The swimming speed of walruses was previously described as 45.3 km/day ($SD = 8.5$, range 36–55 km/day) based on studies in Canada and Greenland (Dietz et al., 2014) or as 66 km (52–84 km) in the Kara Sea (Semenova et al., 2019). We found lower values of 29 km/day. This might be explained by the fact that both Dietz et al. (2014) and Semenova et al. (2019) described walrus speeds during directional migrations, while in this study most of the animals were moving within one area and most of their movement was likely foraging activity. Also, only one walrus carried out directional migration to the northern coast of Novaya Zemlya, with the daily average speed during this transition at 87.2 km/day.

For the first time, sex and age differences were detected for the swimming speed of walruses and, as a result, in the distances covered per day. Immature animals may have moved more in search of food and resting places due to greater competition, whereas large, mature males may be able to defend access to important feeding and resting locations. This is also confirmed by the water depth of the recorded locations: immature walruses were more often recorded in deeper waters (34.9% of locations were in waters deeper than 100 m), while for mature males and females only 19.8%–20% of all locations were below the 100 m isobath. However, findings require confirmation by field observations. The differences in diving behavior may also be explained by the body size, as has been shown for other pinnipeds, including southern elephant seals, *Mirounga leonina* (McIntyre et al., 2010) and gray seals, *Halichoerus grypus* (Beck et al., 2003). Furthermore, it has been shown for Pacific walruses (*O. r. divergens*) that body size imposes physiological limitations on the diving capacity, resulting in differences in foraging dives between free-ranging immature walruses and adult males that are capable of the longest foraging dives (Noren et al., 2015).

4.2 | Area use

The Franz Josef Land archipelago is an important summer-autumn concentration area for walruses (Born et al., 1995; Gjertz et al., 1992; Gjertz & Wiig, 1992; Timoshenko, 2002). During one of the last monitoring studies in the area, 15 regular coastal haul-outs and a few temporary short-term haul-outs were reported in the archipelago (Gavrilo & Martynova, 2017). The animals tagged in this study visited many of the known haul-out sites and migrated between them making use of the entire archipelago. Notably, this is the first study illustrating the active use of the entire area. A previous tagging study of six walruses in the Franz Josef Land archipelago carried out in 1990–1993 (Wiig et al., 1996), did not show such a wide use of the archipelago.

Also, for the first time in this study Victoria Island was shown as the area of high probability of use by the walruses. As opposed to the actively moving walruses of Franz Josef Land archipelago, the animals tagged at Victoria Island never moved farther than 60 km from the island. This could, however, be due to the lack of data, as Wiig et al. (1996) showed that one walrus tagged within Franz Josef Land archipelago visited Victoria Island.

It took the walrus that migrated to the Novaya Zemlya archipelago 5 days to complete the journey (November 16–21, 2020). In 2020, the ice formation in the Franz Josef Land water started in mid-November in the northeastern part of the archipelago, where the migrating animal was at that time. It could be speculated that the forming pack ice forced the animal to move to Novaya Zemlya. It is possible that the tagged male then spent the winter in the Oransky Islands north of Novaya Zemlya, where walruses are found on the ice during the entire ice period (Chapsky, 1936).

The relationship between the walruses of the Franz Josef Land archipelago and the north of Novaya Zemlya remains unclear, although one genetic study reported no differences between the two groups (Shitova et al., 2015). The Atlantic walrus is typically divided into the Svalbard and Franz Josef Land populations (sometimes also united as Svalbard-Franz Josef Land population) and a separate Kara-Barents Sea population, which includes the north of Novaya Zemlya (Andersen et al., 2017; Stewart et al., 2014). This study provides important new evidence of the exchange of individuals between the Franz Josef Land and Kara-Barents Sea populations, although it is yet unclear how typical this exchange is. Notably, despite a rather significant body of evidence suggesting connectivity between walrus populations of Svalbard and Franz Josef Land (Freitas et al., 2009; Lydersen & Kovacs, 2014; Wiig et al., 1996), data in this study did not show migrations to Svalbard, possibly due to the time of year (too late for long-distance migrations) and limited size of the data set (both in terms of number of tagged animals and duration of data collection).

Of particular interest for further research in the context of the ongoing climate change is the period of ice cover formation and changes in animal movements during this period. The changes in the sea ice have been to some extent predicted through modeling; however, there has been little investigation of how these changes will affect walruses (Jay et al., 2012). This study provides limited insight into the impacts of ice on movement patterns, as there was only one animal with a working PTT during the ice formation period. That walrus was in the southwestern part of the archipelago and by the time the ice reached this area, the PTT stopped transmitting. Wintering areas were previously noted in the southern islands of Franz Josef Land (Freitas et al., 2009) and tagged walrus could use this area for winter habitats.

4.3 | Foraging resources

Walruses typically forage in waters less than 80 m deep due to combination of the energy efficiency of the dives and distribution range of their key feeding items, bivalve mollusks (Born et al., 2003; Jay et al., 2001; Noren et al., 2015). Some exceptional cases of foraging activity as deep as >250 m have been recorded (Born et al., 2005), but normally walruses tend to feed in shallow waters to maximize foraging time on the seafloor, and there are also certain physiological constraints, including the ontogeny of muscle biochemistry, preventing walruses from exploiting deeper areas as described for Pacific walruses (Noren et al., 2015). The choice of foraging grounds by walruses is likely determined by the combination of depths, type of bottom sediments, and the structure of bottom communities (Gavrilo & Martynova, 2017). This study is a first attempt to estimate available foraging resources for walruses in Franz Josef Land.

The key foraging items for Atlantic walruses in the research area are the soft-sediment bivalve mollusks. Some polychaetes and other larger invertebrates can also contribute to foraging macrobenthic biomass. Sea urchin, *Strongylocentrotus* spp., was one of the more dominant macrobenthic biomass in the area. It has been previously reported in the gut contents of Atlantic walruses, therefore it can be considered as a foraging item, although the nutritional value of it is less clear (Fisher & Stewart, 1997). The bulk of the diet of Atlantic walruses is formed by large bivalve mollusks, in particular *Mya truncata*, *Hiatella arctica*, and *Serripes groenlandicus* (Born et al., 2003). All three species have been found in the research area and *H. arctica* was the overall dominant species in biomass at most of the stations (Figure 6). *H. arctica* is the key foraging item for the walruses in the area forming 36% of benthic biomass (Figure 7) with average wet weight of a single mollusk of approximately 3 g, and maximum weight of 10 g. Mollusks from Astartidae family are also shown to have an important role in the Atlantic walrus diet in other regions (Gebruk et al., 2021), and although they were not as common across sampling sites, they were important more locally, contributing as much as 82% of biomass at individual stations (*Astarte borealis*, station IE-2021-4). Other mollusk species that had high biomass locally include *Mya truncata* and *Musculus discors*.

The foraging grounds of walruses are typically characterized by the presence of large bivalve mollusks, and relatively high faunal diversity of macrobenthos (Gebruk et al., 2021; Sejr et al., 2000). A total of 299 species of macrobenthic invertebrates were identified in the research area (Kokorin et al., unpublished data). In general, benthic fauna identified in this study is typical for the area (Dahle et al., 2009; Denisenko, 2013); however, biomass values (mean 420 ± 14 g/m^2 with a maximum of 3,994.27 g/m^2) were nearly two times higher than previously reported from Franz Josef Land (maximum value of 2,146 g/m^2 according to Dahle et al., 2009). Observed macrobenthic biomass was also noticeably higher than in the other foraging grounds of Atlantic walruses in the region, e.g., in the Pechora

Sea between the Vaigach and Dolgy Islands (mean biomass of 147 ± 7 g/m^2 with a maximum of 693.47 ± 39.87 g/m^2 (Gebruk et al., 2021) and in the East Greenlandic fjord (maximum biomass of 238 g/m^2; Sejr et al., 2000).

Most recent studies estimate energy needs of an individual adult walrus as approximately 23 kg of foraging biomass/day (Skern-Mauritzen et al., 2022), corresponding to 8.4 tons of macrobenthos annually. Based on the grab samples analyzed in this study, foraging capacity of the research area can be estimated as 200–300 tons of macrobenthic biomass. However, it is important to recognize the limitations of this estimate, including the limitations of the sampling method. Some burrowing mollusks including *Mya truncata* are hidden too deep in the sediment for the benthic grabs to capture them; however, they are still accessible for walruses that can dig them out with a specially adapted digging snout (Kastelein & Mosterd, 1989), and therefore contribution from burrowing in-fauna is likely underestimated.

The densest aggregations of bivalve mollusks were found on the soft sediments within the 15–30 m depth range (Figure 8), which is a very suitable habitat for walrus foraging. Similar depth distribution of foraging macrobenthic biomass was reported in the Pechora Sea (the majority of available macrobenthic biomass was found in a depth range of 25–30 m; Denisenko et al., 2019; Gebruk et al., 2021) and in East Greenlandic fjord (maximum macrobenthic biomass at 35 m according to Sejr et al., 2000). It is likely that the study area is a particularly important habitat for Atlantic walruses because of high species diversity and biomass of macrobenthic invertebrates. However, this work did not show a clear relationship between the habitat utilization by the walruses estimated by the kernel analysis and distribution of macrobenthic biomass—most of the areas of high use by the walruses did not correspond with the stations of maximum macrobenthic biomass (Figures 4, 6, 9). This is probably because the high utilization areas identified by satellite telemetry were near the haul-out sites while the entire area of the archipelago within the 100 m depth range is used for foraging and can be considered an important feeding ground. Perhaps this also indicates a high spatial heterogeneity in the distribution of macrobenthos in this region, and to obtain more reliable data, continuous scanning of the seabed could provide better insight into spatial distribution of macrobenthos than individual grab samples.

4.4 | Conservation considerations and conclusions

The Franz Josef Land archipelago and its surrounding waters in the northern Barents Sea are identified as an Ecologically and Biologically Significant Marine Area (EBSA) by the Convention on Biological Diversity (CBD, 2023) and as an Area of Heightened Ecological Significance by the Arctic Council (AMAP/CAFF/SDWG, 2013) with the importance as the haul-outs and feeding grounds for the Atlantic walruses being one of the key nomination criteria. The archipelago also has a high conservation status in Russia and from 2009 it is included in the Russian Arctic National Park with restrictions on shipping, fisheries, and offshore development, but still allowing limited tourism and scientific research. However, available scientific data on the walrus population of Franz Josef Land remain scarce. This study contributes new and important data on the areas of use within the archipelago as well as on Victoria Island; suggests statistically significant differences between the movement speed and travel distance of male, female, and immature walruses in the area; provides evidence of connectivity between Franz Josef Land and Novaya Zemlya walruses; and describes distribution, biomass, and composition of available macrobenthic foraging resources in the area. To gain a better understanding of the connectivity of populations and the impacts of the retreating sea ice on the habitat use, food availability and migrations of Atlantic walruses in the Barents region, a long-term environmental monitoring program is desired that would encompass satellite telemetry, collection of environmental data, and benthic assessments.

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AUTHOR CONTRIBUTIONS

Maria Solovyova: Conceptualization; data curation; formal analysis; methodology; visualization; writing – original draft. **Anna Gebruk:** Conceptualization; data curation; project administration; writing – original draft; writing – review and editing. **Svetlana Artemyeva:** Conceptualization; methodology; project administration; writing – review and editing. **Vyatcheslav Rozhnov:** Resources; visualization; writing – review and editing. **Artyom Isachenko:** Resources; validation; writing – review and editing. **Renata Lazareva:** Resources; supervision; validation; writing – review and editing. **Pavel Chukmasov:** Data curation; writing – review and editing. **Dmitry Glazov:** Methodology; validation; writing – review and editing. **Yulia Ermilova:** Formal analysis; visualization; writing – review and editing. **Alexander Kokorin:** Data curation; writing – original draft; writing – review and editing. **Maria Mardashova:** Data curation; formal analysis; writing – original draft; writing – review and editing. **Nikolay Shabalin:** Funding acquisition; supervision; writing – review and editing.

ORCID

Anna Gebruk https://orcid.org/0000-0002-2516-8286
Viatcheslav V. Rozhnov https://orcid.org/0000-0002-2142-0763
Dmitry Glazov https://orcid.org/0000-0001-7707-5500

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