Shifts in site use by spring-staging swans *Cygnus* sp., from traditional to artificially reclaimed habitat in the Gulf of Finland

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Abstract

Variation in the abundance and habitat use recorded for three swan species – the Bewick's Swan *Cygnus columbianus bewickii*, Whooper Swan *Cygnus cygnus* and Mute Swan *Cygnus olor* – at their main spring staging areas in the coastal waters of Neva Bay, Gulf of Finland, were studied from 2018–2022. The count sites were grouped into two distinct habitat types: "traditional" (defined as natural shallow coastal water areas with low levels of anthropogenic disturbance, supporting a range of emergent vegetation), and "reclaimed" (defined as the shallow waters created behind artificial sand embankments during and following their creation). The numbers of swans using traditional sites varied widely, but never exceeded 121 Bewick's Swans and 292 Whooper Swans at any one site. At the reclaimed sites, numbers of the two yellow-billed swans increased progressively following completion of the reclamation work, with peak counts ranging from 0–442 Bewick's Swan and up to 160 Whooper Swans. In contrast, Mute Swans in any one area never exceeded two individuals. Surveys of potential food plants used by swans in summers 2021 and 2022 demonstrated the prevalence of Perfoliate Pondweed *Potamogeton perfoliatus* at the main stopover sites close to reclaimed areas, together with Hairlike Pondweed *Potamogeton trichoides* and the green algae *Cladophora glomerata*. These results suggest that, with the continued gradual colonisation by aquatic vegetation of shallow waters formed near reclaimed areas, there is potential for the number of swans feeding in these areas to increase, provided that the sites are protected (*e.g.* from disturbance by human activity) and continue to provide suitable habitats for the swans.

Key words: Bewick's Swan, foraging, migration, Mute Swan, population monitoring, submerged macrophytes, Whooper Swan.

Neva Bay in the Russian part of the Gulf of Finland, Baltic Sea, is well known as a stopover area for migrating waterfowl, including large numbers of spring-staging swans. Birds from the East Atlantic Flyway pass through the area from wintering sites in western Europe to breeding areas in northern parts of European Russia. The shallow coastal waters of Neva Bay offer important areas for swans to rest and feed during migration because spring food resources at stopovers elsewhere in the region are limited, both by the extent and duration of ice cover, and by the general lack of aquatic sites with an abundance of high-energy vegetation as food at a suitable depth for feeding (Nolet & Drent 1998; Nolet *et al.* 2001, 2008; Rees & Beekman 2010; Nuijten *et al.* 2014). Local disruption to swans resting and refuelling during migration can lead to decreases in local staging abundance and, together with conditions encountered at the nesting sites, contribute to reduced breeding success (Beekman *et al.* 2002).

Since 1995, the Northwest European Bewick's Swan *Cygnus columbianus bewickii* population has been in decline (Rees & Beekman 2010; Beekman *et al.* 2019), while numbers of Whooper Swans *Cygnus cygnus* have been increasing (Laubek *et al.* 2019). Surveys conducted in the early 21st century have shown a drop in the numbers of Bewick's Swans staging in Neva Bay during 2012–2018 (decreasing from 460 to 103 individuals), which may be attributable not only to the population decline but to the increasing pace of construction and reclamation of natural shallow water habitats with abundant emergent and submerged vegetation, for conversion to terrestrial habitats (Rymkevich *et al.* 2012; Zaynagutdinova *et al.* 2019), with the smaller numbers of Whooper Swans (5–65 birds) remaining relatively stable over the same period (Zaynagutdinova *et al.* 2019). In contrast, numbers of Mute Swans *Cygnus olor* are currently increasing as the species spreads in the Leningrad region. Since 1990, Mute Swans have bred regularly on the Kurgalsky Peninsula (Kouzov 2016; Kouzov *et al.* 2024) and two Mute Swan nests were found near Kotlin Island in Neva Bay in 2017 (Fedorov 2018). Since then, numbers of Mute Swans nesting in Neva Bay have continued to grow (Zaynagutdinova *et al.* 2020).

Our study aimed to determine whether the distribution and abundance of swans using the main migration stopover sites in Neva Bay have changed in more recent years, between 2018 and 2022. In particular, we tested our prediction that the swans would respond positively to new feeding opportunities as these were created, and to a decrease in anthropogenic disturbance near reclaimed sites following a cessation of construction work in the vicinity. We also investigated the expansion of Mute Swans in the area, considering that the abundance and distribution of this species was less likely to be influenced by construction work in Neva Bay, because it is more closely associated with the large areas of reed beds along the coast of Neva Bay, which provide nesting sites for the species (Zaynagutdinova *et al.* 2019; Kouzov *et al.* 2021, 2024).

Methods

The study was conducted in Neva Bay, in the Russian part of the Gulf of Finland

(59.95°N, 30.00°E), in the spring and summer of 2018–2022. We defined 16 count sites, used as stopovers by swans during their migration. Each site comprised extensive areas of shallow coastal waters, with the survey area for each site determined by the accessible length of the coastline, and observations were made up to 1 km out from the shore (*i.e.* limited by the maximum range of telescopes and ability to identify birds to species level). No swans were found in water areas > 1 km from the shoreline during the surveys, perhaps reflecting an increase in water depth to > 1 m, which would be too deep for the birds to obtain food even by up-ending. The area of each count site was calculated using QGIS and these are presented in the Supporting Materials (Table S1).

For each site, we distinguished between "reclaimed" habitats, which were created by dredging works, and "traditional" habitats with a predominance of natural biotopes. Reclaimed areas (*e.g.* Fig. 1a,b) were previously aquatic areas but are now sandy substrate areas lacking inland water bodies, created for the construction of residential buildings. During the reclamation work, however, areas of shallow water formed around the site as a result of large amounts of sand being deposited as part of the construction process. In due course, Whooper Swans and Bewick's Swans started feeding in these shallow waters and numbers associated with the reclaimed areas were counted during our surveys. "Traditional" areas (Fig. 2) are coastal shallow waters with submerged vegetation, which have an optimal depth for feeding birds and not been observed to have suffered impacts from hydrotechnical works associated with St. Petersburg Flood Prevention Facility Complex (built in 1979–2011). Those constructions changed the water exchange regime with the rest of the Gulf of Finland and contributed to the emergence of larger areas with underwater and surface vegetation in the Neva Bay. The main difference between reclaimed and traditional sites was the proximity to the reclamation activity and the timing of reclamation works (Table 1).

Counts were not carried out regularly at all sites; however, sites with the largest numbers of migrating swans were observed several times over the survey period in most years (Supporting Materials Table S2). The dates of the counts varied from year to year, but at most sites which supported large numbers of swans they covered the entire migration period (Supporting Materials Table S3). The area of coastal water monitored was calculated for each site, based on the length of the survey route along the coastline, with the route being to the maximum possible distance travelled by the counters until restricted by access to the coast. Rather than giving the average density of birds from the intermittent counts, we present maximum values, which better reflect the capacity of the site, taking into account the known extent of the water area being monitored (Supporting Materials Table S1). For the traditional sites, migrating swans were counted in spring on waters along the established survey routes. Surveys on reclaimed sites began when we found or received information from publications, volunteers, and citizen science sources (social networks and applications) about the appearance of any swans in these places.

Figure 1. Reclaimed area Sea Façade in (a) 2008, and (b) 2022.

Figure 2. Traditional swan staging area – "Northern coast of Neva Bay" – with above-water and submerged vegetation.

Since the study was conducted in the city, the likelihood that the birds would not be seen was low. The counts (made using binoculars and telescopes) started before the ice melt and arrival of swans and ended once the last Whooper and Bewick's Swans had left the Neva Bay area, with the number of swans of each species being recorded. In late spring and summer, we also surveyed Mute Swans nesting in the area.

During the summer, to assess the potential feeding resources available to swans, we described the extent of aquatic vegetation in 40 10 × 10 m sample plots at the three reclaimed sites holding the most swans during spring migration (Kanonersky Island, Sea Façade and Lakhta, near Dekabristov Island; sites 8, 9 and 10 in Fig. 3 and Supporting Materials Fig. S1). Vegetation was described by determining the percentage cover within quadrats (1 × 1 m), with 10 quadrats studied within each 10 × 10 m sample plot. The final percentage cover of a 10 × 10 m plot was then calculated as the average value recorded for each plant species in the ten 1 × 1 m quadrats. All plants were identified to species level (Tsvelev 2000). Geobotanical descriptions were conducted at a depth of no more than 1 m, and all sites were characterised by uniform sandy substrates.

Statistical analysis was conducted using STATISTICA 12. Given the small sample sizes and significant deviation of the data

Table 1. Differences in construction work location and schedule at traditional and reclaimed sites.

Traditional sites	Reclaimed sites
Reclamation work during the construction of a complex of protective structures against floods in St. Petersburg, in 1979–2011.	Recent reclamation work took place from 2005–2009 to 2019 directly at the observation sites or close to them.
The sites are located at a distance of 4–5 km from a complex of structures which protect against flooding (except for Western Kotlin).	The sites are located at a distance of 1–2 km from reclamation works at the observation sites.

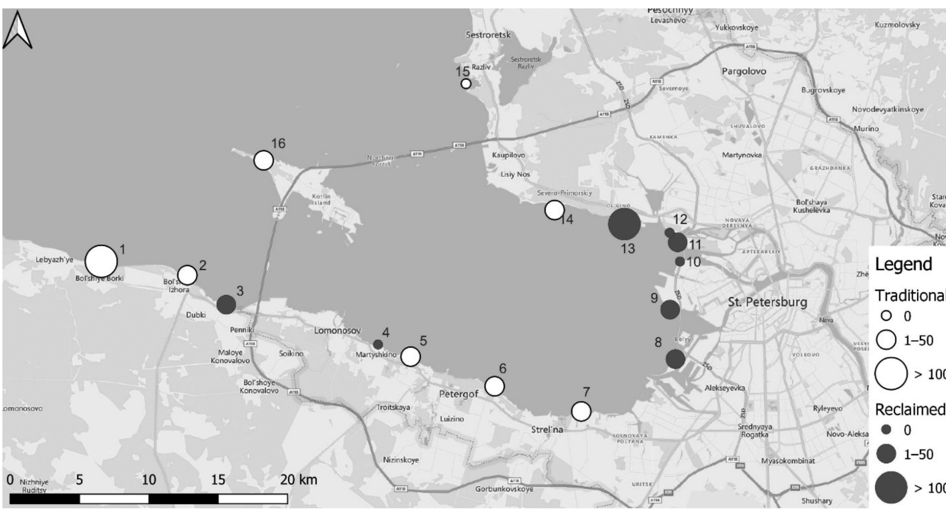

Figure 3. Distribution of Whooper Swans at all sites in the study area during 2018–2022 (maximum numbers for each site).

from a normal distribution (Shapiro-Wilk's test), non-parametric Kruskal-Wallis tests were used to compare the extent of vegetation cover between the reclaimed sites. The swans' distribution was analysed and presented using QGIS. We analysed maximum seasonal numbers and densities, as they reveal the capacity of stopovers. Densities (birds km^{-2}) are presented in parentheses next to the maximum numbers at the site.

Results

Whooper Swan

Only two of the Whooper Swan stopover sites – Chaika-Lebyazhye (a traditional site) and Lakhta-Olgino (a reclaimed site) – were seen to hold > 100 individuals during the study period (Fig. 3).

Up to a maximum of 292 birds (density = 86 birds km^{-2}) were counted among traditional sites (recorded at Chaika-Lebyazhye in 2019), but numbers were lower in 2018, 2020, 2021 and 2022. A maximum of only 24 birds (5 birds km^{-2}) were counted at the traditional sites in 2020 (*i.e.* on the Northern coast of Neva Bay), and 13 (7 birds km^{-2}) in 2022 (at Bolshaya Izhora; see Table 2 and Supporting Materials Table S4).

Maximum daily counts of Whooper Swan on reclaimed sites in the first two years of the study were 57 (27 birds km^{-2}) at Lakhta-Olgino in 2019, increasing to 160 (76 birds km^{-2}) at the same site in 2022 (Table 2 and Supporting Materials Table S4).

Table 2. Maximum number of Whooper Swan per count day at all sites during the study period.

Count site	**Maximum number of individuals per count day**				
	2018	**2019**	**2020**	**2021**	**2022**
Traditional					
1. Chaika-Lebyazhye	85	292	7	7	2
2. BolshayaIzhora	–	–	15	9	13
5. Petergof	0	0	–	3	0
6. Southern coast of Neva Bay	–	0	8	2	6
7. Strelna	0	7	0	8	0
14. Northern coast of Neva Bay	13	0	24	22	6
15. Tarkhovka	–	–	–	0	–
16. Western Kotlin	8	–	–	0	0
Reclaimed					
3. Bronka	0	–	0	2	20
4. Martyshkino	0	–	0	0	–
8. Kanonersky Island	–	–	0	22	10
9. Sea Façade	–	10	31	37	32
10. Dekabristov Island	–	–	–	0	–
11. Zenit Arena	–	–	–	1	–
12. 300th Anniversary of St. Petersburg Park	–	–	0	0	–
13. Lakhta-Olgino	0	57	44	10	160

Total Whooper Swan numbers counted at all reclaimed sites (combined) increased from 0 in 2018 and 67 in 2019 to 222 individuals in 2022, compared with 106 at traditional sites in 2018 and 27 in 2022 (Table 2). The proportion of Whooper Swans recorded on reclaimed sites thus increased from zero in 2018 (when construction work was still ongoing at Lakhta-Olgino; Table 3) to 89% in 2022.

Bewick's Swan

The maximum number of Bewick's Swans counted at traditional sites, 219 birds (density = 65 birds km^{-2}), came from Chaika-Lebyazhye in 2022. Of the other traditional sites, Bolshaya Izhora held 146 (77 birds km^{-2}), also in 2022, whilst counts on the Northern coast of Neva Bay recorded 121 (25 birds km^{-2}) in 2020, 101 (21 birds km^{-2}) in 2018 and 96 (20 birds km^{-2}) birds in 2022 (Fig. 4, Table 4, Supporting Materials Table S5). Numbers declined slightly at Petergof, Southern Neva Bay and Strelna over the study period to 2022 (Table 4).

The highest daily maximum number of Bewick's Swans counted at reclaimed sites was recorded at Lakhta-Olgino with 442 (209 birds km^{-2}) in 2022. Daily maxima also increased at other reclaimed sites, for example at the Sea Façade where numbers rose from 101 (67 birds km^{-2}) in 2020 to 144 (96 birds km^{-2}) in 2022, and at Kanonersky Island from 3 (2 birds km^{-2}) birds in 2020 to 57 (46 birds km^{-2}) in 2022 (Table 4, Supporting Materials Table S5).

Table 3. Timing of completion of alluvial works and appearance of Whooper Swans and Bewick's Swans at the site. The number of years between the cessation of the works and the first appearance of the swans is given in parentheses for each species.

Reclaimed count site	Date of completion of reclamation work	Year first Whooper Swans appeared (no. of years from cessation of reclamation works)	Year first Bewick's Swans appeared (no. of years from cessation of reclamation works)
3. Bronka	2015	2021 (6)	2018 (3)
4. Martyshkino	2015	–	2018 (3)
8. Kanonersky Island	2016	2021 (5)	2020 (4)
9. Sea façade	2014	2019 (5)	2020 (6)
10. Dekabristov Island	2016	–	–
11. Zenit Arena	2016	–	2021 (5)
12. 300th Anniversary of St. Petersburg Park	2009	2021 (12)	–
13. Lakhta-Olgino	2019	2019 (0)	2019 (0)

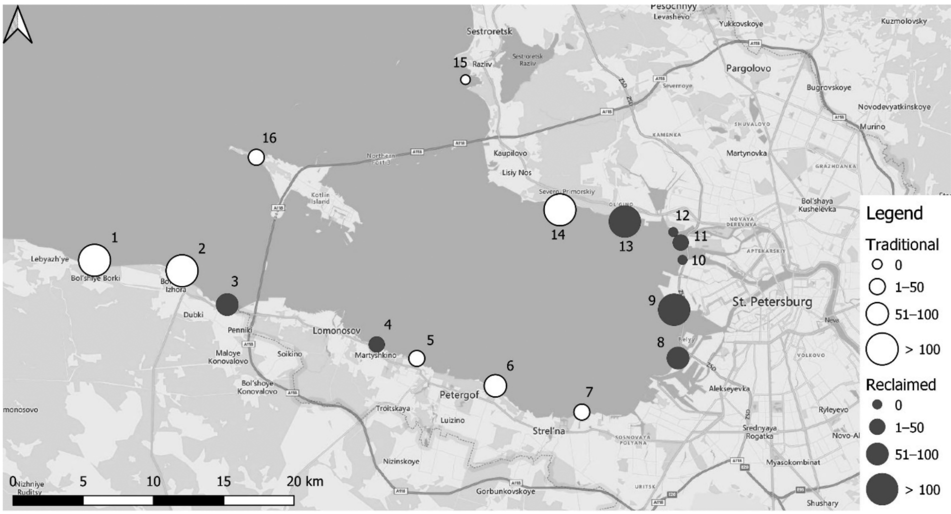

Figure 4. Distribution of Bewick's Swans at all sites in the study area during 2018–2022 (maximum numbers for each site).

In recent years, the distribution of birds has begun to shift towards reclaimed sites, although some traditional sites retain high number of birds, for instance the 219 (65 birds km^{-2}) at Chaika-Lebyazhye and 146 (77 birds km^{-2}) at Bolshaya Izhora in 2022. Bewick's Swans have used traditional sites on the Northern coast of Neva Bay somewhat consistently during 2018–2022 (range = 33–101 birds each year; Table 4), whereas numbers at the reclaimed site of Sea Façade rose from zero to 144 (96 km^{-2}) birds and at Lakhta-Olgino from zero to 442 (209 km^{-2}) birds, with the swans returning within 6 and 0 years respectively after the cessation of construction work at these sites (Table 3, Fig. 4).

Mute Swan

A maximum of eight Mute Swan per count day was recorded among reclaimed sites (at Lakhta-Olgino in 2020) and nine among traditional sites at (Western Kotlin in 2021; Table 5). At two traditional sites (the Northern and Southern Coasts of Neva Bay) five and six individuals were recorded, respectively, in 2021. Numbers failed to exceed three individuals at other traditional areas and the species was largely absent from reclaimed sites (with counts of two birds at Bronka in 2018 and two and eight birds at Lakhta-Olgino in 2019 and 2020; Table 5). The density of Mute Swan at each site is presented in the Supporting Materials (Table S6).

Food availability

One species of submerged macrophyte – Perfoliate Pondweed *Potamogeton perfoliatus* – which is considered a potential food for swans (Dirksen *et al.* 1991) was present in single species stands dominating the sea bed at all reclaimed sites. Hairlike Pondweed *Potamogeton trichoides* and the green algae

Table 4. Maximum number of Bewick's Swan per count day at all sites during the study period.

Count site	Maximum number of individuals per count day				
	2018	2019	2020	2021	2022
Traditional					
1. Chaika-Lebyazhye	17	36	107	8	219
2. BolshayaIzhora	–	–	11	5	146
5. Petergof	5	36	–	4	3
6. Southern coast of Neva Bay	–	0	56	6	1
7. Strelna	0	2	20	2	0
14. Northern coast of Neva Bay	101	20	121	33	96
15. Tarkhovka	–	–	–	0	–
16. Western Kotlin	6	–	–	42	40
Reclaimed					
3. Bronka	4	–	4	60	5
4. Martyshkino	2	–	16	9	–
8. Kanonersky Island	–	–	3	18	57
9. Sea Façade	–	0	101	34	144
10. Dekabristov Island	–	–	–	0	–
11. Zenit Arena	–	–	–	4	–
12. 300th Anniversary of St. Petersburg Park	–	–	0	0	–
13. Lakhta-Olgino	0	100	122	119	442

Cladophora glomerata were also observed to a limited extent at Lakhta-Olgino (Site 13) and Kanonersky Island (Site 8). Green algal growth was not common but was most extensive at Sea Façade.

The percentage cover of Perfoliate Pondweed did not differ significantly between the three reclaimed sites sampled in 2021 (Kruskal-Wallis test: $H_2 = 2.30$, $P = 0.32$, n.s.; Fig. 5a) or in 2022 (Kruskal-Wallis test: $H_2 = 0.85$, $P = 0.65$, n.s.; Fig. 5b). The greatest percentage cover of submerged macrophytes occurred at Sea Façade, with up to 79% cover in some plots. At two plots on Kanonersky Island, a high percentage cover of Perfoliate Pondweed was also recorded – from 70–80% in 2022. The percentage cover of Perfoliate Pondweed across all areas was similar in 2021 and 2022.

The percentage cover of Hairlike Pondweed was generally very much lower and more variable between years, but

Table 5. Maximum number of Mute Swan per count day at all sites during the study period

Count site	Maximum number of individuals per count day				
	2018	**2019**	**2020**	**2021**	**2022**
Traditional					
1. Chaika-Lebyazhye	0	0	2	0	0
2. BolshayaIzhora	–	–	0	0	2
5. Petergof	2	0	–	1	0
6. Southern coast of Neva Bay	–	2	3	6	2
7. Strelna	2	0	2	1	3
14. Northern coast of Neva Bay	2	0	5	5	1
15. Tarkhovka	–	–	–	0	–
16. Western Kotlin	6	–	4	9	–
Reclaimed					
3. Bronka	2	–	0	0	0
4. Martyshkino	0	–	0	0	–
8. Kanonersky Island	–	–	0	0	0
9. Sea Façade	–	0	0	0	0
10. Dekabristov Island	–	–	–	0	–
11. Zenit Arena	–	–	–	0	–
12. 300th Anniversary of St. Petersburg Park	–	–	0	0	–
13. Lakhta-Olgino	0	2	8	0	0

significantly higher at Lakhta-Olgino than at the other two sites in both 2021 (Kruskal-Wallis test: $H_2 = 21.08$, $P < 0.001$) (Fig. 6a) and 2022 (Kruskal-Wallis test: $H_2 = 9.89$, $P = 0.007$; Fig. 6b).

The percentage cover of green algae did not differ significantly between the reclaimed sites in either 2021 (Kruskal-Wallis test: $H_2 = 3.62$, $P = 0.16$, n.s.; Fig. 7a) or in 2022 (Kruskal-Wallis test: $H_2 = 4.877$, $P = 0.087$, n.s.; Fig. 7b). The low level of statistical significance may be due to the high percentage cover of green algae in a few plots on the Kanonersky Island site introducing very high variance in the data.

Discussion

Results of studies conducted in the Neva Bay of the Gulf of Finland since the 2000s indicate that the numbers of Bewick's and Whooper Swans staging at the site each spring is gradually decreasing, which may be

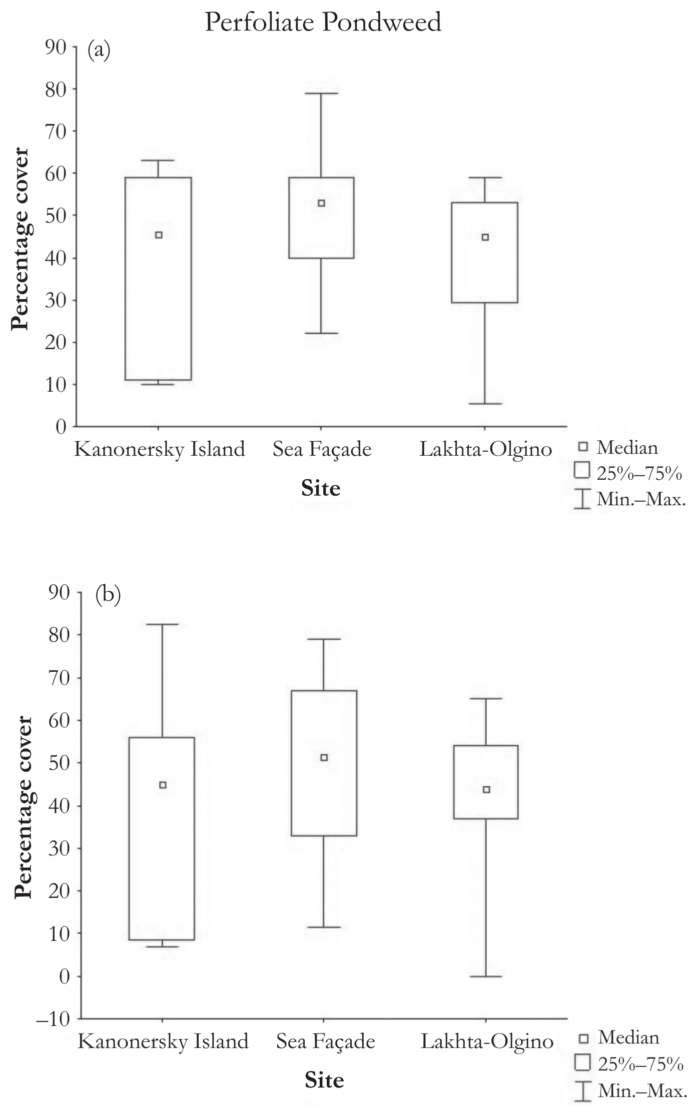

Figure 5. Percentage cover of Perfoliate Pondweed at reclaimed sites in (a) 2021, and (b) 2022.

caused by both natural and anthropogenic factors. Counts in the same area, made in 1975, found *c.* 1,000–2,000 Bewick's Swans and 300–400 Whooper Swan at the mouth of the Smolenka River and on the Lakhtinskaya Shoal, located near the Sea Façade and Lakhta-Olgino sites (Rychkova 2009). Our records showed much lower maximum numbers both in these areas – 442 and 160 individuals, respectively, at Lakhta-Olgino, and 144 and 32 individuals at Sea Façade. The data presented show a

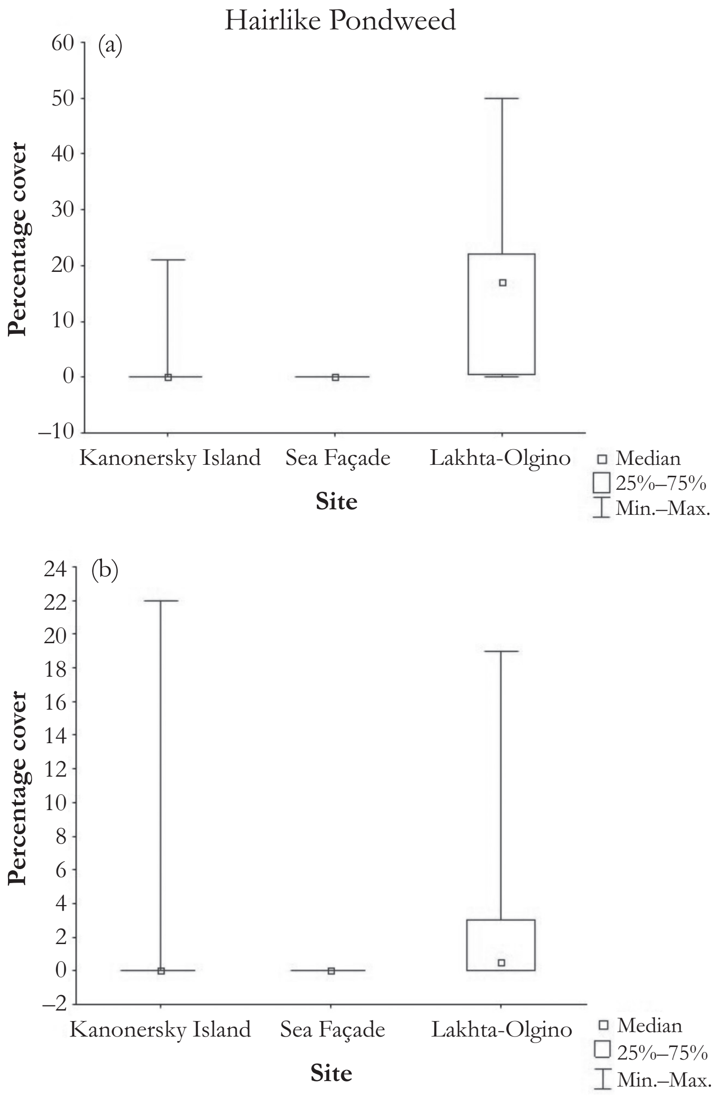

Figure 6. Percentage cover of Hairlike Pondweed in reclaimed sites in (a) 2021, and (b) 2022.

decrease in the total number in the Neva Bay since the mid-20th century, despite differences in the distribution of birds between sites. For surveys up until 2018 (*e.g.* Zaynagutdinova *et al.* 2019), there was no division into traditional and reclaimed sites because the presence of birds was not expected near areas subject to reclamation, especially those located near urban areas, but the swans' distribution has since changed.

Despite the overall long-term decline in swans spring-staging on Neva Bay, numbers

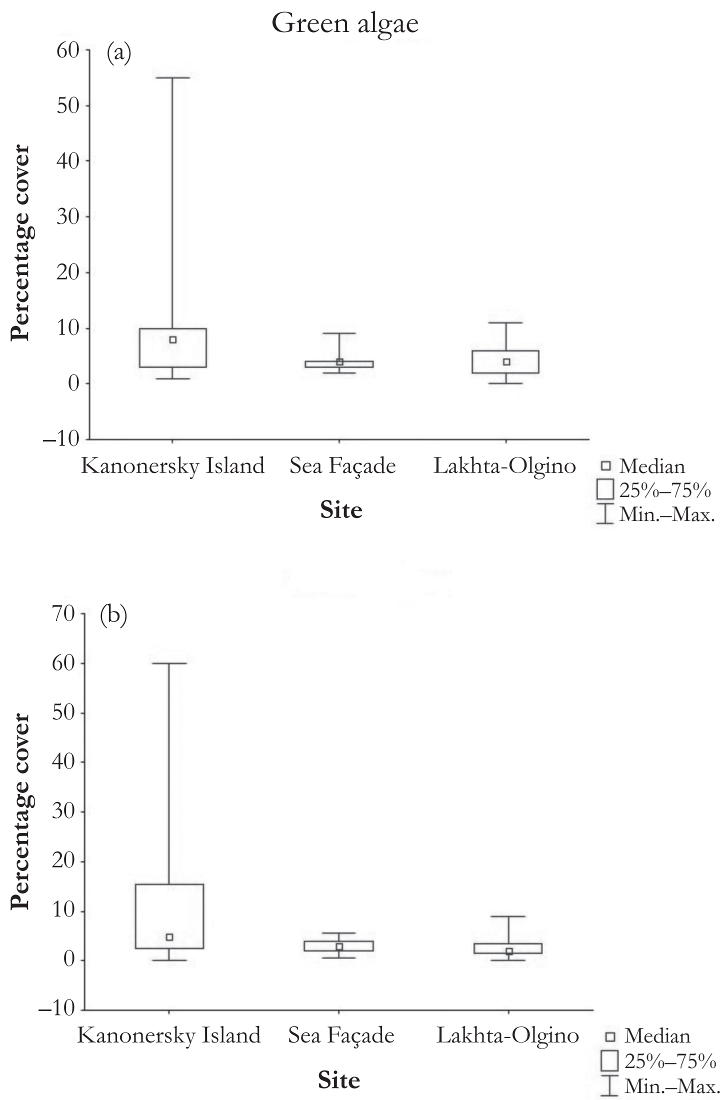

Figure 7. Comparison of the percentage cover of green algae at reclaimed sites in (a) 2021, and (b) 2022.

of Bewick's and Whooper Swans increased near the reclaimed areas during the study period. A sharp decline in the number of birds at Lakhta-Olgino had been observed in 2013, associated with the start of hydraulic engineering work for construction of the Lakhta Centre complex in 2012 (Zaynagutdinova *et al.* 2019), which resulted in an increase in water turbidity which could affect food resources and hence numbers of

Bewick's and Whooper Swans in this area. After declines in both species, numbers increased again to 442 and 160 individuals, respectively, in 2022. In other reclaimed areas, monitoring started only in 2018, when the first swans appeared there. Their numbers have increased to 100–150 individuals per count by 2022. The presence of extensive areas of submerged vegetation in shallow waters near reclaimed land suggests a possible relationship between this and the abundance of both swans species staging these sites.

During 2018–2022, breeding Mute Swans colonised and began to spread in Neva Bay. The first nesting birds were recorded in 2017 near Kotlin Island (Fedorov 2018). Nesting attempts were observed in 2020 on the southern coasts of Neva Bay, when several birds were found to be nesting (Zaynagutdinova *et al.* 2020; Milto 2020). Four nests were found near Kotlin Island in 2020 and five in 2021. Considering the high dispersal capacity of the species, it is expected that the species will continue to further spread east (Krivonosov 1991).

The percentage cover of the Perfoliate Pondweed was high at each of the reclaimed sites. This species is a valuable food resource for swans (Rees & Beekman 2010), growing in abundance at water depths that make it highly accessible for consumption at reclaimed sites. Swans presumably feed on the rhizomes of this species (which germinate from turion buds in May), or on the turions themselves which overwinter at the bottom of ponds, lakes, and coastal waters (Wolfer & Straile 2004). Rhizomes can form a large biomass in sandy bottoms of the reclaimed feeding areas, but are less abundant in sandy-gravel bottoms (Ozimek *et al.* 1976). Considering the high numbers of swans in the areas, Perfoliate Pondweed at spring migration sites near alluvial areas may be of no less importance than Fennel Pondweed *Stuckenia pectinata*, an important swan food on more traditional sites mainly in autumn and winter (Beekman *et al.* 1991; Dirksen *et al.* 1991; Klaassen & Nolet 2007).

It is also necessary to note the potential importance of the green algal species *Cladophora glomerata*, which accumulates biomass in May when the water temperature exceeds 10°C (Whitton 1970). Before the growth season, swans consume the wintering mats of green algae accumulated in the previous summer (Kouzov *et al.* 2021). During the growth season, however, the nutritional profitability of Perfoliate Pondweed will exceed that of algae and be higher when the contribution of green algae to swan diet will likely be insignificant (Gubelit & Berezina 2010; Kouzov *et al.* 2021).

Although of lesser biomass, the Hairlike Pondweed can also potentially be used as food by swans during its growth season at the reclaimed sites.

Further redistribution of birds in the water area of Neva Bay may depend on the implementation of new dredging works to create further reclaimed areas, which can lead to local suppression of underwater vegetation due to mechanical destruction, greater turbidity and increased water depth (Zaynagutdinova *et al.* 2019). Evidence shows that underwater vegetation, in particular Perfoliate Pondweed, can recover from environmental degradation in a short time (Zhigulsky *et al.* 2020). For example, the Lesser Pondweed *Potamogeton pusillus* settles in shallow water denuded of substrates a few years after dredging works (Nowak *et al.* 2015), potentially allowing swans to exploit such a biotope as a feeding area if there are favourable feeding conditions.

It is not currently possible to say whether traditional sites are losing their value for feeding swans. We lack knowledge of the food resources needed to be able to understand these patterns. Coastal shallow waters, created as a result of reclamation activities, should be preserved and protected in the case of construction of new ones. There should also be some regional coordination to ensure the protection of traditional areas of bird migration stopovers, including the maintenance of appropriate levels of food resources for swans within them.

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Photograph: Bewick's Swans at a staging site on the Gulf of Finland, near St Petersburg, by Anton Kubyshkin.