

Seasonal changes in the diet of Mute Swans *Cygnus olor* in the recently colonised eastern Gulf of Finland

SERGEI A. KOUZOV^{1,*}, YULIA I. GUBELIT², ANNA V. KRAVCHUK¹,
ELENA M. KOPTSEVA¹, ELMIRA M. ZAYNAGUTDINOVA³ &
VALENTINA N. NIKITINA¹

¹Department of Applied Ecology, Saint-Petersburg State University, Saint-Petersburg, Russia.

²Laboratory of Freshwater and Experimental Hydrobiology,

Zoological Institute of the Russian Academy of Science, Saint-Petersburg, Russia.

³Department of Vertebrate Zoology, Saint-Petersburg State University, Saint-Petersburg, Russia.

*Correspondence author. E-mail: skouzov@mail.ru

Abstract

Mute Swans have expanded their Russian breeding range since the 1950s, and first colonised the eastern part of the Gulf of Finland in 1987. Diet analysis showed that the pre-breeding and breeding season diet of Mute Swans in this region consists entirely of soft aquatic plants. In late winter and early spring (prior to active vegetation growth) the birds fed on the previous year's growth of green filamentous algae *Chladophora* sp., which had been displaced by currents and storms from wintering mats on the bottom substrate. Diatoms were an increasingly important component of the swans' diet during the pre-nesting period, from a month before egg-laying and also during egg-laying, when diatom abundance was peaking but the growth of vascular aquatic plants and algae had yet to commence. Later, during egg-laying and incubation, Mute Swans began to feed on the new season's growth of aquatic vascular plants and filamentous algae. Given the timing of diatom intake, we suggest that diatoms can play a significant role in enabling Mute Swans in the eastern part of the Gulf of Finland to accumulate the protein and energy reserves required for reproduction.

Key words: diet, faecal samples, feeding ecology, Mute Swan, submerged aquatic vegetation.

Of the Palearctic swan species, the Mute Swan *Cygnus olor* is the largest in size, most strongly associated with water, and has the shortest migration distance and longest breeding season (Cramp & Simmons 1977;

Northcote 1981; Johnsguard 2016). The Mute Swan's bill is also more adapted to filtering its food, whereas the robust beaks of the other swans are better suited to their grubbing and grazing activity (Avilova 1990;

Martynovich 1990). In its natural habitats, the Mute Swan's diet consists mainly of soft aquatic vegetation such as algae and pondweeds, usually avoiding the more fibrous terrestrial and riparian vegetation favoured by Whooper Swans *C. cygnus* and Bewick's Swans *C. columbianus bewickii* (e.g. sedges *Cyperaceae* sp., grasses *Poaceae* sp. and rushes *Juncaceae* sp., Cramp & Simmons 1977; Kondratev 1985; Johnsgard 1978, 2016). When traditional food is limited (e.g. in winter), Mute Swans do feed on terrestrial and riparian vegetation, particularly on pasture grasses and flooded fields (Sears 1989; Wood *et al.* 2013), although aquatic vegetation is still typically preferred. In extreme conditions, Mute Swans can even take animal prey, including catching fish in severe winters on the northern Black Sea (Zhmud 1988) and consuming Zebra Mussels *Dreissena polymorpha* along Polish Baltic Sea coasts in winter (Włodarczyk & Janiszewski 2014).

The aquatic vegetation selected by Mute Swans is well known (Gillham 1956; Cobb & Harlin 1980; Allin & Husband 2003; Naylor 2004; Perry *et al.* 2004; O'Hare *et al.* 2007; Tatu *et al.* 2007; Bailey *et al.* 2008; Sandsten & Klaassen 2008; Gayet 2010; Wood 2012; Gayet *et al.* 2014; Wood *et al.* 2014). However, most studies have focused on the effect of the Mute Swan feeding on plant communities, depletion rates or the effects of the distribution and abundance of particular vegetation on the spatial distribution and numbers of birds. To date, there have been very few publications devoted to the study of the direct qualitative or quantitative composition of the Mute Swan's diet (analysis of the stomach and

oesophagus content or faecal samples). Moreover, most of our current knowledge of Mute Swan diet comes from studies undertaken in the western parts of the native range (e.g. the UK) or from its range as an invasive alien (e.g. in North America). One exception is the detailed description of the spring and summer diet of Mute Swans on the Baltic Sea, based on data collected on the southeast coast of Sweden in the 1950s, which identified 22 species of vascular aquatic plants and algae and 19 animal species in Mute Swan stomach contents (Berglund *et al.* 1963). Our study of the Mute Swan's diet in a more easterly part of its range will help to redress the balance.

From the mid-20th century, numbers of Mute Swan began to grow rapidly and spread (especially northwards) in the Palaearctic, colonising new habitats and encountering new climatic, ecological and foraging conditions (Berglund *et al.* 1963; Jygi 1968; Hilden 1987; Tenovuo 1975, 1976). The species first started nesting in the eastern Gulf of Finland in 1987 (Buzun & Khrabry 1990; Kouzov 2005, 2009; Kouzov & Kravchuk 2014; Kouzov *et al.* 2016). Annually, up to 170 breeding pairs and 520 non-breeding birds were observed here during 2005–2015 (Kouzov 2016; Kouzov & Loseva 2016), with most recorded in the southern sector of the Gulf of Finland (Kouzov & Kravchuk 2016). Numbers of nesting birds have varied more than four-fold, depending on spring phenology, with breeding pairs occupying nesting territories as early as the spring allows, which in very early years may be in the second half of February (Kouzov 2016). Birds arrive at their breeding sites 45–50 days before

nesting, so Mute Swans in the eastern Gulf of Finland generally start egg-laying during 10–20 April, peaking between 20 April and early May (Kouzov 2016). Both the quality and quantity of food available to individual birds during this period therefore are critical to their breeding outcome (Drent & Daan 1980; Birkhead *et al.* 1983).

Despite the increasing abundance of Mute Swans in the Gulf of Finland, little is known to date about the food taken by the birds during the pre-breeding and nesting periods. We therefore analysed faecal samples of this species, collected at the northern boundary of its expanding range, to identify any adaptations in its diet that enabled it to exploit new conditions, and to circumvent any ecological limits on its distribution in this northeast part Europe.

Methods

Study area

Landscape and hydrological zoning. We defined six geographical areas according to landscape characteristics and the hydrological regime in the Russian part of the Gulf of Finland (Tsvetkov & Sorokin 2009), modified to take into account the landscape and habitat characteristics of the coasts and shallow waters. Five were in the eastern part of the Gulf of Finland, and one was more centrally situated (Fig. 1).

District 1. Fresh eutrophic estuary (including Neva Bay and the inner Luga Bay) with extensive Common Reed *Phragmites australis* and Sea Clubrush *Bolboschoenus maritimus* beds. The vegetation comprises many freshwater species of submerged and semi-submerged vascular plants, such as

Lesser Bullrush *Typha angustifolia*, hornworts *Ceratophyllum* sp., White Water Lily *Nymphaea alba*, Yellow Water Lily *Nuphar lutea*, Common Frogbit *Hydrocharis morsus rana*, Water Soldiers *Stratiotes aloides*, Canadian Pondweed *Elodea canadensis*, Broad-leaved Pondweed *Potamogeton natans* and European Water-plantain *Alisma plantago-aquatica*, which are widely distributed here.

District 2. Transitional shallow water area, with water salinity at < 3.5‰ (Ostov 1971). The landscape includes both morainic boulder areas and extensive sandy beaches, with reed and bulrush beds in small shallow bays. The species composition, biomass and spatial extent of submerged vegetation are extremely low in comparison to District 1. Most of the coastal water area comprises open sandy shallow waters with isolated stands of Perfoliate Pondweed *Potamogeton perfoliatus* and Sago Pondweed *Stuckenia pectinata*.

District 3. Island moraine area in the southern part of the Gulf of Finland, where the glacially-formed landscape is characterised by an abundance of boulder banks and islands, including vast sand and pebble spits formed by sea currents. The strongly indented coastlines of the mainland and larger islands result in numerous small bays and capes. The salinity of the water ranges from *c.* 5.1–7.1‰ (Ostov 1971). The *Phragmites australis*, Common Club-rush *Schoenoplectus lacustris* and *Bolboschoenus maritimus* are abundant in places protected from storms (Glazkova 2001). Freshwater submerged vegetation is dominated by *Potamogeton perfoliatus*, *Stuckenia pectinata* and Horned Pondweed *Zannichellia palustris*. Scarcer beds of the marine vascular species Brackish Water Crowfoot *Ranunculus*

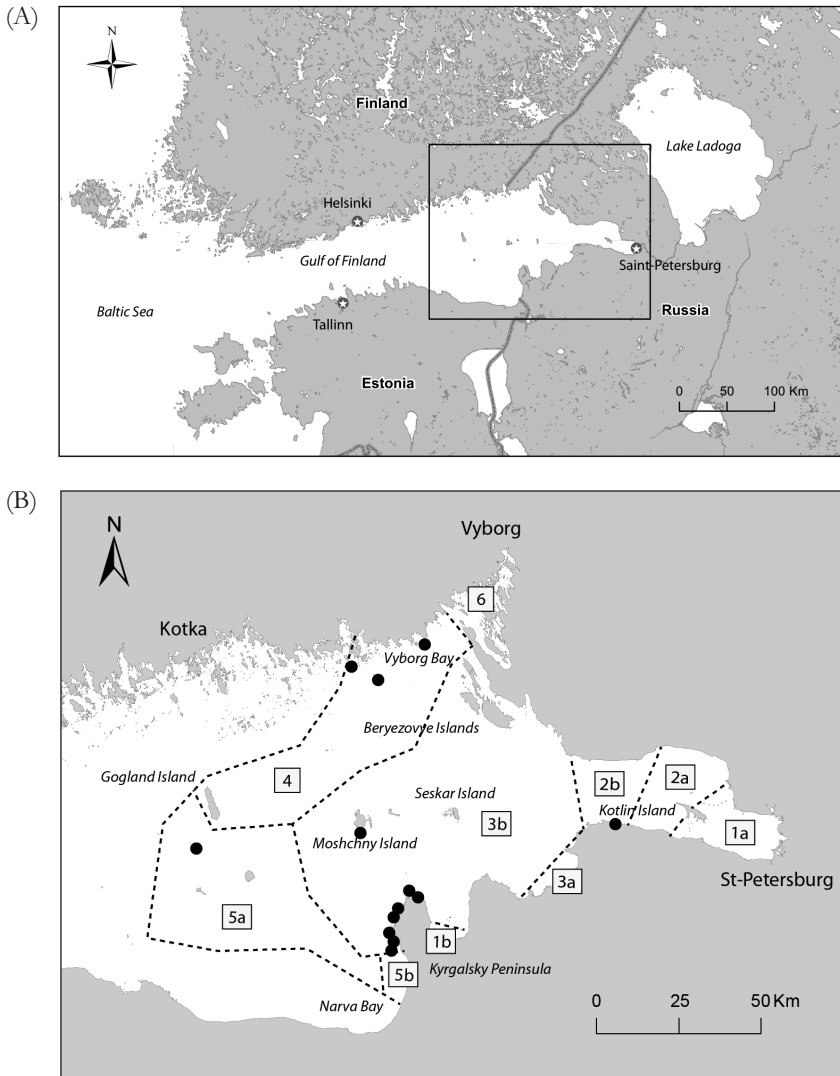


Figure 1. Map showing (A) the location of the study area in the eastern part of the Gulf of Finland, and (B) landscape and habitat zones, along with the faecal sample collection sites. Note: 1 = Fresh river estuaries with rich submerged vegetation (1a = Neva Bay, 1b = Luzhskaya Bay); 2 = Shallow area (2a = zone of open sandy hydro-accumulative beaches, 2b = zone with a predominance of moraine boulder ridges); 3 = Island moraine area (3a = local areas with a predominance of sandy beaches, 3b = zone predominantly of boulder ridges and secondary sand-pebble banks); 4 = Deep rocky district; 5 = area of open sea in the central part of the Gulf of Finland (5a = zone of sandy hydro-accumulative beaches and coastal shoals, 5b = islands in the open sea); 6 = Shallow rocky-moraine area in Vyborg Bay. Black circles = locations where faecal samples were collected.

baudotii, Beaked Tasselweed *Ruppia maritima* and Spiny Water Nymph *Najas marina* occur in this district (Glazkova 2001).

District 4. Deep-water rocky area in the northern part of the Gulf of Finland, where smoothed granite rocks (skerries) dominate. Small deposits of sand, pebbles and boulders occur only locally. Water salinity is about 7.1‰ (Ostov 1971). This area is characterised by a very sharp drop in water depth and complete absence of a shallow zone around the islands. A narrow belt of semi-submerged vegetation along the coastline is present in narrower bays protected from storms. Algal growth dominates the aquatic vegetation, with submerged vascular plant vegetation growing only locally. Species composition of the aquatic vascular plants and algae is the same as in District 3.

District 5. The westernmost area of open water, where islands consist mainly of moraine, pebbles and boulder areas, but with local rock outcrops occurring on Bolshoy Tyuters Island. Although this is a deep-water area, the islands have well-defined shallow waters around their perimeters. Water salinity exceeds 7.1‰ (Ostov 1971). There is no semi-submerged vegetation near the coastline; algae form the main aquatic vegetation in the area, and submerged vascular plants (*Potamogeton perfoliatus*, *Stuckenia pectinata*, *Ranunculus marinus*, *Ruppia maritima* and *Najas marina*) are present only locally where protected from storms (Fig. 1b).

District 6. Shallow rocky-moraine area of Vyborg Bay. Water depths do not exceed 5 m, and water salinity is no more than 3.5‰ (Ostov 1971). Freshwater vegetation is

present only at the top of the bay. Aquatic vegetation in the mouth of the bay is similar to the vegetation in Districts 3 and 4.

Macroalgae communities

Water salinity is one of the main factors determining the composition and distribution of macroalgae in the Baltic Sea (Larsen & Sand-Jensen 2006). Compared to elsewhere in the Baltic Sea, the salinity of the eastern Gulf of Finland is low, varying from 0.2‰ in Neva Bay, up to 4‰ near the Berezovye Islands, and 7‰ near Bolshoy Tyuters Island (Ostov 1971). In this regard, the macroalgae flora of the most desalinated Russian sector of the Gulf of Finland is far poorer than that found in other parts of the Baltic. One hundred and fifty-six species of red, 128 species of brown and 110 species of green macroalgae are known for the Baltic Sea (Nielsen *et al.* 1995), compared to 22 species of green, 15 species of brown and seven species of red macroalgae observed in the Russian sector of the Gulf of Finland (Kovalchuk 2008; Gubelit & Kovalchuk 2010).

Macroalgae reach down to 5.5–6 m in the eastern Gulf of Finland, with the euryhaline freshwater alga *Cladophora glomerata* dominating, forming dense monodominant communities at depths from 0.1–0.2 m to 3.0–3.5 m (Gubelit & Kovalchuk 2010). As salinity increases above 2‰ this community also includes green algae *Ulva intestinalis*, and the marine species *Pylaiella littoralis* and *Ceramium tenuicorne* begin to appear. During summer, macroalgae biomass may form into large aggregates, some accumulating in shallow coastal areas, other transported by currents

to a depth of no more than 5–6 m, where they form wintering algae mats (Gubelit & Kovalchuk 2010).

In the spring, after ice melt, these mats begin to grow, successfully competing with phytoplankton for nutrients, and some of them are transported to the shore, where they can serve as a source of food for herbivores (Gubelit & Berezina 2010; Lehvo & Bäck 2001). When the ice disappears in spring, the first ephemeral species of algae develop at the water's edge in addition to the wintering mats, although they are rapidly replaced by the next generation of algae. Species of the genera *Cladophora* and *Ulva* produce the largest biomass in the Gulf of Finland in one or two biomass peaks during the summer. Typically, peak biomass occurs between the end of May and July, depending on prevailing climatic conditions (Gubelit 2015; Berezina *et al.* 2017).

Distribution of nesting Mute Swan pairs

The majority of the local Mute Swan population (70–175 pairs) nests within District 3 on the Kurgalsky Peninsula, the Seskar Archipelago and on Moschny Island (Bubyreva *et al.* 1993; Noskov *et al.* 1993; Buzun 1997; Kouzov 2005, 2009, 2015b; Kouzov & Kravchuk 2014, 2016; Kouzov & Loseva 2016). Five to 15 pairs nest in District 4: on the island of Maly Fiskar, the Bolshoy Fiskar, Dolgy Reef and Dolgy Kamen archipelagos, and in Dalnaya Bay (Iovchenko *et al.* 2002; Kouzov & Loseva 2015, 2016). Two to five pairs nest in District 5: on Maly Tyuters and Bolshoy Tyuters Islands, and on the Virgin archipelago (Kouzov 2015c, 2016; Kouzov & Loseva

2016). In recent years, 2–3 pairs of Mute Swan began to nest within District 2 in Chernaya Lakhta Bay and near Kotlin Island (Kouzov 2015a; Kouzov & Loseva 2016; Fedorov 2018). In 2020, three breeding attempts were recorded within District 1 in the Neva Bay (Zaynagutdinova *et al.* 2020). The first Mute Swan nested within District 6 on Stoglaz Island in 2019 (Shiryaeva & Kouzov 2019). Mute Swans and Greylag Geese *Anser anser* prefer sandy-boulder shallow waters in the southern part of the Gulf of Finland (Kouzov & Kravchuk 2013; Kouzov & Loseva 2016; Kouzov 2016), in contrast to the Barnacle Goose *Branta leucopsis* which is primarily an arctic-breeding species that (like other arctic birds) nests almost exclusively in the northern part of the gulf, when breeding on the Gulf of Finland (Cerenkov *et al.* 2016; Kouzov *et al.* 2018, 2019). There are also main migration stopover sites of the Bewick's Swans and Whooper Swans in the southern part of the Gulf of Finland (Zaynagutdinova *et al.* 2019). These two species use this region during spring migration and could be the major competitors of Mute Swans in the same area.

In general, the Mute Swans nesting in the Leningrad region currently enjoy favourable conservation status. The population size is growing (Kouzov 2016), and their major feeding, roosting and nesting areas have legal protection. However, increasing recreational pressure and infrastructure construction along the coast of the Gulf of Finland may soon become a threat to the swans (Zaynagutdinova *et al.* 2019). Expanding the network of protected areas, as a compensatory measure for the

construction of ports, therefore, is an urgent issue (Chusov *et al.* 2017).

Data collection and processing

The majority of faecal samples were collected in areas where most of the Mute Swans nest: at the moraine island of District 3 and the deep-water rocky District 4. Both areas have similar water salinity (Tsvetkov & Sorokin 2009) and similar species composition of algae and aquatic vascular plants (Gubelit 2011; Glazkova 2001). The main differences are related to the size of shallow water areas up to 5 m depth where vegetation occurs. Single samples from other areas were not considered in the study.

Fieldwork was conducted from 20 February to the end of June each year during 2014–2017, between St. Petersburg, and the western coast of the Kurgalsky Peninsula, and on the islands in the eastern part of the Gulf of Finland (Mozhny, Seskar, Bolshoy and Maly Tyuters, Dolgy Reef, Bolshoy and Maly Fiscars, and the Dolgy Kamen and Virgins archipelagos; see Fig. 1b).

Material was collected during ground surveys of swan numbers and distribution in 2014–2017. Vegetation samples were collected from Mute Swan feeding sites immediately after observing the birds' feeding behaviour, taking samples of plants which we observed the swans consuming. All available faecal samples were collected immediately after the observations, from shallow water and terrestrial areas where Mute Swans were observed resting or sleeping.

All faecal samples were fixed with 5% formaldehyde solution. We slightly modified

the method used by Owen (1975), by carefully mixing the sample then selecting five parts at random and placing each on a slide for inspection under a binocular microscope. A few drops of water were added, and the plant residues were then spread evenly across the slide using a dissecting needle. Each plant fragment was identified to species level, on the basis of the pattern, colour and shape of the cells, following the identification guidebook for plant remains in peat (Vinogradova *et al.* 1980). A specialist algologist and a specialist in vascular plants both examined each slide. The total amount of plant remains in each field of view was taken as 100%, and the proportion of each species observed was determined to an accuracy of 5%. The percentage of each species present in each faecal sample was then taken as the mean of the values recorded for the five slides. Species observed just once, where a percentage could not be determined, were marked as “present” (“+”) for estimating frequency of occurrence. Frequency of occurrence of species consumed by Mute Swans during the study period was calculated (as a percentage) by dividing the number of samples containing a particular species by the total number of samples examined (Swanson *et al.* 1974).

In analysing the seasonal changes in diet, we assigned samples to one of three periods. (1) 1 February–15 March (16 samples), which marks the end of winter and time of arrival to the nesting area. (2) 16 March–30 April (31 samples), when the birds occupy nesting sites, prepare for breeding, accumulate energy reserves for clutch formation, and begin egg-laying. (3) 1 May–

15 June (40 samples), the incubation and hatching period.

We compared our data with the results of an earlier study of Mute Swan diet at Blekinge, Sweden, which identified the vegetation in 51 stomach contents samples during 1957–1961 (Berglund *et al.* 1963). Their studies were also conducted in the Baltic region, but 50 years ago, in a landscape of moraine shoals and coasts with an abundance of small island archipelagos, similar to the eastern Gulf of Finland.

Statistical analysis

A total of 87 faecal samples were subject to statistical analysis and were grouped into the three time intervals (“phenology” variable, Table 1). Multivariate analysis of variance (MANOVA) was used to determine whether the diets of Mute Swans varied between these three periods (General ANOVA/MANOVA module, StatSoft Statistica 2011). Data from different observation sites and years were combined. MANOVA was used to evaluate the overall variation in seven major food categories, consumed by Mute Swans, including: 1) green alga *Chlorophyta* sp.; 2) brown alga

Phaeophyta sp.; 3) red alga *Rhodophyta* sp.; 4) diatoms *Diatomeae* sp.; 5) thin roots papillae of semi-submerged and near-water herbaceous plants with stiff stems, e.g. *Phragmites australis*, *Bolboschoenus maritimus* and *Agrostis* sp.; 6) fine vegetative parts of submerged aquatic plants *Potamogeton perfoliatus*, *Stuckenia pectinata*, *Zannichèllia palustris*, *Ruppia maritima*; and 7) detritus.

For the statistical analysis, the major food items were grouped into categories based on taxonomic order. At the same time, root papillae and vegetative parts of vascular vegetation were combined into two separate groups (Table 2). We excluded the yellow-green algae *Vaucheria* sp. from the analysis because of their low occurrences in the samples. Data for each food category were summarised as an aggregate percentage of the area on the slide. We used the percentages of food categories as the response variables (Ross *et al.* 2005; Bailey *et al.* 2008). Arcsine square root transformation was applied to the proportions because the error distributions were not normally distributed (Sokal & Rohlf 1995). Wilks’ lambda was used to determine the main effects in the

Table 1. The number of Mute Swan faecal samples collected in each time period, during the 4-year (2014–2017) study.

Time periods	2014	2015	2016	2017	Total
1 February–15 March	2	8	6	0	16
16 March–30 April	12	12	7	0	31
1 May–15 June	17	4	11	8	40
Total	31	24	24	8	87

model. Statistical models were considered statistically significant at $P < 0.05$. Where multivariate tests of the phenology effects were significant, *a posteriori* analysis was performed using Tukey tests to determine exactly which periods were different from the others.

Results

Overview of species composition in the faecal samples

In total, 29 algae species, and eight submerged, semi-submerged and coastal vascular plant species occurred in the faecal samples (Table 2). No remains of aquatic invertebrates were found. Algae in samples were represented by species of *Chlorophyta*, *Phaeophyta*, *Rhodophyta*, *Xanthophyta* and *Bacillariophyta*. Two vascular plant species were represented only by thin root papillae (*Phragmites australis* and *Bolboschoenus maritimus*), and six vascular plant species only by vegetative parts (*Agrostis* sp., *Zannichellia palustris*, *Stuckenia pectinata*, *Potamogeton perfoliatus*, eelgrass *Zostera* sp. and *Ruppia maritima*).

Volume percentage and frequency of occurrence of species in faecal samples

Cladophora sp. comprised the greatest volume of all samples (mean \pm s.e. = $27.7 \pm 3.1\%$; Table 2). Detritus ($11.4 \pm 2.2\%$), *Ulva* sp. ($7.5 \pm 1.6\%$), vegetative parts of *Zannichellia palustris* ($8.7 \pm 1.4\%$) and *Stuckenia pectinata* ($9.6 \pm 1.2\%$), along with *Cladophora* sp. contributed a total of 65% to the volume of the Mute Swans' diet, although percentages of all of these species were less than that of *Cladophora* sp. by 2.5–3 times.

The remaining species each comprised $< 5\%$ of the volume of food in the faecal samples. Among them, the most notable species were *Rhizoclonium* sp. ($4.9 \pm 1.4\%$), *Ceramium* sp. ($3.2 \pm 0.6\%$), *Melosira varians* ($2.3 \pm 0.5\%$), and thin root papillae of *Phragmites australis* ($2.7 \pm 0.8\%$).

The frequencies of species occurrence in the samples were more even than the volumes recorded (Table 3). Highest frequencies in the faecal samples were of species in the *Cladophora* genus and vegetative parts of *Stuckenia pectinata*, at 0.68 and 0.70, respectively. The frequencies of occurrence of *Rhizoclonium* sp. (0.43), vegetative parts of *Zannichellia palustris* (0.47) and detritus (0.47), were similar. Another seven groups had occurrence frequencies ranging between 0.30 and 0.40: *Oedogonium* sp. (0.37), *Ulva* sp. (0.32), *Melosira varians* (0.33), *Navicula* sp. (0.34), *Gomphonema constrictum* (0.32), *occoneis placentula* (0.33) and vegetative parts of *Potamogeton perfoliatus* (0.31).

Digestion of food species

Rockweeds *Fucus* sp. and seaweed *Dictyota* sp. were almost unchanged in faecal samples and probably are not absorbed by birds. Most likely, swans swallow them with other food items. At the same time, only empty shells remained from diatoms in faecal samples, which suggests good digestibility among this group of algae.

Percentages of the main food groups in the swans' diet

Almost half of the Mute Swans' diet (46%) consisted of green algae (*Chlorophyta* sp., Fig. 2). Vegetative parts of vascular submerged and coastal vegetation contributed 22%,

Table 2. Volume (%) of species in the faecal samples of Mute Swans on the Russian part of the Gulf of Finland in 2014–2017.

Species	Mean % (s.e.)			
	1 February– 15 March	16 March– 30 April	1 May– 15 June	Total
Chlorophyta	60.63 (4.03)	45.81 (4.93)	41.00 (4.36)	46.32 (2.85)
<i>Chaetomorpha</i> sp.	0.13 (0.13)	2.23 (0.57)	2.00 (0.64)	1.74 (0.36)
<i>Cladofora</i> sp.	59.94 (4.09)	28.06 (5.44)	14.59 (3.28)	27.73 (3.10)
<i>Microspora amoena</i>	0.00 (0.00)	0.23 (0.20)	0.03 (0.03)	0.09 (0.07)
<i>Mougeotia</i> sp.	0.00 (0.00)	0.35 (0.18)	2.45 (0.72)	1.25 (0.36)
<i>Oedogonium</i> sp.	0.19 (0.19)	1.52 (0.47)	3.44 (0.76)	2.16 (0.41)
<i>Rhizoclonium</i> sp.	0.38 (0.26)	6.19 (3.38)	5.68 (1.37)	4.89 (1.37)
<i>Spirogyra</i> sp.	0.00 (0.00)	0.10 (0.07)	0.08 (0.06)	0.07 (0.04)
<i>Stigeoclonium</i> sp.	0.00 (0.00)	2.10 (0.74)	0.25 (0.25)	0.86 (0.30)
<i>Ulothrix zonata</i>	0.00 (0.00)	0.16 (0.08)	0.05 (0.03)	0.08 (0.03)
<i>Ulva</i> sp.	0.00 (0.00)	4.87 (1.83)	12.45 (2.90)	7.46 (1.57)
Phaeophyta	2.63 (0.98)	0.00 (0.00)	1.75 (0.46)	1.29 (0.30)
<i>Pylayella littoralis</i>	0.00 (0.00)	0.00 (0.00)	1.50 (0.38)	0.69 (0.19)
<i>Fucus</i> sp. + <i>Dictyota dichotoma</i>	2.63 (0.98)	0.00 (0.00)	0.25 (0.15)	0.60 (0.22)
Rhodophyta	0.00 (0.00)	4.16 (1.15)	8.93 (2.49)	5.59 (1.26)
<i>Bangia atropurpurea</i>	0.00 (0.00)	0.00 (0.00)	3.25 (2.29)	1.49 (1.06)
<i>Polysiphonia nigrescens</i>	0.00 (0.00)	0.00 (0.00)	2.00 (0.53)	0.92 (0.27)
<i>Ceramium</i> sp.	0.00 (0.00)	4.16 (1.15)	3.68 (0.90)	3.17 (0.60)
Xanthophyta	0.00 (0.00)	0.87 (0.42)	0.78 (0.28)	0.67 (0.20)
<i>Vaucheria</i> sp.	0.00 (0.00)	0.87 (0.42)	0.78 (0.28)	0.67 (0.20)
Bacillariophyta	0.69 (0.51)	17.68 (2.33)	3.93 (0.95)	8.23 (1.21)
<i>Melosira varians</i>	0.00 (0.00)	3.77 (0.97)	2.13 (0.86)	2.32 (0.54)
<i>Tabellaria fenestrata</i>	0.63 (0.51)	2.29 (0.38)	0.18 (0.09)	1.01 (0.20)
<i>Diatoma elongatum</i>	0.06 (0.06)	2.90 (0.48)	0.20 (0.10)	1.14 (0.22)
<i>Navicula</i> sp.	0.00 (0.00)	2.77 (0.43)	0.40 (0.13)	1.17 (0.21)
<i>Gomphonema constrictum</i>	0.00 (0.00)	2.39 (0.45)	0.35 (0.11)	1.01 (0.20)
<i>Cocconeis placentula</i>	0.00 (0.00)	2.84 (0.55)	0.40 (0.13)	1.20 (0.24)
Other Diatom species	0.00 (0.00)	0.71 (0.21)	0.28 (0.25)	0.38 (0.14)

Table 2 (continued).

Species	Mean % (s.e.)			
	1 February– 15 March	16 March– 30 April	1 May– 15 June	Total
Thin root papillae of <i>Phragmites australis</i> and <i>Bolboschoenus maritimus</i>	5.06 (1.62)	6.48 (3.06)	1.83 (0.70)	4.08 (1.18)
<i>Phragmites australis</i>	3.75 (1.25)	4.48 (1.95)	0.85 (0.42)	2.68 (0.77)
<i>Bolboschoenus maritimus</i>	1.31 (0.55)	2.00 (1.15)	0.98 (0.40)	1.40 (0.46)
Vegetative parts of vascular submerged and coastal plants	9.88 (1.93)	13.06 (3.57)	34.63 (4.94)	22.39 (2.88)
<i>Agrostis</i> sp.	0.00 (0.00)	0.68 (0.34)	2.48 (0.83)	1.38 (0.41)
<i>Zannichèllia palùstris</i>	0.00 (0.00)	6.71 (2.13)	13.78 (2.14)	8.72 (1.35)
<i>Stuckenia pectinata</i>	8.69 (1.91)	5.55 (1.65)	13.08 (2.07)	9.59 (1.22)
<i>Potamogeton perfoliatus</i>	1.19 (0.42)	0.13 (0.08)	2.08 (0.50)	1.22 (0.26)
<i>Zostera</i> sp.	0.00 (0.00)	0.00 (0.00)	0.40 (0.19)	0.18 (0.09)
<i>Ruppia maritima</i>	0.00 (0.00)	0.00 (0.00)	2.83 (0.62)	1.30 (0.32)
Detritus	21.13 (4.40)	11.94 (4.29)	7.18 (2.95)	11.44 (2.24)

detritus 1%, and diatoms *Bacillariophyta* sp. 8% (Table 2). The proportions of other groups (*Phaeophyta*, *Rhodophyta*, thin root papillae of rough semi-submerged vegetation) are almost insignificant (1–6%). Excluding detritus (likely an indigestible fraction of the diet ingested with other food items), diatoms represent the third most abundant source of spring food for swans, reaching 30–40% in several samples.

Changes in the food composition over time

Intake of the seven categories of food differed between sampling periods

(MANOVA, phenology effect: Wilks' $\lambda = 0.30$, $F_{14,156} = 10.08$, $P < 0.001$). *A posteriori* comparisons based on Tukey tests showed that the consumption of green alga differed significantly between the first and third periods (1 February–15 March and 1 May–15 June, $P = 0.043$), with the amount of green algae in the diet decreasing (Fig. 3). In February–middle March, faecal samples also contained more brown algae ($P = 0.001$) but fewer red algae ($P = 0.003$) compared to the second and third periods, respectively. The consumption of diatoms increased sharply in the second period (middle March–April, $P < 0.001$) and decreased

Table 3. Frequency of occurrence (%) of species in the faecal samples of Mute Swans on the Russian part of the Gulf of Finland in 2014–2017.

	1 February– 15 March	16 March– 30 April	1 May– 15 June	Total
	(n = 16)	(n = 31)	(n = 40)	(n = 87)
Chlorophyta	100.00	90.32	85.00	89.66
<i>Chaetomorpha</i> sp.	6.25	45.16	25.00	28.74
<i>Cladophora</i> sp.	100.00	64.52	57.50	67.82
<i>Microspora amoena</i>	0.00	6.45	2.50	3.45
<i>Mougeotia</i> sp.	0.00	16.13	42.50	25.29
<i>Oedogonium</i> sp.	6.25	38.71	47.50	36.78
<i>Rhizoclonium</i> sp.	12.50	35.48	60.00	42.53
<i>Spirogyra</i> sp.	0.00	6.45	5.00	4.60
<i>Stigeoclonium</i> sp.	0.00	25.81	2.50	10.34
<i>Ulothrix zonata</i>	0.00	12.90	5.00	6.90
<i>Ulva</i> sp.	0.00	25.81	50.00	32.18
Phaeophyta	50.00	0.00	30.00	22.99
<i>Pylayella littoralis</i>	0.00	0.00	30.00	13.79
<i>Fucus</i> sp. + <i>Dictyota dichotoma</i>	50.00	0.00	7.50	12.64
Rhodophyta	0.00	32.26	50.00	34.48
<i>Bangia atropurpurea</i>	0.00	0.00	22.50	10.34
<i>Polysiphonia nigrescens</i>	0.00	0.00	30.00	13.79
<i>Ceramium</i> sp.	0.00	32.26	40.00	29.89
Xanthophyta	0.00	22.58	25.00	19.54
<i>Vaucheria</i> sp.	0.00	22.58	25.00	19.54
Bacillariophyta	18.75	80.65	47.50	54.02
<i>Melosira varians</i>	0.00	54.84	30.00	33.33
<i>Tabellaria fenestrata</i>	12.50	61.29	10.00	28.74
<i>Diatoma elongatum</i>	6.25	64.52	12.50	29.89
<i>Navicula</i> sp.	0.00	67.74	22.50	34.48
<i>Gomphonema constrictum</i>	0.00	61.29	22.50	32.18
<i>Cocconeis placentula</i>	0.00	61.29	25.00	33.33
Other Diatom species	0.00	35.48	5.00	14.94

Table 3 (continued).

	1 February– 15 March	16 March– 30 April	1 May– 15 June	Total
	(<i>n</i> = 16)	(<i>n</i> = 31)	(<i>n</i> = 40)	(<i>n</i> = 87)
Thin root papillae of <i>Phragmites</i>				
<i>australis</i> and <i>Bolboschoenus maritimus</i>	50.00	41.94	17.50	32.18
<i>Phragmites australis</i>	43.75	41.94	10.00	27.59
<i>Bolboschoenus maritimus</i>	31.25	25.81	15.00	21.84
Vegetative parts of vascular				
submerged and coastal plants	93.75	48.39	80.00	71.26
<i>Agrostis</i> sp.	0.00	12.90	27.50	17.24
<i>Zannichéllia palústris</i>	0.00	35.48	75.00	47.13
<i>Stuckenia pectinata</i>	87.50	48.39	80.00	70.11
<i>Potamogeton perfoliatus</i>	50.00	9.68	40.00	31.03
<i>Zostera</i> sp.	0.00	0.00	12.50	5.75
<i>Ruppia maritima</i>	0.00	0.00	50.00	22.99
Detritus	93.75	45.16	30.00	47.13

in the third (May–June, $P < 0.001$). The proportion of thin root papillae of *Phragmites australis* and *Bolboschoenus maritimus* did not differ significantly between periods (all $P > 0.10$, n.s.). In May 1–June 15, samples contained more vegetative parts of vascular submerged and coastal plants compared to the first and second periods ($P = 0.020$ and $P < 0.001$, respectively). The amount of detritus was significantly higher in the first period compared to the third ($P = 0.009$).

Green algae, root papillae and vegetative parts of vascular plant aquatic vegetation were all consumed throughout the study periods. In February–middle March, there

were no red algae in samples, and diatoms were present in minimal amounts (Fig. 3), whereas in the second half of March–April there were no brown algae, and in May–first half of June, all types of food were found.

Comparison with the study of Mute Swan diet at Blekinge, Sweden

A comparison of our data with the results of an earlier study in Sweden (Berglund *et al.* 1963) provided further information on the variety of multicellular algae and vascular aquatic plants in the Mute Swans' diet (Table 4). Green algae *Chlorophyta* (*Cladophora* sp.) and submerged vascular aquatic vegetation were predominant in diets from

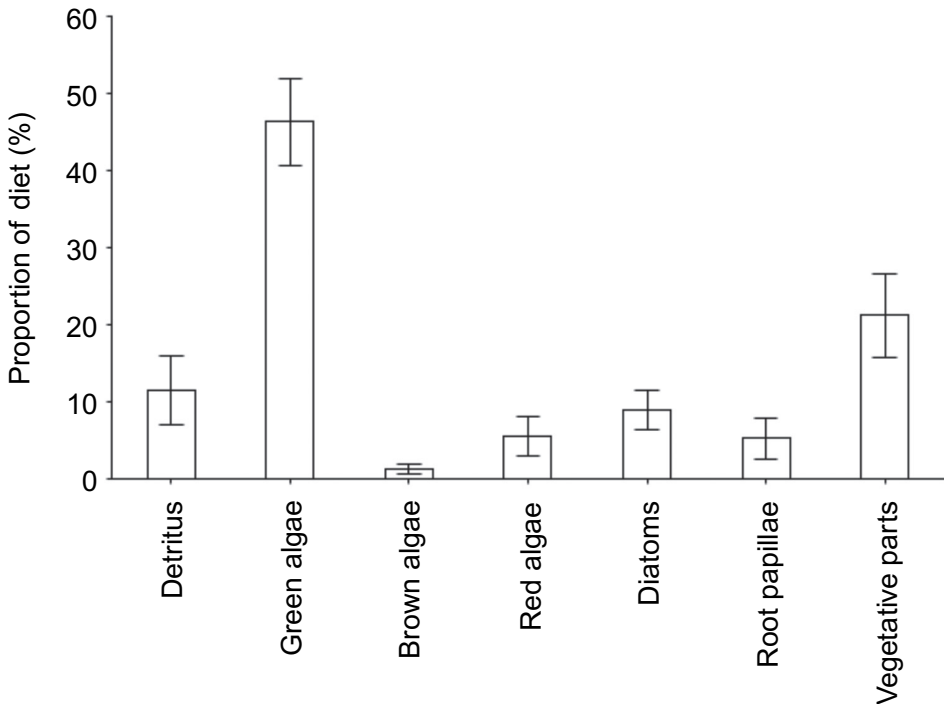


Figure 2. Mean proportions (%) of the main food groups in the faecal samples of Mute Swans on the Russian part of the Gulf of Finland in 2014–2017. Vertical lines represent 95% confidence intervals.

both regions. The proportion of vascular plants in the samples was slightly less in the eastern Gulf of Finland, however, compared to the Swedish coast. Moreover, detritus and diatoms (*Bacillariophyta*) were not found in samples from Blekinge, Sweden, whereas diatoms were relatively frequently found in the faeces collected in the eastern part of the Gulf of Finland (Table 4). The Swedish samples also occasionally included remains of aquatic invertebrates (19 species recorded), in contrast to our samples which were comprised of vegetation only. This can be explained both by the difference in the methods used in the two studies (*i.e.*

analysing faecal samples *versus* stomach contents), and by different climatic conditions influencing food resources. For example, in southern Sweden, in contrast to the eastern part of the Gulf of Finland, vast fields of vegetative vascular aquatic vegetation were present in the spring.

Discussion

Our study shows that the Mute Swan in the eastern Gulf of Finland is a generalist herbivore, with a diet comprised of many species of aquatic plants and algae. The majority of the diet (62.1% of the volume, $n = 87$) consisted of algae. The most common taxa in the diet were the green

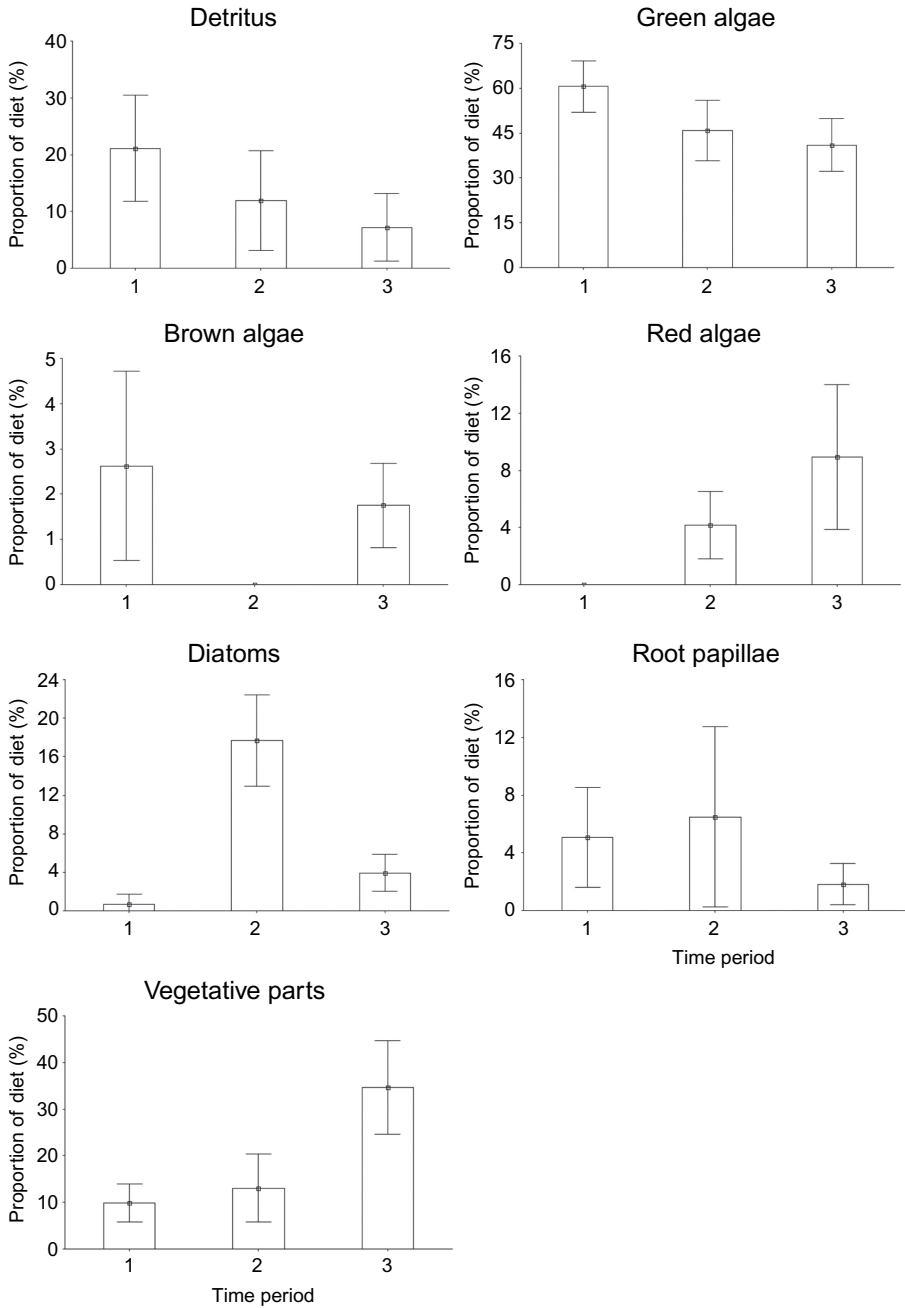


Figure 3. Dynamics of food consumption by Mute Swans in spring (mean values \pm 95% confidence intervals): 1) from 1 February–15 March; 2) from 16 March–30 April; and 3) from 1 May–15 June.

Table 4. Comparative analysis of the species composition for the main systematic groups of plants in the spring diet of Mute Swans in the eastern part of the Gulf of Finland and in Blekinge, Sweden (Berglund *et al.* 1963).

Species	Number of species	
	Eastern part of the Gulf of Finland (87 faecal samples)	Blekinge, Sweden (51 stomach content samples)
<i>Chlorophyta</i>	10	4
<i>Charophyta</i>	0	2
<i>Phaeophyta</i>	4	5
<i>Xanthophyta</i>	1	0
<i>Rhodophyta</i>	3	1
<i>Bacillariophyta</i>	7	0
<i>Magnoliophyta</i>	8	10
<i>Detritus</i>	1	0

algae *Chlorophyta* sp. (46.3%), which concurs with previous studies (Berglund *et al.* 1963; Owen & Kear 1972; Mathiasson 1973; Birkhead & Perrins 1986; Ciaranca *et al.* 1997; Tatu 2007). The Black Swan *Cygnus atratus* (which among the swans is very closely related to the Mute Swan) has also been found to include algae as a major component of its diet (Mitchell & Wass 1995).

The absence of *Phragmites australis* (both its thick rhizomes and young shoots), as well as of *Stuckenia pectinata* tubers in the faecal samples was surprising, given that these species form a significant part of the diets of other large herbivorous waterfowl (Cramp & Simmons 1977; Kondratev 1985; Johnsgard 1978, 2016; Beekman *et al.* 1991; Klaassen & Nolet 2007). This may be a feature of the morphology of the Mute

Swan's bill, which is more adapted to filtering than those of other swan species, which are better suited to grubbing and grazing (Avilova 1990; Martynovich 1990). Nolet *et al.* (2002) found that Bewick's Swans had a 90% assimilation efficiency when feeding on pondweed tubers. The absence of *Stuckenia pectinata* tubers in our samples could reflect it being less abundant and having a more limited distribution than green algae in the study area. On the other hand, these tubers contain much starch (potentially completely digested by swans), so may not have been detectable in the faecal samples despite being ingested by the swans. *Stuckenia pectinata* tubers were beginning to sprout during our spring study period, however, with small stems visible. These are very noticeable, and can easily be

identified in Bewick's Swan or Whooper Swan droppings, yet *Stuckenia pectinata* shoots were detected in very small quantities in faecal samples even for these two species (S. Kouzov *et al.*, unpubl. data). Given that *Stuckenia pectinata* stems were likewise found in very few of the Mute Swan samples, it seems that this food resource is rarely used by the swans at spring stopovers in the eastern part of the Gulf of Finland.

Variation with study location

Differences in the species composition and volume fractions of the different food detected are likely due to variations in local plant community composition in the study area. Comparing our data with the results of earlier observations at Blekinge in Sweden (Berglund *et al.* 1963) therefore is of interest. In both studies, a wide range of multicellular algae and vascular aquatic plants was found in the Mute Swan diet (Table 4). Green algae *Chlorophyta* (*Cladophora* sp.) and submerged vascular aquatic vegetation were predominant in diets from both regions. That the proportion of vascular plants recorded in the diet was slightly less in the eastern Gulf of Finland than on the Swedish coast may reflect the absence of extensive Common Eelgrass *Zostera maritima* and *Ruppia maritima* meadows in the eastern part of the gulf which are present in Sweden. *Stuckenia pectinata* and *Zannichellia palustris*, the most common vascular plants in the sandy shallows of the eastern Gulf of Finland, produce less biomass of vegetative parts and overwintering rhizomes. We therefore suppose that differences between the diets observed in the two areas were related to other characteristics of the foraging

habitats. These include: 1) the absence of yellow-green algae *Xanthophyta* sp. in the samples from Swedish Mute Swans, and 2) *Charophyta* sp., which were most commonly consumed in Sweden, were rare in the brackish-water Gulf of Finland and not often found in the samples of Russian birds.

In addition, we noted two significant differences in the faecal material that we cannot explain by differences in feeding conditions between the two regions. One is the complete absence of detritus and diatoms in samples from Blekinge, Sweden (Berglund *et al.* 1963), which are widely represented in the samples from the eastern Gulf of Finland. These components are common and abundant in all shallow waters of the Baltic region, so we think that their absence is probably attributable to methodological differences. Spring diet of the Swedish swans was studied by sampling the stomach contents of shot birds, with the main aim of determining the species composition of the food, in particular the ratio of animal and plant components. In this case, detritus residues may simply have been ignored. For the same reason, both small and unicellular organisms, including diatoms, were perhaps not counted, a suggestion confirmed by the summer faecal analysis results from the same area presented in the same publication (Berglund *et al.* 1963), where small amounts of diatoms were observed, and detritus content reached 15%.

At the same time, the proportions of these constituents in the spring diet in Blekinge, Sweden should be even higher, because: 1) the diatoms grow in abundance at this time, and 2) detritus is an incidental food consumed when swans forage on

algae. In early spring, in the absence of young algae attached to the stones and of young shoots of vascular aquatic plants its proportion should increase, which was confirmed by our data.

Diatoms are rarely mentioned in reports on the Mute Swans' diet, and when they are they are usually considered as a minor constituent, taken accidentally when the birds are foraging on other items (Berglund *et al.* 1963; Willey & Halla 1972; Baldassarre 2014). However, according to our observations, their average volume share in samples reached 18% at certain stages of the spring period, and in several samples it reached 30–40%. This is likely due to the dense growth of different species of diatoms that form dense epiphytic layers on the threads of green algae (mainly *Cladophora* sp.) during spring growth, when their accessible biomass can be comparable to that of green algae.

Diatoms play an essential role in aquatic food webs (Wasser *et al.* 1989). Products of assimilation by diatoms differ from those of other algae producing carbohydrates. Diatoms produce lipids, the nucleic acid rich phosphate store volutin, and the energy rich storage polysaccharide chrysolaminarin. One hundred grams of diatom organic matter contains 40% proteins, 30% carbohydrates and 30% lipids (Wasser *et al.* 1989) and an energy content of 525 kcal per 100 g, exceeding that of all other groups of algae, as well as being highly digestible. Essential amino acids in the diatoms, which also contain lipids including many unsaturated fats and free fatty acids, include the crucial eicosapentaenoic acid (Wasser *et al.* 1989).

Variation with time of year

The importance of diatoms for Mute Swans in the eastern Gulf of Finland becomes clear if we consider changes in the birds' diet across three different time periods during the breeding season.

Arrival in the nesting area. February and the first half of March mark the end of winter and the time when the swans arrive in their nesting area. The vegetative growth of a new generation of algae and vascular plants has not yet begun. The main food for the birds consists of the remains of *Cladophora* sp. production from the previous summer, which overwintered on the bottom of the gulf in the form of algae mats.

Sixty percent of the material in the swans' faecal samples consisted of *Cladophora* sp., which are brought in some quantity to shallow waters near the shoreline by storms and currents at this time of year. Usually there is a conspicuous mixture of detritus, overwintering parts of *Stuckenia pectinata*, *Fucus* sp., and *Dictyota dichotoma*, which are consumed with the main food. The main product of *Cladophora* sp. assimilation is starch (Wasser *et al.*, 1989). Typically, most herbivorous waterfowl switch to a carbohydrate-based food to provide energy during winter and prior to migration (Beekman *et al.* 1991; Klaassen & Nolet 2007). Moreover, other swan species change their use of food resources during winter, in order to obtain the highest daily rates of net energy gain (Wood *et al.* 2019).

Establishing territories and onset of laying. In the second half of March and April the swans occupy nesting sites in preparation for egg-laying. During this period they accumulate energy reserves for clutch

formation (Thomas 1988). This circumstance requires a transition of diet to supply food rich in proteins, fat and vitamins. However, during this period, there is still no active growth of new generations of forage vegetation; the first growth of *Stuckenia pectinata*, *Zannicbellia palustris* and semi-submerged plants, as well as of green, yellow-green and red algae, occurs only in the second half of April (Chemeris & Bobrov 2020).

The *Cladophora* sp. remains from overwintering mats continue to be the most common foraging resource for swans. The volume share of green algae in faecal samples was 46%. These food resources do not allow birds to switch from a carbohydrate type of food to a protein one. Nevertheless, the spring peak of reproduction of diatoms occurs during this period leading to their epiphytic fouling on filamentous algae. Diatoms overgrow the branching fragments of *Cladophora* sp. (Leskinen 1993). Their average volume in faecal samples was 28%. As mentioned above, the chemical composition of diatoms differs significantly from other groups of algae, and their relative abundance and concentration probably allows birds to compensate for the lack of protein food and energy in the other constituents of their diet, which they need before breeding.

Incubation and hatching period. May and the first half of June is the time for incubation and hatching. During this period, the spring population of diatoms declines, and aquatic vascular plants and algae biomass increase, allowing birds to compensate for the energy expenditure and the deficit of protein and calcium after clutch formation (Drent &

Daan 1980). Young thickets of *Stuckenia pectinata* rich in amino acids and calcium are especially useful in this regard.

Our data allow us to draw some tentative conclusions. The Mute Swan in the eastern Gulf of Finland apparently feeds mostly on soft plant food of aquatic origin. In the eastern Gulf of Finland in late winter and early spring, before the onset of active vegetation growth, the main Mute Swan food resource is the remains the previous year's biomass of green algae *Cladophora* sp., carried by currents and storms to the surface from wintering mats on the bottom of the gulf. Differences in the spring diet of Mute Swans between the eastern Gulf of Finland and southern Sweden (Berglund *et al.* 1963) are most likely due to a lack of extensive underwater meadows of *Ruppia* sp. and *Zostera* sp., which are numerous in the western Baltic, but absent in this part of Russia. Mute Swans begin to feed on the new growth of aquatic vascular plants and filamentous algae after the beginning of the egg-laying and incubation period. Diatoms appear to become an essential component of the Mute Swans' diet in the pre-nesting period (about a month before egg-laying), and also during egg-laying before the onset of active growth of vascular aquatic plants and the new generations of algae. Their consumption probably allows birds to accumulate the protein and energy reserves required for reproduction. We therefore believe that the significant role of diatoms in the diet of swans is due to the timing of the spring peak growth of these algae coinciding with the birds' pre-nesting period.

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Photograph: Mute Swan with downy young in the Gulf of Finland, by Sergei Kouzov.