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A. J. van der Graaf · O. V. Lavrinenko · V. Elsakov
M. R. van Eerden · J. Stahl

Habitat use of barnacle geese at a subarctic salt marsh in the Kolokolkova Bay, Russia

Abstract Along the east Atlantic migratory flyway, goose and swan species rely on the availability of suitable coastal habitats as staging sites during migration and for breeding. Especially for the Russian part of the flyway, detailed descriptions of these habitats in relation to use by herbivores are lacking. We report on salt-marsh characteristics and habitat use by barnacle geese in a recently established breeding site, near the village Tobseda at Kolokolkova Bay in the Pechora Delta, Russia. A classification of plant communities was made and both vegetation and soil properties were measured. Goose visitation was assessed by counting droppings. From the bay towards the dunes there was a gradient of decreasing salinity, along with a gradual shift in plant communities from salt marshes to freshwater bogs, tundra and dunes. Barnacle geese visited salt-marsh communities of the low and middle marsh more than the high marsh and non-saline communities. Two low marsh communities were preferred. Both had high tiller densities and low canopy heights and were dominated by *Carex subspathacea*, a species with high forage quality. Those characteristics are selected by geese, but might be maintained through grazing. The salt marsh at our site bears similarities to other marshes at similar latitudes along the Russian coast and in Canada. We discuss whether processes like grazing facilitation and habitat degeneration through overgrazing occur on our site.

A. J. van der Graaf (✉) · J. Stahl
Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, P.O. Box 14,
9750 AA Haren, The Netherlands
E-mail: a.j.van.der.graaf@biol.rug.nl
Tel.: +31-50-3632028
Fax: +31-50-3635205

O. V. Lavrinenko · V. Elsakov
Institute of Biology, Komi Scientific Centre UrD RAS,
Kommunisticheskaya 28, Syktyvkar, 167982, Russia

M. R. van Eerden
Institute of Inland Water Management and Waste Water Treatment RIZA, P.O. Box 17, 8200 AA Lelystad,
The Netherlands

Introduction

Recently, research on flight energetics and the costs of long-distance migration in waterfowl revealed that migrating geese and swans ultimately depend on "stepping stones" of suitable foraging habitats along the migration route to meet their energy demands for long-distance flight (e.g., Alerstam and Hedenström 1998; Nolet and Drent 1998). The integrity of the flyway depends on the persistence of appropriate staging sites. These sites serve as "fuelling stations" along the migratory route, where birds acquire resources in order to continue their journey and to gather a surplus of reserves that will allow them to initiate clutches upon arrival at the arctic breeding grounds. Along the east Atlantic migratory flyway, linking western Europe with Siberia, barnacle geese (*Branta leucopsis*), dark-bellied brent geese (*B. bernicla bernicla*), tundra bean geese (*Anser serrirostris*), white-fronted geese (*A. albifrons*), Bewick swans (*Cygnus bewickii*) and a large variety of ducks rely almost exclusively on coastal habitats as staging (and breeding) grounds. From temperate to subarctic sites, salt marshes play a central role in our understanding of the migratory schedules of herbivores.

The green wave hypothesis suggests that the migration of avian herbivores to arctic breeding grounds is related to seasonal patterns of plant growth and in particular to changes in the nutrient quality of forage plants. Birds follow the temporal wave of spring growth in forage plants as they migrate North (Owen 1980). The spring production of leaf tissue, which offers nutrients in high concentrations, is the fuel for migration and subsequent breeding. The hypothesis also attempts to explain the traditional restriction of the breeding range of different herbivorous waterfowl species, like geese and swans, to high arctic regions through limitations in food availability and production (Owen 1980). At arctic breeding sites, the birds are confronted with a short time-window in which they

have to lay eggs, incubate and raise their young. It is extremely important for young birds to be able to forage on high-quality vegetation in order to gain sufficient weight to undertake the southward migration to the temperate wintering grounds (Gadallah and Jefferies 1995; Piedboeuf and Gauthier 1999; Person et al. 2003). According to the hypothesis, the quality of food on offer from the peak standing crop in summer in more temperate regions would be insufficient to support the requirements of the birds and their young. However, the recent expansion of the breeding range of a variety of goose species seems to contradict this hypothesis. A species that recently expanded its breeding range from the high Arctic to a wide range of habitats in sub-arctic and temperate regions is the barnacle goose (Van der Jeugd et al. 2003). In this study, we use the barnacle goose as a model to understand the habitat use of herbivorous migratory birds at a subarctic staging and breeding site.

Although salt marshes are key habitats in the life cycle of small avian herbivores like geese, our knowledge of salt marshes around the Arctic Circle of the Old World remains fragmentary. While several salt marshes in the Canadian and North American Arctic are well described (Jefferies 1977; Jefferies et al. 1979; Vince and Snow 1984; Kincheloe and Stehn 1991), descriptions of the salt marshes along the Russian part of the east Atlantic flyway are either lacking, or not accessible in Western literature. In this study, we attempt to fill this gap by describing different plant communities and their characteristics and mapping the zonation of a salt marsh at an important stopover and breeding site for migrating geese in the Pechora Delta in Arctic Russia. We give special attention to habitat use by barnacle geese, as the area forms one of the westernmost breeding sites for the Russian population of this species.

Materials and methods

Study site

Fieldwork was carried out near the village of Tobseda (68°35.296′N, 52°18.183′E), in Kolokolkova Bay on the west coast of the Pechora Delta (Fig. 1). The peninsula, where the village of Tobseda is situated, borders the Pomorsky Channel of the Barentz Sea to the north and the Kambalnichya Pakha Gulf of Kolokolkova Bay to the south (Fig. 1). It is a low coastal terrace, which is being formed in two parallel ways: first, from the sea side due to the accumulation of sand along the open coast as a result of abrasion of the shore and sea bottom and, second, from the Kolokolkova Bay as a result of the sedimentation of clayey deposits transported into the bay by the Neruta River. A dune system has developed along the maritime terrace and salt marshes have established along the shores of Kolokolkova Bay.

The groundwater depth in these marshes is shallow and, therefore, the groundwater salinity is often similar to that of seawater. Moving from the Kolokolkova Bay in the direction of the dunes, the marshes become less saline and gradually turn into sedge-moss bogs where freshwater conditions prevail. Within the marshes, there are a number of small water bodies differing in salinity.

The salt marshes are potentially of great importance for migrating geese and swans. Satellite telemetry shows that dark-bellied brent geese use the area as a stopover site during spring migration (Syroechkovsky and Litvin 1998; Green et al. 2002). On the return migration in autumn, the area again serves as an important staging post (Van Eerden 2000). On earlier expeditions (1996, 1997), large numbers of barnacle geese, tundra bean geese, white-fronted geese and Bewick swans were observed in these marshes (Van Eerden 2000). In the past decade, the area has developed as a breeding area for barnacle geese (Syroechkovsky 1995; Van der Jeugd et al. 2003), probably as an outcome of a reduction in human disturbance, since the nearby village was abandoned.

Vegetation classification and mapping

Vegetation descriptions were made in 48 plots of 4×4 m. All species of vascular plants, mosses and lichens were recorded, following the plant nomenclature of Czerepanov (1995). The abundance of all species was recorded by estimating their percentage cover. The vegetation descriptions were arranged in groups of plots with differing species and/or combinations of species with a high percentage cover. The resulting classification matched that of Leskov (1936), describing coastal salt-marsh communities of the Barentz sea.

Using this classification (Table 1), we determined salt-marsh vegetation zonation along four transects, which were established on different parts of the salt marsh in the summer of 2002 and were considered as four independent replicates (Fig. 1). Transects ran perpendicular to the coastline in order to map zonation from the low salt-dominated marshes to the dunes. Transects were 50 m wide and transects 1–4 were respectively 890, 1130, 1280 and 770 m in length. Transects were situated at least 500 m apart from each other and were numbered from northwest to southeast. Transect 1 was close to the (abandoned) village, transect 2 was located in the goose breeding area and transects 3 and 4 were placed towards the east. Transect 4 was higher in elevation than transect 3 and also traversed another small breeding colony.

In order to determine the vegetation zonation within each transect, we walked a line-transect of 50 m width, with five people evenly spaced over the entire width of the transect. The transect led from the intertidal flat to the dunes; and the plant community was recorded by every person every 10 m, using the classification in Table 1.

Fig. 1 Location of the Pechora Delta area, the village of Tobseda and the transects within the study area. The figure is based on Landsat images (1995/1996)
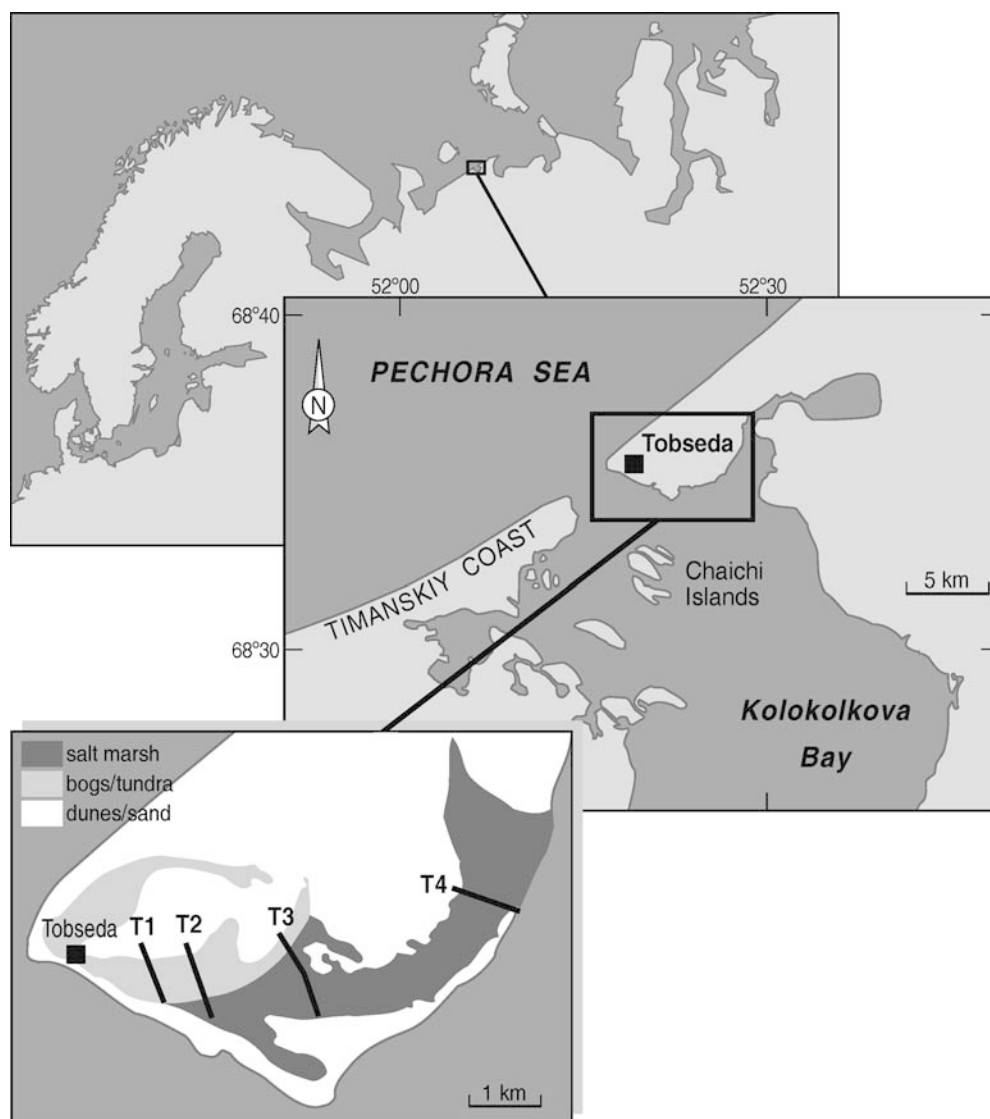
Measurements

For each plant community within each transect, goose droppings were counted. Dropping counts were done mid-July 2002. We assumed that we counted only droppings from the same season and that dropping numbers thus reflected the use of the area in that year. Resting piles were discarded. Dropping counts were made using two different methods and were repeated ten times within each vegetation type for each transect in randomly chosen plots. When droppings were abundant, we counted droppings in plots of 4 m^2. When dropping density was low, we counted plots of 10 m^2. Densities were expressed as x droppings m^{-2}. For all plant communities with dropping densities higher than 1 dropping m^{-2}, we measured tiller density (three replicates, each of 25 cm^2), percentage of grazed tillers (three replicates, each of 25 cm^2) and canopy height (five measurements, to the nearest 0.5 cm), using a sward stick with a styrofoam disc (20 cm diameter, 24 g). In addition, for each

of the plant communities along transects 1, 2 and 3, vegetation cover was estimated in ten randomly selected plots of 4 m^2. Additionally, we collected samples of leaftips (approximately 3 cm) from the most abundant plant species for chemical analysis of forage quality. Table 3 shows the number of replicates for each species. Samples were dried at 60°C for 48 h and thereafter ground and analysed for nitrogen and carbon content, using an automated CNHS analyser (automated element analysis, Interscience EA 1110).

In order to estimate the standing crop, samples of aboveground biomass were taken in all plant communities for all transects at 21–25 July 2002. In each plant community, we sampled the upper 2–3 cm of soil, including the litter layer. We collected three or four round turves with a diameter of 16.6 cm in each plant community. In stands of *Salix reptans*, the aboveground biomass of willow was cut from an area of 1 m^2. Green biomass was cut, sorted and dried to a constant weight at 70°C.

Table 1 Vegetation cover of the plant communities on marshes, combined with a table of the frequency and cover of vascular plants. Roman numerals indicate frequency: I <20%, II 21–40%, III 41–60%, IV 61–80%, V 81–100%. The percentage cover of each taxon was estimated using the following variant of the Braun–Blanquet scale: r ≪1%, $+$ <1%, I 1–5%, $2a$ 6–12.5%, $2b$ 12.6–25%, 3 26–50%, 4 51–75%, 5 76–100%. Entries in bold indicate the indicative species of the plant community. In the *Salix reptans* community, species with a frequency I include *Luzula wahlenbergii* (+) and *Carex concolor* (+)

Diagnostic species	H. tetraphylla	P. phryganodes-C. subspathacea	C. mackenziei-Warnstorfia exannulata	C. subspathacea-S. humifusa	C. subspathacea-dicotyledons	C. deschampsioides-C. glareosa	F. richardsonii-P. palustris	S. reptans-R. rosea
Number of areas	4	9	6	3	5	12	5	4
Vegetation cover (%)	10–60	20–100	90–100	70–100	90–100	90–100	100	100
Covered by monocotyledons (%)	10–60	20–100	60–80	40–100	90–100	90–100	90–100	5–50
Covered by mosses (%)			30–100		10		1–10	20–50
Covered by lichens (%)								1–50
Covered by cryptogamic crusts (algae; %)		20–75		60				
Hippuris tetraphylla	**V/2a-4**							
Puccinellia phryganodes		**V/2a-4**		V/1	V/+-2b	I/r-2b		
Carex mackenziei			**V/4-5**					
Dupontia psilosantha			I/+					
Triglochin palustre			I/r		I/r	I/r		
Carex subspathacea		IV/1-3	III/+	**V/2b-4**	**V/2a-4**	V/+-2b	V/r-1	
Stellaria humifusa		II/+		**V/2a-2b**	**V/1-2b**	V/+-2b	II/r-+	
Potentilla egedii					IV/+-2b	V/+-2a	III/2a-2b	
Plantago schrenkii					IV/r-4	IV/r-3	II/+-1	
Arctanthemum hultenii					**III/+-1**	V/+-2a	V/+-2a	
Carex glareosa						**V/+-5**	IV/+-2b	III/r-+
Calamagrostis deschampsioides						**V/+-4**	V/r-2b	III/r-1
Festuca richardsonii							**V/2b-4**	I/+
Parnassia palustris							**V/+-2b**	III/+
Salix reptans							I/1	**V/2b-4**
Rhodiola rosea							IV/r-+	**V/r-+**
Carex rariflora								V/1-3
Empetrum hermaphroditum								V/1-3

In order to measure electric conductivity, surface water was sampled either in the root zone of plants (*Hippuris tetraphylla*, *Carex mackenzeii*, *Dupontia psilosantha* communities) or in pools that were present in the marsh (all other plant communities; sample sizes are mentioned in Table 1). Soil samples were collected in the rooting zone of plants (0–8 cm), dried to a constant weight at 70°C and homogenised using a porcelain mortar and pistil and sieved with a mesh width of 0.25 mm. Every plant community was sampled once on each transect where present (Table 2). The total nitrogen and carbon contents (% dry matter) were determined by gas chromatography on an automated nitrogen/carbon analyser (ANA-1500) at the Ecoanalit Laboratory (Institute of Biology, Komi Science Centre, Russia).

To get information about the use of the area by other herbivores, we collected data on the presence of other herbivorous birds and mammals. Sightings and counts of birds and mammals were not collected systematically, but were noted. During 10 days, three lines of 20 mousetraps, baited with carrot and peanut butter, were set in the proximity of the village and transect 1 in order to trap small mammals.

The taxonomy of bird species follows the guidelines of the Dutch Commission for Avian Systematics (CSNA).

Statistics

As soil and vegetation properties were measured in different plots with different sample sizes, these data are not appropriate for detailed statistical analyses. Hence, the results are presented in a descriptive manner. All analyses were performed using the statistical package SPSS for Windows ver.11.0.1. Barnacle goose dropping density was log-transformed to reach normality criteria.

Results

Classification of the vegetation

On basis of the vegetation classification, 11 plant communities were recognised within the salt marsh (Table 1). Three plant communities not presented in Table 1 are the *D. psilosantha* community (a community with a dominance of *D. psilosantha*), a community similar to the *C. subspathacea*/dicotyledons community with a dominance of *Plantago schrenkii* and a community that we call "beach wall in colony". The latter was situated on an elevated sandy ridge at the coast and was characterised by a low vegetation cover (10%), of which 77% of the cover was graminoids (36% *Puccinellia phryganodes*, 41% *C. subspathacea*). The remainder was *P. schrenkii* (23%); and many nests of barnacle geese were found in this community. Mosses and lichens are not presented in Table 1, although they were recorded as

Table 2 Soil properties (N:C ratio of sediment, fraction nitrogen in sediment, electrical conductivity of the groundwater) and vegetation properties (total aboveground biomass, tiller density, vegetation height) of all salt-marsh plant communities. Data given are means ± SE, with sample size given in brackets. For tiller density and canopy height, the results of a post-hoc test are given. Different letters denote significant differences at the $P < 0.05$ level

Plant community	Hippuris tetraphylla	Puccinellia phryganodes-Carex subspathacea	Carex mackenziei-Warnstorfia exannulata	Carex subspathacea-Stellaria humifusa	Carex subspathacea-dicotyledons	Calamagrostis deschampsioides-Carex glareosa	Festuca richardsonii-Parnassia palustris	Salix reptans-Rhodiola rosea	beach wall in colony
N fraction in sediment		0.16±0.06 (5)	0.40±0.17 (3)	0.30±0.11 (5)	0.28±0.12 (4)	0.31±0.07 (9)	0.33±0.12 (3)	0.13±0.03 (2)	
Electrical conductivity (μS cm^{-1})	229.5±81.0 (3)	14071.3±3556.5 (8)	182.3±31.0 (6)	17600.0 (2)	4901.3±3245.8 (3)	2453.0±1494.1 (6)	152.7 (1)	125.3 (2)	
Total aboveground dry biomass (g m^{-2})	81.4 (N=1)	59.34±8.25 (N=4)	195.13±14.64 (N=3)	127.20 (N=2)	126.47±6.38 (N=3)	217.02±24.33 (N=4)	221.70 (N=2)	125.03±28.19 (N=3)	
Tiller density (tillers in 25 cm^2)		19.04±1.68 (N=30) ab		26.53±1.93 (N=20) c	20.55±1.44 (N=10) abc	13.68±0.88 (N=20) a			25.27±1.38 (N=10) bc
Canopy height (cm)		1.26±0.06 (N=30) ab		0.83±0.07 (N=20) a	2.13±0.23 (N=10) b	5.05±0.41 (N=20) c			0.70±0.04 (N=10) a

present, especially in the *Salix reptans/Rhodiola rosea* community.

We divided all non-salt-marsh plant communities into the following habitat classes: water/algae, dune/sand, bogs and tundra. This sketchy distinction was made on the basis of indicative species or groups of species (*Carex aquatilis*, *Carex rariflora* and mosses for bog habitat class, a substantial cover of lichens and dwarf shrubs for tundra habitat class) and substratum. We subdivided the salt marsh into three habitat classes, based on their salinity and location with respect to tidal inundation (low, middle, high). The communities belonging to the low salt marsh were the most saline communities: *P. phryganodes/C. subspathacea*, *C. subspathacea/Stellaria humifusa* and the beach wall community in the colony. Plant communities belonging to the middle high salt marsh were more brackish communities: *H. tetraphylla*, *C. mackenziei/Warnstorfia exannulata*, *D. psilosantha*, *C. subspathacea/*dicotyledons, *C. subspathacea/*dicotyledons with *P. schrenkii* dominant and *Calamagrostis deschampsioides/Carex glareosa*. The plant communities of the high salt marsh were *Festuca richardsonii/Parnassia palustris* and *S. reptans/R. rosea*.

For all plant communities, the total nitrogen content of the sediment was very low (<1%). Table 2 gives the electrical conductivity of surface water samples. An average electrical conductivity close to that of seawater (21,000 μS cm^{-1}) was distinctive for pools on sites where the communities *P. phryganodes/C. subspathacea*, *C. subspathacea/S. humifusa*, *C. subspathacea/*dicotyledons and *C. deschampsoides/C. glareosa* were present, i.e., those communities that experienced periodical or occasional flooding by seawater. All other communities showed values more similar to the conductivity of freshwater lakes in the dunes and the high marshes (54.2 μS cm^{-1}). However, high standard errors in conductivity values were recorded for the communities listed above, which shows that there was considerable heterogeneity in salinity of soil and lake water represented by these different vegetation communities. We found no significant correlation between salinity and total aboveground biomass (Pearson correlation = −0.469, $n = 8$, $P = 0.241$).

Description of the transects

From east to west (i.e., from transect 1 to transect 4), we observed a decrease in bog and tundra habitats and an increase in the area occupied by salt-marsh communities, especially plant communities dominated by *P. phryganodes* and *C. subspathacea* (Fig. 2). Some plant communities occurred only in a single transect: the *F. richardsonii/P. palustris* community was present only in transect 3, the *C. subspathacea/*dicotyledons community with *P. schrenkii* dominant was present only in transect 4 and the beach wall community was only found in transect 2.

▶

Fig. 2 Vegetation zonation in the transects, with an indication of the main habitat types. For the salt-marsh habitat types, numbers identify the plant community: *1 Hippuris tetraphylla, 2 Puccinellia phryganodes/Carex subspathacea, 3 Carex mackenziei, 4 Dupontia psilosantha* (not present in Table 1), *5 Carex subspathacea/Stellaria humifusa, 6 Carex subspathacea/*dicotyledons, *7 like 6 but with Plantago schrenkii* dominant, *8 Carex glareosa/Calamagrostis deschampsioides, 9 Festuca richardsonii/Parnassia palustre, 10 Salix reptans/Rhodiola rosea*

Barnacle goose visitation in the plant communities

For the salt-marsh communities, we used a univariate ANOVA with plant community as a fixed factor and transect as a random factor, in order to test for differences in goose visitation between transects and plant communities. We found a significant effect of plant community on goose visitation ($F_{8,9} = 14.201$, $P < 0.001$), no effect of transect ($F_{3,9} = 1.516$, $P = 0.276$) and a strong interaction between transect and plant community ($F_{9,189} = 5.671$, $P < 0.001$).

Because the main differences occurred between plant communities and not between transects, we grouped all data from the different transects for the analysis of habitat use by barnacle geese. A post-hoc Tukey test was used to depict differences between plant communities. All non-marsh plant communities and both the *F. richardsonii/P. palustris* and *S. reptans/R. rosea* communities did not differ in grazing pressure and had significantly lower dropping densities than those recorded for other marsh communities. Dropping densities in these plant communities are shown in Fig. 3. The beach wall community and the *C. subspathacea/S. humifusa* community had a significantly higher dropping density than other communities. All communities that had average dropping densities lower than 1 dropping m^{-2} (non-marsh communities, the *F. richardsonii/P. palustris*, *S. reptans/R. rosea*, *C. mackenzeii/W. exannulata* and *D. psilosantha* communities) were not used for the following analyses.

Vegetation parameters and barnacle goose visitation

Aboveground biomass accumulation was highest in plant communities of the middle and high marshes, where the grasses *C. deschampsioides* and *F. richardsonii* and the sedge *C. glareosa* dominated. The *P. phryganodes/C. subspathacea* community was characterised by a low total net accumulation of biomass (Table 2).

Table 2 gives the average tiller density and canopy height. Both tiller density ($F_{4,85} = 9.180$, $P < 0.001$) and canopy height ($F_{4,85} = 71.076$, $P < 0.001$) were significantly different between plant communities (one-way ANOVA). Overall, the *C. subspathacea/S. humifusa* and breeding beach wall communities had the highest tiller densities and the lowest canopy heights (see Table 2 for results of a post-hoc Tukey test). Table 3 shows the nitrogen content and the C/N ratio of some main forage
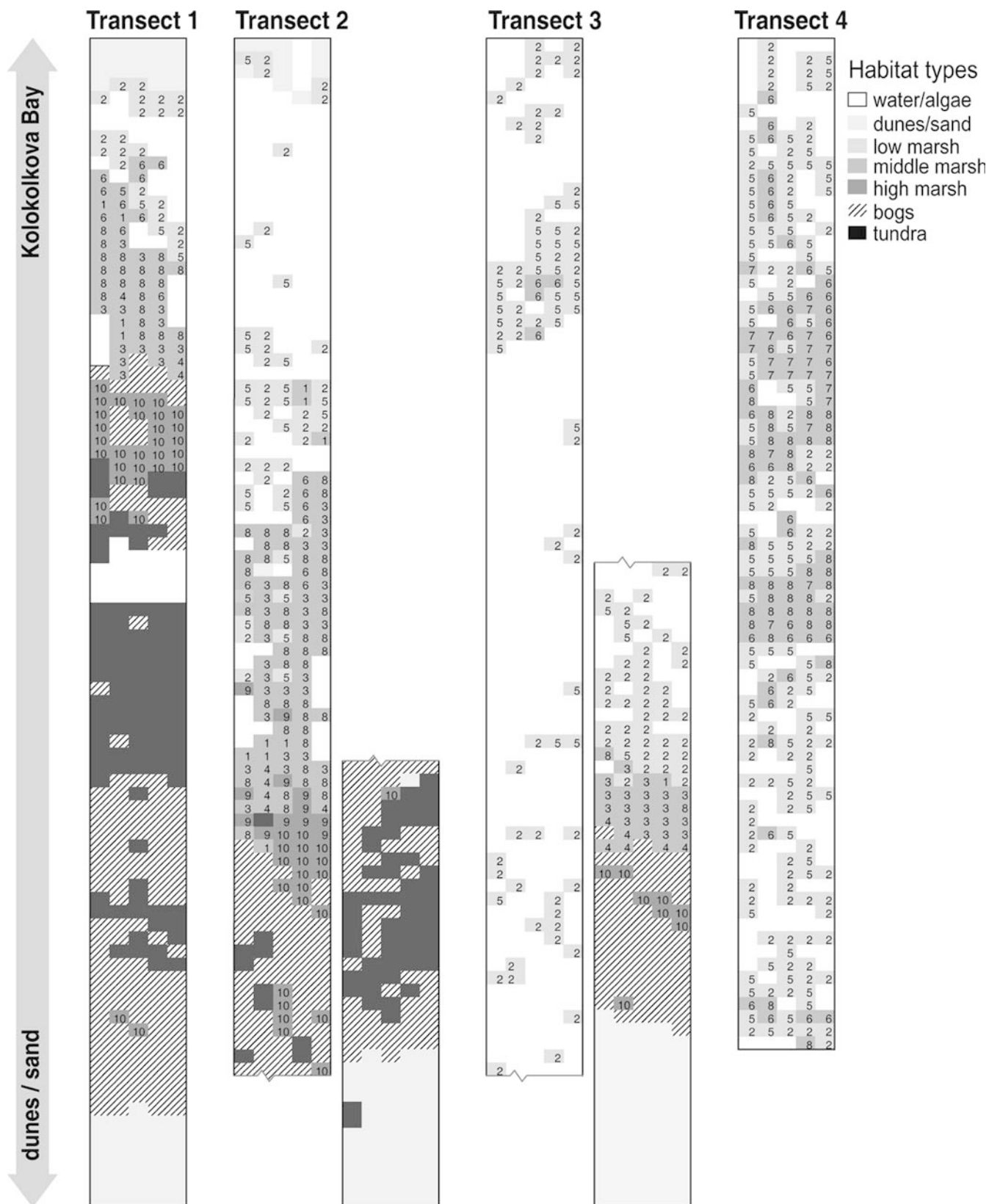
species. The quality of species differed significantly (one-way ANOVA $F_{6,21} = 9.378$, $P < 0.001$). *C. subspathacea* and *T. palustre* seemed to have the highest N content and the lowest C/N ratio. A posthoc-Tukey test shows that *C. subspathacea* had indeed a significantly higher N content than *P. phryganodes* and *C. deschampsioides*, but did not differ significantly from *C. mackenziei*, *C. glareosa*, *C. rariflora* and *P. schrenkii*.
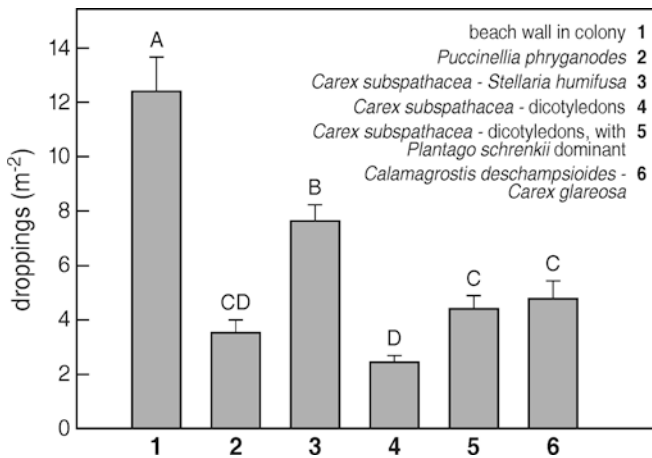
Fig. 3 Cumulative dropping densities for the most important vegetation communities. Communities with dropping densities lower than 1 dropping m^{-2} are left out. *Different letters* denote significant differences derived from a post-hoc Tukey test ($P < 0.05$). Values are averaged for all transects. *Error bars* indicate SEs of the mean. $n = 30$ except for communities 1 ($n = 10$), 4 ($n = 20$) and 5 ($n = 10$)

Table 3 N content and C/N ratio of plant species, ranked on ascending N content. *Different letters* denote significant differences (Tukey post-hoc test with significance level of $P < 0.05$)

Species	n	Nitrogen (% ± SE)	C/N ratio
Festuca richardsonii	1	1.64	27.73
Dupontia psilosantha	1	2.00	22.97
Calamagrostis deschampsioides	3	2.34 ± 0.05 c	19.75
Puccinellia phryganodes	5	2.58 ± 0.22 bc	18.34
Plantago schrenkii	2	2.60	16.17
Carex rariflora	3	2.90 ± 0.02 abc	16.26
Carex glareosa	3	2.92 ± 0.09 abc	15.90
Carex mackenziei	3	3.27 ± 0.14 ab	14.31
Carex subspathacea	9	3.79 ± 0.15 a	11.86
Triglochin palustre	1	4.14	9.69

To investigate whether barnacle geese have a preference for specific vegetation properties, we tested for a relation between barnacle goose dropping density and canopy height and tiller density (univariate ANOVA with plant community as fixed factor and tiller density and canopy height as covariates). We found a significant effect of plant community ($F_{4,83} = 12.657$, $P < 0.001$), tiller density ($F_{1,83} = 5.433$, $P = 0.022$) and canopy height ($F_{1,83} = 5.167$, $P = 0.026$) on dropping density. In this model, tiller density had a positive effect on dropping density, whereas canopy height affected dropping density negatively. Interestingly, the most preferred communities (the beach wall and the *C. subspathacea/S. humifusa* communities) indeed had the highest tiller density and lowest canopy height. When performing the same test for each plant community separately, we found a significant positive relation between canopy height and dropping density only for the *C. subspathacea/S. humifusa* community ($F_{1,17} = 14.149$, $P = 0.002$). Apparently,

the geese favoured higher vegetation in this preferred plant community where canopy height was generally low. Overall, barnacle geese preferred plant communities with low canopy heights.

Other herbivores

White-fronted geese and tundra bean geese occurred in low numbers. Some breeding pairs were found in the area but no flocks of non-breeders were seen. A non-parametric Kruskal–Wallis test showed a significant difference in dropping densities of *Anser* species between plant communities ($\chi^2 = 20.046$, df $= 8$, $P = 0.010$). Most droppings were found in the *D. psilosantha* community and on the beach wall community. No droppings were found in the *C. subspathacea/S. humifusa* and *C. subspathacea*/dicotyledons communities.

A couple of pairs of Bewick swans were observed in the area. Swan grazing differed significantly between plant communities ($\chi^2 = 43.227$, df $= 8$, $P < 0.001$). Droppings were found only in the different bog communities and in the *C. mackenziei/W. exannulata* community. However, moulting groups of more than 100 birds were observed grazing on the *C. subspathacea/* dicotyledons community, just outside the study area.

Droppings of willow grouse (*Lagopus lagopus*) were found only in one bog site outside the transects, (0.63 ± 0.20 droppings m^{-2}, $n = 70$) and on a dry ridge running through that bog (0.95 ± 0.53 droppings m^{-2}, $n = 40$). We found no droppings of reindeer (*Rangifer tarandus*) or mountain hare (*Lepus timidus*) in the area. We did not catch any small mammals on our mousetrap transects, nor did we observe any tracks in the area.

Discussion

The Tobseda salt marsh bears similarities in vegetation composition to other marshes along the Russian coast (Korchagin 1935; Rebristaya 1997; personal observations at Shoyna marsh, Kanin Peninsula) and to marshes at similar latitudes in North America, in particular the marsh at La Pérouse Bay, Canada (Jefferies et al. 1979). Just like that Canadian site, the lower salt marsh here is dominated by *P. phryganodes* and *C. subspathacea* and the soil nutrient content is very low. At the lowest elevation, *P. phryganodes/C. subspathacea* vegetation forms a mosaic pattern with bare soil (Fig. 2). This pattern is probably typical for low salt-marsh areas in subarctic environments, where mechanical disturbance (ice rafting) is prominent; and it has also been described for the Canadian subarctic site (Srivastava and Jefferies 2002). At our site, the mosaic turns into a more distinct zonation along the elevational gradient where the *P. phryganodes/C. subspathacea* community turns into the *C. subspathacea/ S. humifusa* and *C. subspathacea*/dicotyledons communities. All plant communities with high

cover of either *P. phryganodes* or *C. subspathaceae* are preferentially used by foraging geese.

As the Russian subarctic salt marsh at our study site is heavily used by staging, breeding and moulting geese, processes similar to those acting in La Pérouse Bay may play a role: grazing optimisation at modest levels of herbivory and habitat degeneration at high levels due to overgrazing. At the salt marsh at La Pérouse Bay, lesser snow geese (*A. caerulescens caerulescens*) increase the production, density and nitrogen content of their forage plants (*P. phryganodes*, *C. subspathacea*) by grazing (Cargill and Jefferies 1984; Kotanen and Jefferies 1987; Bazely and Jefferies 1989a). This process is an example of grazing optimisation and is caused by an acceleration in nutrient cycling as a result of grazing and subsequent fertilisation of the vegetation by droppings (Bazely and Jefferies 1985; Hik and Jefferies 1990). The negative effects of large numbers of herbivores on their forage plants, which cumulate during habitat degeneration, are initiated by the grubbing of lesser snow geese. As a result of the removal of the insulating mat of plant material, soil evaporation increases, which leads to hypersaline conditions in the upper layers of the soil, thereby reducing the growth of graminoids (Srivastava and Jefferies 1996). In grubbed areas, soil nitrogen and its mineralisation are decreased which, together with the hyper-saline conditions, hamper the re-establishment of plants (Wilson and Jefferies 1996; Walker et al. 2003). Unlike the snow geese in the Canadian Arctic, barnacle geese do not forage destructively. They graze the aboveground plant material and do not grub for belowground plant parts. At our Russian site, we found no evidence of the negative effects of goose grazing on the graminoid sward and we do not expect habitat degeneration as a result of goose foraging to play a role in inducing vegetation change in this Russian subarctic salt marsh. It is likely, however, that grazing optimisation does play a role in this marsh.

Vegetation selection by barnacle geese
at a subarctic marsh

Our data suggest that the geese select forage sites on a combination of the forage parameters of canopy height, tiller density and food quality. It is striking that the two most preferred plant communities both contain the two forage species with highest tissue quality: *T. palustre* and *C. subspathacea*. The preferred communities also had the highest average tiller densities and the lowest average canopy heights. Interestingly, these can either be characteristics selected by the geese, or they can be caused by goose grazing. Grazing reduces canopy height and may increase tiller density in the grazed vegetation (McNaughton 1984; Kotanen and Jefferies 1987; Bazely and Jefferies 1989a). Dense swards of forage plant species are preferred by the geese, as they result in increased food intake rates (Van der Wal et al. 1998). At the same time, geese are known to prefer low canopy heights, as short swards decrease handling time and enhance foraging efficiency (Van der Wal et al. 1998; Hassall et al. 2001; Bos 2002).

For arctic and subarctic systems, several studies demonstrated that the quality of the vegetation is improved through grazing (Gauthier et al. 1995; Post and Klein 1996; Ruess et al. 1997; Fox et al. 1998). The alleviation of nutrient limitation in the vegetation through the addition of herbivore faeces plays an important role in this process (Bazely and Jefferies 1989b; Ruess et al. 1997). Future expeditionary work on the Tobseda marsh will investigate nutrient availability for plant growth at that site and the role of foraging geese within the ecosystem processes.

References

Alerstam T, Hedenström A (1998) The development of bird migration theory. J Avian Biol 29:343–369

Bazely DR, Jefferies RL (1985) Goose faeces: a source of nitrogen for plant growth in a grazed salt marsh. J Appl Ecol 22:693–703

Bazely DR, Jefferies RL (1989a) Leaf and shoot demography of an arctic stoloniferous grass *Puccinellia phryganoides* in response to grazing. J Ecol 77:811–822

Bazely DR, Jefferies RL (1989b) Lesser snow geese and the nitrogen economy of a grazed salt marsh. J Ecol 77:24–34

Bos D (2002) Brent Geese cope with increased levels of primary production in spring by aggregation. PhD thesis, University of Groningen, Groningen

Cargill SM, Jefferies RL (1984) The effects of grazing by lesser snow geese on the vegetation of a sub-arctic salt marsh. J Appl Ecol 21:669–686

Czerepanov SK (1995) Vascular plants of Russia and adjacent states (the former USSR). Cambridge University Press, Cambridge

Fox AD, Kristiansen JN, Stroud DA, Boyd H (1998) The effects of simulated spring goose grazing on the growth rate and protein content of *Phleum pratense* leaves. Oecologia 116:154–159

Gadallah FL, Jefferies RL (1995) Forage quality in brood rearing areas of the lesser snow goose and the growth of captive goslings. J Appl Ecol 32:276

Gauthier G, Hughes RJ, Reed A, Beaulieu J, Rochefort L (1995) Effect of grazing by greater snow geese on the production of graminoids at an arctic site (Bylot Island, NWT, Canada). J Ecol 83:653–664

Green M, Alerstam T, Clausen P, Drent RH, Ebbinge BS (2002) Site use by dark-bellied brent geese *Branta bernicla bernicla* on the Russian tundra as recorded by satellite telemetry: implications for East Atlantic Flyway conservation. Wildl Biol 8:229–239

Hassall M, Riddington R, Helden A (2001) Foraging behaviour of brent geese, *Branta b. bernicla*, on grasslands: effects of sward length and nitrogen content. Oecologia 127:97–104

Hik DS, Jefferies RL (1990) Increases in the net above-ground primary production of a salt-marsh forage grass—a test of the predictions of the herbivore-optimization model. J Ecol 78:180–195

Jefferies RL (1977) The vegetation of salt marshes at some coastal sites in arctic North America. J Ecol 65:661–672

Jefferies RL, Jensen A, Abraham KF (1979) Vegetational development and the effect of geese on vegetation at La Pérouse Bay, Manitoba. Can J Bot 57:1439–1450

Kincheloe KL, Stehn RA (1991) Vegetation patterns and environmental gradients in coastal meadows on the Yukon–Kuskokwim delta, Alaska. Can J Bot 69:1616–1627

Korchagin AA (1935) Vegetation of maritime alluviums of the Mezensky Gulf and Chez Bay meadows and meadow bogs (in Russian). Acta Inst Bot Acad Sci URSS Ser 3:2223–2333

Kotanen PM, Jefferies RL (1987) The leaf and shoot demography of grazed and ungrazed plants of *Carex subspathacea*. J Ecol 75:961–976

Leskov AI (1936) Geobotanical essay of the Malozemelskaya Tundra coastal salt marshes of the Barentz Sea (in Russian). Bot Zh St Petersburg 21:96–116

McNaughton SJ (1984) Grazing lawns: animals in herds, plant form and coevolution. Am Nat 124:863–886

Nolet BA, Drent RH (1998) Bewick Swans refuelling on pondweed tubers in the Dvina Bay (White Sea) during their spring migration: first come, first served. J Avian Biol 29:574–581

Owen M (1980) Wild geese of the world. Batsford, London

Person BT, Herzog MP, Ruess RW, Sedinger JS, Anthony RM, Babcock CA (2003) Feedback dynamics of grazing lawns: coupling vegetation change with animal growth. Oecologia 135:583–592

Piedboeuf N, Gauthier G (1999) Nutritive quality of forage plants for greater snow goose goslings: when is it advantageous to feed on grazed plants? Can J Zool 77:1908–1918

Post ES, Klein DR (1996) Relationships between graminoid growth form and levels of grazing by caribou (*Rangifer tarandus*) in Alaska. Oecologia 107:364–372

Rebristaya OV (1997) Flora of the seas coast habitats in the west Siberian Arctic (in Russian). Bot Zh St Petersburg 82:30–40

Ruess RW, Uliassi DD, Mulder CPH, Person BT (1997) Growth responses of *Carex ramenskii* to defoliation, salinity, and nitrogen availability: implications for geese-ecosystem dynamics in western Alaska. Ecoscience 4:170–178

Srivastava DS, Jefferies RL (1996) A positive feedback: herbivory, plant growth, salinity and the desertification of an Arctic salt-marsh. J Ecol 84:31–42

Srivastava DS, Jefferies RL (2002) Intertidal plant communities of an Arctic salt marsh: the influence of isostatic uplift and herbivory. Ecoscience 9:112–118

Syroechkovsky EE Jr (1995) News in distribution of Barnacle Goose in Russia (in Russian with English summary). Geese Study Group Bull East Eur North Asia 1:39–46

Syroechkovsky EE Jr, Litvin KE (1998) Migrations of Brent geese (*Branta bernicla bernicla*) in Russia (in Russian with English summary). Casarca 4:71–95

Van der Jeugd HP, Gurtovaya E, Eichhorn G, Litvin KYe, Mineev OY, Van Eerden MR (2003) Breeding barnacle geese in Kolokolkov Bay, Russia: number of breeding pairs, reproductive success, and morphology. Polar Biol 26:700–706

Van der Wal R, Van de Koppel J, Sagel M (1998) On the relation between herbivore foraging efficiency and plant standing crop: an experiment with barnacle geese. Oikos 82:123–130

Van Eerden MR (2000) Pechora Delta—structure and dynamics of the Pechora Delta ecosystems (1995–1999). Institute for Inland Water Management and Waste Water Treatment (RIZA), Lelystad

Vince SW, Snow AA (1984) Plant zonation in an Alaskan salt marsh—I. Distribution, abundance and environmental factors. J Ecol 72:651–667

Walker NA, Hendry HAL, Wilson DJ, Jefferies RL (2003) The dynamics of nitrogen movement in an Arctic salt marsh in response to goose herbivory: a parameterized model with alternate stable states. J Ecol 91:637–650

Wilson DJ, Jefferies RL (1996) Nitrogen mineralization, plant growth and goose herbivory in an Arctic coastal ecosystem. J Ecol 84:841–851