BOREAL ENVIRONMENT RESEARCH 26: 1–16 © 2021
ISSN 1797-2469 (online) Helsinki 12 January 2021

Abundance and feeding of fish in the coastal zone of the Neva Estuary, eastern Gulf of Finland

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Received 26 Jul. 2019, final version received 20 Aug. 2020, accepted 13 Nov. 2020

Demchuk A.S., Uspenskiy A.A. & Golubkov S.M. 2021: Abundance and feeding of fish in the coastal zone of the Neva Estuary, eastern Gulf of Finland. *Boreal Env. Res.* 26: 1–16.

Fish inhabiting coastal zone are important link between lower and higher trophic levels in its ecosystems. The aim of this study was to provide more information on the composition of coastal fish and the diet of dominant species in the Neva Estuary, one of the largest estuary of the Baltic Sea. The study showed a diverse coastal fish fauna associated with a large variety of biotopes within the estuary. We identified five freshwater fish species belonging to Cyprinidae, and high abundance of three-spined stickleback probably a consequence of high eutrophication in the coastal zone and extensive green tides of macroalgae. Diet analysis shows that zooplankton is an important food for many core fish species (bleak, three-spined stickleback and perch), whereas chironomid larvae were the main food items for benthivorous fish (roach and gudgeon), and low dependency on non-insect zoobethos.

Introduction

Fish of various species are central for the functioning of whole ecosystem and food webs in the Baltic Sea (Österblom *et al.* 2007; Östman *et al.* 2013, 2016; Kraufvelin *et al.* 2018). With respect to fish communities, coastal areas provide important habitats for spawning, recruitment and foraging for many species and are thereby an important basis for commercial, household and recreational fisheries (Rönnbäck *et al.* 2007; Seitz *et al.* 2014; Bergström *et al.* 2016a). Estuarine areas are especially important as they have a great variety of environmental conditions with significant gradients of abiotic factors providing high heterogeneity of habitats, which are important for spawning, development of young and small fishes and foraging for many non-commercial species. But, human population increases have been particularly rapid in coastal zones around estuaries and have resulted in a multitude of ecological stresses on their ecosystems (Flemer and Champ 2006).

Coastal fish are a resource for commercial and recreational fisheries as well as significant contributors to coastal ecosystem functioning, by linking lower and higher levels of the food web. The coastal zone of the Baltic Sea has diverse fish communities consisting of species of various origins: marine species, freshwater species, and migratory anadromous species. Among them, two functional group of species are especially

Editor in charge of this article: Örjan Östman

important. The first one is piscivores, which are attributed to changes in food web processes through predation, and the second one is cyprinids, which are associated with eutrophication (Bergström *et al.* 2016a). Some declining trends in piscivores and of increases in cyprinids have been observed during the last three decades. A recent rise of stickleback (*Gasterosteus aculeatus*) in different areas of the Baltic Sea has also been recorded (Bergström *et al.* 2016b). This species is important because if it reaches high numbers, it can be a strong predator on the eggs and larvae of other fish. When adult sticklebacks immigrate from the open sea to the coastal zone to spawn, they may dominate fish assemblages during the summer.

The Neva Estuary located in the eastern part of the Gulf of Finland is one of the largest estuaries of the Baltic Sea. Its extensive shallow productive habitats in the coastal zone such as wetlands, vegetated flads/lagoons and sheltered bays as well as more exposed rocky and sandy areas are always utilized by fish across many life history stages including spawning, juvenile development, feeding and migration (Berg 1940; Kuderskiy *et al.* 2007). However, due to St. Petersburg located on its shores, the largest city in the Baltic region, its ecosystem suffers from significant anthropogenic impact. Eutrophication, nutrient and organic pollution, alien species and habitat fragmentation are the major environmental problems in the Neva Estuary (Golubkov 2009b; Gubelit *et al.* 2016; Golubkov *et al.* 2018, 2019). Values of eutrophication indicators in the estuary are among the highest in the Baltic region (Golubkov 2009a; Golubkov *et al.* 2017, 2018).

Eutrophication affects the composition of fish communities. For instance, it often leads to declining trends in piscivores and of increases in cyprinid fish (Ådjers *et al.* 2006; Snickars *et al.* 2015; Bergström *et al.* 2016b). It may also have negative effects on benthic feeding species (HELCOM 2006). Stable isotope analysis of some fish from the coastal zone of the Neva Estuary showed that they mainly used the pelagic-derived carbon for their production (Golubkov *et al.* 2018).

Variable conditions, high anthropogenic press and intensive ship traffic in the region make the Neva Estuary vulnerable to non-ingenious species (NIS) invasion. Moreover, rising temperatures in the northern part of the Baltic Sea due to climate change may increase the risk of the invasions of new species (Holopainen *et al.* 2016).

Coastal fish and their diets in many areas of the Baltic Sea have been well studied (Lankov *et al.* 2006; Rönnbäck *et al.* 2007; Seitz *et al.* 2014; Snickars *et al.* 2015; Bergströmetal.2016b; Ojaveer *et al.* 2017). However, this does not apply to the Neva Estuary and the Russian, eastern part of the Gulf of Finland as a whole. There is little up-to-date data on the composition of coastal fish communities and their diets in this vast Baltic area (Uspenskiy and Naseka 2014; Golubkov *et al.* 2018). In this regard, the purpose of this study was to provide more information on the current composition of coastal fish communities and the diet of dominant species in the Neva Estuary. We tested the hypothesis that the species composition and diet of coastal fish reflect specific conditions in the estuary, including significant environmental gradients, high level of eutrophication and vulnerability to NIS invasions differ from that of other regions of the Baltic Sea.

Material and methods

Study area and field sampling

The Neva Estuary is located in the eastern Gulf of Finland. It consists of three parts: the upper part (Neva Bay), the middle part (Inner Estuary), and the lower part (Outer Estuary; Fig. 1). At the end of 1980s, Neva Bay was separated from the lower parts by the Flood Protective Facility (Dam). It consists of eleven dams separated by broad water passages and ship gates in its southern and northern parts. The surface area of Neva Bay is about 400 km^2; with a salinity range between 0.07–0.20 PSU. The Inner Estuary is brackish-water and is located between the Dam and a longitude of ca. 29°E. The salinity of the surface water in this part of the Neva Estuary ranges 0.5–3.0 PSU. The Outer Estuary is located from the west of 29°E and to the east of the border of territorial waters of Russia. The

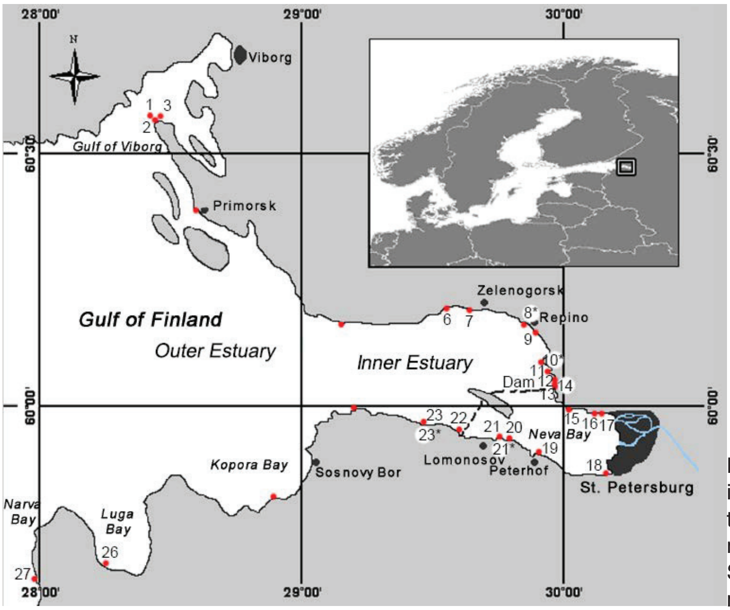

Fig 1. Study area and sampling sites in the Gulf of Finland. Stations for the study of the fish distribution are numbered and marked by black dots. Stations for the study of fish diet are marked with red dots.

salinity of water in the coastal area of its western part can reach 5.0 PSU. Detailed information about the Neva Estuary and its coastal habitats, description of sampling sites and main physical and chemical characteristics are given elsewhere (Telesh *et al.* 2008; Gubelit 2015; Gubelit *et al.* 2016; Berezina *et al.* 2017; Golubkov *et al.* 2017; 2018).

The coastal fish assemblages were investigated in the Neva Estuary during the ice-free season (from May to October) of 2014. Twenty-seven coastal localities were surveyed on the coastal shallows at the depth from 0.5–1.5 m (Fig. 1, Table 1). Fifty-two beach-seine samples (including seasonal replications) were collected in Neva Bay, Luga, Kopora and Narva bays, and in the Gulf of Vyborg. To analyze the diet, fish were collected at eight sites (Fig. 1) in July 2018, which is the period of their active migration and feeding in the shallow coastal zone (Table 1).

Fish were caught using a small hand-towed beach-seine (length: 10 m, wings: 1.5 m high, bag: 3 m, mesh-size: 10 mm on the wings and from 0.5–4 mm in the bag). The distance of hauling varied from 25 m to 90 m, measured by a monocular laser distance meter with an accuracy of 1 m. The distance was shorter than 90 m in some sampling locations, where the depth was more than 1.2 m, and numerous boulders or vegetation were at the bottom. Two or three haulings were made in such cases. All samples were recalculated per 100 m^2 to standardize the data. Fish samples were fixed with 4% formalin.

Table 1. Samplings stations, periods and a number of samples/stations during 2014.

	Neva Bay	Inner Estuary		Outer Estuary	
		South	North	South	North
Station No.	15–21	22–23	6–14	26–27	1–3
Sampling Period					
May–15 June	5/3	3/2	4/3	2/2	—
15 June–15 September	9/8	8/6	12/8	3/3	3/4
15 September–November	4/3	3/2	4/3	—	—

Laboratory procedure and analysis of fish community composition

Species composition, occurrence (V) and relative abundance (RN) of different species in catches, their CPUE, age and size were estimated. The total length (TL) and standard length (SL) to the nearest lower millimeter and total weight (TW) to the nearest 0.001 g were measured. Age was examined by scales and operculums with the purpose of length differentiation of the 0+ y and 1+ y juveniles, and older fishes. The age of no less than 30 specimens were examined for each species. The frequency of occurrence (V) was estimated according to:

$$V = 100 \times a / A, \quad (1)$$

where a is the number of sites where a certain species was recorded and A is the total number of sampling sites.

A species was identified as a core of species, if the frequency of occurrence exceeded 50%. The species was considered secondary if it was recorded in 25–50% of sampling sites; as rare if V was 8–25%; and occasional if V was less than 8% (Uspenskiy and Naseka 2014). The relative abundance in catches (RN) of different fish species was estimated as:

$$\mathrm{RN} = 100 \times n / N, \quad (2)$$

where n is the number of specimens of a certain fish species in sample and N is the total number of fishes in the sample. The species was identified as "dominant" when RN exceeded 50%; "abundant" when RN was more than 10% and less than 50%. Species was "medium in numbers" when RN was 1–10%; "few in numbers" when RN was 0.1–1.0% and "scarce" when RN was less than 0.1% (Tereshchenko and Nadirov 1996). CPUE (catch per unit of effort, individuals/100 m^2) for the beach-seine was estimated as the number of specimens of a certain fish species caught per 100 m^2 (Žiliukas *et al.* 2012):

$$\mathrm{CPUE} = 100 \times n / S, \quad (3)$$

where n is the number of specimens of a certain fish species in the sample and S is the sampled area, measured in m^2.

Laboratory procedure and analysis of food composition

Food composition of five dominant fish species in the surveyed area (*Rutilus rutilus*, *Alburnus alburnus*, *Gasterosteus aculeatus*, *Gobio gobio* and *Perca fluviatilis*) was investigated. Different age stages of these species were numerous at most study sites. Bleak was represented by one-year-old juveniles (1+ y) and older adult fishes (TL 46–100 mm; average 61.8 mm ± 11.0 SD), perch — by young-of-the-year juveniles (0+ y) only (TL 10–49 mm; average 28.1 mm ± 7.8 SD). Stickleback was represented by both young-of-the-year (0+ y) juveniles (average TL 15.9 mm ± 3.4 SD) and adult fishes (1+ y) (TL 48–68 mm; average 57 mm ± 5.1 SD). Roach samples included young-of-the-year (0+ y) (average TL 28.8 mm ± 2.4 SD) and older juveniles (1+ y) (TL 44–86 mm; average 65.3 mm ± 12.7 SD). Gudgeon was represented by older juveniles and adults (1+ y) (TL 58–113 mm; average 75.3 mm ± 12.7 SD), which had been examined together.

Food organisms from 505 intestinal tracts from 19 beach-seine samples (N = 25 on average, min = 15, max = 40 fish in each sample) collected at eight stations (Fig. 1) were identified to the lowest possible taxonomic level (usually species or genus except for some Chironomidae taxa) and counted. The best-preserved specimens were measured with a micrometer eyepiece scale (up to 0.03 mm) for the additional calculations of their biomass, which was estimated as a sum of weights based on allometric equations (Chislenko 1968; Alimov *et al.* 2013) or a ready-average mass (Pertzova 1967). The contribution of each prey items to the overall diet was analyzed using the following three relative metrics of prey amount: percent frequency of occurrence (F_i), percent wet mass of food items in fish intestinal tracts (I_i) and percent composition by quantity (Q_i)(Hyslop 1980):

$$F_i = 100 \times N_i / N, \quad (4)$$

where N_i is the number of fish with food category, i, in their intestinal tracts and N is the total number of analyzed fish.

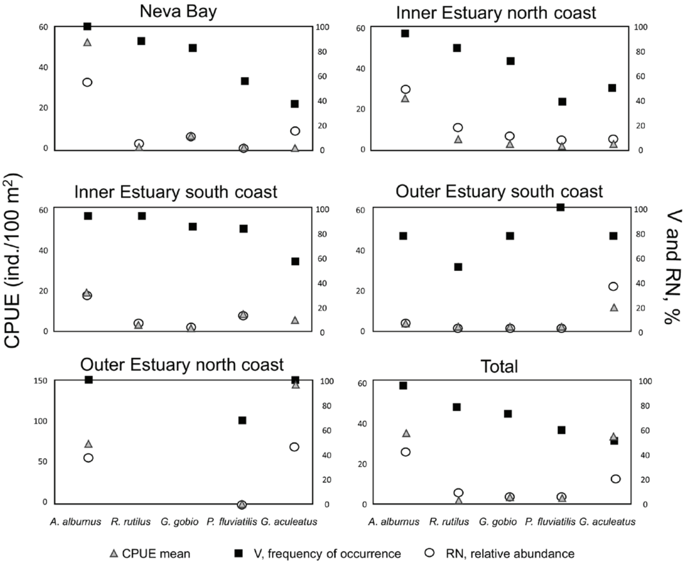

Fig 2. Average CPUE (ind./100 m²), relative abundance (RN, %) and frequency of occurrence (*V*, %) of the abundant fish species in different parts of the Neva Estuary.

$$I_i = 100 \times S_i / S_t, \qquad (5)$$

where S_i is the wet mass of food category, *i*, in all intestinal tracts of a certain fish species, and S_t is the total content wet mass of all food categories in the intestinal tracts of a certain fish species.

$$Q_i = 100 \times D_i / D_t, \qquad (6)$$

where D_i is the number of prey of food category, *i*, and D_t is the total number of prey of all food categories in the whole intestinal tracts. The Index of Relative Importance (IRI) was calculated to assess the significance of prey items:

$$\mathrm{IRI}_i = (\%Q_i + \%I_i) \times \%F_i. \qquad (7)$$

This index is a representative value, because sometimes numerous small organisms overshadow the importance of a few large ones. Different digestive rates distort volumetric mass measurements. Moreover, the estimation of the frequency of occurrence (F_i) is sensitive to sampling errors (Pinkas *et al.* 1971). Taking into account these misleading aspects of assessment of prey significance, individual data categories were expressed as percentages for each fish species in the all their intestinal tracts in total: feeding intensity was measured as index of fullness (FI) calculated at first for each individual, and then averaged per species (Hureau 1970):

$$\mathrm{FI} = 100 \times \mathrm{WS} / \mathrm{TW}, \qquad (8)$$

where WS is the total weight intestinal tracts/stomachs contents and TW is the total weight of the fish.

Statistical analysis was performed using Microsoft Excel 2013, Past ver. 4.0 and Statistica ver. 10. All measured parameters were expressed as a mean ± SD (standard deviation) except CPUE: mean ± SE (standard error). For a formalized estimate of the diet heterogeneity of various fish species throughout the study area, we used the Principal Component Analysis (PCA) for the percent of wet mass of food items in non-empty fish's intestinal tracts (I_i).

Results

Fish diversity and abundance

The coastal fish community of the eastern Gulf of Finland consisted of 30 fish species from 11 families including five invasive species (Table 2). Species from the family Cyprinidae (14 species) composed 47% of the total species richness. The next most numerous family was

Table 2. Average occurrence (*V*), average abundance in catches (RN) and total number of caught individuals (*n*) of fish in the eastern Gulf of Finland in 2014. juv — juveniles; ad — adults; NB — Neva Bay; InnS — Inner Estuary south costal; InnN — Inner Estuary north costal; OutS — Outer Estuary south costal; OutN — Outer Estuary north costal; LS — life stages + marked species occurred in samples; * indicates invasive species.

No.	Species	Occurrence in Samples					*V*	RN	*n*	LS
		NB	InnS	InnN	OutS	OutN	%	%		
	Common species (core fish species)									
1	*Alburnus alburnus* (Linnaeus, 1758), bleak	+	+	+	+	+	94.2	42.5	8870	ad juv
2	*Rutilus rutilus* (Linnaeus, 1758), roach	+	+	+	+		78.8	11.6	688	ad juv
3	*Gobio gobio* (Linnaeus, 1758), gudgeon	+	+	+	+		73.1	8.7	683	ad juv
4	*Perca fluviatilis* (Linnaeus, 1758), perch	+	+	+	+	+	59.6	6.3	311	ad juv
5	*Gasterosteus aculeatus* (Linnaeus, 1758), three-spined stickleback	+	+	+	+	+	51.9	22.2	2862	ad juv
	Secondary species									
6	*Gymnocephalus cernua* (Linnaeus, 1758), ruffe	+	+	+			40.4	9.9	493	ad juv
7	*Blicca bjoerkna* (Linnaeus, 1758), white bream	+	+	+	+		32.7	6.9	207	ad juv
8	*Abramis brama* (Linnaeus, 1758), bream	+	+	+			30.8	8.8	418	juv
9	**Proterorhinus semilunaris* (Heckel, 1837), tubenose goby	+	+	+			30.8	19.9	567	ad juv
10	*Pungitius pungitius* (Linnaeus, 1758), nine-spined stickleback	+	+	+	+		26.9	8.0	175	ad juv
11	*Leuciscus leuciscus* (Linnaeus, 1758), dace	+	+	+			25.0	0.4	32	ad juv
12	*Cobitis taenia* (Linnaeus, 1758), spined loach	+	+	+			25.0	1.7	31	ad juv
	Rare species									
13	*Pomatoschistus microps* (Kroyer, 1838), common goby		+	+	+	+	21.2	20.2	995	ad juv
14	**Romanogobio albipinnatus* (Lukasch, 1933),white-fin gudgeon	+	+				11.5	2.1	29	ad juv
15	*Scardinius erythrophthalmus* (Linnaeus, 1758), rudd	+	+	+			11.5	6.7	27	ad juv
	Occasional species									
16	**Carassius gibelio* (Bloch, 1782), gibel carp	+		+			5.8	1.1	4	juv
17	*Vimba vimba* (Linnaeus, 1758), silver bream		+		+		5.8	1.2	5	juv
18	*Sander lucioperca* (Linnaeus, 1758), pike perch	+	+				5.8	6.0	67	juv
19	**Perccottus glenii* (Dybowski, 1877), rotan	+	+				5.8	30.7	146	ad juv
20	*Coregonus albula* (Linnaeus, 1758), vendace		+	+			3.8	2.2	2	juv
21	*Osmeruse perlanus* (Linnaeus, 1758), european smelt		+	+			3.8	43.7	185	juv
22	*Leucaspius delineatus* (Heckel, 1843), sunbleak	+			+		3.8	4.7	4	ad juv
23	*Phoxinus phoxinus* (Linnaeus, 1758), european minnow				+		3.8	2.8	8	ad juv
24	*Ammodytes tobianus* (Linnaeus, 1758), sand eel				+		3.8	27.3	86	juv

Table 2. (*continued*)

No.	Species	Occurrence in Samples					*V*	RN	*n*	LS
		NB	InnS	InnN	OutS	OutN	%	%		
		Occasional species								
25	*Clupea harengus membras* (Linnaeus, 1760), baltic herring				+		1.9	2.0	3	juv
26	*Leuciscus idus* (Linnaeus, 1758), ide			+			1.9	3.0	1	juv
27	*Squalius cephalus* (Linnaeus, 1758), european chub	+					1.9	1.2	2	juv
28	*Barbatula barbatula* (Linnaeus, 1758), stone loach	+					1.9	0.6	1	ad
29	**Neogobius melanostomus* (Pallas, 1811), round goby				+		1.9	1.5	2	ad juv
30	*Pomatoschistus minutus* (Pallas, 1770), sand goby				+		1.9	1.1	2	ad juv

Gobiidae (four species and 13%). The family Percidae included three species (10%) and the family Gasterosteidae was represented by two species (7%). Another seven families were represented by one species each (in total 23%).

The core species of ichtyocoenosis on the surveyed sites were *A. alburnus*, *G. gobio*, *P. fluviatilis*, *R. rutilus* and *G. aculeatus* (Table 2). The secondary species (seven fish species) were generally not abundant except in some samples. Half of the fish species (15 species) was labelled occasionally occurring and three species were rare.

Bleak occurred in the whole surveyed area (Fig. 2) (*V*: 75–100% in a total 94% of all sampled sites), its *V* was lowest on sites of the southern coast of the Outer Estuary. Roach mainly occurred in Neva Bay and the Inner Estuary (*V*: 83–91%). The occurrence of gudgeon was similar between all sampling areas (*V*: 72–82%) with the exception for the northern coast of the Outer Estuary. Perch occurred irregularly (*V*: 39–100%), and was most common in the shallow parts of the southern coast of the Inner (*V* = 82%) and Outer estuaries (*V* = 100%). Bleak was the most abundant within the core species (RN = 42.5%; CPUE 34 ± 9 individuals/100 m^2) in the surveyed area (Table 2) and identified as the dominant (RN > 50%) species in 18 samples. Other abundant species were three-spined stickleback (RN = 22.2%; CPUE 33 ± 8 individuals/100 m^2) and roach (RN = 11.6%; 6 ± 2 individuals/100 m^2). Perch (RN = 6.3%; 8 ± 5 individuals/100 m^2) and gudgeon (RN = 8.7%; 8 ± 3 individuals/100 m^2) were identified as a "medium in numbers" species.

Bleak predominated in catches during the whole sampling season with the maximum in autumn. Sticklebacks were presented locally in the coastal zone and primarily during the first half of summer (June–July), because of the mass spawning migrations of adults to the shores in spring and the equally retreat of the juveniles at the end of summer. Other species did not demonstrate such differences in CPUE during the season. Roach was the most numerous in the sites along the northern coast of the Inner Estuary (6 ± 2 individuals/100 m^2). The highest average density of *Gobio gobio* was recorded for the sites in Neva Bay (8 ± 3 individuals/100 m^2) and a similar abundance (8 ± 5 individuals/100 m^2) was observed for *Perca fluviatilis* in the samples from the southern coast of the Inner Estuary.

The core and the secondary species were observed in samples during the whole season. The shallow coastal habitat was mainly inhabited by juvenile fish (1+ y) in the spring and early summer and by the young-of-the-year (0+ y) in the second half of the summer. The size-age composition differed for the each species during the season (Table 3).

Fish diet

Prey from eight major taxonomic groups were identified: crustaceans (Copepoda, Cladocera,

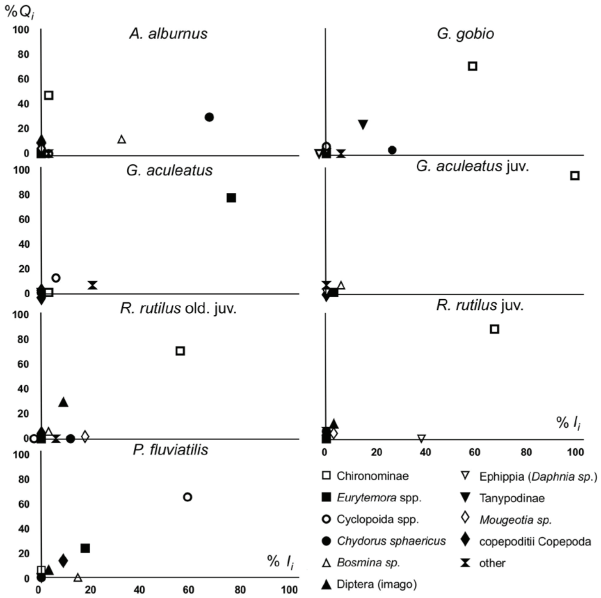

Fig 4. Plots of quantity (y-axis; %Q_i) vs. wet mass of food items in fish intestinal tracts (x-axis; %I_i). Each point corresponds to one prey item.

Ostracoda and Amphipoda), molluscs (Bivalvia and Gastropoda) and insects (Chironomidae, other Diptera and Ephemeroptera) were found in the intestinal tracts of fishes (Table S1 in Supplementary Information). Of the total 505 intestinal tracts, 56 were empty; 36 prey types were identified in the remaining 449 non-empty intestinal tracts. Six prey types from them constituted more than 85% of the total intestinal tracts contents. Chironomids, dipterans (imago), cladocerans and copepods (each by 2 different prey items) were the most frequent preys of all investigated fish species. A complete list of prey taxa, their relative proportion in the non-empty intestinal tracts, most frequently encountered preys and IRI% of all prey items are given in Table S1 in Supplementary Information.

Older juveniles of roach mainly consumed insects (larvae and imago) that were found in > 90% of roach specimens and constituted 80% of their total diet. Index of Relative Importance of Chironominae larvae was 62%, and Diptera (imago) was 22%. Young-of-the-year roach had less diverse diet com-

Table 3. Size and age composition of the most common fish species in beach-seine catches. Percentage indicates the proportion of specimens of represented length in the species catches.

Species	May–June		August–September	
	0+	1+ and older	0+	1+ and older
A. alburnus	—	29–57 mm 100%	9–46 mm 99.2%	54–108 mm 0.8%
G. aculeatus	12 – 19 mm 7%	42 – 67 mm 93%	15–47 mm 22%	53 – 65 mm 78%
G. gobio	—	41 – 116 mm 100%	14 – 48 mm 73%	53–121 mm 27%
P. fluviatilis	20–26 mm 29%	52–185 mm 71%	10–68 mm 79%	78–226 mm 21%
R. rutilus	—	39 – 67 mm 100%	18 – 56 mm 19%	56–122mm 81%

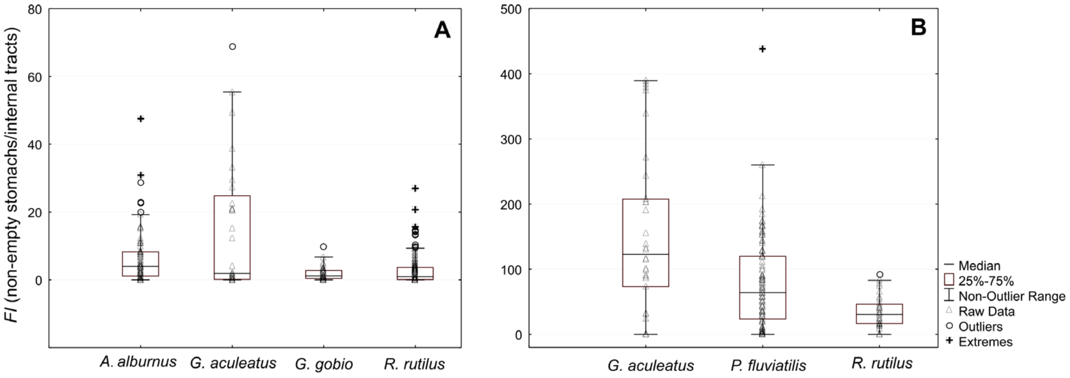

Fig 5. Feeding intensity of all core fish species as mean fullness of non-empty stomachs/internal tracts (FI). Box Plot of FI severally grouped by adult/older juveniles (A) and young-of-the-year juvenile (B) fishes. The horizontal bar in the middle of each box is the median, the box indicates the quartiles (25th and 75th percentiles) of values and the whiskers indicate the non-outlier range.

pared with adult fish (6 components vs. 16 in adults). The main components were Chironomid larvae (IRI$_i$ = 79%) and ephippia of Daphnia (IRI$_i$ = 17%). Feeding of adult bleak consisted of planktonic and benthic organisms. The most frequent of planktonic were *Chydorus sphaericus* (present in > 80% intestinal tracts, IRI$_i$ = 46%) and *Bosmina sp*. (F_i = 35%, IRI$_i$ = 20%). Among the benthic preys, the most significant part of the diet consisted of Chironomid larvae (F_i = 40%, IRI$_i$ = 23%), which were one of the most common benthic macroinvertebrates in the study area. Different species of them (group of species of Chironominae and Tanypodinae larvae) also formed > 70% of the diet of older (+1 y) gudgeon juveniles (I_i) and were found in 100% of intestinal tracts. Index of Relative Importance of Chironominae larvae was 64%, and Tanypodinae larvae was 17%. Besides chironomids, cladocerans (*C. sphaericus*, *Alona sp.*) were important prey items. The frequency of occurrence of these species was 49% and 22%, respectively. However, their relative proportion was not more than 9% in common (Table S1 in Supplementary Information; Fig. 4).

Feeding of adult three-spined sticklebacks was different from that of cyprinid species. The dominant taxa in their stomachs were planktonic organisms in conjunction accounting for > 90% of the food biomass, and found in > 85% of stomachs. Other preys (10 items) were also represented in the stomachs, but their cumulative contributions never exceeded 10–20% of the total amount of food items. Among planktonic organisms, species of the genus *Eurytemora* were the most important preys for stickleback (IRI$_i$ = 76%, F_i = 53% I_i = 66%). In addition, there were stickleback eggs in their stomachs (F_i = 25%). However, sticklebacks showed greater feeding variability among the stations of the study area, in particular, they consumed benthic organisms at some stations and planktonic ones at the other stations. Juveniles (young-of-the-year) feeding was less diverse compared with the feeding of adult fish. Chironominae larvae were the main food component and reached up to 90% of stomach content (IRI$_i$ = 95%, F_i = 83%). The food composition of perch juveniles (young-of-the-year) differed from the food composition of stickleback juveniles, and mostly included planktonic species. They consumed *Cyclopoida* spp. (I_i = 49%, IRI$_i$ = 60%) and *Eurytemora* spp. (I_i = 22%, IRI$_i$ =19%) (Table S1 in Supplementary Information; Fig. 4).

Feeding activity, fullness index

The index of fullness significantly differed between fish species (ANOVA, $F_{6–20}$ = 4.53, p = 0.004; Fig. 5) and increased with decreasing body size, from older juveniles of gudgeon and roach, to young-of-the-year juveniles of sticklebacks and perch.

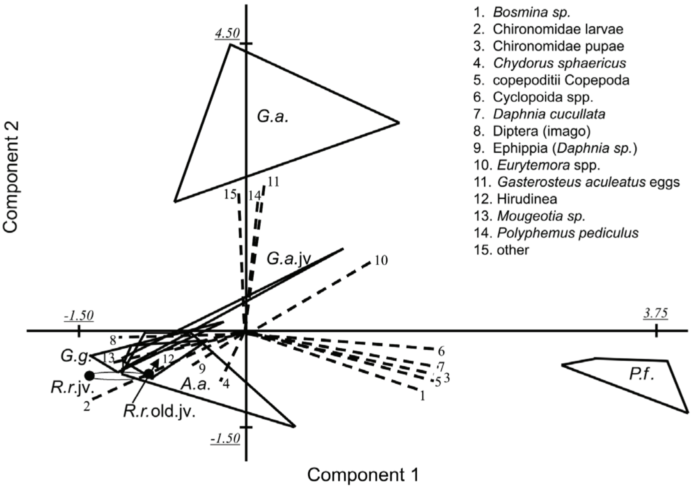

Fig 6. Results of PCA for all core fish by similarities in the diet composition of fishes. G.a.— *G. aculeatus*; G.a.jv. — *G. aculeatus* juv.; P.f. — *P. fluviatilis* juv.; R.r.jv — *R. rutilus* juv.; R.r.old. jv — *R. rutilus*; A.a. — *A. alburnus*, G.g. — *G. gobio*.

Older juveniles of roach had the highest (28%) and young-of-the-year perch had the lowest (5%) proportion of empty internal tracts/stomachs, on average. The percentage of empty internal tracts/stomach were 25% among adult sticklebacks, while gudgeon and bleak had 14% and young-of-the-year juvenile of roach and stickleback juveniles had 11% each.

The feeding activity for bleak, as revealed by the proportion of empty internal tracts and fullness index, was relatively uniform across the different sites in the Neva Estuary. The lowest proportion of empty stomachs and the highest feeding activity for three-spined stickleback juveniles was recorded in the Outer Estuary (Koporskaya and Vyborg bays). The highest feeding activity of adult sticklebacks in terms of stomach fullness index (F_{I} = 19‱) were observed also in Vyborg Bay. In contrast, higher feeding activity for all age of juvenile roach (*R. rutilus*) and perch were in the coastal zone of the Inner Estuary, especially along its northern coast. At the northern stations, the proportion of the empty internal tracts/stomachs was the lowest and the index of fullness was the highest (F_{I} about 6‱ in older juveniles roach and up to 116‱ in perch juveniles). Gudgeon, *G. gobio*, had the lowest fullness index among all investigated fish species at about 2‱. The lowest proportion of empty internal tracts was in Koporskaya Bay (5%; Table 4).

Differences in diet composition of fish

According to PCA, the first and second components (38% and 26% of variance) show mainly fish feeding habitat (benthic-feeding and planktonic-feeding) and diet differences of adult sticklebacks and the other fish species. Interpretation of the remaining components (about 36% of total variance) is difficult to assess (Fig. 6).

Two clouds of points are located separately; they are formed by the samples of perch juveniles and adult sticklebacks from all sampling stations. A feature of the diet composition of perch juveniles was the abundance of different planktonic preys (Cyclopoida spp, copepoditii Copepoda, *Daphnia cucullata* (G.O. Sars, 1862)). The diet of adult sticklebacks was distinguished by the presence of unique and great variety of relatively uncommon prey items (group of species — others, eggs of sticklebacks themselves and *Polyphemus pediculus*), as well as the propensity to consume *Eurytemora* spp. Clouds of bleak and stickleback juveniles are more stretched by the first component than others (Fig. 6). Their feeding was characterized by the presence of a significant portion of planktonic crustaceans in the diets along with benthic organisms (Table S1 in Supplementary Information). Clouds of other fishes overlapped and benthic organisms dominated in the diet in the whole study area (Fig. 6).

Discussion

Our study showed that the species richness of coastal fish in the Neva Estuary is large relative to other areas of the Gulf of Finland. For example, the number of fish species in the northern coastal zone of the central and western parts of the Gulf of Finland was 21 (Lappalainen *et al.* 2000), while in our study, 30 species of fish were found (Table 2). The current composition of fish communities in the Neva Estuary, presented in our study, shows a high similarity with previously published checklists (Berg 1940; Grib 1949; Kuderskiy *et al.* 2007), with the exception of several invasive species (*P. glenii*, *P. semilunaris*, *R. albipinnatus*, *C. gibelio*, *N. melanostomus*, see Table 2) that were not represented in previous publications. This relatively large species richness of coastal fish is apparently associated with a wide gradient of salinity in the estuary and a large variety of aquatic biotopes.

In our study, the dominant fish species was bleak (Table 2). In contrast, bleak occurrence and abundance in Finnish coastal waters were significantly lower (Lappalainen and Urho 2006; Kallasvuo *et al.* 2011). Beyond the oligohaline parts of the Neva Estuary (Neva Bay and Inner Estuary), CPUE and relative abundance of freshwater fishes decline notably (Fig. 2). At the shallow brackish water biotopes in the Latvian coastal zone, freshwater fishes as *A. alburnus* and *R. rutilus* mainly comprised less than 10% of fish abundance (Ustups *et al.* 2003). In the Polish coastal waters, where sticklebacks and gobies were most numerous, freshwater roach and perch were few (Sapota and Skóra 1996).

Table 4. Feeding intensity of fish species in different parts of the study area. Mean fullness of all stomachs/internal tracts (FI,‱) and proportion of empty stomachs/internal tracts (%). N B – Neva Bay; Inn. S – Inner Estuary south coastal; Inn. N – Inner Estuary north coastal; Out. S – Outer Estuary south coastal; Out. N – Outer Estuary north coastal.

Species	Number of fish	Station	FI (all intestinal tracts)	Proportion of empty intestinal tracts
A. alburnus	7	Inn. S (st. No 23)	8.2	0%
	11	Inn. N (st. No 10)	16.5	0%
	12	N B (st. No 5)	7.9	0%
	20	Inn. N (st. No 8)	4.7	12%
	21	Out. S (st. No 25)	6.2	29%
G. aculeatus	7	Inn. S (st. No 23)	0.6	0%
	6	Inn. S (st. No 24)	0.8	33%
	19	N B (st. No 5)	19.2	26%
G. aculeatus juv.	3	Inn. S (st. No 23)	0.0	100%
	3	Inn. S (st. No 24)	57.7	50%
	11	Out. N (st. No 4)	184.6	14%
	13	Out. S (st. No 25)	146.0	0%
G. gobio	18	Inn. S (st. No 24)	2.6	5%
	3	Inn. N (st. No 10)	0.0	100%
	2	Inn. N (st. No 8)	0.0	100%
	15	Out. S (st. No 25)	1.1	13%
P. fluviatilis	18	Inn. S (st. No 23)	29.4	6%
	10	Inn. N (st. No 10)	70.5	0%
	25	N B (st. No 5)	58.5	16%
	37	Inn. N (st. No 8)	116.1	3%
R. rutilus old juv.	21	N B (st. No 5)	3.1	5%
	36	N B (st. No 5)	4.6	25%
	29	Out. N (st. No 4)	1.3	24%
	10	Inn. N (st. No 8)	6.0	10%
	29	Out. S (st. No 25)	1.4	62%
R. rutilus juv.	22	Inn. N (st. No 10)	37.9	11%
	10	N B (st. No 5)	11.9	20%

Another factor structuring fish community in the Baltic Sea is eutrophication (Lappalainen *et al.* 2000; HELCOM 2006; Snickars *et al.* 2015; Bergström *et al.* 2016a; Kraufvelin *et al.* 2018). It favors cyprinids at the expense of percid and coregonid fish species (HELCOM 2006; Bergström *et al.* 2013, 2016a). These groups of fish species are used as indicators of environmental conditions and food webs in coastal habitats in the Baltic Sea (Bergström *et al.* 2013, 2016a; Otto *et al.* 2018). Moreover, a recent manyfold increase in the abundance of three-spined stickleback may result in further eutrophication symptoms through inducing of trophic cascades and regulation of invertebrate grazers (Bergström *et al.* 2015).

The Neva Estuary is one of the most eutrophic parts of the Baltic Sea, and the degree of eutrophication of which has increased in recent decades due to high anthropogenic pressure and adverse climatic changes (Golubkov *et al.* 2017; Golubkov and Golubkov 2020). The composition of fish community in the estuary also reflects this high degree of eutrophication. The Cyprinid together with three-spined stickleback were the most common and abundant fish species in the studied area (Table 2). These species were part of the core of ichthyocenoses. Most of the other cyprinid species were subdominants and considered as secondary species. Although the piscivorous perch was common, its abundance was considerably lower than of three above mentioned core species (Table 2).

Currently, seven invasive (NIS) species accounted for about 15% of the total fish species richness in the Neva Estuary. Most of them are still rare or occasional species (Table 2), but the number of NIS has significantly increased in the last three decades. Three of them (*Neogobius melanostomus*, *Proterorhinus semilunaris* and *Romanogo bioalbipinnatus*), were first found in the estuary at the beginning of the century. The recent increase in the number of new invasions is probably related to a global trend (Cohen and Carlton 1998) and is the result of intensive shipping activities and high anthropogenic impact in the region.

The large number and abundance of fish in coastal biotopes makes them a central element of trophic links in shallow aquatic environments in the Baltic Sea. Most fish feed on zoobenthos (Bubinas and Ložys 2000; Tomczak *et al.* 2009; Snickars *et al.* 2015). Bubinas and Ložys (2000) showed that the main food components of fish inhabiting the coastal zone of the southern Baltic Sea are mainly molluscs, worms (Polychaeta), Gammaridae and also zooplankton and other fish species. According to our results (Fig. 6), it is possible to conclude that in the shallow eastern Gulf of Finland, benthic-feeding species also dominated over planktonic-feeding. This confirms that the coastal waters are important in linking zoobenthos and fish, because of the many coastal fish species feed on benthic preys in these habitats (Snickars *et al.* 2015; Golubkov *et al.* 2018). However, our feeding data also show that planktonic prey and insects constitutes a relative larger part of fish diet in the coastal zone of the Neva Estuary compared to many other coastal areas of the Baltic Sea.

The reason for the lower occurrence of benthic invertebrate in the fish diet in the Neva Estuary may be the intensive macroalgae *Cladophora glomerata* and *Ulva intestinalis* blooms (green tides) in the summer (Berezina and Golubkov 2008; Golubkov *et al.* 2018). These blooms lead to near bottom temporary deoxygenation of water beneath algal mats caused by the decomposition of detached macroalgae and result in deterioration of bottom animal communities (Berezina and Golubkov 2008). Under these conditions, the opportunistic chironomid species resistant to hypoxia and able to rapidly colonize biotopes after the cessation of hypoxia dominate the bottom invertebrate communities at many sites of the Neva Estuary (Berezina and Golubkov 2008; Berezina *et al.* 2017; Golubkov *et al.* 2018). The zooplankton of the upper layers of the water is also apparently less susceptible to near-bottom hypoxia under the algal mats.

Roach is a freshwater fish species that has benefited from coastal eutrophication in the Baltic Sea (Lappalainen *et al.* 2004; HELCOM 2006). We found that roach in the Neva Estuary mostly fed on a few taxa such as chironominae larvae, other Diptera (larvae and imago) and algae called *Mougeotia sp*. The diet of juvenile roach is meager, almost entirely consisting of chironomids larvae (Table S1 in Supplementary Information). Our results somewhat contradict the data of Lappalainen *et al.* (2001), Bubinas and Ložys (2000) and Rask *et al.* (1998), whom reported that molluscs are the most important food items for roach: up to 50–85% of the intestinal tracts content (Rask *et al.* 1998; Bubinas and Ložys 2000; Lappalainen *et al.* 2001). However, we studied the food composition only in juvenile roach, which were caught in shallow waters (Table 4). Perhaps in the diet of older individuals, mollusks play a greater role.

The diet of young-of-year perch juveniles was more diverse compared with the diet of roach, taking into account the number of taxa and the frequency of occurrence of all dominant taxa in stomachs (Table S1 in Supplementary Information). The nature of perch diet depends on the biotope and various environmental conditions. In the Neva Estuary, perch was mainly planktivorous (Fig. 6), consuming small-sized copepods (Cyclopoida spp. and *Eurytemora* spp.) of up to half of its stomach content (Table S1 in Supplementary Information). In the Gulf of Riga, perch mainly consumed various stages of *Eurytemora affinis*, and besides that, cladocerans and pelagic larvae of benthic invertebrates (Lankov *et al.* 2006). However, according to other research the main food components of perch juveniles are amphipods, Mysidae, Chironomidae larvae and molluscs (Bubinas and Ložys 2000). Of these taxa, only Chironomidae larvae were found in intestinal tracts of juvenile perch in the Neva Estuary (up to 10% stomach content).

Three-spined stickleback, both adults and juveniles, is generally considered as an opportunistic feeder that adjusts its food intake according to prey availability (Demchuk *et al.* 2015; Rybkina *et al.* 2016; Ojaveer *et al.* 2017; Lajus *et al.* 2020). In the brackish Baltic Sea, stickleback abundance has increased more than ten-fold during the last decade (Bergström *et al.* 2015). Currently, it dominates fish assemblages in some coastal areas during summer, when adults immigrate from the open sea to spawn (Ljunggren *et al.* 2010; Sieben *et al.* 2011; Park *et al.* 2013). In coastal waters, stickleback may reach high abundances and may be a potential predator on eggs and larvae of fish (Bergström *et al.* 2015). We found juveniles of other fish species in their stomachs at one sample size, confirming they feed on fish eggs and larvae, but only at one sampling site and of low importance (IRI_i) in the Neva Estuary. At the other stations, the feeding spectrum of adult sticklebacks was composed by planktonic organisms: *Eurytemora* spp., Cyclopoida spp. or benthic chironomids and their own eggs. Feeding on these prey taxa have also been recorded in the Baltic Sea by others (Kostrichkina 1970; Peltonen *et al.* 2004; Ojaveer *et al.* 2017). In general, these studies found more planktonic than benthic preys in stickleback diets, possibly because their fish samples had been taken at the open sea.

Bleak is a more specialized column water feeder, feeding primarily on zooplankton during its whole life (Politou *et al.* 1993; Vinni *et al.* 2000; Vašek and Kubečka 2004). The food composition of bleak differs depending on their environment. Bleak actively feeds on zooplankton, consuming cladocerans, copepods and imago of dipterans but also flying insects (Politou *et al.* 1993; Bubinas and Ložys 2000; Vašek and Kubečka 2004; Mehner *et al.* 2005). Bubinas and Lozys (2000) showed a similar result throughout the Baltic Sea. Furthermore, bleak is a fast-moving species living near the surface, which mainly chases its preys (Haberlehner 1988). This fact can explain a large number of hard-to-reach imago of flying insect in the bleak diet in the Neva Estuary.

Gobio gobio tended to consume different species of chironomid larvae and other benthic food components in the Neva Estuary. Cladocerans (*Chydorus sphaericus*, *Alona sp.*) constituted a small part of its diet (Table S1 in Supplementary Information). Similar feeding patterns have been observed in other areas. For example, gudgeon in the Larraun River (northern Spain) fed mainly on benthic macroinvertebrates (Chironomidae, Anomopoda and Trichoptera larvae) as well as in our study, although terrestrial invertebrates and plant material were also consumed (Oscoz *et al.* 2003). Several authors recorded, that it feeds on detritus, invertebrates (predominately chironomid larvae) and plants (Valladolid and Przybylski 1996; Artaev and Ruchin 2013). Gudgeon from the Netherlands, on the contrary, is characterized by a higher capacity to feed on sessile algae, phytoplankton, and zooplankton, and a lower capacity for utilizing fish and insects (Nagelkerke *et al.* 2018). Based on these data we can conclude that there are significant differences in the feeding habits of gudgeon, depending on study area.

In our study, the highest shares of empty stomachs (intestinal tracts) was observed for roach (28%) and the index of fullness was lowest for the older juveniles of roach and gudgeon. This could imply potential difficulties in finding food and food limitation. In contrast, the low share of empty stomachs in small perches (5%) feeding on zooplankton in the Neva Estuary indicates more favorable feeding conditions in the pelagic zone in comparison with bottom biotopes, including availability of suitable preys.

Conclusion

Our study showed that the Neva Estuary has a rather rich fauna of coastal fish species. This, apparently, is associated with a large variety of biotopes within the estuary. A characteristic feature of its fish fauna is a significant number of NIS and freshwater species belonging to the family Cyprinidae. This is obviously due to the high degree of eutrophication of the estuary, in the coastal zone of which green tides of opportunistic macroalgae are observed in the summer. These tides lead to periodic benthic hypoxia and deterioration of benthic invertebrate communities. In this regard, the diet of benthic fish was dominated by chironomids, which often predominate in fresh waters with a high degree of eutrophication. Unlike some other coastal areas of the Baltic Sea, where fish mainly feed on zoobenthos, in the Neva Estuary, zooplankton and insects are an important food for the core fish species (bleak, three-spined stickleback and perch).

Acknowledgements: The study was supported by the State Contracts nos. AAAA-A18-118042390186-9 and AAAA-A19-119020690091-0 with the Russian Ministry of Science and Education, transboundary Russian-Finnish project TOPCONS ENPI 2011-022-SE511. We sincerely thank Zhidkov Z.V. and Naseka A.M. for help with collecting fish samples. We thank Drs. Dmitry Lajus,Nadezhda Berezina and Yulia Gubelit, Prof. Örjan Östman and the anonymous reviewer for valuable comments, which helped to improve the early version of the manuscript.

Supplementary Information: The supplementary information related to this article is available online at: http://www.borenv.net/BER/archive/pdfs/ber26/ber26-001-016-supplement.pdf

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