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Article

Diversity of food spectra of vendace in the water bodies of Eurasia

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Abstract. The composition and relative importance of food organisms in the food bolus were analyzed for two species (forms) of vendace: European vendace *Coregonus albula* and sardine cisco *C. sardinella* from water bodies of Russia (Yaroslavl, Vologda, Kaliningrad, Arkhangelsk and Murmansk Oblasts; Altai, Novosibirsk, and Krasnoyarsk Krais; Republic of Karelia, Komi Republic, and Yamalo-Nenets Autonomous Okrug), Finland, Sweden, Norway, Lithuania, and Poland. Vendace is a typical planktivorous fish in most lakes of the boreal zone, but euryphagous consuming significant number of benthic invertebrates in the northern water bodies of Eurasia. Both forms of vendace are characterized by feeding plasticity, diversity of the food spectrum and its seasonal and spatial variability. The ecological and geographical features of the lakes precondition the composition and abundance of food organisms, thus influencing the food spectrum of vendace.

Keywords: *Coregonus*, fish nutrition, trophic links, plankton, benthos, feeding plasticity, euryphagy, productivity.

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Introduction

Vendace are whitefish of the genus *Coregonus*, which differ from other representatives of this genus by the large number of gill rakers and the superior mouth (the lower jaw is longer than the upper one). Such mouth structure is typical for fish that feed in the water column and in the surface water layer. Vendace is an important component of the boreal, subarctic and arctic aquatic ecosystems of the Palaearctic. European vendace *Coregonus albula* (Linnaeus, 1758), sardine cisco *C. sardinella* Valenciennes, 1847, and two other species of whitefishes (peled *C. peled* (Gmelin, 1789) and Penzhin omul *C. subautumnalis* (Pallas, 1776)) are identified as evolutionarily closest taxa; they form a single complex of species (*Coregonus sardinella* complex) (Politov, 2017).

The European vendace, *C. albula*, inhabits in Russia numerous lakes in the basins of the Baltic, Barents and White Seas and the Volga River (Borovikova and Makhrov, 2012; Reshetnikov, 1980). In the open reaches of the Rybinsk Reservoir (Volga River), vendace occurs everywhere in feeding aggregations with other species of pelagic fish and their juveniles, such as Black Sea sprat *Clupeonella cultriventris* (Nordmann, 1840), European smelt *Osmerus eperlanus* (Linnaeus, 1758), zope *Ballerus ballerus* (Linnaeus, 1758), bleak *Alburnus alburnus* (Linnaeus, 1758), sichel *Pelecus cultratus* (Linnaeus,

1758) and Percidae (Kiyashko and Slyn'ko, 2003; Polovkova and Permitin, 1981; Ryby..., 2015). European vendace entered this reservoir in the 1940s, presumably from the Lake Beloe via the Sheksna River (Kiyashko and Slyn'ko, 2003). In the Vologda and Arkhangelsk Oblasts, vendace is widespread in the lakes belonging to the basins of Onega, Northern Dvina and Mezen rivers. In the Kenozero National Park, it forms geographically and reproductively isolated populations; the most numerous of them inhabit lakes Kenozero and Lekshmozero (Dvoryankin, 2009). In the Kaliningrad Oblast, a large oligotrophic Lake Vishtynetskoe is the only water body inhabited by the European vendace (Krivopuskova et al., 2014).

In the Gulf of Finland and in large lakes Onega and Ladoga, vendace *C. albula* is represented by two forms. The small-size form of this species (body length up to 25 cm) is widespread throughout the entire water area, and the large-size form (ripus, or kilets, *Coregonus albula* subsp. *ladogensis*) reaching up to 34 cm in length, is found mainly in the areas with significant depths. In the lakes of Karelia, *C. albula* was found in more than 270 lakes, it is one of the main species of commercial fish in most of them, including Lake Syamozero (Berezina et al., 2021; Pokrovsky, 1953; Sterligova et al., 2002; Sterligova and Il'mast, 2016). It is numerous in the subarctic lakes of the Murmansk Oblast, including Lake Imandra (Zubova and Kashulin, 2019).

The small-size form of *C. albula* is also common in water bodies of Great Britain, Germany, Lithuania, Estonia, and Poland; its populations are especially numerous in Finland, Sweden, and Norway (Bukelskis and Umbrasaite, 2016; Czarkowski et al., 2007; Mamcarz and Bloniarz, 1995; Sarvala et al., 2020; Scharf et al., 2008; Schulz et al., 2003; Viljanen, 1983). In many European countries, *C. albula* populations are currently considered vulnerable and endangered due to the negative effects of warming, eutrophication, overfishing, and fish introductions (Sarvala et al., 2020; Winfield et al., 2017).

The basin of the Pechora River is the boundary between sardine cisco and European vendace ranges (Borovikova and Makhrov, 2012). According to main characters, vendace inhabiting the Usa River, a tributary of the Pechora River (described as *Coregonus sardinella marisalbi* Berg, 1916), occupies an intermediate position between the European and Siberian forms, but to some traits, it is much closer to the European vendace (Reshetnikov, 1980).

The sardine cisco *C. sardinella* is distributed from the White Sea to the east to the Bering Sea, it inhabits the Anadyr and Amguema rivers and the lakes of Chukotka (Nikulina et al., 2018). It is common in the subarctic lakes and rivers of the Bolshezemelskaya Tundra (a part of North Russian Plain). In the Malozemelskaya Tundra, *C. sardinella* is abundant in the lakes of the upper reaches of large rivers, such as the Lakes Kharbeyskie, Lakes Vashutkiny, and some others (Borovikova and Makhrov, 2012; Kuchina and Solovkina, 1970; Sidorov and Reshetnikov, 2014). In Kamchatka, the sardine cisco lives in the Lake Tkhuklu and in the basin of the Oblukovina River. It is also found in the Kara Bay, the mouths of the rivers of the Western Yamal, on the islands of the Arctic Ocean (Kolguev Island, Novosibirskie Islands), and in the transbaikalian Lake Baunt (Reshetnikov, 1980).

C. sardinella lives as well in the Arctic lakes of the Pechora-Pyasinskaya lake-river system of the Putorana Plateau (Lakes Norilskie, including Lama and Melkoe) in harsh hydrological conditions with a very short and cool summer, which lasts about two months, starting in the end of June (Nikulina and Romanov, 2019). In the Lake Taimyr, vendace is characterized by low growth rate, since this lake is the northernmost habitat for this species and is characterized by the least amount of the annual heat (Popov, 2007). In the Krasnoyarsk Krai, in particular in the reservoirs of the Taimyr Peninsula, the Putorana Plateau and the Yenisei River, the greatest diversity of local herds of sardine cisco is observed (Kizhevatov, 2007).

All forms of vendace are important commercial fish species in Russia and Europe (Popov, 2007; Sarvala et al., 2020). The sardine cisco is one of the most important commercial species of whitefishes beyond the Arctic Circle in the permafrost zone, in the basins of the Khatanga River (Balakhna and Khet forms), Yenisei River (Turukhansk and Kara forms), and Kolyma River (Bogdanov and Bogdanova, 2008; Kirillov and Fedorova, 2010; Nikulina et al., 2018; Sergienko, 2015). The vendace flesh is characterized by a high content of omega-3-polyunsaturated fatty acids, macro- and microelements, and vitamins (Gnedov, 2009). Large and fat vendace from the Lake Pleshcheyevo (town of Pereslavl-Zalessky), or "Pereslavl herring", was included in the menu of tsars during the reign of Alexei Mikhailovich (1629–1676, reigned from 1645 until the death); since 1675, according to his decree, the vendace in this lake was taken under protection. Nowadays, it is still included in the Red List of the Russian Federation. There is a high content of essential amino acids in the tissue proteins of sardine cisco (Lebedeva and Abramov, 2015). This is especially important for the indigenous people of the northern regions of Russia living in a harsh climate (including Yakutia), since a person's need for valuable protein may mostly be met by including vendace in the diet, especially as raw flesh (Abramov et al., 2018).

Vendace species are traditionally considered planktivorous, feeding mainly on zoo- and ichthyoplankton (Chernyaev, 2017). However, their feeding on zoobenthos, water-surface insects, and other food components is increasingly described in

the scientific literature (Berezina et al., 2018; Liso et al., 2011; Scharf et al., 2008; Zubova and Kashulin, 2019). In the lakes and rivers of the Pasvik Nature Reserve (northern Norway), fish (nine-spined stickleback) were a part of the food spectrum of the small European vendace *C. albula* (body length 11–19 cm), which was associated with the scarcity of zooplankton (Liso et al., 2011). The share of fish reached 20% of the food bolus by mass, the rest was formed by aerial insects, Cladocera, Copepoda, and by small number of benthic organisms (Liso et al., 2011; Reshetnikov et al., 2020). The food spectrum of large forms of *C. albula*, Ladoga vendace (ripus) and Onega vendace (kilets), fish fry, smelt, and fry of vendace (kannibalism) were also found along with zooplankton, mysids, and chironomids (Babiy and Sergeeva, 2003; Reshetnikov, 2004). Apparently, vendace may consume different food, and its food spectrum may change in different types of habitats. In this regard, we aim to analyze the qualitative composition of the food of European vendace (*Coregonus albula*) and sardine cisco (*C. sardinella*) inhabiting various regions of Eurasia.

Materials and methods

The material was the available published data on the composition and relative content of food organisms in the food bolus of small-sized forms of two vendace species (*Coregonus albula* and *C. sardinella*) from the water bodies of Russia (Yaroslavl, Vologda, Kaliningrad, Novosibirsk, Arkhangelsk and Murmansk Oblasts; Altai Krai and Krasnoyarsk Krai; the Republics of Karelia and Komi Republic Yamalo-Nenets Autonomous Okrug), Finland, Sweden, Norway, Lithuania and Poland. The frequency of occurrence and the share by abundance and weight (%) of various food components in the food bolus of fish (Popova and Reshetnikov, 2011).

Results and discussion

Central Russia

Lake Pleshcheyevo is one of the lakes in the Volga River basin rich in European vendace *C. albula* (Gerasimov et al., 2019). From May through October, planktonic Cladocera are the main food for vendace in this reservoir, benthic organisms are recorded in the food bolus only occasionally (Khal'ko et al., 2019). Large cladocerans such as *Leptodora kindtii* (Focke, 1844) and *Bythotrephes brevimanus* (Lilljeborg, 1901) and small crustaceans *Bosmina* spp. and *Daphnia longispina* (O.F. Müller, 1785) are the most important in the diet of vendace in this lake, when their frequency of occurrence may reach 100% (Table 1). Nauplii and copepodites of Copepoda were abundant in the food bolus in more than 70% of the studied fish. The larvae of dragonflies and chironomids were recorded singly (Khal'ko et al., 2019).

In summer, European vendace feeds mainly on cladocerans of the genera *Bosmina*, *Chydorus*, *Leptodora*, and *Bythotrephes* in the pelagic zone of the open reaches of the Rybinsk Reservoir, where average zooplankton biomass reaches 1.5–2.0 g/m^3 (Kiyashko and Slyn'ko, 2003). As a rule, the frequency of occurrence of these crustaceans is 100% in the fish stomach, and their relative importance may reach 90%. For example, in the stomach of one vendace (body length 16.3 cm), there were 1400 specimens of *Chydorus sphaericus* (O.F. Müller, 1776), 753 specimens of *Bosmina coregoni* Baird, 1857, and 232 specimens of *Bythotrephes longimanus* (Leydig, 1860) (Kiyashko and Slyn'ko, 2003). By autumn, the stomach filling indices of vendace and other fish usually decreased (down to 0.514%) (Kiyashko and Slyn'ko, 2003). A decrease in the feeding intensity of vendace in the open reaches of the reservoir is associated with a seasonal decrease in the zooplankton abundance, when in some years, the zooplankton biomass was 20 times and even more lower by autumn than in summer (Lazareva and Sokolova, 2018). The mass development of cladocerans, which make up the main food of vendace, takes place in the surface water layer. Therefore, European vendace during the growing period keeps in the upper 5–10-m water layer. It descends to the bottom habitats only as the spawning period starts, in October–November, so a change in the food composition may also occur. Therefore, the food spectra of vendace caught in the sublittoral of the reservoir differs from that of fish from the pelagic group (Table 1). Amphipod crustaceans *Gmelinoides fasciatus* (Stebbing, 1899), which dominated in the benthos during the sampling period (October), comprised 90% by weight of the diet of coastal fish (Berezina and Strel'nikova, 2010).

In Lake Pleshcheyevo, vendace does not consume much zoobenthos in the autumn period, as noted in the Rybinsk reservoir, since the zooplankton production in this lake is quite high throughout the season (Stolbunova, 2006). *Daphnia cucullata* (Sars, 1862), *Bosmina coregoni,* and *Eudiaptomus graciloides* (Lilleborg, 1888) dominate in zooplankton by biomass in September–October. At the same time, the biomass of zooplankton is quite high (up to 21 g/m^3) both in the littoral zone among aquatic vegetation and in the deep-water part of the lake.

Northwest Russia

In the Lake Ladoga and Lake Onega, copepods and cladocerans are main food components of the small-sized *C. albula* (body length 10–14 cm); the quantitative ratio of different species in the fish food bolus varies depending on the season and the biomass distribution in the reservoir. In Lake Onega, the vendace larger than 14 cm also feeds on chironomid larvae and pupae throughout the season, in addition to cladocerans and copepods; in August, chironomids

Table 1. Species and groups of invertebrates forming the food basis of vendace in various water bodies of Eurasia.

Lake	Month	Fish length, mm	Dominant food items	Reference
Rybinskoe (Volga River)	VIII–X	85–180	*Bosmina coregoni* *Bythotrephes* spp. *Leptodora kindtii* *Chydorus sphaericus* *Gmelinoides fasciatus*	Kiyashko and Slyn'ko, 2003; Berezina and Strelnikova, 2010
Pleshcheyevo	VI–X	150–210	*Leptodora kindtii* *Bythotrephes brevimanus* *Bosmina coregoni* *B. longirostris* *Daphnia longispina* *Megacyclops viridis*	Khal'ko et al., 2019
Ladoga	V–IX	100–140	*Asplanchna priodonta* *Daphnia* spp. *Bosmina* spp. *Holopedium gibberum* *Eudiaptomus gracilis* *Sida crystallina* *Polyphemus pediculus*	Kuchko et al., 2017
Onega	VI–IX	100–186	*Bosmina longimanus* *Leptodora kindtii* *Limnocalanus macrurus* *Eurytemora lacustris*	Mal'tseva, 1983
Syamozero	VII–IX	123–195	*Leptodora kindtii* *Bythotrephes cederströmii* *Eudiaptomus gracilis* *Bosmina coregoni* *Daphnia longispina* *D. cristata*	Sterligova et al., 2002; Sterligova and Il'mast, 2016
Vishtynetskoe	VII–IX	100–180	*Leptodora kindtii* *Bythotrephes longimanus* *Daphnia cucullata* *Heterocope appendiculata* *Chydorus ovalis,* *Eudiaptomus graciloides*	Krivopuskova et al., 2014; Mychkova et al., 2017
Vozhe	V–IX	–	*Bosmina coregoni* *Heterocope appendiculata* pupae and larvae of aquatic insects	Zuyanova et al., 1994
Krivoe	VI–X	135–170	*Gammarus lacusris* *Monoporeia affinis* *Phryganea bipunctata* *Ephemera vulgata* *Sphaerium nitidum* *Bosmina longirostris* *Sida crystallina* *Megacyclops* spp.	Berezina et al., 2021; Berezina et al., 2018
Imandra	VII–IX	86–180	*Centroptilum* spp. *Cricotopus* spp. *Psectrocladius* spp. *Prodiamesa* spp. *Diamesa* spp. *Stictochironomus* spp. *Euglesa* spp. Limnephilidae	Zubova and Kashulin, 2019; Zubova et al., 2020

Lake	Month	Fish length, mm	Dominant food items	Reference
Medve	VII–IX	184–250	*Leptodora kindtii* *Bosmina* spp.	Wiêski, 2002
Leginske	V–VII, XI–II	170–265	*Bythotrephes* spp. *Daphnia cucullata* *Eudiaptomus* spp. *Cyclops* spp.	Szypuła, 1965
Khazhikovske	III–VI	161–181	*Cyclops strenus* *Daphnia* spp.	Mamcarz and Błoniarz, 1995
Suomunyarvi	IV–X	82–234	*Bosmina coregoni* *Daphnia* spp. *Cyclops scutifer* *Heterocope appendiculata*	Viljanen, 1983
Bolmen	VII–X	–	*Bosmina coregoni* *Holopedium gibberum*	Hamrin, 1983
Melaren	VI–X	112–280	*Bosmina longispina* *Limnocalanus macrurus* *Heterocope appendiculata*	Northcote and Hammar, 2006
Golodnaya Inlet	VII–VIII	150–190	*Bosmina* spp. *Daphnia* spp. *Chydorus* spp.	Fadeeva, 1999
Korovinskaya Inlet	VII–VIII	160–200	Cladocera imagoe and pupae of Chironomidae	Kornilova and Panova, 1964
Bolshoi Kharbei	VII–IX	150–190	Cladocera larvae of Chironomidae mollusks	Sidorov, 1974
Lama and Melkoe	VII–VIII	170–250	*Bosmina* spp. *Limnocalanus grimaldii* *L. macrurus* imagoe, larvae, and pupae of Chironomidae	Vershinin and Sycheva, 1964; Romanova, 1948
Ob Bay	II–III, VIII–IX, XII–I	90–270	*Bosmina* spp. *Daphnia* spp. *Senecella calanoides* *Bythotrephes* spp. *Limnocalanus macrurus* *Monoporea affinis* *Cyclops* spp. *Heterocope* sp. *Onisimus* sp.	Leshchinskaya, 1962; Stepanova, 2017; Stepanova and Stepanov, 2006; Yukhneva, 1955;
Kolyma River	VIII–X	80–180	*Bosmina longirostris* *Limnocalanus macrurus* Planorbidae Pisidiidae Odonata	Fedorova et al., 2011

comprise more than 70% by mass of the food bolus (Mal'tseva, 1983). In these lakes, during the summer and until early September, vendace usually stays in the warmest upper 5–10-m water layer due to the largest accumulation of plankton here (Nikolaev, 1983).

According to Ya.A. Kuchko et al. (2017), in northern Lake Ladoga at the beginning of summer, rotifers *Asplanchna priodonta* (Gosse, 1850), *Kellicottia longispina* (Kellicott, 1879), and *Keratella cochlearis* (Gosse, 1851) along with copepods of the genera *Mesocyclops* and *Thermocyclops* constitute the basis of the vendace ration (75% by mass of all consumed organisms); during this period, the share of crustacean zooplankton in the natural communities is low. As the waters warm up and throughout the summer, vendace consumes most significant cladocerans of pelagic zooplankton (*Daphnia cristata* (Sars, 1862), *D. longispina, Holopedium gibberum* (Zaddach, 1855), *Bosmina coregoni,* and *B. longirostris* (O.F. Müller, 1785)) and copepods (*Eudiaptomus gracilis* (Sars, 1863) and *Cyclops strenuus* (Fisher, 1851)), as well as representatives of the littoral fauna of the thickets: *Sida crystallina* (O.F. Müller, 1776), *Polyphemus pediculus* (O.F. Müller, 1785), *Ceriodaphnia quadrangula* (O.F. Müller, 1785), *Macrocyclops albidus* (Jurine, 1820), and *Megacyclops viridis* (Jurine, 1820) (Kuchko et al., 2017).

In autumn, other zooplankton species dominate in the pelagic and littoral of Onega and Ladoga lakes, but the food composition of vendace remains similar to the summer period, when cladocerans make up 90% of its ration (Sterligova et al., 2002).

Large crustaceans *Leptodora kindtii, Bythotrephes cederströmii* Schödler, 1877, *Bosmina* spp., *H. gibberum,* and *E. gracilis* are main forms of zooplankton consumed by vendace in Lake Syamozero, southern Karelia (Sterligova and Il'mast, 2016). During insect swarming, vendace switches to this prey; aerial insects may bring up to 99% by mass of the food bolus. In spring, copepod crustaceans are the main food for vendace in the boreal lakes of Karelia, with *E. gracilis* being the absolute dominant (81.8%). Cladocerans are basis of ration of vendace (body length of 12.3–19.5 cm) in summer and autumn, when *Bosmina coregoni, Daphnia longispina, D. cristata, B. cederströmii,* and *L. kindtii* are the main food objects. Rotifers are noted in small numbers. The share of copepods in the summer months is small (3.2%), but increases in autumn (31.7%).

In the lakes of the Arkhangelsk Oblast, vendace has nearly no food competition with other species (Dvoryankin, 2009). In the Lake Kenozero, cladocerans of the genus *Daphnia* are the main components (96.5%) of its diet in the autumn period (Dvoryankin, 2009). In the Lake Lekshmozero, cladocerans *Daphnia* (61.3%) and *Bosmina* (27%) are the main food for vendace, the share of copepods reach 11.5% by abundance; larvae of chironomids, caddis flies, and aerial insects constitutes less than 1% (Dvoryankin, 2009).

In the Lake Vishtynetskoe, representatives of the genus *Daphnia* (47.5% according to the index of relative importance) and copepods (37.5%) dominate in the vendace diet (Krivopuskova et al., 2014). In summer, high selectivity for large representatives of zooplankton (*Leptodora kindtii* and *Bythotrephes longimanus*) has been revealed. These two cladoceran species are presented in the food bolus of vendace in large numbers even when their biomass in the lake is low. Benthic organisms (larvae of chironomids and oligochaetes) and rotifers are also found in the food bolus, but their proportion is less than 1%. The presence of chironomid pupae in the food bolus of vendace is noted in the period preceding the swarming of these insects. Changes in the diet of vendace are noted when the places of its localization change. For example, during abnormally warm periods in the Lake Vishtynetskoe, vendace descends down to cooled near-bottom water layers; during homothermy, the population is dispersed throughout the lake, approaching shallow water; benthic invertebrates dominate in the diet of vendace during this period (Krivopuskova et al., 2014).

In the Lake Vishtynetskoe, there is a seasonal change in the species composition of food items in the diet of vendace. In autumn, *Daphnia cucullata, B. longimanus, L. kindtii, Chydorus ovalis* (Kurz, 1875), as well as rotifers dominate in the food bolus of fish. At the same time, the copepods *E. graciloides, Heterocope appendiculata* (Sars, 1863), harpacticides, and plants are the additional food objects. In the winter post-spawning period, vendace feeds mainly on copepods (35%), zooplankton species dominanting in winter (over 89% of total abundance), and plants (28.6%) (Mychkova et al., 2017). *E. graciloides* and *H. appendiculata* contribute 45.5% and 29.9% by mass, respectively.

Northern Russia

In the subarctic lakes of Russia, characterized by a low zooplankton productivity, benthic invertebrates are increasingly found in the vendace food spectrum (Berezina et al., 2021; Berezina et al., 2018). In Lake Vozhe (northern Vologda Oblast, upper reaches of the Onega River), the food spectrum of *C. albula* expands, showing specific seasonal peculiarities (Zuyanova et al., 1994). From May to autumn, zooplankton and insect imagoes are the main food objects; however, a frequent change of dominant planktonic species leads to the change in the food spectrum. Thus, in spring and early summer, *Bosmina coregoni* and *Heterocope appendiculata* were the main food objects, in August, these were *Cyclops, Diaptomus*, and *Daphnia* (Zuyanova et al., 1994). Pupae and larvae of aquatic insects (chironomids,

mayflies, caddis flies, and dragonflies) are noted in the food bolus quite often; sometimes aquatic mites, nematodes, oligochaetes, plant debris, and phytoplankton are also found.

In the Lake Imandra, vendace feeds mostly on benthic organisms. Benthic invertebrates are found in 67% of vendace specimens (up to 15 cm length), and zooplankton, only in 25% of studied vendace specimens (Zubova et al., 2020). The index of the relative importance of zoobenthos exceeds sixfold the index of zooplankton (Table 1). Large vendace (body length > 15 cm), the food bolus is presented by 94.7% by the representatives of macrozoobenthos: larvae and pupae of chironomids, caddis flies Limnephilidae, bivalve mollusks of the genus *Euglesa*, bugs, and nematodes (Zubova and Kashulin, 2019). The larvae of chironomids of the genera *Centroptilum, Cricotopus, Diamesa, Prodiamesa, Psectrocladius,* and *Stictochironomus*, as well as the larvae of Coleoptera of the genus *Dytiscus,* were the dominant groups of benthic organisms in the diet of vendace. Amphipods, larvae of stoneflies, and gastropods of the genus *Valvata* make up 17% by mass in the food bolus. Therefore, according to the type of food, the European vendace in Lake Imandra is characterized as an omnivorous predator preferring macrozoobenthos.

Vendace of small northern lakes in Karelia (Krivoe, Nizhnee Starushech'e) are characterized by high seasonal variability in nutrition and the contribution of various groups of benthos and plankton to their diet (Berezina et al., 2018; Berezina et al., 2021). Analysis of stable nitrogen and carbon isotopes in fish tissues and their potential food sources revealed four trophic levels in the food webs of Lake Krivoe and highly pronounced euryphagy. In summer, the fish was characterized by a mixed diet, using food resources of predominantly benthic origin in both coastal and deep habitats (Berezina et al., 2018). Among them, bottom amphipods *Gammarus lacustris* Sars, 1863 and *Monoporeia affinis* (Lindström, 1855) accounted for 67–75% of the assimilated food of fish, planktonic crustaceans, 2–5%. These data are somewhat contradict the results of the analysis of fish stomachs: for example, the contribution of zooplankton in food bolus may reach 22% in summer and early autumn (Berezina et al., 2018). In contrast to summer and autumn, in the ice winter-spring period, the share of planktonic crustaceans and insect larvae in the food bolus of vendace was rather high (37–54% and 24–42%, respectively), while amphipods (*G. lacustris, M. affinis*) accounted for less than 20%. In general, macroinvertebrates were the main food resource of vendace in small subarctic lakes throughout the year, but crustacean plankton was also important in its diet; its role especially increased in the autumn-winter period (Berezina et al., 2021; N.A. Berezina, unpublished data, 2020−2021).

Europe

Analysis of publications on the feeding of small-sized vendace *C. albula* in boreal lakes in a number of European countries evidences that zooplankton is the basis of its nutrition. At the same time, cladocerans and copepods are dominant zooplankton representatives in all lakes (Table 1).

In the small lakes of Lithuania, in the summer-autumn period, *C. albula* consumes a wide range of prey, 19 taxa (Bukelskis and Umbrasaite, 2016), being a typical planktivore. In all lakes, cladocerans, copepods, and chironomid larvae prevail in their diet. The vendace also consumed the mollusks *Bithynia* and *Dreissena* (Lake Chichiris) and mysids (Lake Daugai).

In Lake Wigry (northeastern Poland), a close relationship between the food spectrum of vendace and seasonal dynamics of abundance and species diversity of zooplankton has been observed (Czarkowski et al., 2007). In spring and autumn, vendace feeds on large copepods *Cyclops vicinus* Ulyanin, 1875 and *Eudiaptomus graciloides*, in summer, these are cladocerans (*Daphnia cucullata, D. cristata,* and *D. hyalina* Leydig, 1860); larvae and pupae of amphibiotic insects (*Chaoborus* sp. and *Microtendipes* sp.) are recorded in small numbers.

In the lakes of Finland, Germany, and Sweden, European vendace (*C. albula*) is known primarily as planktivorous, i.e. it feeds mainly on seasonally abundant zooplankton such as cladocerans and copepods, with a small addition of insect larvae (Mamcarz and Błoniarz, 1995; Schulz et al., 2003; Viljanen, 1983). If such large food items as *Bythotrephes longimanus*, *Leptodora kindtii*, and mysids are available, they become dominant in the diet (Scharf et al., 2008; Schulz et al., 2003; Viljanen, 1983). Benthic organisms (larvae of chironomids and amphipods) are noted as single and sporadic food components (< 2%) in the vendace diet (Northcote and Hammar 2006; Scharf et al., 2008).

Some studies have revealed patterns in the food preferences of vendace; for example, mysids were consumed in different seasons of the year, while nauplii of copepods were always avoided (Scharf et al., 2008). Mysids were found in large numbers in the stomachs of vendace, when their abundance in the pelagic zone was high alongside a low availability of mesozooplankton.

According to selectivity indices, vendace usually prefers large species of cladocerans and copepods in Finnish lakes (Viljanen, 1983); therefore, changes in its food spectrum reflect seasonal changes in the zooplankton community and depend on the abundance of available food organisms.

Bolshemelskaya Tundra and Malozemelskaya Tundra

Vendaces are numerous in the lakes of the Malozemelskaya Tundra. In the Lake Golodnaya

Guba, vendace (body length up to 19 cm) feeds on cladocerans of the genera *Bosmina, Chydorus,* and *Daphnia* in July–August (Kornilova, 1967; Fadeeva, 1999). Chironomid larvae and pupae, as well as their imagoes, are also occasionally found in the food bolus of these fish. A characteristic feature of this lake, as well as of other water bodies of northern latitudes, is low feeding capacity for planktivorous fish, since the abundance of the genera *Bosmina, Chydorus, Daphnia, Conochilus*, as well as *Keratella cochlearis* and *Kellicottia longispina*, is low, from 0.3 to 0.6 g/m^3 (Imant et al., 2018).

In the Usa River, in autumn, *C. sardinella* (15–21 cm) feeds mainly on imagoes of aerial insects, three quarters (72.8%) of the food bolus were presented by them (Borovskaya and Novoselov, 2020). High values of the proportion of adult insects in the food bolus coincided with the moments of their emergence from the water after metamorphosis. Diptera Simuliidae (24–51% by weight), Mycetophilidae, Muscidae, and Chironomidae prevailed among these insects in the stomachs of vendace. Aquatic insect larvae living on the sediment surface (larvae of chironomids, coastal flies, caddis flies, stoneflies, and mayflies) were less important in the diet of vendace, accounting for 24% by weight.

In August–September, the Pechora vendace migrates to rivers to spawning grounds, it usually keeps in the surface water layer, so it feeds on the surface, collecting insect imagoes: midges and mosquitoes (Solovkina, 1962). In the delta and estuary of the Pechora River, vendace feeds on planktonic and benthic invertebrates (Fadeeva, 1999). In the floodplain and riverbed water bodies of the Pechora River, at the end of July, *C. sardinella* consumes crustaceans in significant quantities (Zvereva et al., 1953). European vendace, feeding directly in the riverbed and its tributaries, feeds mostly on insect imagoes (both terrestrial and aquatic forms), as well as on benthic invertebrates (Solovkina, 1962). Larvae of chironomids, caddis flies, mayflies, and stoneflies were found in the food spectrum. Zooplankton was rare in the stomachs of the vendace feeding at the riverbed.

In the Pechora River delta, vendace has the opportunity to feed on plankton only during warm years. During these periods, cladocerans, chironomid pupae, and insect imagoes form the basis of its summer diet (Kornilova and Panova, 1964). In cold years, in the river delta and in the Korovinskaya Inlet of the Pechora Bay, the development of zooplankton is insufficient to fully support vendace needs (Kornilova, 1970).

In the Lake Bolshoi Kharbei (basin of the Pechora River, eastern part of the Bolshezemelskaya Tundra), as in other tundra lakes, extremely warm years alternate with extremely cold ones (Loskutova, 2002). The food spectrum of vendace in the Kharbei Lakes in warm years (August–September) is usually represented by zooplankton (> 50%), while in cold years, vendace feeds mainly on benthic invertebrates, such as chironomid larvae and mollusks (Sidorov, 1974). The food spectrum of fish living in different lakes varies greatly. For example, in the Lake Bolshoi Kharbei, in a warm year, cladocerans (67% by weight) dominated in the diet of vendace, while these were copepods in the Vashutka Lakes (Kuchina and Solovkina, 1970; Sidorov and Reshetnikov, 2014).

Western and Eastern Siberia

The shallow (down to 20 m deep) Gulf of Ob (the estuary of the Ob River) is covered by ice for most of the year (240 days). River waters, carrying micronutrients and heat from the south, mix here with the cold salty waters of the Kara Sea, which promotes specific hydrological and hydrochemical conditions favorable for the mass development of plankton and benthos and for the reproduction of vendace.

Almost all fish living in the Gulf of Ob feed on benthos; only vendace and smelt consume zooplankton. According to V.S. Yukhneva (1955), in summer, in the Gulf of Ob, vendace feeds mainly on planktonic crustaceans of the genera *Daphnia, Bosmina, Cyclops*, etc. (Table 1). Vendace from the middle part of the bay prefers crustaceans of the genus *Heterocope* and the family Diaptomidae, and in the northern part, the food is mainly presented by *Senecella calanoides* Juday, 1923, *Bosmina* sp., and *Daphnia* sp. (Leshchinskaya, 1962).

In the Gulf of Ob, the food spectrum of vendace in autumn and winter differs significantly from that in summer. In September and October, vendace (body length 16–27 cm) consumes amphipods *Monoporeia affinis*, which may make up 100% of the stomach contents (up to 600 ind. per fish) (Stepanova and Stepanov, 2006). In December–January, copepod *Limnocalanus macrurus* G.O. Sars, 1863 and mysids were found in its diet in addition to *M. affinis*. At the same time, about half of the studied fish were actively feeding. In February–March, calanoids, among which *L. macrurus* dominated (up to 100% by biomass) were still the main food items for vendace (Stepanova, 2017). The frequency of occurrence of amphipods (most often *Onisimus* spp.) was 25%, mysids, 12%. Therefore, during the ice period, vendace in the Gulf of Ob is characterized by a mixed diet with a predominance of large crustaceans.

In the lakes of the Norilsk-Pyasinskaya lake-river system, characterized by a harsh climate, vendace is characterized by high feeding plasticity (Nikulina and Romanov, 2019; Popov, 2007) and a mixed type of diet, including zooplankton, zoobenthos, and aquatic vegetation (Romanova, 1948; Sycheva and Luk'yanchikov, 1964). According to N.V. Vershinina and A.V. Sycheva (1964), young vendace living in the coastal areas of the Putorana Plateau (lakes Lama

and Melkoe) feed on rotifers, crustacean plankton, chironomid larvae and pupae, and insect imagoes. The food spectrum of adult fish (body length up to 25 cm) feeding in the pelagic zone is narrower; it mainly includes cladocerans of the genus *Bosmina*, large calanoids *Limnocalanus grimaldii* (Guerne, 1886) and *L. macrurus*, and, to a lesser extent, larvae and pupae of chironomids. The rotifers and copepods usually dominate in zooplankton of these lakes (total average biomass of 0.5 g/m^3), while more than 40 species of chironomids and amphipods inhabit zoobenthic communities (Zadelenov et al., 2017).

The food spectrum of vendace in the high-latitude Lake Taimyr varies from year to year depending on the plankton and benthos development during the very short summer. For example, vendace in the Lake Taimyr fed exclusively on copepods in the pelagic zone, only occasionally eating chironomid larvae (Greze, 1957), but according to other authors Taimyr vendace consumed mainly benthos (amphipods and mysids), as well as aerial insects (Malinina et al., 1988). In the spring, during the flood, shallow bays and inlets are formed around the Lake Taimyr for 3–4 weeks, which serve as additional feeding grounds for vendace. In summer, the zooplankton biomass in the lake is low (0.16–0.23 g/m^3), while zoobenthos is well developed, especially in bays, where its biomass reaches 5.6 g/m^2 (Kiyashko, 1995). Moreover, 57% of the fish were with empty stomachs. In well-warmed bays of the Lake Taimyr, the vendace food spectrum consists of amphipods, chironomid larvae, ostracods, and mollusks (Kiyashko, 1995).

In the northern Krasnoyarsk Krai, in the Khatanga River and Khatanga Bay, the diet of vendace was mostly presented by the larvae of chironomids and caddis flies, amphipods, mysids, and aquatic plants (Lukyanchikov, 1967; Romanov, 1997; Romanov and Karmanova, 2005). Zooplankton was poorly represented in the diet of vendace in Khatanga River, since it was extremely scarce in the river. Turukhansk vendace from the middle and lower reaches of the Yenisei River, as well as from other water bodies of Siberia, is characterized by a mixed type of feeding. However, in some years, vendace predominantly feeds on zooplankton, and in other years, on benthic invertebrates (Popov, 2007; Ustyugov, 1972, 1976).

The larvae of dragonflies and other insects (more than 50% of the frequency of occurrence), mollusks and amphipods were the main food components of underyearlings in the Kolyma River (Fedorova et al., 2011). In the two-year-old vendace, the proportion of mollusks from the families Planorbidae and Pisidiidae increased. In fish of older age groups, insect larvae dominated in the diet. In the lower reaches of the Kolyma River, where the zooplankton was characterized by high share of rotifers, cladocerans *Bosmina longirostris* and copepods *Limnocalanus macrurus* (total abundance from 17 to 121 thousand ind./m^3), vendace nevertheless preferred to feed on benthic invertebrates (Fedorova et al., 2011).

Conclusions

Analysis of the feeding of European vendace and sardine cisco in various water bodies of Eurasia (both temperate and high latitudes) evidences that its food spectrum is quite wide: from small forms of phytoplankton and zooplankton to large benthic crustaceans, insect larvae, mollusks, and even fish. Despite the fact that vendace is more adapted to feeding on small crustaceans in the water column by the structure of its jaw apparatus, it can also easily feed on benthic invertebrates.

Water bodies located in the boreal zone of Europe and Russia (Lake Pleshcheyevo, lakes of the southern Karelia, Lake Ladoga, Lake Onega, Lake Vishtynetskoe, Lake Lekshmozero, Lake Kenozero, etc.) are characterized by a fairly high development of the zooplankton community during the growing period of vendace; thus, the dietary needs are fully met by crustacean zooplankton. At the same time, feeding mainly on cladocerans and copepods, vendace always prefers larger objects, such as representatives of the genera *Leptodora, Bythotrephes,* and *Limnocalanus*. In most water bodies, where seasonal variability of the qualitative and quantitative indicators of zooplankton is observed, caused by both the peculiarities of hydrological conditions and the specificity of the biological cycles of zooplankton species, vendace may alter the feeding strategy in accordance with the emerging trophic conditions. If large benthic objects are available, it can successfully feed on them, preferring primarily crustaceans and insects, but if this prey becomes unavailable, vendace may also consume mollusks, fish, and phytobenthos. Including all kinds of the most abundant benthic organisms, planktonic animals, and aerial insects, vendace has adapted to life in various reservoirs of different latitudes and even in the very harsh conditions of Siberia and the Arctic, where it is still one of the most valuable fishing objects. Vendace has high feeding plasticity along with poor development of the food base; therefore, its food spectrum is very diverse and variable both in regard to the season and latitude, being highly dependent on biodiversity and productivity of the reservoir.

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References

Abramov, A.F., Salova, A.F., Salova, T.A., Stepanov, K.M., Efimova, A.A. et al., 2018. Pishchevaya i biologicheskaya tsennost' presnovodnykh ryb rek Yakutii [Nutritional and biological value of freshwater fish of the rivers of Yakutia]. SibAK, Novosibirsk, Russia, 154 p. (In Russian).

Babiy, A.A., Sergeeva, T.I., 2003. Krupnaya ryapushka kilets – *Coregonus albul*a Onezhskogo ozera [Large vendace kilets – *Coregonus albula* of Lake Onega]. *Voprosy ikhtiologii [Journal of Ichthyology]* **41** (3), 345–351. (In Russian).

Berezina, N.A., Litvinchuk, L.F., Maksimov, A.A., 2021. The food spectrum of fishes in connection with the composition of zooplankton and zoobenthos in a subarctic lake. *Inland Water Biology* **4**, 406–416.

Berezina, N.A., Strelnikova, A.P., Maximov, A.A., 2018. The benthos as the basis if vendace *Coregonus albula* and perch *Perca fluviatilis* diet in an oligotrophic sub-Arctic lake. *Polar Biology* **41**, 1789–1799.

Berezina, N.A., Strelnikova A.P., 2010. The role of the introduced amphipod *Gmelinoides fasciatus* and native amphipods as fish food in two large-scale north-western Russian inland water bodies: Lake Ladoga and Rybinsk Reservoir. *Journal of Applied Ichthyology* **26** (s2), 89–95. https://doi.org/10.1111/j.1439-0426.2010.01493.x

Bogdanov, N.A., Bogdanova, G.I., 2008. Promysel ryapushki v basseyne reki Khatangi [Fishing for vendace in the Khatanga River basin]. *Materialy Vserossiyskoy konferentsii s mezhdunarodnym uchastiyem "Problemy i perspektivy ratsional'nogo ispol'zovaniya vodnykh bioresursov Sibiri v KHKHI veke" [Materials of the All-Russian conference with international participation "Problems and prospects of the rational use of aquatic biological resources of Siberia in the XXI century"].* Krasnoyarsk, Russia, 243–246. (In Russian).

Borovikova, E.A., Makhrov, A.A., 2012. Izucheniye populyatsiy perekhodnoy zony mezhdu yevropeyskoy i sibirskoy ryapushkami (*Coregonus*): rol' sredy obitaniya v vidoobrazovanii [Study of populations of the transition zone between European and Siberian vendace (*Coregonus*): the role of habitat in speciation]. *Printsipy ekologii [Environmental Principles]* **4**, 5–20. (In Russian).

Borovskoy, A.V., Novoselov, A.P., 2020. Pishchevye otnosheniya sigovykh vidov ryb v nizhnem techenii reki Usa v osenniy period [Trophic relations of coregonid fish species in the lower reaches of the Usa River in autumn]. *Trudy Karel'skogo nauchnogo tsentra RAN [Proceedings of the Karelian Scientific Centre of the Russian Academy of Sciences]* **5**, 44–58. (In Russian). https://doi.org/10.17076/eco1196

Bukelskis, E., Umbrasaite, V., 2016. Pishchevaya spetsializatsiya ryapushki (*Coregonus albula*) v ozerakh Litvy [Food specialization of vendace (*Coregonus albula*) in Lithuanian lakes]. In: Mikheeva, T.M. (ed.), *Ozernye ekosistemy: biologicheskiye protsessy, antropogennaya transformatsiya, kachestvo vody [Lake ecosystems: biological processes, anthropogenic transformation, water quality].* Belarus State University, Minsk, Belarus, 285–286. (In Russian).

Chernyaev, Zh.A., 2017. *Vosproizvodstvo sigovykh ryb. Ekologo-fiziologicheskiye osobennosti razmnozheniya i razvitiya [Whitefish reproduction. Ecological and physiological characteristics of reproduction and development]* KMK, Moscow, Russia, 329 p. (In Russian).

Czarkowski, T.K., Martyniak, A., Kapusta, A., Wójcik, A., Bowszys, M., Wziątek, B., Szamańska, U., Kozłowski, J., 2007. Feeding ecology of vendace, *Coregonus albula* (L.), in Lake Wigry (Northeastern Poland). *Archives of Polish Fisheries* **15** (2), 117–128.

Dvoryankin, G.A., 2009. Populyatsionnye kharakteristiki ryapushki Kenozerskogo natsional'nogo parka [Population characteristics of vendace in the Kenozero National Park]. *Materialy XVIII Mezhdunarodnoy konferentsii "Biologicheskiye resursy Belogo morya i vnutrennikh vodoyemov yevropeyskogo severa" [Materials of the XVIII International Conference "Biological Resources of the White Sea and Inland Water Bodies of the European North"].* Karelian Scientific Centre of the Russian Academy of Sciences, Petrozavodsk, Russia, 179–183. (In Russian).

Fadeeva, G.V., 1999. Pitaniye nel'my v zimniy period v nizov'yakh reki Pechory [Feeding of nelma in winter in the lower reaches of the Pechora river]. *Tezisy dokladov mezhdunarodnoy konferentsii "Biologicheskie osnovy izucheniya, osvoyeniya i okhrany zhivotnogo i rastitel'nogo mira, pochvennogo pokrova Vostochnoy Fennoskandii" [Abstracts of the international conference "Biological foundations of the study, development and protection of flora and fauna, the soil cover of Eastern Fennoscandia"].* Petrozavodsk, Russia, 167–168. (In Russian).

Fedorova, E.A., Filippova, D.S., Ivanov, E.V., Sobakina, I.G., Ushnitskaya, L.A., Solomonov, N.M., Sokolova, V.A., 2011. Izucheniye pitaniya dominiruyushchikh vidov ryb v nizhnem techenii r. Kolymy [Study of the feeding of dominant fish species in the lower reaches of the Kolyma River]. *Bioekologiya [Bioecology]* **4**, 265–268. (In Russian).

Gerasimov, Yu.V., Malin, M.I., Borisenko, E.S., Zhdanova, S.M., Tsvetkov, A.I., Smirnov, A.K., 2019. Pishchevoye povedeniye i pitaniye ryapushki (*Coregonus albula*) v ozere Pleshcheyevo v period temperaturnoy stratifikatsii [Feeding behavior and nutrition of vendace (*Coregonus albula*) in Lake Pleshcheyevo during the period of temperature stratification]. *Materialy II Mezhdunarodnoy konferentsii "Ozera Evrazii: problemy i puti ikh resheniya". Chast' 2 [Materials of the II International Conference "Lakes of Eurasia: Problems and Ways to Solve". Part 2].* Kazan, Russia, 234–239. (In Russian).

Gnedov, A.A., 2009. Kachestvennye pokazateli produktsii iz ryapushki sibirskoy (*Coregonus sardinella* Valenciennes) – perspektivy polnogo ispol'zovaniya [Quality indicators of production from Siberian vendace (*Coregonus sardinella* Valenciennes): prospects for full use]. *Vestnik KrasGAU [Bulletin fo Krasnoyarsk State Agrarian University]* **5**, 177–180. (In Russian).

Greze, V.N., 1957. Osnovnye cherty gidrobiologii ozera Taymyr [The main features of the hydrobiology of Lake Taimyr]. *Trudy Vsesoyuznogo gidrobiologicheskogo obshchestva [Proceedings of the All-Union Hydrobiological Society]* **8**, 183–218. (In Russian).

Hamrin, S.F., 1983. The food preference of vendace (*Coregonus albula* L.) in South Swedish forest lakes including the predation effect on zooplankton population. *Hydrobiologia* **101**, 121–128. https://doi.org/10.1007/BF00008664

Imant, E.N., Zavisha, A.G., Studenova, M.A., Novoselov, A.P., Levitsky, A.L., 2018. Sravnitel'naya kharakteristika kormovoy bazy ryb raznotipnykh ozor Severnogo rybokhozyaystvennogo basseyna [Comparative characteristics of the food supply for fish of different types of lakes in the Northern fishery basin]. *Materialy III Mezhdunarodnoy konferentsii "Aktual'nye problemy planktonologii" [Materials of the III International conference "Actual issues of planktonology"].* Atlantic Branch of the Russian Federal Research Institute of Fisheries and Oceanography, Kaliningrad, Russia, 86–90. (In Russian).

Kizhevatov, Ya.A., 2007. K biologii i rasnrostraneniyu ryapushki sibirskoy (*Coregonus sardinella* Valenciennes, 1848) v nekotorykh rekakh YANAO [On the biology and distribution of sardine cisco (*Coregonus sardinella* Valenciennes, 1848) in some rivers of the Yamalo-Nenets Autonomous Okrug]. *Nauchny vestnik YaNAO [Scientific Bulletin of the YNAO]* **2**, 54–60. (In Russian).

Kirillov, A.F., Fedorova, E.A., 2010. K izucheniyu vosproizvodstva sibirskoy ryapushki *Coregonus sardinella* (Salmoniformes, Coregonidae) reki Kolymy [On the study of the reproduction of the sardine cisco *Coregonus sardinella* (Salmoniformes, Coregonidae) of the Kolyma River]. *Voprosy rybolovstva [Fisheries Issues]* **11** (2), 232–240. (In Russian).

Kiyashko, V.I., 1995. Kormovye resursy itroficheskiye svyazi osnovnykh promyslovykh ryb ozera Taymyr [Forage resources and trophic relationships of the main commercial fish of Lake Taimyr]. *Tezisy dokladov Mezhdunarodnoy konferentsii "Biologicheskiye resursy Belogo morya i vnutrennikh vodoyemov yevropeyskogo Severa" [Abstracts of the International Conference "Biological Resources of the White Sea and Inland Waters of the European North"].* Petrozavodsk State University, Petrozavodsk, Russia, 35–36. (In Russian).

Kiyashko, V.I., Slyn'ko, Yu.V., 2003. Struktura pelagicheskikh skopleniy ryb i sovremennaya trofologicheskaya situatsiya v otkrytykh plesakh Rybinskogo vodokhranilishcha posle vseleniya chernomorsko-kaspiyskoy tyul'ki [The structure of pelagic fish accumulations and the current trophological situation in the open reaches of the Rybinsk reservoir after the introduction of the Black Sea-Caspian tulka]. *Materialy rossiysko-amerikanskogo simpoziuma "Invazii chuzherodnykh vidov v Golarktike" [Materials of the Russian-American Symposium "Invasions of Alien Species in the Holarctic"].* IBIW RAS, Borok, Russia, 259–271. (In Russian).

Khal'ko, N.A., Tereshchenko, L.I., Malina, Yu.I., Bazarov, M.I., 2019. Seasonal and interannual changes in the feeding spectrum of vendace (*Coregonus albula* L.) in Lake Pleshcheyevo. *Inland Water Biology* **12** (S1), 98–102. https://doi.org/10.1134/S0320965219030100

Kornilova, V.P., 1967. Ikhtiofauna ozera Golodnaya guba del'ty Pechory [Ichthyofauna of Lake Golodnaya Bay of the Pechora River delta]. *Materialy rybokhozyaystvennykh issledovaniy*

Severnogo basseyna [Fisheries research materials of the Northern Basin] **9**, 32–41. (In Russian).

Kornilova, V.P., 1970. Ikhtiofauna nizov'ev Pechory i Pechorskogo zaliva Barentseva moray [Ichthyofauna of the lower reaches of the Pechora and the Pechora Bay of the Barents Sea]. *Materialy rybokhozyaystvennykh issledovaniy Severnogo basseyna [Fisheries research materials of the Northern Basin]* **13**, 5–44. (In Russian).

Kornilova, V.P., Panova, N.A., 1964. Nekotorye dannye po pitaniyu sigovykh Golodnoy i Korovinskoy gub del'ty Pechory [Some data on the feeding of whitefishes in Golodnaya and Korovinskaya bays of the Pechora River delta]. *Materialy rybokhozyaystvennykh issledovaniy Severnogo basseyna [Fisheries research materials of the Northern Basin]* **2**, 38–45. (In Russian).

Krivopuskova, E.F., Masyutkina, E.A., Sokolov, A.V., Shibaeva, M.N., 2014. Kharakteristika sostava pishchi ryapushki (*Coregonus albula*) ozera Vishtynetskogo (Kaliningradskaya oblast') v sovremennykh usloviyakh [Characteristics of the food composition of vendace (*Coregonus albula*) of Lake Vishtynetsky (Kaliningrad Oblast) in modern conditions]. *Izvestia KSTU [News of Kaliningrad State Technical University]* **3**, 9–16. (In Russian).

Kuchina, E.S., Solovkina, L.N., 1970. Ryapushka ozer Bol'shezemel'skoy tundry [Vendace of the lakes of the Bolshezemelskaya Tundra]. *Biologicheskiye osnovy ispol'zovaniya prirody Severa [Biological bases of using the nature of the North].* Komi Book Publishing House, Syktyvkar, USSR, 276–281. (In Russian).

Kuchko, Ya.A., Il'mast, N.V., Kuchko, T.Yu., Milyanchuk, N.P., 2017. Zooplankton kak kormovaya baza yevropeyskoy ryapushki shkhernogo rayona severnoy chasti Ladozhskogo ozera [Zooplankton as a food base for European vendace in the skerry region of the northern part of Lake Ladoga]. *Uchenye zapiski PetrGU. Obshchaya biologiya [Scientific notes of Petrozavodsk State University. General Biology]* **2** (163), 39–45. (In Russian).

Lazareva, V.I., Sokolova, E.A., 2018. Zooplankton pelagiali vodokhranilishcha [Zooplankton of the pelagic zone of the reservoir]. In: Lazareva, V.I. (ed.), *Struktura i funktsionirovaniye ekosistemy Rybinskogo vodokhranilishcha v nachale XXI veka [The structure and functioning of the ecosystem of the Rybinsk reservoir at the beginning of the XXI century].* IBIW RAS, Moscow, Russia, 213–238. (In Russian).

Lebedeva, U.M., Abramov, A.F., 2015. Osnovy ratsional'nogo pitaniya naseleniya Yakutii [Fundamentals of rational nutrition of the population of Yakutia]. M.K. Amosov North-Eastern Federal University, Yakutsk, Russia, 246 p. (In Russian).

Leshchinskaya, A.S., 1962. Zooplankton i bentos Obskoy guby kak kormovaya baza dlya ryb (Trudy Salekhardskogo statsionara AN SSSR. Ural'skiy filial. Vyp. 2) [Zooplankton and benthos of the Ob Bay as a food base for fish (Proceedings of the Salekhard Station of the USSR Academy of Sciences. Ural Branch. Is. 2)]. Ural'skiy Rabochiy, Sverdlovsk, USSR, 80 p. (In Russian).

Liso, S., Gjelland, K.Ø., Reshetnikov, Y.S., Amundsen, P.A., 2011. A planktivorous specialist turns rapacious: piscivory in invading vendace *Coregonus albula*. *Journal of Fish Biology* **78**, 332–337. https://doi.org/10.1111/j.1095-8649.2010.02831.x

Loskutova, O.A., 2002. Bentos ozerno-rechnykh sistem vostochnoyevropeyskoy tundry [Benthos of lake-river systems of the East European tundra]. In: Taskaev, A.I. (ed.), *Vozobnovimye resursy vodoyemov Bol'shezemel'skoy tundry (Trudy Komi NC UrO RAN. Vyp. 169) [Renewable resources of water bodies of the Bolshezemelskaya tundra (Proceedings of the Komi Scientific Center of the Ural Branch of the Russian Academy of Sciences. Is. 169)].* Komi Scientific Center of the Ural Branch of the Russian Academy of Sciences, Syktyvkar, Russia, 44–57. (In Russian).

Lukyanchikov, F.V., 1967. Ryby sistemy reki Khatanga [Fish of the Khatanga River System]. In: Vershinin, N.V. (ed.) *Ryby i kormovye resursy basseynov rek and vodokhranilishch Vostochnoy Sibiri [Fish and food resources of river basins and reservoirs in Eastern Siberia].* Siberian Research Institute of Fisheries, Krasnoyarsk Branch, Krasnoyarsk Regional Scientific and Technical Society of the Food Industry, Krasnoyarsk, USSR, 11–93. (In Russian).

Malinin, L.K., Poddubny, A.G., Permitin, I.E., 1988. Struktura populyatsiy, pitaniye i prostranstvennoye raspredeleniye ryb v ozere Taymyr [Population structure, nutrition and spatial distribution of fish in Lake Taimyr]. All-Russian Institute for Scientific and Technical Information. No. 1147-I88. Moscow, USSR, 55 p. (In Russian).

Mal'tseva, V.V., 1983. Pitaniye ryapushki i koryushki severo-vostochnoy chasti Onezhskogo ozera [Feeding of vendace and smelt in the northeastern part of Lake Onega]. *Ryby Onezhskogo ozera i*

ikh khozyaystvennoye ispol'zovaniye [Fish of Lake Onega and their economic use]. Trudy GosNIORKH [Proceedings of State Scientific Institute of Lake and River Fisheries] **205**. Promrybvod, Leningrad, USSR, 79–91. (In Russian).

Mamcarz, A., Bloniarz, W., 1995. Diet of *Coregonus albula* L. in eutrophic Lake Charzykowskie (Pomerania, Poland). *Archiv für Hydrobiologie* **46**, 79–88.

Mychkova, A.V., Krivopuskova, E.V., Shibaeva, M.N., 2017. Zooplankton pribrezhnoy chasti ozera Vishtynevskogo v zimniy period i ego rol' v pitanii evropeyskoy ryapushki (*Coregonus albula* L.) [Zooplankton of the coastal part of Lake Vishtynevsky in winter and its role in the feeding of European vendace (*Coregonus albula* L.)]. *Vestnik molodezhnoy nauki [Bulletin of Youth Science]* **3** (10), 24. (In Russian).

Nikolaev, I.I., 1983. Ekologicheskaya geterogennost' zooplanktona Onezhskogo ozera i yeye znacheniye v dinamike chislennosti osnovnykh planktofagov etogo vodoyema – ryapushki i koryushki [Ecological heterogeneity of zooplankton in Lake Onega and its significance in the dynamics of the abundance of the main planktophages of this reservoir – vendace and smelt]. *Ryby Onezhskogo ozera i ikh khozyaystvennoye ispol'zovaniye. Trudy GosNIORKH [Fish of Lake Onega and their economic use. Proceedings of State Scientific Institute of Lake and River Fisheries]* **205**. Promrybvod, Leningrad, 67–79. (In Russian).

Nikulina, Yu.S., Borovikova, E.A., Budin, Yu.V., 2018. Morfologicheskaya differentsiatsiya rechnykh i ozernykh populyatsiy ryapushek (r. *Coregonus*) basseynov morey Karskogo i Laptevykh [Morphological differentiation of river and lacustrine populations of vendace (genus *Coregonus*) of the Kara and Laptev seas]. Uchenye zapiski RGGMU [Scientific notes of the Russian State Hydrometeorological University] **51**, 162–175. (In Russian).

Nikulina, Yu.S., Romanov, V.I., 2019. Biologicheskaya kharakteristika ryapushek nekotorykh ozer plato Putorana [Biological characteristics of vendace in some lakes of the Putorana Plateau]. *Materialy V Mezhdunarodnoy konferentsii "Sovremennoye sostoyaniye vodnykh bioresursov" [Materials of the V International Conference "Current state of aquatic biological resources"].* Novosibirsk State Agrarian University, Novosibirsk, Russia, 106–110. (In Russian).

Northcote, T.G., Hammar, J., 2006. Feeding ecology of *Coregonus albula* and *Osmerus eperlanus* in the limnetic waters of lake Malaren, Sweden. *Boreal Environmental Research* **11** (3), 229–246.

Pokrovsky, V.V., 1953. Ryapushka ozer Karelo-Finskoy SSR [Vendace of the lakes of the Karelo-Finnish SSR]. Gosudarstvennoye izdatel'stvo Karelo-Finskoy SSR, Petrozavodsk, USSR, 107 p. (In Russian).

Politov, D.V., 2017. Coregonids of Russia: Evolutionary genetic approach in assessment of the current state of biodiversity *Fundamental and Applied Limnology* **189** (3), 181–192. https://doi.org/10.1127/fal/2017/0814

Polovkova, S.N., Permitin, I.E., 1981. Ob ispol'zovanii kormovogo zooplanktona nagul'nymi opleniyami ryb-planktofagov [On the use of forage zooplankton by feeding flooding of planktophagous fish]. In: Poddubny, A.G. (ed.), *Vnutripopulyatsionnaya izmenchivost' pitaniya i rosta ryb [Intrapopulation variability in fish nutrition and growth].* Academy of Sciences of the USSR, Yaroslavl, USSR, 3–35. (In Russian).

Popova O.A., Reshetnikov Yu.S., 2011. O kompleksnykh indeksakh pri izuchenii pitaniya ryb [On complex indices in the study of fish nutrition]. *Voprosy ikhtiologii [Journal of Ichthyology]* **51** (5), 712–717. (In Russian).

Popov, P.A. 2007. *Ryby Sibiri: rasprostraneniye, ekologiya, vylov [Fish of Siberia: distribution, ecology, catch].* Novosibirsk State University, Novosibirsk, Russia, 526 p. (In Russian).

Reshetnikov, Yu.S., 1980. Ekologiya i sistematika sigovykh ryb [Ecology and taxonomy of coregonids]. Nauka, Moscow, USSR, 300 p. (In Russian).

Reshetnikov, Y.S., 2004. Coregonid fishes in Arctic waters. *Annales Zoologici Fennici* **41**, 3–11.

Reshetnikov, Yu.S., Sterligova, O.P., Anikieva, L.V., Koroleva, I.M., 2020. Proyavleniye neobychnykh svoystv u ryb v novoy situatsii na primere ryapushki *Coregonus albula* i koryushki *Osmerus eperlanus* [Manifestation of unusual properties in fish in a new situation on the example of vendace *Coregonus albula* and smelt *Osmerus eperlanus]*. *Voprosy ikhtiologii [Journal of Ichthyology]* **60** (3), 352–363. (In Russian).

Romanov, V.I., 1997. K biologii ryapushek basseyna reki Khatanga [On the biology of vendace in the Khatanga river basin]. *Materialy*

nauchnoy konferentsii, posvyashchennoy 50-letiyu deyatel'nosti Novosibirskogo otdeleniya SibrybNIIproyekt "Biologicheskaya produktivnost' vodoyomov Zapadnoy Sibiri i ikh ratsional'noye ispol'zovaniye" [Materials of the scientific conference dedicated to the 50th anniversary of the activity of the Novosibirsk branch of SibrybNIIproject "Biological productivity of reservoirs in Western Siberia and their rational use"]. Novosibirsk, Russia, 145–147. (In Russian).

Romanov, V.I., Karmanova, O.G., 2005. Ekologiya sibirskoi ryapushki Khantaiskogo vodokhranilishcha v period stabilizatsii urovnevogo rezhima [Ecology of the sardine cisco of the Khantai Reservoir during the stabilization of the level regime]. *Materialy Vserossiyskoy konferentsii "Sovremennye problemy gidrobiologii Sibiri" [Materials of the All-Russian conference "Modern problems of hydrobiology of Siberia"]. Tomsk, November 14–16 2001.* Tomsk, Russia, 212–222. (In Russian).

Romanova, G.P., 1948. Pitaniye ryb v nizhnem Yeniseye [Feeding of fishes in the lower reaches of the Yenisei River]. *Trudy Sibirskogo Otdeleniya Vsesoyuznogo nauchno-issledovatel'skogo instituta ozernogo i rechnogo khozyaystva. Ekonomika [Proceedings of the Siberian Branch of the All-Union Scientific Research Institute of Lake and River. Economy]* **7** (2), 151–200. (In Russian).

Ryby Rybinskogo vodokhranilishcha: populyatsionnaya dinamika i ekologiya [Fish of the Rybinsk Reservoir: Population Dynamics and Ecology], 2015. Gerasimov, Yu.V. (ed.). Filigran, Yaroslavl, Russia, 418 p. (In Russian).

Sarvala, J., Helminen, H., Ventelä, A.-M., 2020. Overfishing of a small planktivorous freshwater fish, vendace (*Coregonus albula*), in the boreal lake Pyhäjärvi (SW Finland), and the recovery of the population. *Fisheries Research* **230,** 105638. https://doi.org/10.1016/j.fishres.2020.105664

Scharf, J., Krappe, M., Koschel, R., Waterstraat, A., 2008. Feeding of European cisco (*Coregonus albula* and *C. lucinensis*) on the glacial relict crustacean *Mysis relicta* in Lake Breiter Luzin (Germany). *Limnologica* **38** (2), 147–158. https://doi.org/10.1016/j.limno.2007.12.001

Schulz, M., Kasprzak, P., Anwand, K., Mehner, T., 2003. Diet composition and food preference of vendace (*Coregonus albula* (L.)) in response to seasonal zooplankton succession in Lake Stechlin. *Archiv für Hydrobiologie* **58**, 215–226.

Sergienko, L.L., 2015. Sibirskaya ryapushka kak ob'yekt rybovodstva [Siberian vendace as an object of fish farming]. *Vestnik rybokhozyaystvennoy nauki [Bulletin of Fisheries Science]* **2** (1), 69–77. (In Russian).

Sidorov, G.P., 1974. Rybnye resursy Bolshezemelskoi tundry [Fish resources of the Bolshezemelskaya tundra]. Nauka, Leningrad, USSR, 164 p. (In Russian).

Sidorov, G.P., Reshetnikov, Yu.S., 2014. Lososeobraznye ryby vodoyemov yevropeyskogo Severo-Vostoka [Salmonid fishes of water bodies of the European North-East]. KMK, Moscow, Russia, 346 p. (In Russian).

Solovkina, L.N., 1962. Ryby srednego i nizhnego techeniya r. Usy [Fish of the middle and lower reaches of the Usa River]. In: Zvereva, O.S. (ed.), *Ryby basseyna r. Usy i ikh kormovye resursy [Fish of the Usa River basin and their food resources].* USSR Academy of Sciences, Moscow – Leningrad, USSR, 88–135. (In Russian).

Stepanova, V.B., 2017. Pitaniye ryb v Obskoy gube Karskogo morya v podledny period [Fish feeding in the Ob Bay of the Kara Sea during the ice period]. *Vestnik rybokhozyaystvennoy nauki [Bulletin of Fisheries Science]* **4** (4 (16)), 94–100. (In Russian).

Stepanova, V.B., Stepanov, S.I., 2006. Znacheniye reliktovykh rakoobraznykh v pitanii sigovykh ryb v podledny period [The value of relict crustaceans in the diet of coregonids in the ice period]. *Vestnik ekologii, lesovedeniya i landshaftovedeniya [Bulletin of Ecology, Forestry and Landscape Science]* **6**, 142–145. (In Russian).

Sterligova, O.P., Il'mast, N.V., 2016. Dinamika populyatsii yevropeyskoy ryapushki *Coregonus albula* Syamozera (Respublika Karelia) [Population dynamics of the European vendace *Coregonus albula* in Syamozero (Republic of Karelia)]. *Sibirskiy ekologicheskiy zhurnal [Siberian Ecological Journal]* **2**, 177–183. (In Russian).

Sterligova, O.P., Pavlov, V.N., Il'mast, N.V., Pavlovsky, S.A., Komulainen, S.F., Kuchko, Ya.A. 2002. Ekosistema Syamozera (biologicheskiy rezhim, ispol'zovaniye) [Ecosystem of Syamozero (biological regime, use)]. Karelian Scientific Centre of the Russian Academy of Sciences, Petrozavodsk, Russia, 119 p. (In Russian).

Stolbunova, V.N., 2006. Zooplankton ozera Pleshcheyevo [Zooplankton of Lake Pleshcheyevo]. Nauka, Moscow, Russia, 152 p. (In Russian).

Sycheva, L.I,. Lukyanchikov, F.V., 1964. Nekotorye dannye po pitaniyu lososevidnykh ryb basseyna Khatangi [Some data on the nutrition of salmonids in the Khatanga basin]. *Sbornik kratkikh soobshcheniy i dokladov o nauchnoy rabote po biologii i pochvovedeniyu [Collection of short communications and reports on scientific work in biology and soil science].* Irkutsk State University, Irkutsk, USSR, 99–105. (In Russian).

Szypuła, J., 1965. Odżywianie się sielawy – *Coregonus albula* (L.) w Jeziorze Legińskim [Feeding of vendace – *Coregonus albula* (L.) in Legińskie Lake]. *Zeszyty naukowe Wyższej Szkoły Rolniczej w Olsztynie* **437** (20), 213–224. (In Polish).

Ustyugov, A.F., 1972. Ekologo-morfologicheskaya kharakteristika sibirskoy ryapushki *Coregonus albula sardinella* (Val.) basseyna reki Yenisey [Ecological and morphological characteristics of the Siberian vendace *Coregonus albula sardinella* (Val.) of the Yenisei River basin]. *Voprosy Ikhtiologii [Journal of Ichthyology]* **12** (5), 211–218. (In Russian).

Ustyugov, A.F. 1976. K biologii i promyslu ryapushki r. Yenisey [To biology and trade of vendace of the Yenisei River]. In: Ioganzen, B.G. (ed.), *Problemy ekologii [Problems of Ecology]* **4**, Tomsk State University, Tomsk, USSR, 149–156. (In Russian).

Vershinin, N.V., Sycheva, A.V., 1964. Pishchevye vzaimootnosheniya ryb Noril'skoy ozerno-rechnoy sistemy [Trophic relationships of fish in the Norilsk lake-river system]. In: Krasikov, S.P. (ed.), *Rybnoe khozyaystvo Vostochnoy Sibiri. Trudy Sibirskogo otdeleniya GosNIORKH [Fisheries of Eastern Siberia. Proceedings of the Siberian Branch of State Scientific Institute of Lake and River Fisheries]* **8**, Krasnoyarsk, USSR, 185–199. (In Russian).

Viljanen, M., 1983. Food and food selection of cisco (*Coregonus albula* L.) in a dysoligotrophic lake. *Hydrobiologia* **101**, 129–138. https://doi.org/10.1007/BF00008665

Wiêski, K., 2002. Feeding of vendace in Lake Miedwie (NW Poland). *Electronic Journal of Polish Agricultural Universities. Series Fisheries* **5**, 1.

Winfield, I.J., Fletcher, J.M., James, J.B., 2017. The 'reappearance' of vendace (*Coregonus albula*) in the face of multiple stressors in Bassenthwaite Lake, U.K. *Fundamental and Applied Limnology* **189** (3), 227–233. https://doi.org/10.1127/fal/2016/0799

Yukhneva, V.S., 1955. Godovoy tsikl pitaniya tazovskoy ryapushki (*Coregonus sardinella* Val.) [Annual feeding cycle of the Tazovskaya vendace (*Coregonus sardinella* Val.)]. *Zoologicheskiy zhurnal [Zoological Journal]* **34** (1), 158–161. (In Russian).

Zadelenov, V.A., Dubovskaya, O.P., Bazhina, L.V., Glushchenko, L.A., Isaeva, I.G. et al., 2017. Novye svedeniya o biote ozer zapadnoy chasti plato Putorana [New data on the biota of lakes in the western part of the Putorana Plateau]. *Zhurnal Sibirskogo Federal'nogo Universiteta. Biologiya [Journal of the Siberian Federal University. Biology]* **10** (1), 87–105. (In Russian).

Zvereva, O.S., Kuchina, E.S., Ostroumov, N.A., 1953. Ryby i rybny promysel srednego i nizhnego techeniya Pechory [Fish and fishery in the middle and lower reaches of the Pechora River]. Academy of Sciences of the USSR, Moscow–Leningrad, USSR, 230 p. (In Russian).

Zubova, E.M., Kashulin, N.A., 2019. Pitaniye siga *Coregonus lavaretus* (L.), evropeyskoy ryapushki *C. albula* i evropeyskoy koryushki *Osmerus eperlanus* v oz. Imandra [Feeding of whitefish *Coregonus lavaretus* (L.), European vendace *C. albula*, and European *smelt Osmerus eperlanus* in Lake Imandra]. *Trudy XVI Fersmanovskoy nauchnoy sessii GI KNTs RAN [Proceedings of the XVI Fersmanov's Scientific Session of the Geological Institute of Kola Scientific Centre of RAS].* Apatity, Russia, 203–207. (In Russian).

Zubova, E.M., Kashulin, N.A., Terentyev, P.M., 2020. Sovremennye biologicheskiye kharakteristiki siga *Coregonus lavaretus*, evropeyskoy ryapushki *C. albula* i evropeyskoy koryushki *Osmerus eperlanus* ozera Imandra [Modern biological characteristics of the whitefish *Coregonus lavaretus*, European vendace *C. albula,* and European smelt *Osmerus eperlanus* of Lake Imandra]. *Vestnik Permskogo universiteta. Seriya Biologiya [Perm University Bulletin. Biology Series]* **3**, 210–226. (In Russian). https://doi.org/10.17072/1994-9952-2020-3-210-226

Zuyanova, O.V., Bolotova, N.L., Zuyanov, E.A., 1994. Pitaniye ryapushki iz ozer Beloe i Vozhe [Feeding of vendace from lakes Beloe and Vozhe]. *Materialy V Vserossiyskogo soveshchaniya "Biologiya i biotekhnika razvedeniya sigovykh ryb" [Materials of the V All-Russian meeting "Biology and biotechnology of whitefish breeding"].* St. Petersburg, Russia, 67–68. (In Russian).