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Feeding of Whitefish *Coregonus lavaretus pidschian* (Coregonidae) in the Lower Reaches of the Northern Dvina River

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Abstract—Analysis was performed of the feeding of whitefish in the basin of the Northern Dvina River, including the tributary of the first order—Emtsa River and the middle course of the river, its delta part, and sites of the near-mouth offshore. It was established that, according to the pattern of feeding, whitefish is a euryphage with sufficiently wide food spectrum, including over 40 groups of food organisms at the level of classes, orders, families, and genera. The bulk of its feeding is formed by aquatic larvae of insects (mainly chironomid larvae), secondary food consists of mollusks, crustaceans, worms, and sponges. Changes in the feeding of whitefish depending on habitats, food biotopes, and difference with respect to years and seasons of the year, as well as on the age of fish, were revealed. Sufficiently high feeding intensity, as well as small changes in the feeding of whitefish in different years and at different sections of the channel indicate stable feeding conditions in the middle part of the Dvina basin. Food possibilities of the delta and the near-mouth offshore also satisfy trophic demands of the feeding school of whitefish.

Keywords: basin of the Northern Dvina River, general pattern of feeding of whitefish *Coregonus lavaretus pidschian*, euryphagy, dominant and secondary food objects, spatial, temporal, and age changes in the feeding, feeding intensity

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INTRODUCTION

It is known that feeding of fish is among the factors determining ecology, physiology, and behavior (feeding migrations) of commercial species and can serve as an indicator during elaboration of the strategy of rational use of fish stock. In the complex of fish-cultural studies, the study of feeding of fish makes it possible to give an objective estimate of the state of species within their ranges. In a practical aspect, information on specific features of feeding of commercial fish can be used during exploration of their aggregations, performance of acclimatization measures, determination of the growth rate and population dynamics, and, as a final result, of the state of their stock (Popova, 1979; Novoselov and Fefilova, 1998, 1999).

White Sea whitefish assigned to a group of anadromous Arctic Siberian whitefish (Berg, 1948; Pravdin, 1950, 1954) belongs to a subspecies of oligorakered whitefish *Coregonus lavaretus pidschian* inhabiting basins of the rivers of the Arctic Ocean (Shaposhnikova, 1974; Reshetnikov, 1980). It is widespread uniformly over the coast of the White Sea, preferring sea regions of lower salinity in the period of feeding and fresh river waters during spawning. For spawning, it enters many White Sea rivers (Kovda, Keret, Kandalaksha, Kem, Onega, Northern Dvina, and others) and ascends them to sites of natural spawning, sometimes to considerable distances (Altukhov et al., 1958; Novikov, 1964).

The range of the Northern Dvina whitefish embraces the entire basin of the Northern Dvina River, including its upper and middle parts and tributaries, as well as delta and the near-mouth offshore in the adjacent zone of Dvina Inlet. In numerous channels of the delta and in shallow waters of the near-mouth offshore, whitefish feeds up to sexual maturation and winters, spawners return here after spawning, and juveniles that migrated down from the spawning grounds feed here. They stay in the delta zone throughout the year, fish of older age groups distribute for summer feeding more widely near islands and along coasts of the bays of Dvina Inlet (Novoselov, 2000).

Since the end of the 1950s, Northern Dvina basin began to experience a strong anthropogenic load, which led to its pollution with oil products, phenols, organic substances, iron ions, and other components. A stable tendency appeared for an increase in river waters of biogenic elements, suspended substances, and general water mineralization. In the zone of large industrial complexes of lumber and woodworking branch of industry, MAC, according to main pollutant components, turned out to be multifold exceeded, as a result of which water state ceased to meet the requirements for fish-cultural and sanitary-domestic kinds of water use (Manakov, 1988; Yurovskaya, 1988).

Incessant pollution of Dvina waters was accompanied by a total decrease in the numbers of Salmoniformes in the basin, including Northern Dvina whitefish (Koz'min, 1988; Novoselov and Koz'min, 1991). If more than 40 t of whitefish was obtained in the period of 1954 to 1959 only at the near-mouth offshore, the average annual volume of its catch declined to 30 t in 1960–1962, and approximately 10 t of whitefish were caught in the period of 1965 to 1980 in the entire Northern Dvina basin, i.e., three times less (Novikov, 1964; Elsukova, 1981). Presently, there is no specialized whitefish fishery in the Northern Dvina River—fish are trapped by fishing gear only as an additional catch in all types of fishery and is used in mass by the local population as an object of amateur fishery in the winter subglacial period (Novoselov and Bushueva, 1996; Novoselov, 1998).

Note that scientific literature contains rather fragmentary information dedicated to both general pattern of feeding of Northern Dvina whitefish (Epishin and Elsukova, 1990; Novoselov and Fefilova, 1999; Fadeeva and Novoselov, 2002) and to its more private aspects (Novoselov and Fefilova, 1998; Borkichev et al., 1999; Novoselov, 1999a, 1999b). At the same time, a need arose for an all-round analysis and generalization of all available data on the state of Northern Dvina whitefish to restore numbers, formation of the commercial stock, and elaboration of ways for its rational use. One aspects of such analysis is assessment of the spatial-temporal, seasonal, and age dynamics of feeding of Northern Dvina whitefish at feeding sites since conditions and efficiency of feeding are among main factors forming the commercial numbers of commercially demanded fish species.

MATERIALS AND METHODS

The study of feeding of whitefish was carried out during performance of seasonal surveys in the channel and delta parts of the Northern Dvina River and in sections of the near-mouth offshore (Sukhoe More Inlet and water area of Mulyug and Kumbysh islands) (Fig. 1), as well as in the channel part of the river (at sections of the village of Kargovino and near Siiskii Island), and at one of lower tributaries of the first order—the Emtsa River. Altogether, 365 gastrointestinal tracts of the whitefish were collected and processed.

The collection, as well as laboratory and statistical material processing, were performed according to the Manual on Feeding and Food Interactions of Fishes in Natural Conditions (*Metodicheskoe posobie*..., 1979). Feeding intensity was calculated as total indices of gastrointestinal tracts fullness and expressed in decimiles and percentage for each kind of food from the total amount. Compared to tables in the text, data are rounded off to 1 or 0.1% according to the rule of two significant figures (Tereshchenko and Reshetnikov, 2000). Analysis of the qualitative and quantitative composition of the food of whitefish was performed separately for different sites of the lower part of the Northern Dvina basin, seasons, years, and age groups of fish. Seasonal and age changes in the feeding were expressed as diagrams performed using standard programs.

RESULTS

General Pattern of Feeding of Whitefish

From published data (Reshetnikov, 1980), we know that northern water bodies are characterized by comparatively poor and rather variable food resources that do not provide food requirements of fish dwelling in water bodies of northern latitudes and, of Coregonidae, in particular.

Analysis of the contents of gastrointestinal tracts of whitefish in the lower part of the Northern Dvina basin (at different sections, in different seasons and years) indicates eurybiontic pattern of its feeding. Its food spectrum in the study period was sufficiently wide and consisted of individuals of six taxa of higher order at a level of types. It included over 30 groups of food organisms at the level of classes, orders, families, genera, and species. In the food composition of the Northern Dvina whitefish, Coelenterata, moss animacules, worms, mollusks, arthropods, that included classes of Arachnida, Crustacea, and insects, remains of fish and their eggs, as well vegetation remains and detritus were recorded (Table 1).

In the quantitative respect, during analysis of the combined sample for all analyzed sites, more than a half of the feed of the Northern Dvina whitefish (60%) consisted of insects. They were represented by both larvae that enter into the composition of benthic communities and by adult forms (imago) after their metamorphosis consumed by the whitefish both in the water column and from its surface. Among larval forms, representatives of the order Diptera (55% on average) that included larval chironomids (54%), gadflies, biting midges, and limoniids dominated. Representatives of the orders Ephemeroptera, Trichoptera, and Copeoptera, as well as of Megaloptera and bugs, were less important in the feeding of whitefish.

A noticeable role in the feeding of whitefish was played by mollusks (17% by weight) that included two groups: Bivalvia (12%) and Gastropoda (4%). Among the former, representatives of the genus *Macoma* dominated, and those of the genus *Limnea* dominated among the latter. Vegetation remains were recorded in gastrointestinal tracts of whitefish in a slightly smaller amount. The importance of crustaceans in the feeding of whitefish was relatively small (6%); whitefish consumed juvenile fish and their eggs (3%) and Coelenter-

Fig. 1. Scheme of location of sites of material collection (◆) on feeding of the Northern Dvina whitefish in the lower part of the Northern Dvina River and premouth offshore.

ata at freshened marine biotopes, worms, and detritus in still smaller amounts. The total index of fullness of gastrointestinal tracts (TIF) was relatively low, averaging 94‰ for all samples. Analysis of contents of gastrointestinal tracts of whitefish demonstrated that the intensity and pattern of feeding of whitefish considerably changed at different sections of the lower part of the Dvina basin (Table 1), varying depending on the sampling site, season of the year, and the age of feeding fish (spatial, seasonal, and age variation of feeding).

Feeding of Whitefish in the Lower Tributary of the First Order—the Emtsa River

Food spectrum. According to the generalized sample, the total food spectrum of whitefish in the Emtsa River included representatives of two taxa of food objects at the level of types—mollusks and arthropods, as well as fish remains and vegetable food components. The importance of insects in the feeding of whitefish had a pronounced dominant pattern, their amount comprised 84% of the weight of all food boluses. In the diet of the whitefish, insects were represented by four groups of food objects. Among them, representatives of the order Diptera (81%), which included larval chironomids (75%), biting midges (4%), gadflies (1.2%), and limoniids (1.0%), dominated. Aquatic larvae of orders Trichoptera, Ephemeroptera, and Megaloptera were recorded in an inconsiderable amount (Table 1).

Among mollusks that comprised 12.3% of the weight of food boluses, gastropods that belonged to the

Table 1. General pattern of feeding of whitefish in the lower part of the Northern Dvina basin, % by weight

Food components	Emtsa River—tributary of the first order	Channel part	Delta	Near-mouth offshore		Common spectrum at all sites
				desalinated Sukhoe More Inlet	marine water area of Mudyug Island	
1. Zooplanktonic organisms	**–**	**–**	**–**	**0.5**	**0.2**	**0.5**
Sciphous medusas	–	–	–	–	0.1	<0.1
Copepoda	–	–	–	0.5	0.1	0.4
2. Benthic organisms						
Hydroid polyps	–	–	–	–	16.6	1.4
Moss animalcules	–	0.1	–	–	–	<0.1
Nematodes	–	–	0.1	0.1	–	<0.1
Oligochaetes	–	–	0.6	–	–	0.1
Polychaetes	–	–	–	–	10.1	0.9
Bivalves:	**2.7**	**–**	**5.3**	**14.6**	**35.8**	**12.6**
genus *Sphaerium*	0.8	–	–	0.2	–	0.2
genus *Pisidium*	1.9	–	5.3	3.8	–	3.2
genus *Mya*	–	–	–	0.4	–	0.2
genus *Macoma*	–	–	–	10.2	35.6	8.9
genus *Mytilus*	–	–	–	–	0.2	<0.1
Gastropoda:	**9.6**	**–**	**7.0**	**2.7**	**1.8**	**4.0**
genus *Limnae*	7.2	–	0.6	2.7	1.8	2.7
genus *Valvata*	2.4	–	0.1	–	–	0.3
genus *Planorbis*	–	–	0.1	–	–	0.1
genus *Physa*	–	–	6.2	–	–	0.9
Arachnoidea:	**–**	**0.1**	**–**	**–**	**–**	**–**
Crustacea:	**0.7**	–	**10.0**	**4.8**	**13.3**	**5.5**
Amphipoda	0.3	–	10.0	4.3	8.3	4.7
Cumacea	–	–	–	–	0.4	<0.1
Ostracoda	0.4	–	–	0.1	–	0.1
Mysidacea	–	–	–	0.4	4.6	0.6
Insects larvae:	**84.3**	**70.1**	**72.6**	**53.3**	**4.1**	**57.0**
Chironomidae	74.7	58.3	66.3	52.1	4.1	53.6
Heleidae (biting midges)	3.8	–	0.2	–	–	0.5
Limoniidae (limoniids)	1.0	–	0.3	–	–	0.2
Tabanidae (gadflies)	1.2	–	3.4	0.2	–	0.8
Trichoptera (caddis flies)	1.8	5.3	0.8	0.1	–	0.5
Ephemeroptera (mayflies)	1.7	5.5	0.2	–	–	0.6
Megaloptera (Megaloptera)	0.1	–	1.4	–	–	0.2
Coleoptera (water beetles imago)	–	0.1	–	0.9	–	0.5
Hemiptera (water bugs imago)	–	0.9	–	–	–	0.1
3. The remaining organisms	**2.7**	**29.7**	**4.4**	**24.0**	**18.1**	**17.8**
Fish	0.1	–	–	5.2	–	3.0
Fish eggs	–	–	–	1.3	–	1.0
Aerial insects	–	29.6	0.2	–	–	2.7
Vegetation	2.6	0.1	4.2	17.5	6.4	10.1
Detritus	–	–	–	–	11.7	1.0
Total:	**100.0**	**100.0**	**100.0**	**100.0**	**100.0**	**100.0**
Average index of fullness, ‰	71.7	166.8	71.5	118.4	28.1	94.0
Number of fish, ind.	46	24	55	209	31	365

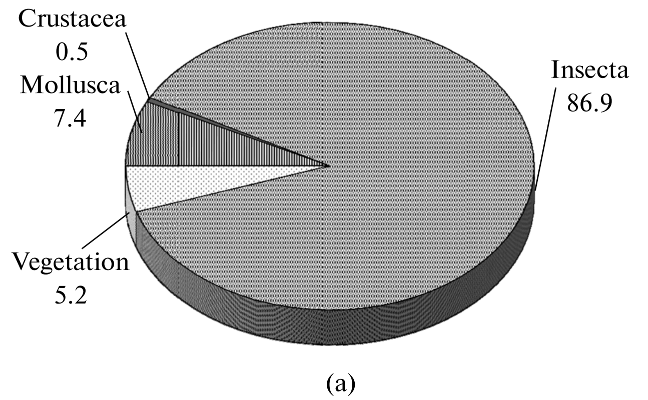
genera *Limnea* and *Valvata* dominated (9.6%). Of Bivalvia, mollusks of the genera *Pisidium* and *Sphaerium* were found in gastrointestinal tracts of whitefish. In a considerably smaller amount (2.6%), plant residues were recorded in the food spectrum. The importance of crustaceans in the feeding of whitefish in the Emtsa River was very small, fish remains were recorded in single gastrointestinal tracts. The total index of fullness of gastrointestinal tracts of whitefish in the Emtsa River was low and comprised approximately 72‰.

Annual changes in feeding. Analysis of the collected material demonstrated that the feeding of whitefish in the Emtsa River in the prevernal period of two compared years (1996 and 1997) did not differ considerably. In the samples of both years, the food spectrum of whitefish included the same taxa of mollusks, crustaceans, insects, and vegetation. In 1997, in gastrointestinal tracts of whitefish, fish remains were recorded, which was not recorded in 1996.

In March 1996, the bulk of its feeding was formed by larval insects (87%) represented by Diptera (84% by weight) and Trichoptera (3%) (Fig. 2). Among Diptera, larval chironomids dominated (76% by weight), larvae of biting midges, gadflies, and limoniids played a considerably smaller role. In the feeding of whitefish, mollusks (7.4%) and vegetable food remains (5.2%) had approximately equal importance. Mollusks were represented by mussels of the genus *Pisidium* and gastropods of the genus *Valvata*. Of Crustacea, in the food spectrum of whitefish, representatives of the order Ostracoda were present in very limited amounts. The average index of fullness of gastrointestinal tracts in 1996 was 37‰.

In March 1997, whitefish fed mainly on larval insects (82%) that were represented more widely in a species respect. Besides dominating Diptera (78%) and Trichoptera, larvae of Ephemeroptera, Megaloptera, and Plecoptera were recorded in the food bolus of whitefish. Among Diptera, larval chironomids also prevailed (73%), and representatives of the families of mayflies, alder and snake flies, and stone flies were present as secondary and accidental food. The consumption of mollusks was slightly higher in species and quantitative respect than in 1996. The total amount in food spectra of mollusks increased to 16% by weight; bivalves were represented by the genera *Pisidium* and *Sphaerium*, and gastropods were represented by the genera *Limnea* and *Valvata*. The importance of crustaceans, vegetation, and fish was also small (Fig. 1). The average total index of fullness of gastrointestinal tracts in March 1997 increased to 100‰.

Age changes in feeding. Since food composition of whitefish in the Emtsa River in the considered years did not differ considerably, we used a generalized sample that included individuals of five groups at an age of 2+ to 6+ years during analysis of age changes in the feeding.



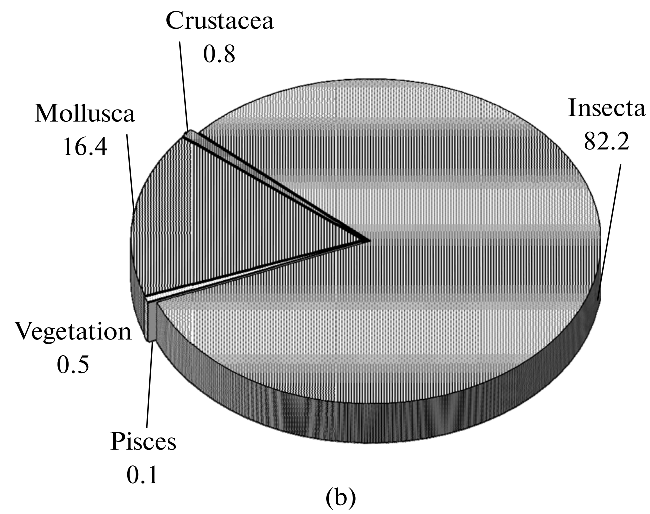


Fig. 2. Food composition of whitefish in the Emtsa River—tributary of the first order of the Northern Dvina in (a) 1996 and (b) 1997, %.

Food spectrum of whitefish at **an age of 2+** included larvae of insects (88%), mollusks (9%), crustaceans (0.3%), and vegetable residues (2.5% by weight). Among insects, larvae of Diptera had dominant importance (86%), and larvae of mayflies and caddis flies played an insignificant role in feeding. Of Diptera, larvae of chironomids, biting midges, limoniids, and gadflies were found in gastrointestinal tracts of whitefish. Mollusks were represented by gastropods of the genus *Limnea* and bivalves of the genera *Sphaerium* and *Pisidium*, while crustaceans were represented by representatives of the orders Ostracoda and Amphipoda (Fig. 3).

The total food spectrum of whitefish at **an age of 3+** remained practically constant and also included larval insects (89.5%), mollusks (9.9), crustaceans (0.5%), and vegetable residues (0.1% by weight). Among insects, larvae of Diptera had dominant importance (85%), larvae of Ephemeroptera and Trichoptera played an insignificant role in feeding. Diptera were represented by larval chironomids, biting midges, and limoniids. Among gastropods that were a secondary

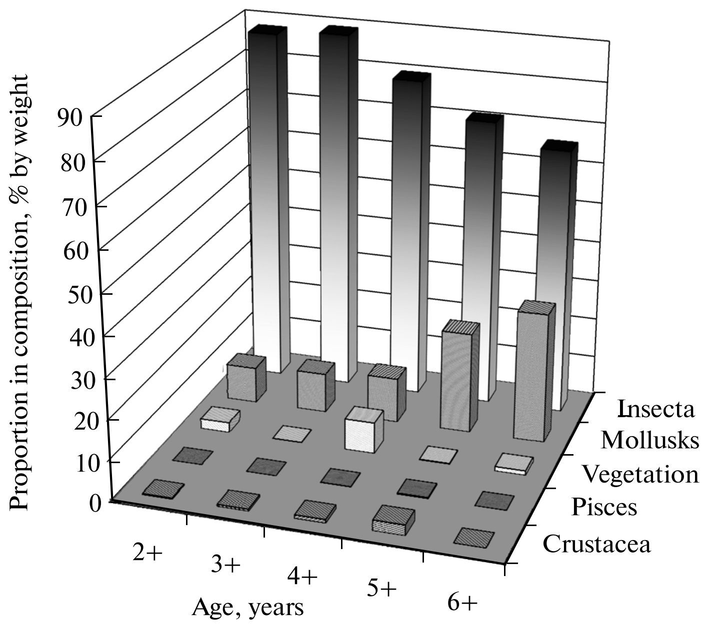


Fig. 3. Age changes in feeding of whitefish in the Emtsa River—tributary of the first order of the Northern Dvina.

food, representatives of the genera *Limnea* and *Valvata* were recorded; among bivalves representatives of the genera *Sphaerium* and *Pisidium* were recorded. Of crustaceans, representatives of the order Ostracoda were recorded in small amounts.

Feeding of whitefish at **the age of 4+** was represented by the same food objects. At the same time, the amount of larval insects in gastrointestinal tracts slightly decreased to 80.0% by weight; among them, the consumption of Diptera (75%) represented mainly by larval chironomids decreased. On the other hand, the role of larval biting midges and gadflies increased. At the former level in gastrointestinal tracts, larval limoniids, caddis flies, and mayflies were recorded, and larval stone flies appeared in insignificant amounts. The importance of mollusks in feeding slightly increased (11% by weight), and the amount of gastropods (until 10.9%) represented as before by the genera *Limnea* and *Valvata* increased. Vegetation was also recorded in gastrointestinal tracts of whitefish, and digested fish remains appeared.

The food spectrum of whitefish at **an age of 5+** remained without changes, while the amount of larval insects in gastrointestinal tracts continued to decline and comprised approximately 72% by weight. Among them, consumption of Diptera that were as before represented mainly by larval chironomids (68%) decreased (to 69%), and the role of larval biting midges and limoniids also slightly decreased. In feeding of six-year-old individuals, no larvae of gadflies, stone flies, and mayflies were recorded. Larvae of caddis flies were recorded at the former level, larvae of alder and snake flies were first recorded in feeding. In the feeding of whitefish, the role of mollusks continued to increase (up to 25%), the quantity of gastropods represented as before by the genera *Limnea* and *Valvata* increased (up to 14%). The amount of bivalves, among which the genera *Spherium* and *Pisidium* were represented in equal amounts, also increased (up to 11%). The role of crustaceans, order Amphipoda and digested fish remains, increased insignificantly up to 2.6 and 0.3%, respectively. Vegetable food was consumed weakly by whitefish at an age of 5+.

In whitefish at **an age of 6+**, no crustaceans and remains of fish food were recorded in gastrointestinal tracts. The amount of larval insects declined to 66% by weight, and species diversity of the consumed organisms also decreased. Larvae of stone flies, alder and snake flies, mayflies, and gadflies dropped out from the food spectrum. Diptera represented mainly by larval chironomids dominated, and insects of the families Heleidae and Limoniidae were recorded singly. Almost one third of the contents of food boluses began to be occupied by mollusks, among which bivalves were represented exclusively by the genus *Pisidium* and among gastropods represented by the genus *Valvata* (Fig. 3).

Analysis of average values of TIF of whitefish indicates moderate intensity of the feeding of whitefish in the prevernal period (March). Its average value over the entire sample comprised approximately 72‰, and maximum index of TIF was in whitefish at an age of 2+ years (87‰); then the intensity of its feeding decreased and comprised 54‰ in whitefish at an age of 6+ years with the growth of whitefish.

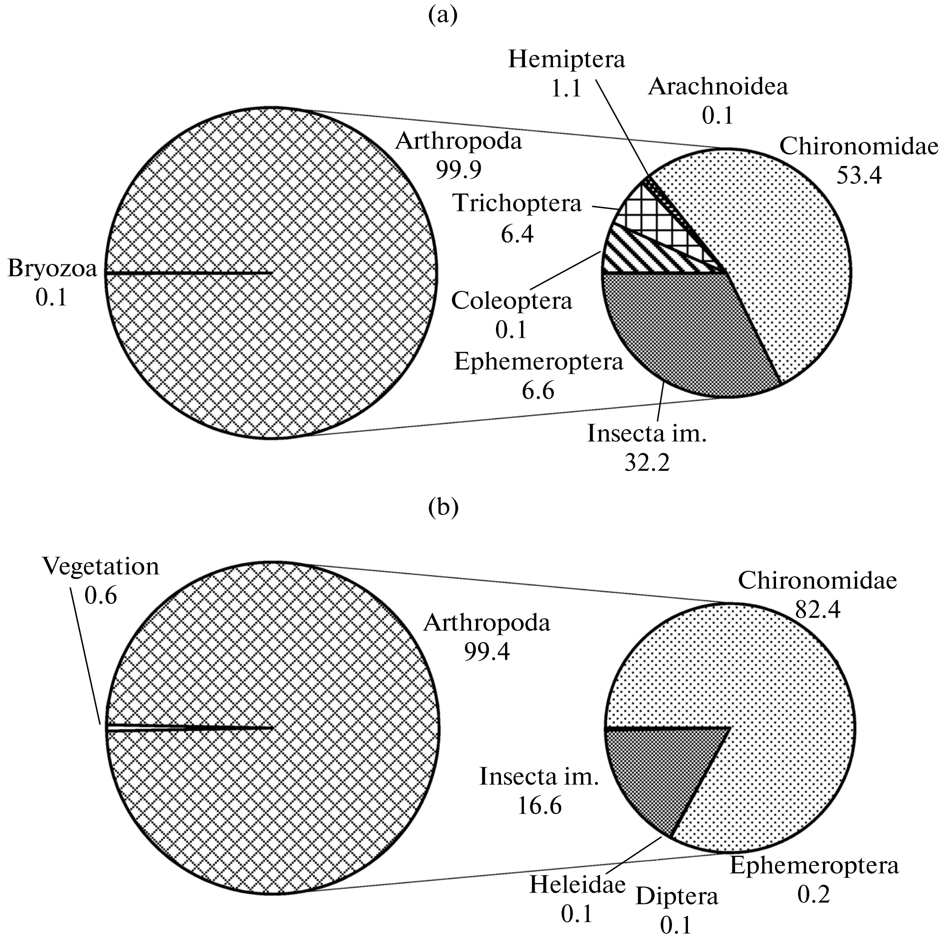


Fig. 4. Food composition of whitefish in the channel part of the lower reaches of the Northern Dvina River, %: (a) Siiskii Island (216 km from the mouth) and (b) village of Korgovina (300 km from the mouth).

Feeding of Whitefish in the Channel Part of the Lower Reaches of the Northern Dvina River

To assess feeding of whitefish in the lower reaches of the Northern Dvina River, fish composition of whitefish was analyzed at two sites: near village of Kargovina (the 300th km from the river mouth) and near Siiskii Island (the 216th km of the river from the mouth).

General pattern of feeding. According to results of laboratory processing of gastrointestinal tracts of whitefish caught at the considered sites, the total food spectrum included three groups of food objects at the level of macrotaxa: moss animalcules, arthropods, and vegetable food components. The importance of insects in the feeding of whitefish had a pronounced dominating pattern, and their amount comprised 99.7% of the weight of all food boluses. The food diet of whitefish was represented by five groups of food objects among which Diptera (larval chironomids, as well as imago) dominated. Larvae of mayflies, caddis flies, and water bugs were recorded in a small amount. Remains of higher aquatic vegetation were found in single gastrointestinal tracts (Table 1). The total index of fullness of gastrointestinal tracts of whitefish in the middle reaches of the Northern Dvina River in September 1997 comprised approximately 160‰.

Spatial changes in feeding. The food spectrum of whitefish caught near Siiskii Island included dominant arthropods and biting midges recorded only in single gastrointestinal tracts. The main portion of food boluses (99%) consisted of insects among which six groups of food objects that had different importance in the feeding of whitefish were distinguished. The bulk of its food was formed by Diptera represented exclusively by larval chironomids (53%) and by adult forms of insects (32%). Larvae of mayflies and caddis flies occurred in gastrointestinal tracts of whitefish in a considerably smaller amount; the proportion of larval beetles and bugs was insignificant (Fig. 4). The average total index of fullness of gastrointestinal tracts of whitefish near Siiskii Island was 166‰.

At the site near the village of Kargovina, the food composition of whitefish was represented only by insects (99%), and remains of aquatic vegetation accounted for the remaining part. Insects in gas-

Table 2. Age changes in the feeding of whitefish in the channel part of the lower reaches of the Northern Dvina River, % by weight

Food components	Age group, years					Total
	1+	2+	3+	4+	6+	
1. Benthic organisms	**72.7**	**72.5**	**99.2**	**51.2**	**94.5**	**70.3**
Bryozoa (moss animacules)	0.3	–	–	–	–	0.1
Arachnoidea (Arachnida)	–	0.1	–	–	–	0.1
Ephemeroptera (mayfles)	1.4	6.3	–	–	–	5.5
Trichoptera (caddis flies)	19.9	0.2	–	2.2	–	5.3
Chironomidae (chironomids)	47.7	65.6	97.1	48.5	94.2	58.3
Heleidae (biting midges)	–	0.1	2.1	0.5	–	0.1
Coleoptera (aquatic insects)	–	0.1	–	–	0.3	0.1
Hemiptera (aquatic bugs)	3.4	0.1	–	–	–	0.8
2. The remaining organisms:	**27.3**	**27.5**	**0.8**	**48.8**	**5.5**	**29.7**
Aerial insects	27.3	27.0	0.8	48.8	5.5	29.6
Vegetation	–	0.5	–	–	–	0.1
Total:	**100.0**	**100.0**	**100.0**	**100.0**	**100.0**	**100.0**
Average index of fullness, ‰	87.1	192.5	246.8	160.9	180.7	168.6
Number of fish. ind.	6	14	1	2	1	24

trointestinal tracts were represented by dominant larval Diptera (82%) and imago (17%). Among Diptera, larval chironomids comprised the dominant part, larvae of biting midges and mayflies were recorded in a very small amount (Fig. 4). The total average index of stomach fullness of whitefish at the site of the village of Kargovina comprised 170‰.

Age changes. To analyze age changes in the feeding of whitefish from the channel part of the lower reaches of the Northern Dvina River, a generalized sample was taken from both analyzed sites. The sample consisted of individuals of five age groups from 1+ to 6+ years, among which no fish at an age of 5+ years were recorded.

The food spectrum of juvenile whitefish at **an age of 1+** included only arthropods (99.7%) and moss animalcules (0.3% by weight) in the study period. Among insects, larvae of Diptera represented exclusively by larval chironomids (48%), caddis flies (20%), and imago of insects (27%) had dominant importance. Bugs and larvae of mayfles played a small role in the feeding of whitefish (Table 2).

The total spectrum of feeding of whitefish at **an age of 2+** was distinguished by high diversity. Among arthropods, preference was given to insects that comprised 99.7% by weight; vegetable residues were recorded in single gastrointestinal tracts. Among insects, larvae of Diptera (66%) represented mainly by larval chironomids, as well as adult forms of insects (27%), had considerable importance. Larvae of mayflies and caddis flies were recorded in an insignificant amount. Larvae of biting midges, bugs, spiders, and beetles occurred only in single gastrointestinal tracts of whitefish.

Whitefish at **an age of 3+** consumed only insects among which larvae of Diptera that comprised 97% of the weight of food bolus dominated numerically. In the weight respect, larval chironomids dominated (97%), larval biting midges accounted for the remaining part. Adult forms of insects also played no significant role in the feeding of whitefish of this age group (Table 2).

The food spectrum of the feeding of whitefish at **an age of 4+** also consisted only of larval insects, among which the proportion of larval Diptera and adult forms of insects was approximately equal (49% each). Among Diptera, larval chironomids considerably dominated over larval biting midges. Larval caddis flies were recorded in gastrointestinal tracts of whitefish in an inconsiderable amount.

Whitefish at **an age of 6+** fed exclusively on larvae, among which also Diptera represented only by larval chironomids (94% by weight) dominated. Adult insects at an imago stage and beetles were found in the gastrointestinal tract in a small amount.

Analysis of values of average total indices of stomach fullness of whitefish indicates sufficiently high feeding intensity of whitefish in the middle current of the Northern Dvina River in the autumn period. Its average value over the entire sample comprised approximately 174‰, and minimal index was in whitefish aged 1+ years (87‰). Fish fed most intensively at an age of 2+ and 3+ (182 and 247‰, respectively). In individuals aged 4+ and 6+, the total index

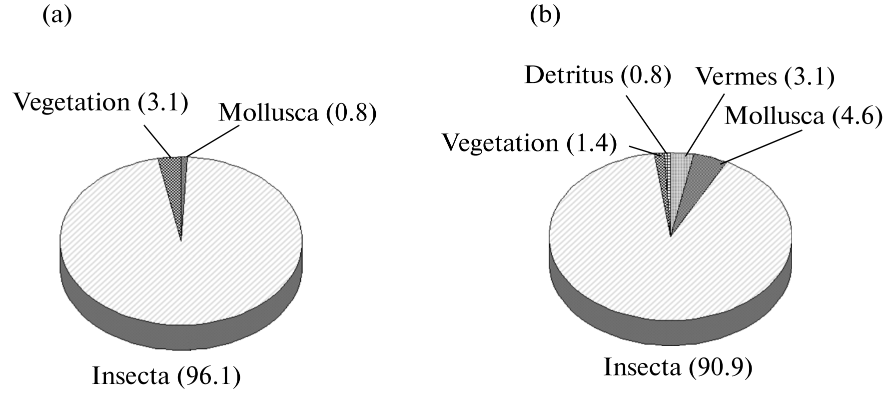


Fig. 5. Food composition of whitefish in the delta part of the Northern Dvina River at channel flow biotopes, %: (a) Maimaks channel and (b) Kuznechikha channel.

of fullness of gastrointestinal tracts was close to the average value (Table 2).

Feeding of Whitefish in the Delta Part of the Northern Dvina River

During study of the feeding of whitefish in the delta part of the Northern Dvina River, we took samples at different biotopes: both in arms of the delta proper (in Maimaks and Kuznechikha channels) and in its salinized part at Archangelsk and Chizovskii biotopes of the lower delta of *limnetic type* with daily impact of tidal currents). As a whole, according to the delta part, the food spectrum of whitefish was represented by larval insects (73%), mollusks (12%), crustaceans (10%), worms (approximately 1%), and vegetation (4%) (Table 1). The numeric ratio of concrete groups of food objects considerably varied depending on the studied biotopes.

At sites of *channel flow type* (Maimaks and Kuznechikha channels), dominant objects in the feeding of whitefish were larval crustaceans that comprised 96 and 91%, respectively, in the Maimaks and Kuznechikha channels. Diptera represented mainly by larval chironomids dominated among them at both sites; larvae of biting midges and limoniids in both channels were recorded in an inconsiderable amount. Larvae of gadflies lacking in the feeding of whitefish in the Maimaks channel and in the Kuznechikha channel were found in a considerable amount, averaging approximately 14%. Representatives of the order Trichoptera played no considerable role in the feeding of whitefish either in Maimaks or Kuznechikha (Fig. 5).

Of secondary objects, no worms were recorded in the Maimaks channel; in the Kuznechikha channel, they comprised 3% by weight and were represented by oligochaetes and nematodes. Mollusk consumption by whitefish was also inconsiderable. In the Maimaks channel, their proportion by weight was 0.8% (gastropods), and that in the Kuznechikha channel was 4.6% by weight (bivalves). The amount of consumed vegetation was approximately equal and comprised 1–3%. The average index of fullness of gastrointestinal tracts in Maimaks (71‰) was slightly higher than in Kuznechikha (50‰).

At biotopes of the lower delta with the impact of tidal currents (Arkhangelsk and Chizhovskoe), the use by whitefish of different food objects turned out to be more uniform, without drastic domination of any group (Fig. 6). The importance of larval *insects* in the feeding of whitefish here was slightly lower compared to that in channels and comprised 53% at Archangelsk biotopes and still less at Chizhovskie biotopes—9%. Among them, bivalves were dominant as before: they were represented by larval chironomids (51.1%) and biting midges (0.1%) at Archangelsk biotopes and by larval chironomids (1.1%) and limoniids (0.6% by weight) at Chizhovskie biotopes. Besides them, larval caddis flies represented by the family Agraulea, larval mayflies, and adult insects were recorded in small amounts in the food of whitefish at Archangelsk biotopes. At Chizhovskie channel flow biotopes, caddis flies included representatives of the families Brachicentrus and Polycentropus; order Megaloptera comprised 7% by weight of the entire food bolus.

Mollusks had approximately equal importance in the feeding of whitefish in the lower delta comprising 37% by weight at Archangelsk biotopes and 34% at Chizovskie biotopes. The qualitative composition of the consumed mollusks considerably differed. At Archangelsk biotopes, dominant were bivalves represented mainly by mollusks from the genus *Pisidium*; at Chizovskie biotopes, gastropods were dominant, among which representatives of the genus *Physa* dominated. The importance of vegetation and detritus in the feeding of whitefish at both considered sites was small. The average index of fullness of gastrointestinal tracts at Arkhangelsk biotopes was considerably lower (28‰) than at Chizhovskie biotopes (122‰).

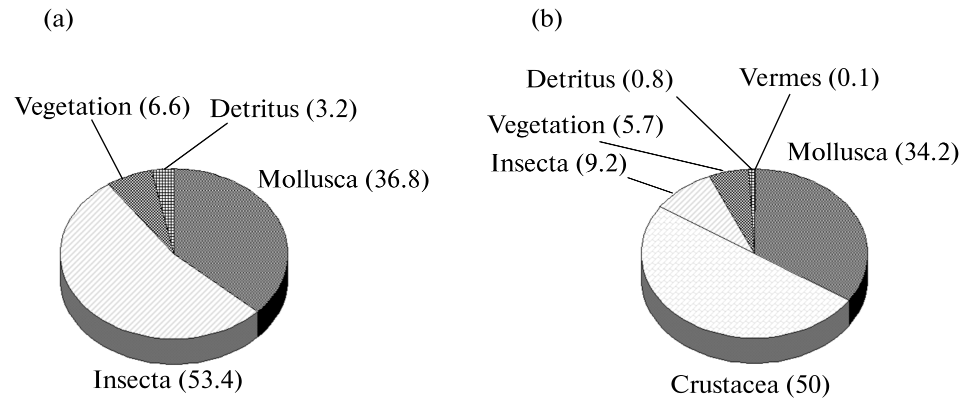


Fig. 6. Food composition of whitefish in the delta part of the Northern Dvina River at biotopes of the lower delta, %: (a) Arkhangelskii and (b) Chizhovskii.

Feeding of Whitefish at Sites of the Near-Mouth Offshore (Sukhoe More Inlet)

Sukhoe More Inlet is located at the near-mouth offshore of the Northern Dvina River between Mudyuzhskii Island and the river bank (Fig. 1). It is extended from the south (the northern extremity of Murovoi Island) to the north (up to the cape foot limiting Novaya Promoina Strait). The total extent of the inlet is 27.8 km; average width is 4.0 km at maximum width of 5.5 km and minimal width of 0.9 km. The area of the water area of the Sukhoe More is 99.0 km^2, including the zone dried during tide off. The distinctive feature of the bay is its shallowness—dominant depths at low tide during ebb do not exceed 0.5–0.8 m. Deeper sites, up to 3–4 m, are at the alignment of Sennaya Cape and in the Novaya Promoina Strait. Depths exceeding a 5-m mark are in the strait between Lebedin and Mudyuzhskii islands, as well as in the Zheleznye Vorota Strait with an increase in depth up to 8–9 m at adjoining sites (Novoselov and Bushueva, 1996).

The bulk of feeding of whitefish in Sukhoe More Inlet was formed by insects (55%) and mollusks (17%) (Table 1). The former were represented mainly by aquatic larval chironomids and in an inconsiderable amount by larvae of beetles, caddis flies, and gadflies. Among mollusks bivalves dominated (14.6%) in the feeding of whitefish; they included representatives of the genera *Macoma*, *Pisidium*, and *Mya*. Of gastropods, mollusks of the genus *Limnae* were recorded in an inconsiderable amount. Crustaceans and sometimes eggs of fish served as secondary food, nematodes were found singly. Sukhoe More Inlet is a shallow water body of a limnetic type with sufficiently high dynamics of aquatic masses as a result of wind mixing and tidal phenomena. Therefore, in the gastrointestinal tracts of whitefish, remains of aquatic vegetation were present in sufficient amount. It is more likely that vegetation is swallowed by fish accidentally at collection of invertebrate animals.

Seasonal changes in the feeding of whitefish. It is known that seasonal changes in the feeding of fish are pronounced in the shift of dominant food objects in a temporal aspect. Analysis of these changes allows one to assess the direction and intensity of food migrations of valuable commercial species and promotes their rational use (Novoselov, 1999a).

In the winter subglacial period (December–April), the pattern of feeding of whitefish in the Sukhoe More was characterized by sufficiently wide diversity; its food spectrum included worms, mollusks, crustaceans, insects, and aquatic vegetation. About a half of the contents of gastrointestinal tracts of whitefish was accounted for by mollusks (45% by weight), and the proportion in feeding of crustaceans (18%), larval insects (15%), and vegetation (21%) was approximately similar (Table 3). The low feeding intensity (average total index of fullness of gastrointestinal tracts comprised 61‰) is related most probably to a decreased metabolism in the period of minimal biological activity in the subglacial period (period of ecosystem stagnation). In different months of the winter season, both total feeding intensity of whitefish and priority of use by them of different food kinds changed (Novoselov and Fefilova, 1998).

In **December**, the food spectrum of whitefish consisted almost entirely of mollusks that dominated in weight respect (98%) and were found almost in half of all gastrointestinal tracts (Fig. 7a). Among them, bivalves played a dominant role in the feeding (96%), and only a small proportion (approximately 2%) was accounted for by gastropods. Of bivalves, *Macoma* dominated, and representatives of the genus *Mya* were in a considerably smaller amount. The proportion of vegetable residues was also insignificant. The role of crustaceans, among which gammarids prevailed, that comprised only 0.5% by weight turned out to be still smaller. Aquatic larval insects were recorded singly. The total index of fullness of gastrointestinal tracts was sufficiently high (at the expense of domination of mollusks) and comprised 102.1‰.

Table 3. Seasonal changes in the feeding of whitefish in Sukhoe More Inlet in the period from December to November, % by weight

Food components	Periods of the year			Total
	subglacial	of open water		
		spring (May–June)	autumn (September–October)	
1. Zooplanktonic organisms	**–**	**0.4**	**0.3**	**0.4**
Copepoda	–	0.4	0.3	0.4
2. Benthic organisms	**78.8**	**60.6**	**88.5**	**66.9**
Worms (Nematoda)	0.4	–	–	–
Bivalvia:				
genus *Mya*	2.5	–	–	–
genus *Macoma*	41.6	6.8	–	5.3
genus *Sphaerium*	–	0.3	–	0.2
Gastropoda:				
genus *Limnae*	1.0	2.9	0.2	2.2
Amphipoda	18.5	0.4	1.9	0.7
Mysidacea	–	0.1	–	0.1
Ostracoda	–	0.4	–	0.3
Insects larvae (Insecta)				
Trichoptera (caddis flies)	0.1	0.5	0.1	0.4
Chironomidae (chironomids)	13.3	49.2	80.4	56.3
Heleidae (biting midges)	0.1	–	–	–
Limoniidae (limoniids)	–	–	0.5	0.2
Tabanidae (gadflies)	1.1	–	–	–
Coleoptera (aquatic beetles)	0.2	–	5.4	1.2
3. The remaining organisms:	**21.2**	**39.0**	**11.2**	**32.7**
Fish eggs	–	10.1	–	7.8
Aerial insects	–	0.5	6.3	1.8
Vegetation	21.2	28.4	4.9	23.1
Total:	**100.0**	**100.0**	**100.0**	**100.0**
Average index of fullness, ‰	60.9	177.6	96.8	159.2
Number of fish, ind.	35	44	13	57

In **January**, both by occurrence (100%) and by weight (67%), remains of higher aquatic vegetation dominated in the composition of food spectrum. Of animals, crustaceans (16%) and insects (15%) had equal importance in weight respect (Fig. 7b). Crustaceans were represented only by gammarids and insects were represented by Diptera, among which only larval chironomids were recorded. The remaining components in January had no considerable importance in the feeding of whitefish. Worms in total comprised approximately 2% by weight; their main part was represented by oligochaetes, and only a small part was represented by nematodes. The role of mollusks whose shell remains were recorded only in single gastrointestinal tracts of whitefish was very inconsiderable. The total index of fullness in January was 7.4‰.

In **February**, the total spectrum of feeding of whitefish narrowed to three groups of food organisms because of dropping out from it of worms and mollusks. As for the quantitative respect, the main food objects remained the same as before (vegetation, crustaceans, and insects); however, their importance changed considerably (Fig. 7c). The proportion of vegetation dominant in January declined from 67 to 13%. At the same time, in the feeding of whitefish, the role of crustaceans represented as before exclusively by gammarids considerably increased, their proportion increased from 16 to 65%. The importance of larval insects also slightly increased (from 15 to 22% by

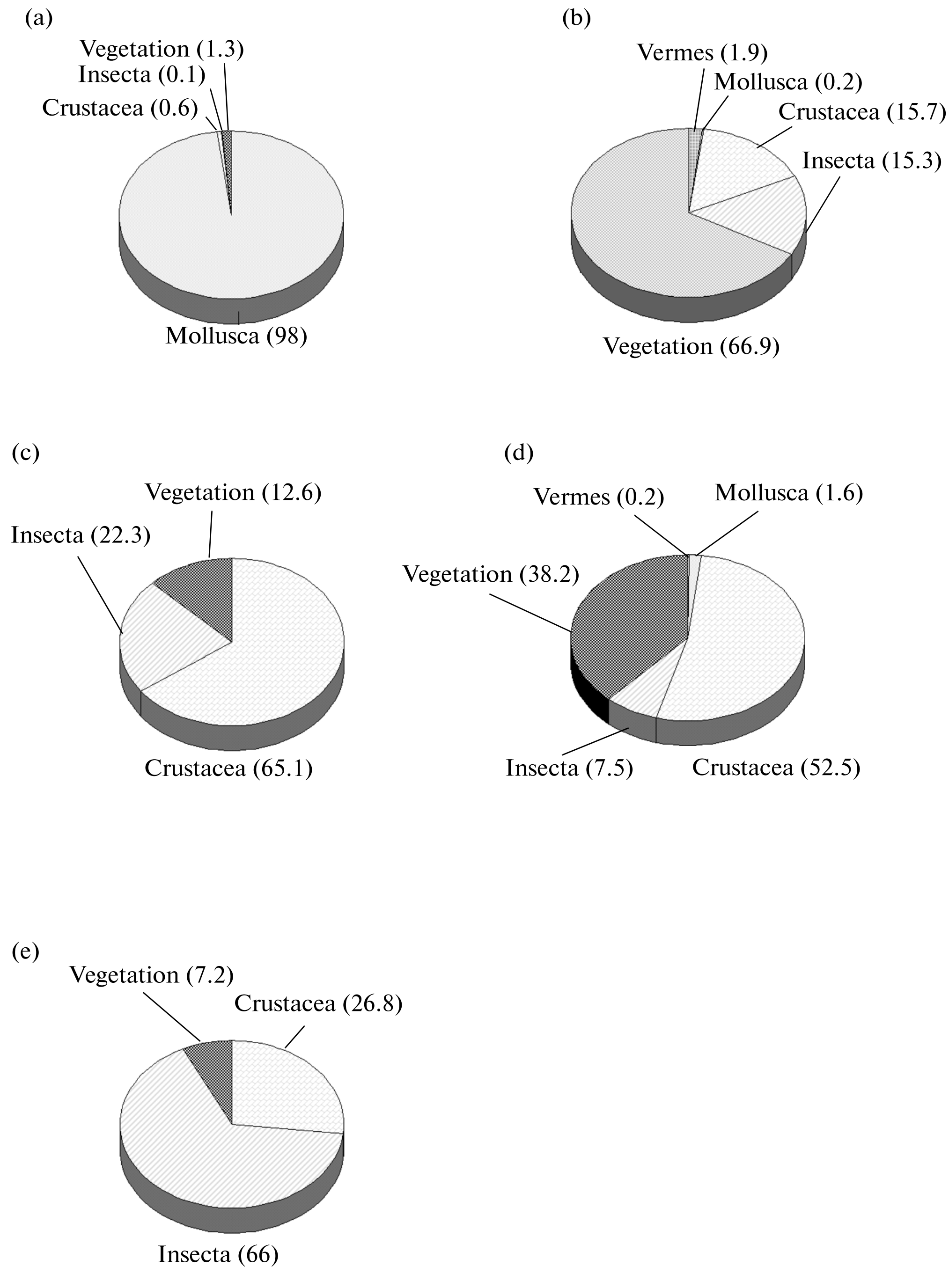


Fig. 7. Food composition of whitefish in Sukhoe More Inlet in the winter subglacial period, %: (a) December, (b) January, (c) February, (d) March, and (e) April.

weight). Among them, caddis flies stopped to occur, and larvae of biting midges appeared in an insignificant amount in the group of Diptera, parallel to larval chironomids. The total index of fullness of gastrointestinal tracts of whitefish in February increased to 15.2‰.

In **March**, the food spectrum of whitefish by main groups of food objects was similar to that in January. The proportion in feeding of vegetable food increased up to 38% compared to that in February (Fig. 7d). In the food diet, worms (only oligochaetes), as well as mollusks represented exclusively by the genus *Limnea*, again appeared in small amount. The proportion in feeding of whitefish of crustaceans as before represented by gammarus continued to remain dominant (52%). The proportion of insects on the whole declined to 7.5%; among the group of Diptera, the

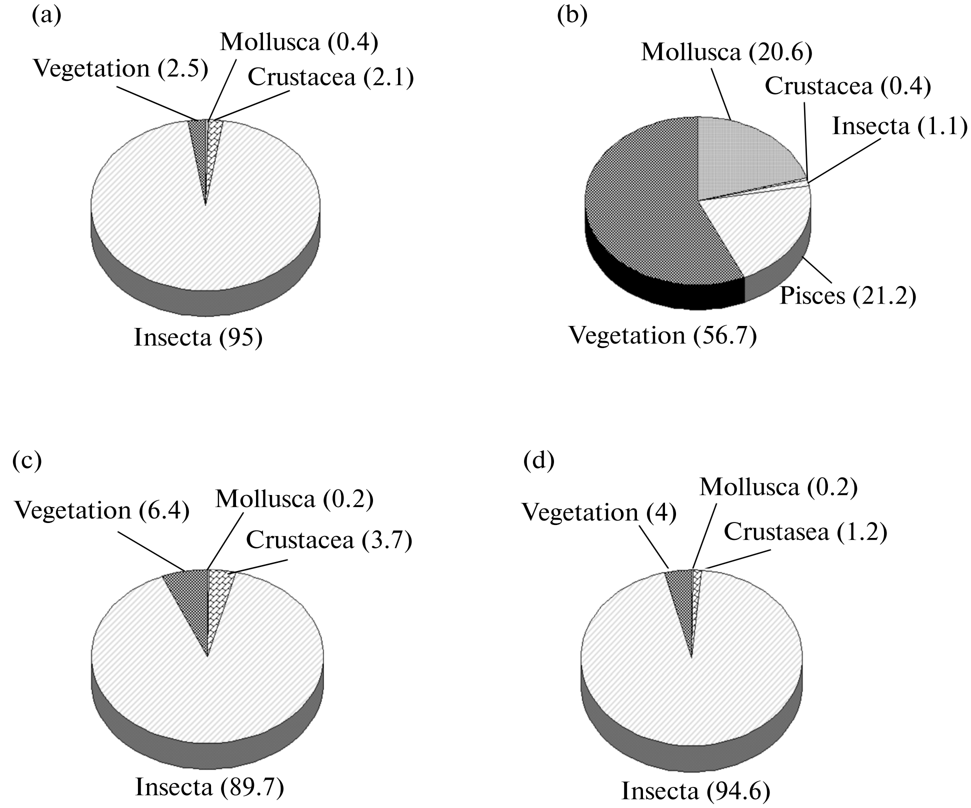


Fig. 8. Food composition of whitefish in Sukhoe More Inlet in the period of open water, %: (a) May, (b) June, (c) September, and (d) October.

amount of larval chironomids decreased to 2.5%. Larval gadflies that appeared in the food spectrum had considerable amount in the weight respect, although they occurred only in single gastrointestinal tracts of whitefish. The total index of fullness continued to increase and comprised 25‰ on average in March.

In **April**, the food spectrum of whitefish narrowed again to three groups in the same way as in February (crustaceans, insects, and vegetation). The proportion of vegetable food components and crustaceans represented as before by gammarids decreased. Insects whose total weight comprised 66% of the weight of the entire food bolus assumed dominant importance in the diet of whitefish in April (Fig. 7e). Among them, larvae of Diptera, mainly of chironomids, dominated. Larvae of beetles and caddis flies were recorded in considerably smaller amounts in gastrointestinal tracts. Larvae of caddis flies were represented by *Brachicentrus* sp., *Hydropsiche* sp., and *Agraulea* sp. that first appeared in the food spectrum. The total index of fullness also continued to increase and comprised 57.5‰ on average in April.

In the period of **open water**, the total food spectrum of whitefish hardly changed in a qualitative respect; however, instead of worms, the eggs of spring-spawning fish consumed by whitefish in the post-spawning period (June) appeared in its gastrointestinal tracts (herring, smelt, Cyprinidae and Percidae). In the quantitative respect during the vegetation period, insects noticeably dominated (60% by weight); whitefish consumed to a considerably smaller extent vegetation (23%), mollusks (8%), eggs of fish (8%), and crustaceans (1%) (Table 3).

In the **spring–summer months** (May–June), the bulk of food of whitefish was formed by insects (50%) represented mainly by Diptera (larval chironoimds). Vegetation was recorded in gastrointestinal tracts of whitefish in a slightly smaller amount, and mollusks and eggs of spring-spawning fish played similar role in its feeding (Table 3). Mollusks were represented by Bivalvia and Gastropoda. Among Bivalvia, representatives of the genera *Macoma* and *Sphaerium* occurred, and one genus *Limnae* occurred among Gastropoda. The role of crustaceans that included representatives of the orders Amphipoda, Ostracoda, Copepoda, and Mysidacea was insignificant on the whole. Food composition also considerably differed by months.

In **May**, the bulk of food of whitefish in the Sukhoe More was formed by insects (95%), among which Diptera represented by larval chironomids were dominant, and larval caddis flies were found in some gastrointestinal tracts only in rare cases. Other food components, particularly vegetation, crustaceans, and mollusks, played a very insignificant role (Fig. 8a).

Among crustaceans, copepods, ostracods, amphipods, and mysids were recorded; among mollusks, only representatives of the genus *Limnae* were recorded. The average total index of fullness of gastrointestinal tracts comprised approximately 182‰ in May.

In **June** in connection with emergence of adult forms of insects, their larvae were not recorded in the feeding of whitefish, in some gastrointestinal tracts, air forms (imago) of insects that fish collected from the water surface were found. The amount of consumed crustaceans considerably decreased; only amphipods and mysids were present in the food spectrum. At the same time, in June, in gastrointestinal tracts of whitefish, the amount of mollusks considerably increased (up to 21%), among which bivalves represented by the genera *Macoma* and *Sphaerium* dominated. Representatives of gastropods were recorded only in an inconsiderable amount and were represented exclusively by the genus *Limnae*. The bulk of food boluses of whitefish in this period was formed by vegetable food (57%) and eggs of spring-spawning fish (mainly of White Sea herring) that comprised almost a quarter of the contents of all gastrointestinal tracts in the weight respect (21%) (Fig. 8b). The average total index of fullness was 173‰ in June.

In **autumn months** (September–October), the food spectrum of whitefish narrowed to four groups of food objects due to absence in its feeding of the fish eggs (Table 3). The bulk of food again (as in May before emergence) was formed by insects (93%) represented mainly by larvae that entered into the composition of benthic communities in this period. Among them, Diptera dominated, whose composition included larval chironomids and limoniids. Larvae of caddis flies and beetles were represented insignificantly. Adult forms of insects were recorded in the feeding of whitefish in a moderate amount (6.3%); the remaining groups of food objects were represented insignificantly and comprised: vegetable food—5%; crustaceans—2%; and mollusks—less than 1% by weight.

In different **autumn months**, food composition of whitefish in the Sukhoe More did not differ considerably. Both in September and October, the bulk of its feeding was formed by larval insects, comprising 90 and 95% by weight, respectively (Figs. 8c and 8d). They were represented mainly by Diptera, among which larval chironomids dominated as before. In September in gastrointestinal tracts of whitefish, larval caddis flies were recorded in an insignificant amount that were lacking in October, but there were no larval limoniids that appeared in food composition in October. In September, aerial insects were also consumed more intensively; they accounted for 16% by weight. The consumption by whitefish of mollusks and crustaceans in different autumn months did not differ considerably. The total average index of fullness of gastrointestinal tracts comprised 61‰ in September and 120‰ in October.

Interannual Changes in the Feeding of Whitefish in the Sukhoe More Inlet

To reveal tendencies in the change of the feeding pattern of whitefish in a long-term aspect, annual material collected in the autumn period (October) during several years (from 1993 to 1997, 2002, 2007, and 2012) was analyzed. Analysis of obtained data demonstrated that the feeding pattern of the Northern Dvina whitefish in the Sukhoe More Inlet did not change significantly in different years. The bulk of its feeding was formed by aquatic larval insects, whose amount varied in different years from 27 (in 1995) to 95% by weight (in 1996 and 2012) (Fig. 9). Among them in all years, larvae of Diptera dominated, comprising 79% on average by weight and represented by larval chironomids. Such groups of organisms as mollusks, crustaceans, and vegetation did not play a considerable role in the feeding of whitefish, and they were secondary food objects.

Note that the autumn period of 1995 does not fit into a general picture: the bulk of feeding at that time was also formed by benthic organisms, but their ratio in the food spectrum considerably differed from other years. Larval insects that comprised in other years over 90% of the contents of gastrointestinal tracts, in 1995 occupied only 27%. At the same time, the amount of mollusks that in other years played a very insignificant role in the feeding of whitefish considerably increased and comprised 61%. Feeding intensity in the autumn periods of the studied years was rather high and varied within 149‰ in 1993 to 69‰ in 2012. The exception was again made by October 1995 when feeding intensity drastically declined to 52‰ (Table 4). This could be related to a catastrophe that occurred in August 1995 at Kotlasskii Pulp and Paper Industrial Complex and caused mortality of food organisms not only in the Vychegda and Northern Dvina rivers but also at sites of the premouth offshore. The numbers of more vulnerable benthic larval insects towards October drastically declined as a result of the anthropogenic impact, as a result of which whitefish was induced to pass to feeding on mollusks more resistant to pollution. In June 1997, whitefish also passed from benthic larval insects to feeding on mollusks and vegetation, but this was connected with seasonal reasons and was determined by mass emergence of adult forms of insects.

Age Changes in the Feeding Pattern of Whitefish

During analysis of age changes in the feeding of whitefish in the Sukhoe More, we took a generalized sample of spring–summer collections (May–June) in which almost all age groups characterizing its feeding school (from 2+ to 6+ years) were represented. We found that the bulk of feeding of fish of all age groups was formed by aquatic larval insects, and they were more intensively consumed by individuals of junior age groups (at an age of 2+ and 3+)—from 48 to 63% of the weight of food boluses. With growth of fish, at an

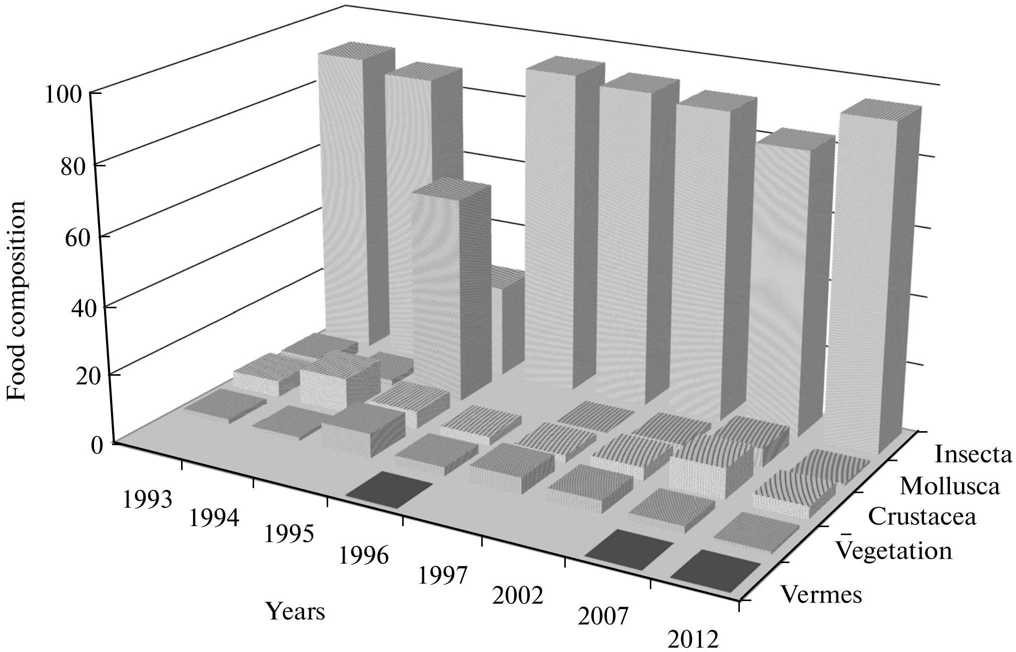


Fig. 9. Annual changes in food composition of whitefish in Sukhoe More Inlet, %.

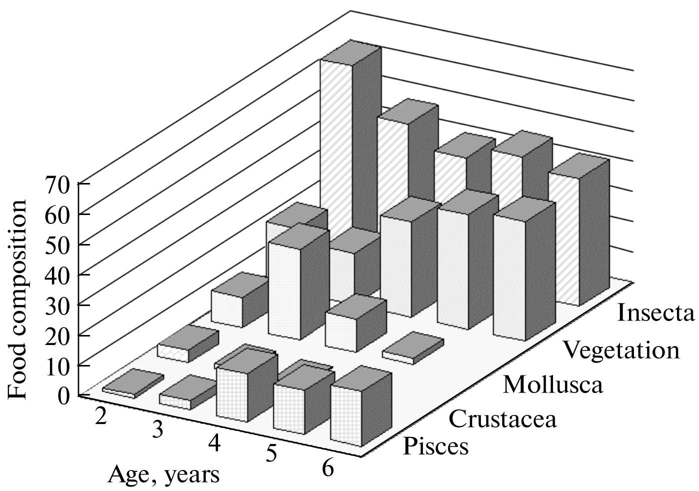


Fig. 10. Age changes in food composition of whitefish in Sukhoe More Inlet, %.

age of 4+…6+, the amount of larval insects declined to 45–41% (Fig. 10). Among them in all age groups, Diptera represented exclusively by larval chironomids dominated. Larval caddis flies were recorded only in single gastrointestinal tracts of whitefish at an age of 3+ and 6+.

Crustaceans in an insignificant amount were present only in food spectra of fish of junior age groups and comprised 4% in three-year olds (2+), 2% in four-year olds (3+), and less than 1% in five-year olds (4+). With growth of fish, the consumption by them of mollusks also decreased: from 10–30% in fish at an age of 2+ and 3+ years to 2% in fish at an age of 5+ years (Fig. 10). They were represented mainly by Bivalvia (genus *Macoma*) present in gastrointestinal tracts of almost all analyzed individuals. The role of gastropods was considerably smaller; they were present in an insignificant amount in the feeding of fish of only two age groups: 3+ and 4+ years. The amount of herring eggs consumed in June with growth of fish increased from 1% in fish at an age of 2+ years to 18% in seven-year-old (6+) individuals, and consumption of vegetation increased from 21 to 39%, respectively. It is known that herring eggs are spawned on vegetation; therefore,

Table 4. Feeding of whitefish in Sukhoe More in the autumn period (October) in different years, % by weight

Food objects	1993	1994	1995	1996	1997	2002	2007	2012	Total
1. Zooplanktonic organisms Copepoda	**0.2**	**8.1**	**0.0**	**0.0**	**0.3**	**2.3**	**5.7**	**0.0**	**2.1**
2. Benthic organisms:	**98.3**	**90.8**	**92.8**	**97.4**	**88.5**	**93.9**	**91.4**	**97.7**	**92.7**
Worms (Nematoda)	–	–	–	0.3	–	–	0.4	0.2	0.1
Bivalvia									
genus *Pisidium*	3.4	1.2	60.7	–	–	2.6	5.2	0.7	7.6
Gastropoda (Gastropoda)									
genus *Limnae*	–	–	–	–	0.2	–	0.1	–	0.1
genus *Planorbis*	–	0.1	–	–	–	–	–	–	0.1
genus *Valvata*	–	0.4	–	–	–	–	0.3	–	0.1
Crustacea (Crustacea)									
Amphipoda	3.6	2.1	3.7	2.3	1.9	2.0	3.3	0.7	2.6
Mysidacea	1.0	–	1.5	0.1	–	2.2	–	0.4	0.6
Ostracoda	–	–	–	0.1	–	–	–	–	–
Larvae of aquatic insects (Insecta)									
Trichoptera (caddis flies)	0.2	0.1	0.1	0.7	0.1	0.9	0.4	0.3	0.3
Chironomidae (chironomids)	89.3	86.6	26.8	93.9	80.4	84.8	80.0	92.8	79.0
Limoniidae (limoniids)	–	–	–	–	0.5	–	–	–	0.1
Coleoptera (aquatic beetles imago)	0.8	0.3	–	–	5.4	1.4	1.7	2.6	2.1
3. The remaining organisms:	**1.5**	**1.1**	**7.2**	**2.6**	**11.2**	**3.8**	**2.9**	**2.3**	**5.2**
Aerial insects	–	–	–	–	6.3	–	0.7	1.4	1.8
Vegetation	1.5	1.1	7.2	2.6	4.9	3.8	2.2	0.9	3.4
Total:	**100.0**	**100.0**	**100.0**	**100.0**	**100.0**	**100.0**	**100.0**	**100.0**	**100.0**
Average index of fullness, ‰	149.1	100.1	52.4	111.3	96.8	107.4	121.2	68.7	109.5
Number of fish, ind.	18	10	12	8	33	17	24	5	**127**

on eating eggs, whitefish also seizes vegetation. The feeding intensity of whitefish with growth did not change considerably and varied from 121 to 166‰. Note that in the late-1970s also at sites of the delta and near-mouth offshore, whitefish juveniles in the first year of life consumed zooplankton (cladocerans and copepods). In the second year of life, planktonic organisms comprised already approximately half of the contents of gastrointestinal tracts, and the remaining part was accounted for by larval chironomids. In the third and fourth years of life, whitefish almost completely passed to feeding on larval chironomids. In whitefish at an age of 4+, the role of mollusks gradually increased, and they formed the bulk of the diet at an age of 5+ and 6+ (Elsukova, 1981).

Feeding of Whitefish in the Premouth Offshore (Water Area of Mulyug Island)

General feeding pattern. In the marine biotope, the food composition of whitefish was relatively uniformly distributed over the main groups of food objects without considerable domination of any (Table 1). Its food spectrum included mollusks (38%), Coelenterata (17%), crustaceans (13%), worms (10%), as well as insects (4%), vegetable residues (7%), and detritus (12%) (Novoselov, 1999b).

The most mass group—mollusks—was represented mainly by bivalves and by gastropods in a considerably smaller amount. Among bivalves, the genus *Macoma* dominated; representatives of the genus *Mytilus* were recorded singly, and gastropods consisted only of the genus *Limnae*. Isopods and mysids dominated of crustaceans in the food composition of whitefish in the sea water area, and Cumacea and Copepoda occurred in a considerably smaller amount. Coelenterata were represented mainly by hydroid polyps (17%) and singly by sciphoid medusas, worms were represented exclusively by polychaetes, and insects were represented by larval chironomids. The average total index of fullness of gastrointestinal tracts of whitefish near Mulyug Island comprised 28‰ in the study period. During analysis of the food composition of whitefish in different months, change in the feeding on some objects in a seasonal aspect was revealed.

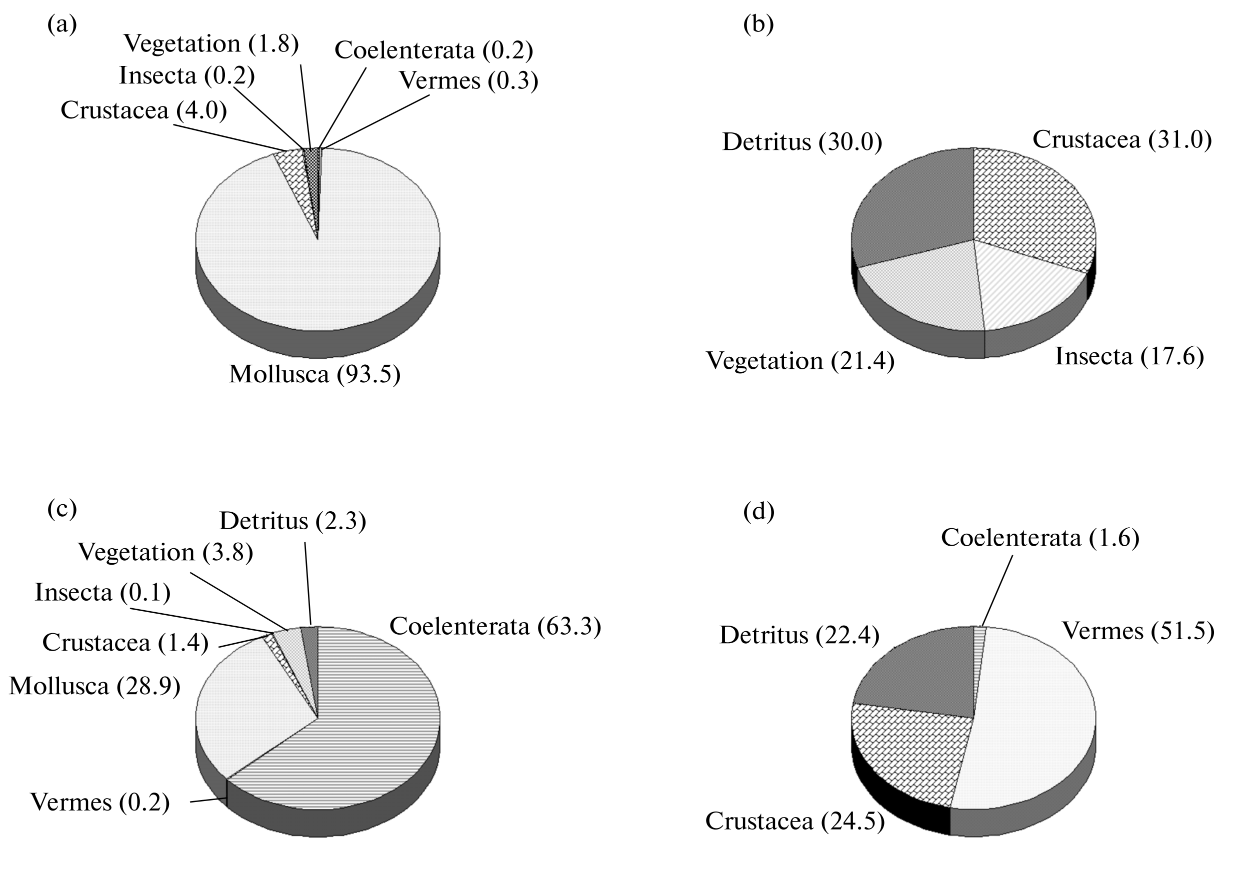


Fig. 11. Food composition of whitefish at the marine water area near Mudyug Island in the spring–summer period, %: (a) May, (b) June, (c) July, and (d) August.

Seasonal changes in feeding. In **May**, bulk of food (94% of weight of food boluses) was formed by bivalves (88%) and gastropods (6%), crustaceans, vegetation, worms, larval insects, and Coelenterata played an inconsiderable role (Fig. 11). The average index of fullness in May was 44‰. In June, the total food spectrum slightly narrowed due to dropping out from it of mollusks that dominated in May, as well as of worms and Coelenterata. At the same time, consumption by whitefish of crustaceans (up to 31%) and larval insects (up to 17%) increased. Among the first, amphipods dominated as before, and larval chironomids dominated among the second. The importance of vegetation and detritus also considerably increased in the feeding of whitefish, which is related to the period of spring storms and appearance of a considerable amount of detritus and vegetable residues in the water column. The average index of fullness in June was approximately 29‰.

In **July** in the food spectrum of whitefish, shift of dominant food objects was observed: Coelenterata appeared in mass, which comprised approximately two thirds and mollusks comprised approximately one third of the contents of all gastrointestinal tracts. The amount of worms, crustaceans, larval insects, vegetation, and detritus decreased approximately to the level of May. The average index of fullness in June was 27‰. In **August**, in the food composition of whitefish, worms (52%), crustaceans (24%), and detritus (22%) began to dominate. If worms were as before represented by polychaetes, mysids and Cumacea began to dominate among crustaceans. The average index of fullness of gastrointestinal tracts in August was minimal and comprised 2‰. In other words, during vegetative season in the food of whitefish over the water area of Mudyug Island mollusks dominated in May, crustaceans and vegetation dominated in June, Coelenterata and mollusks dominated in July, and worms and crustaceans dominated in August.

DISCUSSION

The data obtained characterize the Northern Dvina whitefish as an euryphage with a sufficiently wide food spectrum that undergoes changes depending on habitats (spatial), food biotopes (biotopic), different years (annual), seasons of the year (temporal), as well as age of fish (age).

Spatial changes in feeding. In a spatial aspect, change of the feeding pattern of whitefish occurs from the tributary of the first order—Emtsa River to sites of premouth offshore. In the Emtsa River and in the channel part of the Northern Dvina River, the main food object were aquatic larvae of Diptera; in particular, larval chironomids and larvae of other insects were consumed in an inconsiderable amount. Difference in the feeding of whitefish at these sites was pronounced by the fact that mollusks were present in almost all gastrointestinal tracts in the Emtsa River, among which gastropods of the genus *Limnea* dominated. In the channel part of the Northern Dvina River up to one third of the contents of food boluses consisted of aerial insects at the stage of imago, which is explained by their mass emergence in the sampling period (Table 1).

In the delta of the Northern Dvina River already in the zone of tidal phenomena, the dominant role in the feeding of whitefish of larval chironomids retained (66%); at the same time, crustaceans of the order Amphipoda appeared in the food spectrum. Mollusk consumption remained at the same level, but change of dominant groups occurred at the same time. Among gastropods, mollusks of the genus *Physa* began to play a dominant role in feeding, and bivalves of the genus *Pisidium* appeared in almost the same amount. The amount of remains of aquatic vegetation in gastrointestinal tracts increased to 4%.

At sites of premouth offshore in the desalinated Sukhoe More Inlet, aquatic larvae of chironomids still continued to occupy a dominant position, although not so clearly pronounced (slightly more than half). Mollusks among which bivalves of the genus *Macoma* dominated at this site began to play a considerable role in the feeding of whitefish. In the same amount (17%) in gastrointestinal tracts of whitefish, remains of aquatic vegetation that comes to the water column as a result of storm phenomena were recorded in a sufficient amount. Sukhoe More Inlet is a single site of the lower reaches of the Northern Dvina where herring eggs were recorded in the composition of its food spectrum (5%).

In the marine water area near Mudyug Island, the food composition of whitefish changes cardinally. The dominant role in the feeding of whitefish is now played by mollusks (37%), among which bivalves of the genus *Macoma* dominate; the amount of gastropods of the genus *Limnea* remains insignificant. Larval chironomids (as freshwater objects) ceased to have significant importance in the feeding of whitefish in the marine water area; at the same time, Coelenterata appeared in an equal amount in the food bolus—hydroid polyps, worms Polychaeta, and detritus.

In other words, when there is movement from tributaries of the first order downstream the river up to marine sites of the premouth offshore, successive decrease of the importance in the feeding of whitefish of larval insects dominant at all sites is observed. If they comprised approximately 85% of the weight of food boluses in the Emtsa River and more than 99% in the middle course of the Dvina, their amount declined to 70% in the delta part of the Dvina and up to 30% at sites of the premouth offshore. At the same time, the importance of mollusks successively increased from 12% in the Emtsa River to 30% in the offshore, and that of crustaceans increased from 1 to 10%. Besides, in the delta part of the Dvina and at sites of the premouth offshore, there appeared worms, Coelenterata, and detritus in the food composition of whitefish that were absent in the food spectra of whitefish in the Emtsa River in the middle course of the Dvina.

Biotopic changes in the delta of the Northern Dvina manifested themselves in a less wide food spectrum of whitefish of freshwater channel sites (channels) compared to lower brackish water biotopes of a limnetic type (Fig. 12). With movement to the sea, common groups of food objects in the food composition (worms, mollusks, aquatic larval insects—chironomids and remains of aquatic vegetation) were supplemented by crustaceans of the order Amphipoda that comprised half of the contents of gastrointestinal tracts of whitefish at Chizhovskie biotopes and detritus. In a quantitative respect, the proportion of mollusks consumed by whitefish increased from 1–5% in channels to 34–37% at flooded biotopes. At the same time at brackish water biotopes compared to channel biotopes, the amount of consumed worms (nematodes and oligochaetes disappeared but leeches appeared) and larval chironomids decreased.

Annual changes. In the Emtsa River in different years, the pattern of feeding of whitefish in March hardly differed. The bulk of feeding was formed by larval insects in both 1996 and 1997 (87 and 92% by weight, respectively), among which larval chironomids dominated. The amount of mollusks in gastrointestinal tracts did not exceed 7–16%; that of crustaceans did not exceed 0.5–0.8% and that of vegetation did not exceed 5.2–0.5% (Fig. 2).

During several years (from 1993 to 1997) in Sukhoe More when observations were performed in the autumn period (October), feeding of whitefish did not change considerably, i.e., was sufficiently stable. The bulk of food was formed by larval insects. The importance in feeding of mollusks, crustaceans, and vegetation was small. The exception was made by the autumn period of 1995 when the amount of larval insects that comprised more than 90% of the contents of gastrointestinal tracts in other years drastically decreased (up to 27%). This could be related to a catastrophe that occurred in August at Kotlasskii Pulp and Paper Industrial Complex and caused mortality of food organisms not only in the Vychegda and Northern Dvina rivers but also at sites of the premouth offshore. The numbers of more vulnerable benthic larval insects towards October drastically decreased as a result of the anthropogenic impact because of which whitefish had to pass to feeding on mollusks more resistant to pollution (Fig. 9).

Seasonal changes. In Sukhoe More, the pattern of feeding of whitefish considerably changed throughout

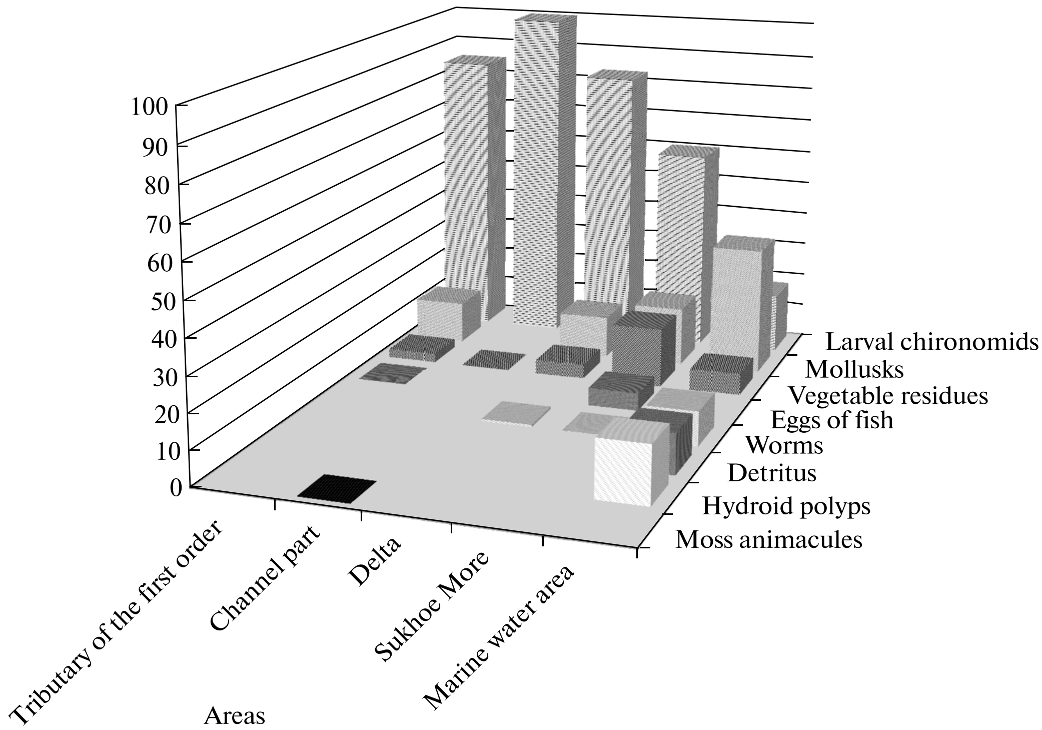


Fig. 12. Biotopic changes in the food spectrum of whitefish in the Northern Dvina River, % by weight.

the year. In the period of open water (vegetation season), the bulk of its feeding was formed by larval insects, mainly chironomids. Mollusks and crustaceans were secondary food objects. In June in connection with mass emergence of insects, their importance fell to almost zero. Whitefish induced to pass to other kinds of food consumed vegetation, mollusks, and herring eggs in mass. In autumn months (September–October), larval insects again occupied a dominant position in the composition of the food spectrum. In the winter subglacial period, from December to March, the feeding of whitefish also underwent considerable changes. In December, mollusks dominated (98%); in January, vegetation food comprised approximately 70% by weight. In February and March, crustaceans dominated in the food of whitefish. In April, consumption of larval insects that in the preemergence period became more accessible for whitefish benthophage increased (Figs. 7, 8).

Age changes. The results of studies demonstrated that change of dominant food organisms occurs in whitefish with growth of fish. In the Emtsa River, with age of fish, an increase in consumption of mollusks from 9% in fish aged 2+ to 32% in seven-year old fish (at an age of 6+) and crustaceans, respectively, in individuals at an age of 5+ years was observed. At the same time, the amount of consumed larval insects decreased from 88 (age 2+) to 66% (age 6+) (Fig. 3). In the channel part of the Dvina, whitefish of all age fed exclusively on larval insects (99–100%), and the importance of larval chironomids increased with age. The amount of larval caddis flies and bugs with growth of fish decreased. In Sukhoe More, the proportion in feeding of vegetable food and eggs (in the spring period) increased with age of fish. The importance of mollusks, on the contrary, decreased from 10% in individuals aged 2+ to 2.1% at an age of 5+ years. Fish of elder age groups also consumed in smaller amounts crustaceans and larval insects (Fig. 10).

CONCLUSIONS

In summary, note that whitefish in the basin of the lower reaches of the Northern Dvina River according to pattern of feeding is an euryphage with a wide spectrum of feeding, including over 40 groups of food objects. The bulk of its feeding is formed by benthic larval insects (mainly larval chironomids) and mollusks (mainly bivalves). At the same time, it easily passes to other kinds of food depending on feeding at different food biotopes (spatial feeding variation), seasons of the year (seasonal variation), and age specific features (age feeding variation). Crustaceans, worms, and sponges are secondary food kinds. In the spring period in its feeding at sites of premouth offshore, a predation element appears, and it can consume eggs of the herring and other spring-spawning fish in considerable amounts. Because of anthropogenic factors (volley accident waste of pollutants) affecting food resources, the food spectrum of whitefish can change considerably. At the same time, rather high feeding intensity indicates that food possibilities of the lower part of the basin of the Northern Dvina River (tributaries, channel part of the river, delta, and premouth offshore) to full measure satisfy trophic demands of the feeding school of the Northern Dvina whitefish.

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