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ORIGINAL ARTICLE

Feeding patterns of the *Perca fluviatilis* (Linnaeus, 1758) in running and stagnant water bodies in Northwest Russia

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Abstract

The feeding habits of *Perca fluviatilis* in the water bodies of the lake-river system of the Pista River (White Sea basin) from May to October were studied. The stomach contents of the perches were analyzed. The occurrence frequency of food items and ratio to the total mass of the food bolus were calculated using standard methods. The contents of the stomachs were described using the index of fullness, the occurrence of major groups of food items and their relative importance. The taxonomic richness of the fish's food supply was estimated by the regression models, which describe the accumulation of food items with an increase in the number of examined stomachs. There was no substantial differentiation in the taxonomic composition of food items between the river and the lake. Zoobenthos prevailed in the spring and summer everywhere, and fish was the second dominant food item. The river displays two distinctive features in this time: a) the poor contribution of the zooplankton due to its scarcity in running water and b) the use of fish as food items by smaller perches. A considerable decrease in the taxonomic richness model values of food items and increase in the number of empty stomachs indicate deterioration of feeding conditions in autumn. Therefore, perch begins to consume the imago of aerial insects, which fell into the water, and fish more actively. However the season feeding spectrum is considerably restructured only in the river, where fish becomes the major type of food. The transition to a predatory mode of life seems to compensate for the shortage of other food resources. The results of the study show that a running water regime transforms the feeding patterns of perch. In a fluvial environment, the contribution of zooplankton decreases markedly and perches use fish as food more actively. The fish and aerial insects become the main food of perch in the river in autumn.

Keywords: European perch, Lake-river ecosystem, Feeding spectrum, Food supply richness, Predation.

INTRODUCTION

The river perch inhabits freshwater bodies in Europe and Northern Asia (Berg 1948; Kottelat & Freyhof 2007). In Northwest Russia, it is one of the most numerous species occurring in lakes and rivers, including mountain rivers. Its feeding spectrum consists of various animal groups. Juveniles mainly feed on zooplankton. As they grow, their ration is enriched with zoobenthos, aerial insects, fish and amphibians (Sterligova et al. 2016). The ration is dominated by the most accessible food items. Therefore, the contents of fish stomachs indicate the perch's food supply in various water bodies and their possible adaptation to the existing environment. The plasticity of food selection is an essential constituent of species' adaptive potential. As a new resource emerges, the perch begins to actively use it. For instance, in Lake Onega, it uses a Baikal amphipod, as invader (Georgiev et al. 2022), and in water bodies with aquaculture it uses food for trout (Onishchenko et al. 2020).

The numerous studies of perch were carried out at materials from lakes and reservoirs (e.g. Allen 1935; Popova & Sytina 1977; Lappalainen et al. 2001; Wziątek et al. 2004; Ceccuzzi et al., 2011; Jacobsen et al. 2015), including in the study area (Pervozvansky 1986). The feeding habits of the species in stagnant waters of various latitudinal zones are well known, but feeding on river rapids are insufficiently studied. Fast-flowing waters are not typical habitats for the species (Berg, 1948), to live in running water bodies, the perch has to obtain food in a specific manner. Successful food adaptation is usually believed to be due to the structure of the jaw apparatus and the alimentary system, but some parameters that are not directly related to feeding, e.g. body shape and hydrodynamic characteristics, also diverge (Aleev 1963; Dgebuadze 2001). Typical rheophilic species, e.g. Atlantic

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salmon, brown trout and grayling differ in behavior from fish living in stagnant water. Rheophilic species commonly inhabit their own sites which are unaffected by strong currents, from which they rush for food into the running water. Their major food items are benthic and planktonic organisms carried away by running water (so-called invertebrate drift), terrestrial insects falling into the water and small-sized lake fish migrating downstream. Active feeding in water flow is provided by their good rheoreaction, rapid rushing and physical strength (Pavlov 1979). We suggest that in these conditions perches use a foraging strategy similar to salmonids. The specimen physical capabilities, in particular the burst swimming speed (Shustov & Gorbach 2023), apparently allow perch to snatch food items from the water flow succesfully.

Food preferences of perch in different ages and habitats are known in detail (e.g. Persson 1983; Pervozvansky 1986; Rask 1986; Persson & Greenberg 1990; Hjelm et al. 2000; Horppila et al. 2000; Estlander et al. 2010; Radenković et al. 2022). A total data on feeding spectrum in lakes of Northern Russia allow to indicate three ecological forms (races) which differ in body size, habitats and feeding patterns (Sterligova et al. 2016).The main food of dwarf perch in small forest lakes with poor food supply is zooplankton. Coastal "herbal" form in large lakes usually feed on zoobenthos, and deep-water perches early begin to feed on fish. In the lakes in the study area, perches become predators when they reach a length of approximately 10 cm, specimens larger than 30 cm feed exclusively on fish (Pervozvansky 1986). Knowledge of river perch, especially in fast-flowing mountain rivers, is insufficient, and differences in feeding patterns of the species between lakes and rivers is not obvious, because available data were obtained from different locations at different times.

The purpose of our study was to reveal the distinctive feeding patterns of the species in running water. We assumed that a running water regime, which is an essential factor in the formation of an environment necessary for the existence of organisms in a water body, has a considerable effect on the food supply and, hence, the feeding of perch. The natural variability of the environment was minimized by selecting the water bodies of one lake-river system, in which perch feeding was studied during the same time intervals.

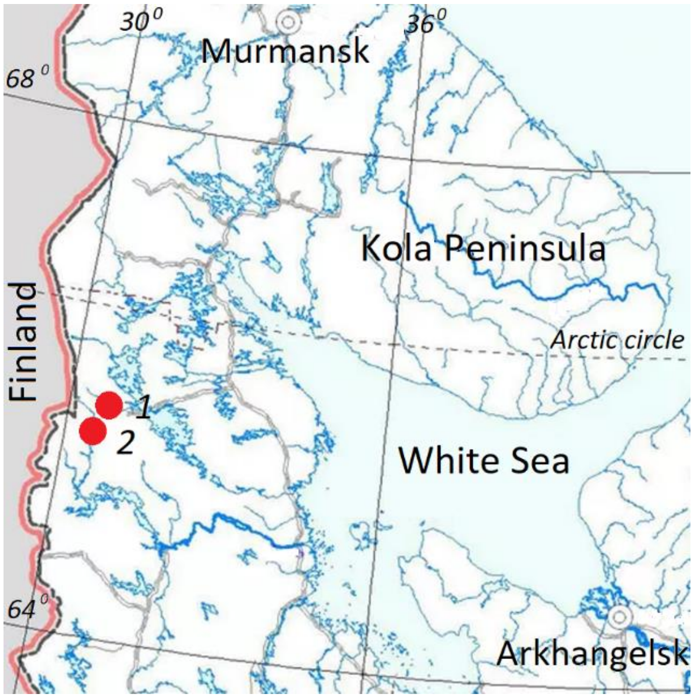

Fig.1. Study water bodies: 1 – Pista River near Kushevanda village, 2 – Lake Pistojärvi.

MATERIAL AND METHODS

The specimens were collected from the water bodies of the Pista River's lake-river system (White Sea basin) (Fig. 1) in May-October, 2016. In accordance with the local thermal regime, the study period was divided into three seasons: spring (May-June), summer (July-August) and autumn (September-October), because ice on water bodies breaks up as late as May, water is heated by July, and ice is formed as early as September. A total of 375 fish samples (Table 1) were caught using a fishingrod on Pista River's rapids near Kushevanda village (N 65.696°, E 30.496°) and in Lake Pistojärvi (N 65.524°, E 30.529°). The mass and total length of each fish were measured, digestive tract was removed and fixed in 4% formalin. The fixed materials were examined in the laboratory under a 10× binocular microscope, the food items being determined to the lowest possible

Table 1. Number and sizes examined perches in the Pista River and Pistajarvi Lake.

Indices	Spring		Summer		Autumn	
	River	Like	River	Like	River	Like
Number of fish	50	65	91	78	52	39
Total length, cm						
Range	9–28	10–27	9–35	9–27	9–25	11–26
Median	14.5 13.1–15.7	17.9 16.6–19.0	14.7 13.6–15.7	17.6 15.5–18.8	16.6 15.3–17.4	19.7 17.7–21.5
Total length of predatory perches, cm						
n	14	19	31	22	24	14
Minimum	11.3–15.6	18.6–19.8	9.4–13.5	18.6–19.7	13.0–16.1	19.5–19.9
Median	18.7 15.6–21.3	22.0 20.0–23.0	18.2 16.0–19.9	22.6 20.3–24.0	18.1 17.5–19.3	22.5 19.9–23.5

Note. n – number of predatory perches, the median confidence intervals were obtained by the bootstrap method.

taxonomic group and weighed. The number of food items was counted, their occurrence frequency (F_i,%) and ratio to the total mass (P_i,%) of the food bolus were calculated (Hyslop 1980). Predatory perches were identified by the remains of fish in food boluses.

The contents of the stomachs of the perch were described using the index of fullness (IF,‱), the occurrence of major groups of food items (F_i,%) and their relative importance (IRI,%). The total index of fullness for each fish was calculated as $IF=10\times m_i/m_k$, where m_i the bolus mass (mg) and m_k is fish mass (g). The relative significance of a food item in perch feeding in the lake or river in each season was calculated as $IRI=(F_iP_i/\Sigma\ F_iP_i)\times100$ (Hyslop 1980; Popova & Reshetnikov, 2011). The diversity of the fish's food supply was described by analogy with the species diversity of parasite communities using the accumulation curves $s=a\times n^b$ (Ieshko et al. 2023), in which parameter a predicts the number of items in the food bolus of the first fish analyzed, the parameter b shows how the number of food items, s, grows with the increasing number of the fish analyzed, n.

The frequency distribution in the samples was checked for normality using Lilliefors' formula (L). The variation range of values was calculated by simple non-parametric boot- strapping with the number of tests B=1000. Confidence intervals were set using the percentile method (Shitikov & Rosenberg 2013). The conjugation of the variability of the relative significance indices of a food item (IRI) was checked by Pearson's correlation method (r). The values were compared using a randomization test (MCR – Monte Carlo Randomization) with B=1000. The significance of differences, p, in such an approach is a corrected fraction of null-model combinations (empirical values difference is not more than randomized difference, $|d_{\text{obs}}|\leq|d_{\text{ran}}|$, correspondingly $L_{\text{obs}}\leq L_{\text{ran}}$ for Lilliefors' criterion and $|r_{\text{obs}}|\leq|r_{\text{ran}}|$ for Pearson's correlation coefficient) relative to the total number of tests, B. The standard value α=0.05 is accepted as the critical value for p. The data were processed in MS Excel and R 4.0.1 using the basic functions and functions of the 'nortest' package (Gross & Ligges 2015; R Core Team 2022).

RESULTS

Because the frequency distributions of the indices values studied deviated from the normal law ($L>0.102$, MCR-test: $P<0.046$), we assessed differences of the samples by their medians. The fish varies in length from 9 to 35 cm (Table 1). The specimens caught in the river in each season were smaller than those caught in the lake (MCR-test: $P<0.010$). In autumn, fish from the river were more large than those caught in spring and summer (MCR-test: $P<0.017$) and perches with empty stomachs occurred more often (MCR-test: $P<0.018$). Other differences in body length were statistically insignificant (MCR-test: $P>0.072$). The variability of fullness indices (IF, Table 2) was mostly stochastic (MCR-test: $P>0.136$), but smallest value shown for

Table 2. The feeding spectrum of perch in the Pista River and Pistajarvi Lake.

Indices	Spring		Summer		Autumn	
	River	Like	River	Like	River	Like
n	50	65	91	78	52	39
Index of fullness of stomach (*IF*,‱)						
Range	3–1410	5–474	1–1220	5–1550	1–883	5–466
Median	70.2 35.4–104.0	46.5 34.5–62.0	53.5 30.0–83.5	57.0 47.0–68.5	71.0 41.0–103.5	73.0 52.0–90.0
Share of empty stomachs, %	10.0 2.0–18.0	4.6 0.0–10.8	5.5 1.1–9.5	10.3 3.8–16.7	19.2 9.6–30.8	5.1 0.0–12.8
Frequency of occurrence (*F*,%) and index of relative importance of food items (*IRI*,%)*						
Zooplankton	18.0 (1.7) 2.5–20.5	20.0 (14.0) 2.5–20.5	22.0 (2.4) 0.0–12.8	19.2 (13.5) 2.6–23.1	5.7 (1.1) 0.0–7.7	12.8 (6.0) 2.5–23.1
Zoobenthos	66.0 (78.3) 48.7–79.5	55.4 (66.2) 38.4–69.2	73.6 (81.6) 53.8–84.6	51.3 (67.0) 43.6–74.4	28.8 (16.9) 18.0–46.2	48.7 (42.4) 33.3–64.1
Aerial insects	18.0 (9.0) 10.3–35.9	16.9 (10.0) 12.8–41.0	11.0 (2.0) 0.0–12.8	12.8 (8.0) 10.3–35.9	21.2 (21.0) 10.2–33.3	20.5 (15.4) 10.2–33.2
Fish	28.0 (11.0) 12.8–41.0	27.7 (9.8) 20.7–51.2	35.2 (14.0) 23.1–53.8	28.2 (11.5) 15.4–46.2	44.2 (61.0) 28.2–59.0	35.9 (36.2) 20.5–51.3

Note. n – number of stomachs examined, * – the confidence interval indicated F, the value of the IRI index is given in brackets. The median confidence intervals were obtained by the bootstrap method.

fish caught in spring in the lake differed from the maximum values obtained for the river in spring and for the river and lake in autumn, MCR-test: $P<0.030$).

The perch fed in river and lake on the common local water organisms. Zooplankton consists of small-sized crustaceans, such as water fleas (*Cladocera* Latreille, 1829) and copepods (*Copepoda* Milne-Edwards, 1840). Zoobenthos is composed of molluscs (*Mollusca* Linnaeus, 1758), water sowbugs (*Asellus aquaticus* Linnaeus, 1758), larvae and pupae of chironomids (*Chironomidae* Newman, 1834) and ceratopogonids (*Heleidae* Newman, 1834), caddis fly (*Trichoptera* Kirby, 1813) and beetle (*Coleoptera* Linnaeus, 1758) larvae, as well as mayfly (*Ephemeroptera* Linnaeus, 1758), stonefly (*Plecoptera* Burmeister, 1839) and dragonfly (*Odonata* Fabricius, 1793) nymphs. Fish and arial insects contributed markedly to the formation of the fish ration. The fish species used as food were roach (*Rutilus rutilus* Linnaeus, 1758), bleak (*Alburnus alburnus* Linnaeus, 1758) and sculpin (*Cottus koshewnikowi* Gratzianow, 1907). The pieces of fish in the food bolus of river perch are found in smaller specimens. Differences in minimum body length and median values for the predatory perch were statistically significant in all seasons (MCR-test: $P<0.031$).

The perch's food was dominated by zoobenthos but in stomaches of the specimens caught from the river in autumn pieces of fish were most common (Table 2). Differences in the occurrence of zooplankton and zoobenthos in food boluses, were mainly stochastic (MCR-test: $P>0.068$). They were much lower only for fish from the river caught in autumn (MCR-test: $P<0.030$). The occurrence of fish and aerial insects was relatively stable (MCR-test: $P>0.102$).

The index of relative significance (*IRI*), smoothing the disproportion of food items differing in occurrence frequency and body mass, is the most variable for planktonic organisms. The values in fish from the lake were several times higher than in fish from the river (Table 2). A low in the contribution of zooplankton to the perch ration in spring and summer was offseted high abundance of zoobenthos. In autumn, *IRI* value was lowest for zoobenthos and highest for fish and arial insects. The significant inverse relationships between zoobenthos – aerial insects ($r=-0.949$, MCR-test: $P=0.003$) and between zoobenthos – fish ($r=-0.926$, MCR-test: $P<0.002$) were revealed.

The parameters of the power models, which describe the accumulation of food items with an

Table 2. Parameters of the power models $s=a\times n^b$, there is the accumulation of food items s with an increase in the number of studied fish n.

Body of water	Parameters		*lim*	R^2	*Me*	*lim*
Spring						
River	*a*	5.33	3.54–7.50	0.728	5.39	4.97–5.58
	b	0.22	0.12–0.33		0.22	0.21–0.23
Like	*a*	5.44	4.11–7.21	0.769	5.39	5.23–5.62
	b	0.23	0.16–0.30		0.23	0.22–0.24
Summer						
River	*a*	6.10	4.18–8.09	0.734	6.06	5.81–6.24
	b	0.18	0.11–0.27		0.18	0.17–0.19
Like	*a*	5.94	3.79–7.79	0.653	6.07	5.88–6.39
	b	0.18	0.11–0.29		0.18	0.17–0.19
Autumn						
River	*a*	2.80	1.14–5.10	0.804	2.73	2.52–3.03
	b	0.36	0.20–0.60		0.29	0.28–0.31
Like	*a*	4.39	2.86–5.94	0.805	4.39	4.27–4.66
	b	0.29	0.20–0.41		0.37	0.37–0.40

Note. The differences of the coefficients a and b from zero are significant for all models (Student's test, t>91.4, $P<0.001$), lim – the confidence interval obtained by the bootstrap method, R^2 – the determination coefficient, Me – the median of the series of bootstrap values of the parameters and their confidence intervals lim.

increase in the number of the stomachs examined, clearly demonstrate the trend described, indicating a significant decline in the perch's food richness in autumn (Table 3). The variation range of the models' parameters largely overlapped, indicating a stochastic type of their differences (MCR-test: $p>0.486$). Significant differentiation was revealed only by analyzing secondary statistics, such as the median values in the model parameter series obtained by bootstrapping. In the river and in the lake, the number of food items (measure of taxonomic richness, parameter *a*) increased in summer and decreased in autumn, and their accumulation rate (measure of heterogeneity of food supply, parameter *b*) displayed a reverse trend (MCR-test: $P<0.001$). Both parameters differed significantly for perches caught from the river and lake in autumn (MCR-test: $P<0.001$).

DISCUSSION AND CONCLUSIONS

The study of food boluses of perches caught from the water bodies of the Pista River's lake-river system has supported the findings about the food spectrum in the study area (Pervozvansky 1986). The food supply of the species is naturally poorer than in more southern areas (Popova & Sytina 1977; Rask 1986; Horppila et al. 2000; Lappalainen et al. 2001). In the group proportion of food items perches from Pista River were not differ from Lake Pistojärvi.

The occurrence of zooplankton, zoobenthos, arial insects and fish during the spring-summer season was stable (Table 2), and all the differences shown were random. The perch's distinctive feeding pattern is based on the distribution of the organisms used with regard to their relative importance index (*IRI*). A small number of zooplankton in the stomachs of river perch is due to a considerable decline in the abundance and biomass of water fleas and copepods on river rapids (Smirnov et al. 1978). The shortage of this food is compensated by the increased active consumption of other food items, primarily zoobenthos. Its relative significance in the food from the river perch is higher than that from the lake perch. Another distinctive feature is better feeding conditions in the river in spring, as indicated by substantial differences in the corresponding indices of fullness of stomach (*IF*). The improvement of feeding conditions is explained by an increase in the intensity of drifting provoked by the seasonal dynamics of the vertical migration of amphibious insects at that time (Muller 1974; Smirnov et al. 1978).

In autumn the perch feeding changes markedly: the abundance of zooplankton decreases, most insects, forming the bulk of zoobenthos, fly away, and their aquatic stages at that time are mainly demonstrated by eggs and juveniles (Yavorskaya 2020). Hence, the contribution of the above aquatic organisms to the perch food decreases. The reduction in the food supply to autumn and winter were shown in other studies (e.g. Horppila et al. 2000; Wziątek et al. 2004; Radenković et al. 2022), with the only difference being that unfavorable conditions in north comes in late in the summer. The perch begins to use large numbers of other food items, e.g. fish and the imago of aerial insects that fall into the water. The parameters of accumulation curves summarize the trend described, indicating a significant decrease in the perch's food richness in autumn. Correlation analysis of *IRI*-values supports the existence of feedback between zoobenthos and air-borne insects and between zoobenthos and fish.

It should be noted that in autumn the perch's feeding spectrum is considerably restructured only for perches from the river, where the main type of food is fish, while air-borne insects and zoobenthos are less common. Transition to predation could be due to two factors. First, fish that inhabit the stagnant water of the lake and are carried away by currents are disoriented and become easy prey in running water. It is known that juvenile salmon reared in ponds with no water circulation are carried away by currents after their release into the river and are poorly fed for at least one month (Shustov et al. 1980). The other factor is the shortage of available food items, e.g. invertebrates, which makes the perch feed on fish. The number of empty stomachs in the river perch increased significantly in autumn, indicating the deterioration of feeding conditions. Transition to a predatory mode of life compensates for the shortage of zoobenthos in the river. The high median value of the index of fullness, which was the same as that obtained for the lake perch, was primarily due to fish consumption. The growing amount of fish in the ration also seems to be due to an increase in the body length of the river perch in autumn relative to the same in spring-summer. It is known that the perch's rushing speed- body size ratio is a power function (Shustov & Gorbach 2023). The increase in physical strength with an increase in body size enables the fish to use more mobile types of food and hunt in running water.

The results of the study showed that in the Pista River, perches begin to feed on fish when they reach about 10 cm in length, whereas 20-cm specimens become predators in Lake Pistojärvi. These estimates differ from the data for some lakes in the study area, where the perch shows a transition to predation upon reaching of 10 cm in length (Pervozvansky 1986). The differentiation may indicate the local or inter-annual specificity of the food supply. Perch flexibly adapts to actual conditions (e.g. Persson et al., 2000; Beeck et al. 2002; Frankiewicz & Wojtal-Frankiewicz 2012) and as example the 0+ age cohort can split into a slow-growing planktivorous and a fast-growing piscivorous cohort during their first months of life (Borcherding 2006).

To sum up, the results of the study support our assumption that a running water regime transforms the feeding spectrum of perch, which is normal in stagnant water. In a fluvial environment, the contribution of zooplankton as a food item decreases markedly; the perch begins to use fish as food earlier. Because of the shortage of other food items in autumn, fish become a major type of food. Large fish, which can rush for food more rapidly, seem to easily obtain food from running water and are better adapted to living in a fluvial environment.

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مقاله کامل

الگوهای تغذیه *Perca fluviatilis* (Linnaeus, 1758) در آب های جاری و راکد در شمال غربی روسیه

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چکیده: عادات غذایی *Perca fluviatilis* در بدنه‌های آبی سیستم دریاچه-رودخانه، رودخانه پیستا (حوضه دریای سفید) از ماه می تا اکتبر مورد مطالعه قرار گرفت. محتویات معده سوف‌ها مورد تجزیه و تحلیل قرار گرفت. فراوانی حضور اقلام غذایی و نسبت آن به جرم کل غذای جویده شده با استفاده از روش‌های استاندارد محاسبه شد. محتویات معده با استفاده از شاخص سیری، وجود گروه‌های اصلی مواد غذایی و اهمیت نسبی آنها توصیف شد. غنای طبقه‌بندی منابع غذایی ماهی توسط مدل‌های رگرسیونی تخمین زده شد که تجمع مواد غذایی را با افزایش تعداد معده‌های بررسی شده توصیف می‌کند. هیچ تفاوت قابل توجهی در ترکیب طبقه‌بندی اقلام غذایی بین سیستم رودخانه و دریاچه وجود نداشت. Zoobenthos در بهار و تابستان و ماهی دومین ماده غذایی غالب بود. رودخانه در این زمان دو ویژگی متمایز را نشان می‌دهد: الف) سهم ضعیف زئوپلانکتون به‌دلیل کمبود آن در آب جاری و ب) استفاده از ماهی به‌عنوان اقلام غذایی توسط سوف‌های کوچکتر. کاهش قابل توجه مقادیر مدل غنای طبقه‌بندی اقلام غذایی و افزایش تعداد معده خالی نشان‌دهنده بدتر شدن شرایط تغذیه در پاییز است. بنابراین، ماهی سوف شروع به مصرف حشرات می‌کند که در آب افتاده‌اند و ماهی را فعال‌تر می‌کند. با این حال، طیف تغذیه فصلی به‌طور قابل توجهی فقط در رودخانه تغییر ساختار می‌یابد، جایی که ماهی به نوع اصلی غذا تبدیل می‌شود. به‌نظر می‌رسد گذار به شیوه زندگی شکارچی، کمبود سایر منابع غذایی را جبران می‌کند. نتایج مطالعه نشان می‌دهد که رژیم آب جاری الگوهای تغذیه سوف را تغییر می‌دهد. در یک محیط رودخانه‌ای، سهم زئوپلانکتون به‌طور قابل توجهی کاهش می‌یابد و سوف‌ها از ماهی به‌عنوان غذا فعال‌تر استفاده می‌کنند. ماهی‌ها و حشرات در پاییز غذای اصلی ماهی سوف در رودخانه را تشکیل می‌دهند.

کلمات‌کلیدی: سوف اروپایی، اکوسیستم دریاچه-رودخانه، طیف غذایی، غنای ذخیره غذایی، شکار.