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Seasonal Dynamics of Feeding and Food Relationships of Juveniles of Salmonidae in the Basin of the Kol River (Western Kamchatka)

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Abstract—Feeding of different-age juveniles of Salmonidae with a long freshwater period of life (coho salmon *Oncorhynchus kisutsch*, cherry salmon *O. masou*, king salmon *O. tschawytscha*, Dolly Varden char *Salvelinus malma*, East Siberian char *S. leucomaenis*, and Kamchatka steelhead *Parasalmo mykiss*) in the basin of the Kol River (western Kamchatka) in the summer–autumn period was studied. Comparative analysis of their foraging in tributaries of different types, off-channel habitats, and the mainstem of the river in the period of July to September is provided. Spectra of consumed foods, indices of stomach fullness, and degree of food similarity between juveniles of different species and age classes at different sites of the river system were estimated. At each concrete river site and in each concrete period of time, juveniles of the studied species exhibit low selectivity and feed on highest mass and easily accessible groups of food objects. Biotopical determination of feeding is typical of juveniles of all species. In the course of the vegetation period in juveniles of Salmonidae in the basin of the Kol River, frequent change of the consumed food and increase in indices of stomach fullness occur. The results obtained indicate dynamic mosaicism of trophic relations of juveniles of salmonids that formed in the ecosystem of the Kol River.

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Keywords: salmonids, Salmonidae, juveniles, foraging, degree of food similarity, food competition, food resources, ecosystem of salmon river

INTRODUCTION

Pacific salmon of the genus *Oncorhynchus* and other fishes of the family Salmonidae in the basin of the northern Pacific are among the most important species of bioresources, and investigations related to study of diverse aspects of their biology and ecology continue many years. In recent years, an ecosystemic approach assumes an ever-increasing importance (Augerot, 2005; Stanford et al., 2005; Shuntov and Temnykh, 2008, 2011; Pavlov et al., 2009). Analysis of productivity and structural-functional organization of the ecosystem of a salmonid river is based on results of study of diverse relations between fish species at different stages of their life cycle. It is considered that the freshwater phase of the life cycle of anadromous salmonids, during which growth of juveniles and their preparation to outmigration to the sea occur has a principal value in the dynamics of the numbers of populations (Birman, 1985; Groot and Margolis, 1991; Bugaev, 1995; Karpenko, 1998; Quinn, 2005). Formation of the yield of generations in a freshwater period considerably depends on the efficiency of utilization of food resources of the river system. In this connection, it seems important to study feeding of juveniles of salmonids in a multispecies community of Kamchatka rivers.

There is comprehensive literature on the feeding of juveniles of different species of salmonids in the rivers of the basin of the Pacific Ocean; however, most papers concern analysis of feeding of separately taken species (Semko, 1956; Zorbidi, 1970, 2010; Gritsenko, 1973; Zhul'kov, 1974; Volobuev et al., 1985; Vvedenskaya et al., 2003; Kirillova and Kirillov, 2006; Malyutina and Savvaitova, 2009). Only in single papers, issues concerning feeding of jointly dwelling species are considered, and some aspects of interspecific trophic relations are assessed (Volovik, 1964; Churikov, 1975; Esin et al., 2009). On Kamchatka, the most complete evidence on the feeding of juveniles of salmonids and on the assessment of their food resources (specific features of feeding of separate fish species, seasonal and diurnal dynamics of drift and benthic communities) belongs to few aquatic systems, mainly to the basin of the Bolshaya River on the western coast of the peninsula (Vvedenskaya and Travina, 2008; Esin et al., 2009; Zkharova and Khiarenko, 2009; Travina and Yarosh, 2010). Data on other rivers are fragmentary and, as a rule, belong to one species. Seasonal changes in the pattern of feeding of juveniles, especially under conditions of joint habitation, remain poorly studied.

At the same time, detailed evidence on the feeding of juveniles of salmonids is of interest for understanding regularities of functioning of ecosystems of salmon rivers of Kamchatka.

The purpose of this investigation is to study seasonal changes in the feeding of uneven-aged juveniles of salmonids with a prolonged period of life in the basin of the Kol River (western Kamchatka) and assessment of interspecific trophic relations under conditions of joint habitation.

MATERIALS AND METHODS

Our own collections in 2008 in the basin of the Kol River were material for the study of feeding of juveniles of salmonids.

The Kol River is located on the west coast of Kamchatka, in the southern part of Sobolevskii district of Kamchatka krai; it originates in spurs of the Central Kamchatka Ridge and inflows the Sea of Okhotsk. Its extent along the main channel is approximately 130 km, width in the mouth is 72 m, water discharge in the mouth is 60 m^3/s at the base flow, and area of drainage basin is 1580 km^2. The river has a mountain and piedmont pattern from the river headwaters to the estuary; floodplain is strongly developed, its width at some sites reaches 5 km. A multitude of tributaries that by their type are divided into two groups—mountain and tundra—inflow the river. In the tributaries, especially in tundra ones, species diversity of salmonid juveniles and their density and biomass are high (Pavlov et al., 2009). All over its extent, the river is characterized by diverse combination of the main channel, side channels, springbrooks and oxbows; at their greater extent, off-channel habitats dominate over the main channel by length and area (Pavlov et al., 2009; Gruzdeva et al., 2011a). On the whole, the system of the Kol River has a high degree of mosaicism of geomorphological structure: practically each site of the main river channel, tributary or off-channel habitats are characterized by a peculiar combination of temperature regime, parameters of the water flow, fractional composition of bottom substrate, degree of manifestation of silty load, structure of plant communities at banks, etc. (Pavlov et al., 2009). Correspondingly, species composition and biomass of invertebrates considerably vary at different sites of the river system (Yarosh et al., 2009).

Floodplain ortho- and parafluvial springbrooks are a typical element of the structure of the Kol River system. Parafluvial springbrooks—short (50–150 m), shallow (20–40 cm) floodplain lotic water bodies with feeding at the expense of hyporheic ground waters—are located at river spits or low floodplain terraces; they inflow the main channel or secondary channels, and are usually inundated by flood waters. Their length, water content, and configuration vary after each flood (Stanford et al., 2005; Pavlov et al., 2009; Kuzishchin, 2010). The total extent of parafluvial springbrooks in the floodplain of the middle course of the Kol River reaches 10.7 km per 1 km of the main channel. Orthofluvial springbrooks are more extended (400–1300 m) and deep (30–80 cm), their feeding occurs at the expense of ground waters of the alluvial flow and phreatic ground waters; they flow among high river terraces and inflow lateral tributaries of the second to third order. An old forest with an age of more than 50 years grows at banks. The configuration of banks does not change during many years, and water content varies insignificantly throughout the year. They are not flooded by floodplain waters, and water in them remains transparent and colorless (Stanford et al., 2005; Pavlov et al., 2009; Kuzishchin, 2010). The total extent of orthofluvial springbrooks in the floodplain of the middle course of the Kol River reaches 6.4 km per 1 km of the main channel.

Preliminary studies of distribution of juveniles of salmonids performed in 2003–2007 demonstrated that numerous para- and orthofluvial springbrooks are keystone elements of the system of the Kol River for summer–autumn foraging of the salmonid juveniles with a long freshwater period of the life cycle. Densities of juveniles (of all species) in spring streams are considerably higher than in the main river channel. Considering the rather considerable area of springbrooks, one can assume that the overwhelming majority of juveniles of salmonids feed precisely in them (Pavlov et al., 2009; Gruzdeva et al., 2011a, 2011b). In this connection, collection of material for analysis of feeding and food relations of juveniles of salmonids were performed mainly in the off-channel habitats: of two parafluvial spring and one orthofluvial spring streams, two tributaries—Skvichik stream (of the tundra type) and Simovyi stream (of the mountain type). For comparison, material from the main channel of the Kol River in its lower course was collected (Fig. 1).

Fish were captured at limited sites (polygons) of the listed water courses. At selection of localization of polygons and its borders (sizes), we proceeded from the fact that each polygon should satisfy the following conditions: (1) juveniles of all species of salmonids should inhabit the polygon in a ratio typical for the entire water body on the whole (tributary or springbrook); (2) on the polygon, there should be all typical elements of the structure of the given water body and all types of biotopes (shallow shoreline, secluded zone, eddy pit, etc.) inhabited by juveniles of different species of salmonids; (3) the polygon, according to its hydrogeomorphological characteristics should to a maximum extent correspond not only to the given water body (tributary, spring stream) but also to other water bodies of the same type; (4) sizes of polygons should be sufficient for collection of representative samples of juveniles of each species and more or less comparable between themselves, at least for water bodies of similar type.

As a result of analysis of the structure of the river system according to satellite depictions (platform ICONUS, NASA, United States) and direct study of the Kol River system, several polygons were selected (Table 1). Characteristics of polygons are comparable between themselves. In the tributaries and orthofluvial

Fig. 1. Scheme of the Kol River and the site of material collection (Δ): (*1*) parafluvial springbrook 1, (*2*) parafluvial springbrook 2, (*3*) orthofluvial springbrook, (*4*) tributary of tundra type (Skvichik stream), (*5*) tributary of mountain type (Simovyi stream), (*6*) site of the main channel at a distance of 13.2 km from the stream.

springbrooks of the capture zone, there are two stretches separated by one riffle; in parafluvial springbrooks, ther is one stretch limited by riffles. Thus, polygons selected for performing studies are maximum standardized, and in full measure reflect the pattern of water bodies and are typical for the basin of the Kol River. In this connection, results of studies can be considered as representative for the entire river basin.

Material was collected thrice for the field season at the beginning of July (immediately after spring flood and termination of the mass seaward migration of pink salmon *O. gorbuscha* and chum salmon *O. keta*), in mid-August (period of summer base flow), and in mid-September (low water, after termination of mass spawning of pink salmon). It is known that the intensity of feeding of juveniles of salmonids considerably varies during the day—sometimes it is highest at night, while sometimes it is highest in the daytime (Shapovalov and Taft, 1954; Zorbidu, 1970, 1977, 2010; Sandercock, 1991; Wiphli, 1997; Noble et al., 2005; Kirillova and Kirillov, 2006; Chebanova, 2009). In our study, material was collected everywhere from 11:00 a.m. to 2:00 p.m. under similar weather conditions and maximum illumination, as it is considered that juveniles of salmonids feed in the light hours of the day more intensively precisely under such conditions (Fausch and White, 1981; Bechara et al., 1992, 1993). Water temperature in water bodies during capture of fish varied from 8 to 11°C; after catch, juveniles were immediately fixed in 4% solution of formaldehyde.

A total of 3223 individuals of all species and age classes of salmonids were studied, sample sizes according to water bodies and the time of collection are given in respective tables and figures.

In each fish, fork length (*FL*) and body weight were measured and sex and age were determined. Within the sample, juveniles of all species were separated into young-of-the-year (0+) and parrs at an age of 1+. In the overwhelming majority of sites, these fish accounted for more than 95% of the numbers and biomass. Juveniles of an older age were rare and were excluded from the analysis.

Fixed material was processed under laboratory conditions. Food composition was studied by the counting–gravimetric method (Shorygin, 1952; *Rukovodstvo po izucheniyu*..., 1961). The total weight of the food bolus and separate components was determined with an accuracy to 0.001 g; when possible, the number of objects of each group was recounted. For classification of food organisms, Kheisin key (1962) and Hauer and Resh tables (2006) were used, food organisms were determined up to family or subfamily. In this connection, the following groups of organisms are distinguished in our study in the food bolus: larvae of amphibiotic insects—stone flies (Plecoptera), mayflies (Ephemeroptera), caddis flies (Trichoptera),

Table 1. Characteristic of polygons at which material for analysis of feeding of juveniles of Salmonidae in the basin of the Kol River was collected

Index	Polygon/zone of capture					
	lower course of the tundra tributary/two stretches separated by one riffle	middle course of the mountain tributary/two stretches separated by one riffle	parafluvial springbrook 1/–80% of the length of the entire stream, long shallow stretch	parafluvial springbrook 2/~75% of the length of the entire stream, long shallow stretch	orthofluvial; springbrook/two stretches separated by one rapid total ~10% of the stream length	main channel in the lower course/site of shallow shoreline along gently sloping bank
Size:						
—length, m	103	91.8	84.5	73.6	73.6	93.5
—average weighed width, m	3.11	2.86	3.31	2.65	5.44	4.01
—total area, m^2	308.5	252.4	260.7	188.4	389.7	369.3
—average depth, m	0.31	0.28	0.39	0.33	0.43	0.32
Bottom substrate, %:						
—boulders	–	30	–	–	–	5
—gravel	50	10	50	60	60	45
—pebble	30	55	20	-	30	30
—sand	20	5	30	40	10	20
Silt, % of the area	–	–	25	35	15	–
Vegetation on banks:						
—tree	Willow and chosenia at an age of 30–50 years, crowns of trees cover up to 50% of the water plane	Willow and alder at an age of >50 years, crowns of trees completely close water plane	Willow at an age of ~10 years, crowns of trees completely close water plane	Alder at an age of 50–70 years, crowns of trees completely close water plane	Willow at an age of 60–80%, crowns of trees close >90% of the water plane	Separate willows at an age of 20–30 years, crowns slightly hang over water
—grass	Nettle, meadowsweet, grasses	Groundsel, meadowsweet, nettle	Grasses and nettle	Nettle, meadowsweet, groundsel	Nettle, meadowsweet, groundsel	Nettle, grasses
General characteristic	Typical by structure for ~75% of the length of the given tributary and similar to other tundra tributaries of the Kol River in their lower and middle course	Typical by structure for ~80% of the length of the given tributary and similar to most mountain tributaries of the Kol River in their lower and middle course	Typical floodplain springbrook, similar by structure to ~60% of streams in the middle and lower course of the Kol River	Typical floodplain springbrook, similar by structure to ~40% of streams in the middle course of the Kol River	Typical springbrook, similar by structure to overwhelming majority of orthofluvial streams in the middle course of the Kol River	Typical site of coastal shallow shoreline in the lower and middle course of the Kol River

Tree vegetation—willow *Salix* sp., chosenia *Chosenia arbutifolia*, alder *Alnus* sp.; grass vegetation—nettle *Urtica* sp., meadowsweet *Filipendula tschatica*, grpundsel *Senecio cannabifolius*.

chironomids (Chironimidae) (up to subfamily); larvae of ground insects—butterflies (Lepidoptera), (caterpillars), weevils (Curculionidae), flies (Muscidae) (maggots); imago of ground insects (Insecta)—beetles (Coleoptera), bivalves (Diptera), worms (Oligochaeta); eggs of salmonids; and fish. Nonfood objects (plant remains, small and large sand grains with a size of 1.5–7.0 mm) were considered separately. Parallel to capture of fish, benthos samples were collected using a Stanford–Hauer benthic net over an area of 0.5 m^2 (Hauer and Resh, 2006). In the sample, composition of the most important groups of invertebrates was assessed. For several groups of invertebrates (larvae of caddis flies, mayflies, stone flies, flies); their length and width were measured since the width of a food organism best correlates with diameter of mouth opening (Mikheev, 1984, 2006). For a more accurate determination of the size and weight of prey in stomachs of fish, regression equation of body length–fragment length was calculated; further, biomass of prey was calculated using regression equation of body length–wet mass (Borutskii, 1960; Balushkina and Vinberg, 1979; Mikheev, 2006).

Index of stomach fullness (ISF) was calculated as the ratio of the weight of food bolus and the weight of fish and expressed in prodecimilles (0+). For calculations of food similarity, Shorygin index of food similarity (1952) and index of overlapping of food niches (Schoener, 1970, 1971) were used.

Material was processed by methods of standard univariant analysis (Lakin, 1990), and mass proportions of feeding components were used in calculations. Besides, cluster analysis was used to compare pattern of feeding. It is known that mathematical analysis of feeding of fish has several limitations related first of all to an abnormal distribution of characters (Mikheev, 2006), while the use of methods of multidimensional statistics requires normal distribution of the used characters (James and McCulloch, 1990). Therefore, analysis of distribution of mass proportions of this or another component was performed in the samples. In most cases, the observed distributions had a strong positive excess, i.e., in different individuals, no noticeable differences by the quantitative composition of feeding components in the food bolus were revealed. Apparently, it is determined by sufficiently limited areas of biotopes on which fish samples were collected; therefore, the pattern of feeding of all individuals in the sample was similar. In this connection, we considered it justifiable to use the method of cluster analysis.

RESULTS

Feeding of Juveniles of Salmonids at Different Sites of the River Kol System

Tundra tributary. In the lower course of the tributary, juveniles of five species of salmonids dwell: coho salmon *Oncorhynchus kisutsch*, cherry salmon *O. masou*, Dolly Varden char *Salvelinus malma*, East Siberian char *S. leucomaenis*, and Kamchatka steelhead *Parasalmo mykiss*. Juveniles practically do not ascend from the main course of the river to the tributary. According to numbers and biomass in the low reaches of the tundra tributary, juveniles of coho salmon and Dolly Varden char dominate: in the aggregate, juveniles of these species comprise 48–56% of the numbers (proportions of coho salmon and Dolly Varden char are nearly equal), while smaller numbers are typical of cherry salmon (17–22%), Kamchatka steelhead (16–19%), and East Siberian char (approximately 10%). In the summer–autumn period, juveniles of salmonids are represented mainly by two age classes—fingerlings (0+) and two-year olds (1+). In rare cases, single three-year olds (2+) of Dolly Varden char, East Siberian char, and Kamchatka steelhead were found. The average density of all fish at the site in July, August, and September comprises 3.39, 2.88, and 4.02 ind./m^2, respectively. Throughout the season, a regular increase in the average body length and weight of juveniles of most species, except two-year olds of East Siberian char and cherry salmon is observed (Table 2). In August–September, spawning of pink salmon takes place in the lower course.

Juveniles of salmonids of all species and all age classes actively fed during summer and autumn: no individuals with empty stomachs were found (Table 2). Nevertheless, stomach fullness of juveniles of different species varied throughout the period of observations. Fingerlings of salmonids had the highest indices of ISF in September, while stomach fullness of fingerlings of different species had an ambiguous pattern. In coho salmon and Kamchatka steelhead, ISF increased throughout the summer–autumn period; two-year olds of cherry salmon, on the contrary, were characterized by a decrease in stomach fullness in the period from July to September, two-year olds of Dolly Varden char had the highest ISF in August, and two-year olds of East Siberian char at this time had, on the contrary, minimal ISF.

At the beginning of July, in the tundra tributary, juveniles of salmonids use a wide spectrum of allo- and autochtonous organisms as food. Juveniles of different species and different age are characterized by considerable differences in the pattern of feeding. In the feeding of juveniles of coho salmon, imago of terrestrial insects and their larvae comprise a considerable proportion. In fingerlings of coho salmon, approximately 75% of the weight of food bolus consists of larvae of butterflies (caterpillars) and weevils dwelling on leaves of willow and grass plants and imago of insects (Culicidae, Chironomidae, and Coleoptera) dwelling on leaves of semi-aquatic vegetation.

In parrs of coho salmon (1+), up to 40% of food bolus are occupied by larvae of mayflies, stone flies, and caddis flies (the so-called "EPT group"—Ephemeroptera, Plecoptera, Trichoptera); approximately 40% are oligochaetes (aquatic and terrestrial)

Table 2. Length and weight of the body, index of stomach fullness in juveniles of Salmonidae in Skvichik stream—tundra tributary of the Kol River

Species	Month	Age, years	Length, mm	Weight, g	Index of stomach fullness, ‱	n, ind.
Coho salmon	July	0+	49.6 (34–65)	1.9 (0.5–3.7)	131.6 (64–292)	25
		1+	86.1 (75–102)	8.8 (5.4–13.3)	62.7 (24–319)	34
	August	0+	56.4 (45–68)	2.6 (1.3–4.7)	122.9 (168–384)	33
		1+	84.9 (71–100)	9.4 (4.5–14.4)	244.1 (144–858)	33
	September	0+	60.6 (49–75)	3.5 (1.7–6.8)	299.1 (101–862)	30
		1+	100.3 (86–113)	15.7 (9.7–23.1)	322.3 (176–938)	39
Cherry salmon	July	0+	54.7 (39–66)	2.6 (0.8–4.5)	172.4 (85–672)	23
		1+	98.8 (72–123)	12.6 (4.4–20.8)	118.8 (76–347)	20
	August	0+	63.4 (56–73)	3.69 (2.1–6.7)	218.8 (88–530)	23
		1+	102.6 (95–113)	16.9 (13.1–21.8)	116.2 (56–269)	23
	September	0+	64.1 (52–71)	4.2 (2.3–6.4)	288.8 (136–837)	30
		1+	88.4 (76–116)	10.8 (6.7–21.8)	111.5 (80–506)	29
Dolly Varden char	July	0+	43.7 (31–70)	1.3 (0.4–4.9)	166.2 (50–275)	33
		1+	108.5 (74–138)	15.9 (5.2–29.2)	87.4 (49–308)	33
	August	0+	49.7 (46–58)	1.4 (1.0–2.1)	176.7 (85–506)	30
		1+	101.1 (81–121)	13.3 (6.9–22.4)	157.2 (31–442)	26
	September	0+	61.0 (48–72)	3.0 (1.3–5.7)	349.9 (128–927)	28
		1+	118.0 (104–134)	21.9 (14.5–31.9)	121.4 (89–567)	30
East Siberian char	July	0+	48.7 (46–54)	1.8 (1.4–2.4)	224.1 (173–257)	23
		1+	125.9 (88–169)	26.7 (8.1–59.3)	117.9 (95–556)	21
	August	0+	57.3 (54–63)	2.4 (2.1–3.1)	218.9 (101–955)	27
		1+	127.0 (87–159)	29.1 (9.1–62.6)	154.5 (81–748)	23
	September	1+	102.1 (76–151)	19.1 (6.4–51.6)	332.4 (155–987)	27
Kamchatka steelhead	July	1+	104.4 (72–150)	16.8 (5.7–39.9)	87.4 (38–273)	28
	August	0+	38.6 (36–41)	0.9 (0.8–0.9)	215.3 (111–311)	25
		1+	109.3 (79–163)	19.4 (6.1–54.2)	158.7 (86–291)	23
	September	0+	54.2 (49–61)	2.1 (1.6–3.3)	339.9 (132–876)	22
		1+	118.0 (113–123)	21.7 (19.3–24.1)	304.2 (195–512)	22

Here and in Tables 3–7: beyond the parentheses—average value of the index, in parentheses—limits of its variation; n is number of studied fish.

and approximately 20% are imago of insects (Fig. 2a). The diet of fingerlings of Dolly Varden char by almost 70% consists of small larvae of caddis flies (Apataniidae and Glossosomatidae) and stone flies (mainly Perlodidae and Chloroperlidae); larger two-year olds of Dolly Varden char feed on a different set of foods: almost 50% of their diet consist of larvae of stone flies and approximately 45% consist of larvae of chironomids (Orthocladiinae, Diamesinae, and Chironominae). In the feeding of two-year olds of Kamchatka steelhead and East Siberian char, fish food has considerable importance: 43–46 and 33–37%, respectively. As a rule, small (*FL* up to 27–34 mm) fingerlings of Dolly Varden char become prey of Kamchatka steelhead, while East Siberian char feeds on small fingerlings of coho salmon $FL \leq 38$ mm.

In July, juveniles of all species at an age of 1+ demonstrate territorial behavior; among fingerlings, it is most pronounced in East Siberian char, cherry salmon, and Dolly Varden char. Fingerlings of coho salmon stay in small schools, 4–10 ind. each, at sites of the tributary with a weak current.

In August, food composition of juveniles of all species and age classes considerably varies (Fig. 2b). Fingerlings of cherry salmon reduce consumption of oligochaetes (their proportion in the food bolus is less than 20%) and begin to feed more intensively on caterpillars and imago of insects (total proportion of

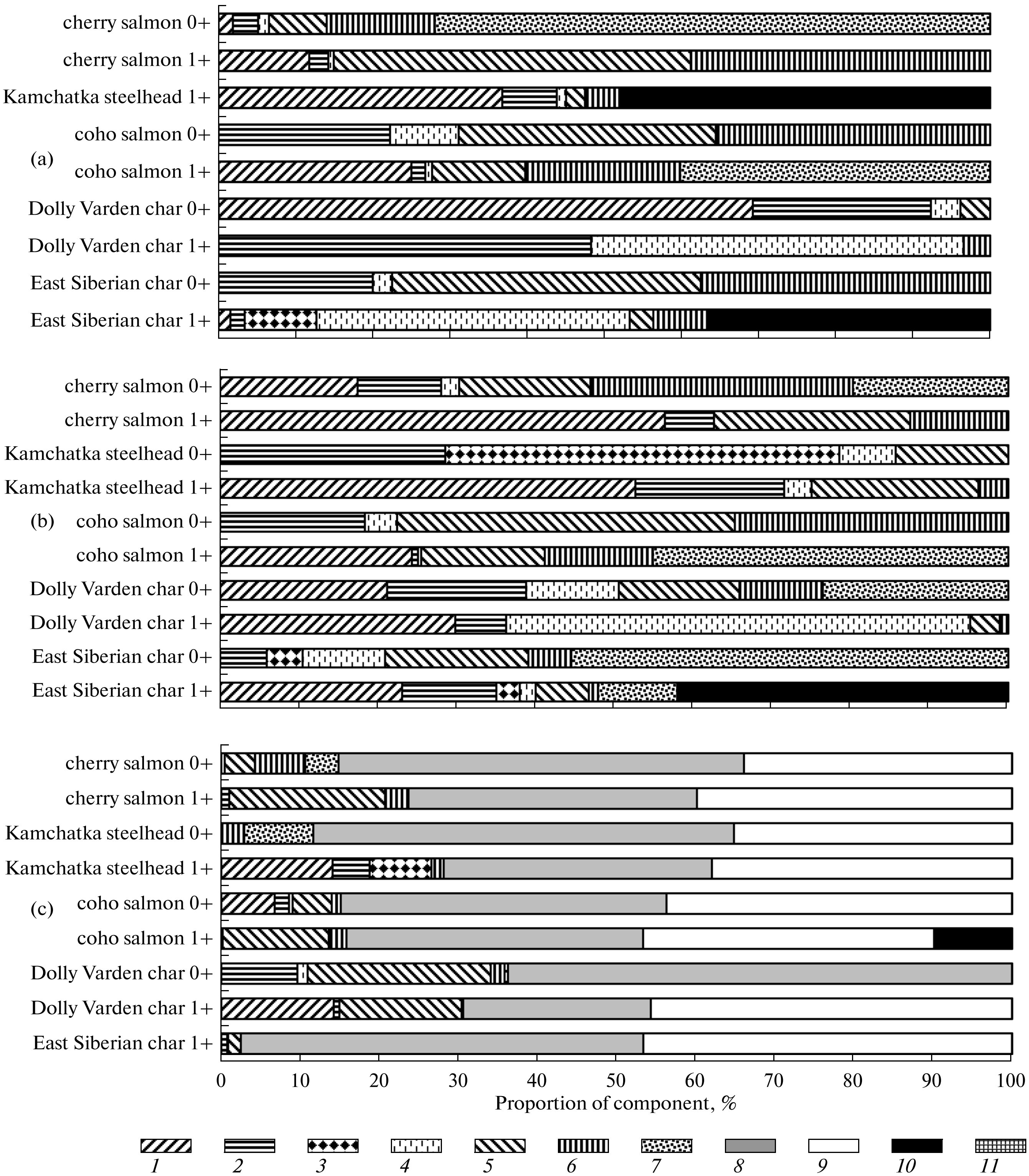

Fig. 2. Spectra of feeding of juveniles of Salmonidae in Skvichik stream–tundra tributary of the Kol River in different months: (a) July, (b) August, (c) September. (*1*) larvae of caddis flies, (*2*) larvae of stone flies, (*3*) larvae of mayflies, (*4*) larvae of chironomids and moths, (*5*) caterpillars, (*6*) imago of insects, (*7*) oligochaetes, (*8*) larvae of flies, (*9*) eggs of Pacific salmon *Oncorhynchus* sp., (*10*) fish, (*11*) mollusks.

~50%). Two-year olds of cherry salmon drastically increase consumption of larvae of caddis flies, mainly Brachycentridae (>55%), and simultaneously decrease consumption of caterpillars and imago of insects. At the same time, two-year olds of Kamchatka steelhead begin to more intensively consume larvae of EPT group (total proportion >70%). Fingerlings of Kamchatka steelhead, as well as two-year olds, feed on larvae of amphibiotic insects; however, in them, early larvae of mayflies (Baetidae and Heptageniidae) play an important role in feeding. Different-age juveniles of coho salmon continue to retain differences in feeding. In two-year olds, ground oligochaetes have considerable importance, while they are lacking in the diet of fingerlings and caterpillars and imago of insects occupy the most important place. Food spectrum of juveniles of Dolly Varden char slightly varies: in two-year olds, the proportion of caddis flies increases due to the consumption of large larvae of Limnephilidae, but the consumption of larvae of stone flies decreases, fingerlings actively consume aquatic oligochaetes (up to 23%). Among juveniles, only two-year olds of East Siberian char lead a predatory mode of life, consuming, as in July, mainly fingerlings of coho salmon (proportion of fish in the food bolus increases to 43%). In August, a noticeable decrease in imago of ground insects and an increase in the role of oligochaetes and caterpillars (except for Kamchatka steelhead) are a typical feature of feeding of juveniles of most species of salmonids. Thus, in August also, juveniles of salmonids continue to feed on ground objects but not those as in July. Apparently, this is related to seasonal processes—rapid growth of larvae of butterflies on semiaquatic vegetation and washout of them and of ground oligochaetes by rain. In single cases (1 ind. of salmon trout, 2 ind. of coho salmon, and 1 ind. of East Siberian char), one–two ants (Hymenoptera) were found in the food bolus.

In September, feeding of all juveniles of salmonids, as in August, changes considerably. At this time in the lower and middle course of the tributary, mass spawning of pink salmon, its mass death, and decomposition of carcasses occur. Juveniles of all species and age classes pass to feeding on eggs of pink salmon and larvae of flies (maggots). The proportion of these two components in feeding drastically dominates from 63% in fingerlings of Dolly Varden char to 96% in two-year olds of East Siberian char (Fig. 2c). At the same time, juveniles of salmonids as before consume larvae of amphibiotic insects and caterpillars. It is noteworthy that only two-year olds of coho salmon consume fish food in September (~10%); their own fingerlings become their prey.

In September, a change in behavior of juveniles occurs. All species pass to a shoaling habit. To a maximum degree, it is typical of cherry salmon, Dolly Varden char, and coho salmon: schools consisting of fingerlings and two-year olds form in these species. At feeding on eggs or larvae of flies, juveniles of all species and size groups consume them simultaneously.

On the whole, during the entire season, juveniles of salmonids feed on any invertebrates accessible for them by size.

Piedmont tributary. Juveniles of four species of salmonids—coho salmon, cherry salmon, Dolly Varden char. East Siberian char inhabit the tributary; here, spawning grounds of Pacific salmon (cherry salmon, chum salmon, sockeye salmon *O. nerka*, coho salmon, pink salmon) and chars (Dolly Varden and East Siberian char) are located. By numbers, juveniles of cherry salmon dominate—in all years of observations, their proportion in catches was 32–38%; juveniles of Dolly Varden were 22–29%, coho salmon were 20–26%, and East Siberian char were 11–16%. During the summer–autumn period, the proportion of species at the site remained more or less similar. The average density of all fish at the polygon in July, August, and September comprised 2.76, 6.75, and 6.32 ind./m^2, respectively.

In the piedmont tributary, juveniles of all species of salmonids in the summer–autumn period fed intensively, no fish with empty stomachs were found. Stomach fullness of juveniles varied throughout the season of observations: in different-age juveniles of coho salmon, lamprey, and East Siberian char, maximum indices of ISF were recorded in September, and those in juveniles of cherry salmon were recorded in August (Table 3).

In the period of observations in the piedmont tributary, juveniles of all species were represented by two age classes—fingerlings and two-year olds. In rare cases, three-year olds of Dolly Varden, East Siberian char, and precocious males of cherry salmon of age class 2+ were found. During the season, an increase in indices of average length and body weight of juveniles occurs (Table 3). ISF of fingerlings of coho salmon regularly increases from July to September, while maximum values of the index are observed in August in two-year olds of coho salmon. A similar picture was found in fingerlings and two-year olds of cherry salmon—maximum values of ISF are observed in August. An increase in ISF from July to September is typical for all juveniles of Dolly Varden and East Siberian chars. Juveniles of different species in the summer–autumn period feed differently. For instance, all juveniles of coho salmon feed less intensively in July than juveniles of other species; high values of ISF were revealed in cherry salmon and East Siberian char. In August, minimal stomach fullness is recorded in uneven-aged juveniles of Dolly Varden char, and maximum is recorded in juveniles of cherry salmon. In September, maximum values of ISF are typical of different-age juveniles of East Siberian char, while minimal are typical of juveniles of coho salmon and cherry salmon.

At the beginning of *July*, maximum diversity of food organisms is observed in the food bolus of juve-

Table 3. Length and weight of the body, index of stomach fullness in juveniles of Salmonidae in Simovyi stream—mountain tributary of the Kol River

Species	Month	Age, years	Length, mm	Weight, g	Index of stomach fullness, ‰o	n, ind.
Coho salmon	July	0+	50.8 (33–62)	2.15 (0.4–3.8)	79.0 (33–189)	36
		1+	79.4 (67–93)	6.32 (3.7–9.7)	70.3 (18–148)	30
	August	0+	53.1 (40–65)	2.32 (0.9–4.8)	246.2 (173–725)	37
		1+	87.3 (71–102)	10.20 (6.2–18.6)	406.9 (189–1218)	29
	September	0+	56.6 (51–62)	2.6 (1.7–3.8)	340.4 (138–741)	30
		1+	101.4 (92–115)	17.7 (13.6–25.9)	249.2 (119–791)	30
Cherry salmon	July	0+	53.9 (42–63)	2.35 (1.2–3.6)	125.4 (78–292)	22
		1+	92.3 (75–109)	10.1 (5.0–15.4)	135.4 (85–659)	28
	August	0+	63.1 (50–73)	4.03 (1.9–6.9)	360.8 (127–1154)	30
		1+	102.5 (88–122)	16.4 (10.0–29.7)	565.2 (189–1128)	27
	September	0+	66.0 (57–76)	4.90 (2.5–8.2)	352.6 (125–917)	30
		1+	116.7 (85–154)	24.8 (10.2–61.0)	206.7 (116–665)	37
Dolly Varden char	July	0+	45.0 (36–69)	1.12 (0.5–3.1)	125.1 (68–333)	20
		1+	97.3 (83–121)	9.78 (5.4–17.7)	124.9 (79–897)	26
	August	0+	46.1 (37–55)	1.32 (0.7–2.2)	113.2 (113–539)	28
		1+	105.0 (80–152)	16.9 (6.6–50.8)	337.0 (192–1295)	26
	September	0+	59.3 (50–71)	2.71 (1.5–4.7)	421.1 (166–1240)	20
		1+	128.5 (106–165)	34.8 (17.8–64.6)	480.3 (182–1381)	20
East Siberian char	July	0+	46.0 (36–58)	1.35 (0.6–2.5)	132.3 (81–367)	20
		1+	102.1 (72–149)	14.1 (3.6–35.9)	117.2 (83–453)	35
	August	0+	52.4 (45–62)	1.96 (1.2–3.0)	181.2 (82–929)	21
		1+	106.6 (75–167)	19.5 (6.6–57.6)	365.6 (124–1290)	29
	September	0+	60.3 (50–69)	3.11 (1.7–5.2)	467.7 (165–1267)	30
		1+	120.0 (97–170)	30.2 (15.7–80.1)	672.7 (192–2790)	35

niles of different species (Fig. 3a). Different-age juveniles of coho salmon feed in their overwhelming majority on imago of insects (firstly, on beetles, total proportion >50%), caterpillars, and larvae of weevils (total proportion >20%). In coho salmon, the degree of similarity in the pattern of feeding of small fingerlings and larger two-year olds is high. The high proportion of beetles in the feeding of juveniles of coho salmon is determined by specific features of the structure of the stream floodplain. It runs through a mature alder-willow forest that forms a continuous canopy above the stream. Numerous beetles and their larvae that feed on leaves of trees constantly fall into water and become prey of fish. Caterpillars and larvae of weevils that also dwell on leaves of semi-aquatic plants are second in feeding of juveniles of coho salmon. In total, imago of insects, caterpillars, and larvae of beetles comprise 72–86% of the food bolus in fingerlings and 78–84% in two-year olds of coho salmon. Small larvae of stone flies and blackflies (Simuliidae) have a smaller importance in their feeding. In food boluses of all juveniles, we found no larvae and pupae of chironomids, which is determined by their extremely low occurrence in the composition of benthic invertebrates in the considered mountain tributary.

In other species of salmonids, considerable differences in feeding between fingerlings and two-year olds were found. In two-year olds of Dolly Varden char, cherry salmon, and East Siberian char, the proportion of occurrence of fish food in stomachs is high: >50% in Dolly Varden and >80% in cherry salmon and East Siberian char. Their feeding is based on small fingerlings of Dolly Varden and coho salmon; in many cases, cannibalism is observed. In fingerlings of these species, the main components of feeding are imago of insects, caterpillars, larvae of weevils, and amphibiotic insects. In this or another combination these groups of organisms have predominant proportion in the feeding of juveniles. Feeding of fingerlings of cherry salmon and East Siberian char is based on imago of insects (beetles), caterpillars, and larvae of weevils; larvae of stone flies have smaller importance (more frequently

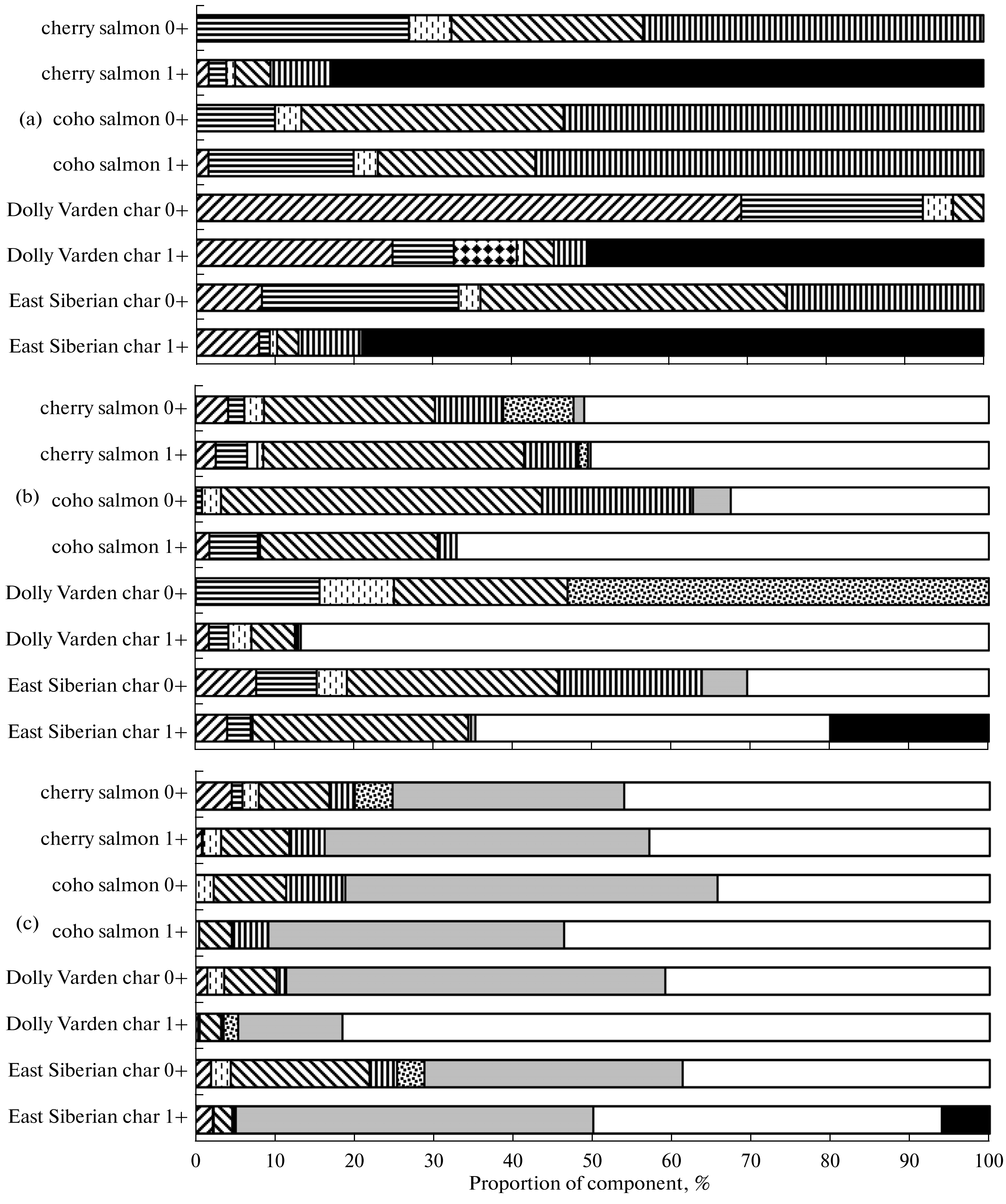

Fig. 3. Spectra of feeding of juveniles of Salmonidae in Simovyi stream–piedmont tributary of the Kol River in different months: (a) July, (b) August, (c) September; designations see in Fig. 2.

Perlodidae, less frequently Chloroperlidae). Compared to cherry salmon, fingerlings of East Siberian char consume considerably more small larvae of caddis flies (Apataniidae). Fingerlings of lamprey consume mainly larvae of caddis flies (Apataniidae, Limnephilidae, and Glossosomatidae) and, to a smaller degree, larvae of stone flies (Perlodidae).

In July, a clearly defined territorial behavior and preference by each species of a definite microbiotope at the site of the tributary is typical of all juveniles, both fingerlings and two-year olds.

In *August* spawners of cherry salmon enter the tributary and their mass spawning begins. The pattern of feeding of juveniles of salmonids changes considerably—the eggs of salmon trout begin to play a dominant role for all species: its proportion in different species varies from 33% in fingerlings of coho salmon to 87% in two-year olds of Dolly Varden (Fig. 3b). Caterpillars are second in importance feeding component: 100% occurrence in fingerlings and two-year olds of all species; their proportion in the food bolus varies from 7% in two-year olds of Dolly Varden to 34% in fingerlings of coho salmon. At this time, juveniles of salmonids drastically decrease consumption of larvae of weevils and amphibiotic insects, although the biomass of the latter in August is high (9787 mg/m^2). Juveniles consume a few larvae of blackflies (Simuliidae), although their numbers (4254 ind./m^2) and biomass (6684 mg/m^2) are high and they completely cover the posterior side of boulders forming ground at many sites. Only fingerlings of Dolly Varden according to pattern of feeding considerably differ from juveniles of other species of salmonids. They do not consume eggs of Cherry salmon, since the sizes of their mouth are too small to swallow large (up to 6 mm) eggs. At the same time, observations of behavior of juveniles demonstrated that fingerlings of Dolly Varden constantly make attempts to seize eggs of cherry salmon; however, they are unsuccessful and the final result is that sooner or later an egg falls from the mouth and is eaten by larger fish of its own or alien species. Nevertheless in August, compared to July, a drastic change in the structure of feeding occurs in fingerlings of Dolly Varden: they pass to ground oligochaetes, whose proportion in the food bolus exceeds 50%.

In August, behavior of juveniles cardinally changes: they demonstrate schooling behavior with formation of multi-species schools consisting of fish of different size. When feeding on eggs of cherry salmon, the school of juveniles tries to occupy a place in immediate vicinity of running spawners. An individual that seized an egg makes a dart to the side and its place is occupied by another that is located, as a rule, downstream the current. During feeding, constant displacement of the school members occurs; from a detached view, these displacements seem chaotic. At the same time, no aggressive behavior of some school members towards the others was recorded.

In *September*, a considerable change in the pattern of feeding of all species is observed again. At this time, mass spawning of Pacific salmon (late chum salmon, sockeye salmon, and coho salmon) and chars (Dolly Varden and East Siberian char) occurs. After spawning, salmon carcasses are washed ashore by the current to banks where they decompose and serve as food for larvae of flies. Rainy weather typical for September on western Kamchatka leads to a variable regime of the tributary level; as a result, mass washout of maggots to the channel occurs where they are actively eaten by salmon juveniles. Thus, in September in the piedmont tributary, easily accessible foods related to spawning activity of salmonids (eggs and larvae of flies) appear, and, as a result, all juveniles of salmonids inhabiting piedmont tributaries feed on these foods. The total proportion of these two components in food boluses varies from 72% in fingerlings to 95% in two-year olds of East Siberian char (Fig. 3c). In September, even fingerlings of Dolly Varden already reach sizes allowing them to efficiently feed on large eggs of salmonids. According to our observations, fingerlings are capable of swallowing eggs on reaching the following length: lamprey—55 mm; coho salmon—51–52 mm; cherry salmon and East Siberian char—50 mm. In September, larvae of amphibiotic insects, terrestrial insects (imago and larvae), and oligochaetes represent insignificant by proportion feeding components for juveniles of salmonids in the piedmont tributary and are found more frequently in fingerlings than in larger fish—two-year olds. No fish food in stomachs of juveniles at this time was found.

In September, as in August, juveniles demonstrate a clearly pronounced schooling behavior.

Parafluvial springbrooks. Feeding of salmonids was studied in two typical parafluvial springbrooks (PSS-1 and PSS-2) spaced apart by 20 km (Fig. 1). The distinction of springbrooks involves the degree of development of plant succession: on banks of one, a young willow forest grows, grass vegetation is represented only by cereals, while the other runs through an old alder-willow forest, grass cover of its banks is represented by nettle, meadowsweet, and ragwort (Table 1).

In parafluvial springbrooks, juveniles of salmonids are represented mainly by juveniles of coho salmon and Dolly Varden of two age classes 0+ and 1+. In September, PSS-1 fingerlings of sockeye salmon ascend from the main channel. Juveniles of other species occur rarely; however, their numbers are low (<1%), and species and age composition are variable. In the springbrooks studied by us, juveniles of East Siberian char, king salmon *O. tschawytscha*, and cherry salmon were recorded singly. The ratio of different-age juveniles of coho salmon and Dolly Varden throughout the period of observations is nearly equal. The average density of all fish in PSS-1 in July, August, and September comprise 4.36, 4.12, and 4.21 ind./m^2 and that in PSS-2 is 4.26, 4.78, and 4.42 ind./m^2, respectively.

Table 4. Length and weight of the body, index of stomach fullness of juveniles of Salmonidae in the parafluvial spring stream 1, lower course of the Kol River

Species	Month	Age, years	Length, mm	Weight, g	Index of stomach fullness, ‰o	*n*, ind.
Coho salmon	July	0+	39.6 (32–50)	1.01 (0.4–2.0)	158.4 (79–318)	30
		1+	62.5 (48–75)	2.82 (1.3–4.7)	422.6 (275–1108)	25
	August	0+	49.6 (34–59)	1.98 (0.7–3.8)	202.5 (179–415)	30
		1+	76.3 (47–91)	6.52 (3.5–10.1)	656.3 (224–1305)	24
	September	0+	54.6 (48–68)	2.31 (1.1–4.1)	288.3 (192–505)	30
		1+	86.1 (77–97)	8.34 (6.0–10.6)	677.4 (265–1322)	25
Dolly Varden char	July	0+	43.4 (33–52)	1.00 (0.1–1.8)	119.3 (93–220)	30
		1+	65.9 (54–74)	2.86 (1.5–4.2)	288.5 (212–454)	25
	August	0+	49.0 (40–61)	1.30 (0.1–2.4)	146.7 (112–285)	30
		1+	84.6 (71–97)	6.67 (3.7–8.8)	387.4 (295–663)	25
	September	0+	58.3 (47–71)	1.97 (0.7–4.3)	185.4 (139–306)	30
		1+	105.5 (82–118)	15.2 (6.7–28.9)	400.2 (211–934)	25
Sockeye salmon	September	0+	47.6 (31–65)	1.14 (0.1–3.5)	121.4 (93–177)	40

Table 5. Length and weight of the body, index of stomach fullness in juveniles of Salmonidae in the parafluvial spring stream 2, middle course of the Kol River

Species	Month	Age, years	Length, mm	Weight, g	Index of stomach fullness, ‰o	*n*, ind.
Coho salmon	July	0+	41.3 (33–52)	1.05 (0.2–2.2)	169.3 (128–269)	50
		1+	68.3 (50–75)	3.03 (1.6–5.3)	345.5 (188–713)	50
	August	0+	54.8 (36–62)	2.17 (0.4–4.2)	215.6 (168–676)	50
		1+	81.4 (52–100)	7.11 (4.1–16.3)	705.5 (424–933)	50
	September	0+	61.1 (39–72)	2.20 (0.7–4.5)	297.4 (189–553)	50
		1+	100.3 (69–120)	11.21 (3.6–23.4)	653.5 (479–1015)	50
Dolly Varden	July	0+	42.2 (32–55)	0.95 (0.1–1.9)	136.5 (98–238)	50
		1+	73.4 (55–82)	3.77 (1.8–8.3)	359.6 (228–604)	50
	August	0+	48.8 (34–62)	1.33 (0.3–2.8)	178.5 (139–386)	50
		1+	89.3 (62–105)	7.32 (2.3–18.8)	479.6 (377–895)	50
	September	0+	60.3 (34–69)	2.07 (0.4–4.1)	202.5 (156–388)	50
		1+	113.4 (79–124)	22.5 (3.8–30.2)	524.7 (398–753)	50

Throughout the summer–autumn period, the average length and weight of the body of fish in both spring streams regularly increases (Tables 4 and 5). Stomach fullness of fish increases—indices of ISF in both species increase from July to September; in juveniles of Dolly Varden, they are lower than in juveniles of coho salmon. Noteworthy are very high values of ISF in August and September typical both of fingerlings and two-year olds of coho salmon and Dolly Varden (Table 4). No considerable difference in the intensity of feeding of juveniles in different springs was revealed. In the year of collecting seasonal samples on feeding and in all other years of observations in parafluvial springbrooks, no individual with an empty stomach was recorded among juveniles of all species.

Unlike river tributaries, in parafluvial springbrooks, no drastic seasonal changes in the pattern of feeding are observed. On the whole during the summer–autumn period, composition of food organisms in springbrooks remains similar (Figs. 4 and 5). Larvae and pupae of chironomids play a key role in the feeding of coho and Dolly Varden, which reflects their high numbers in benthos of spring streams. The total biomass of chironomids of all subfamilies varies from 78.3

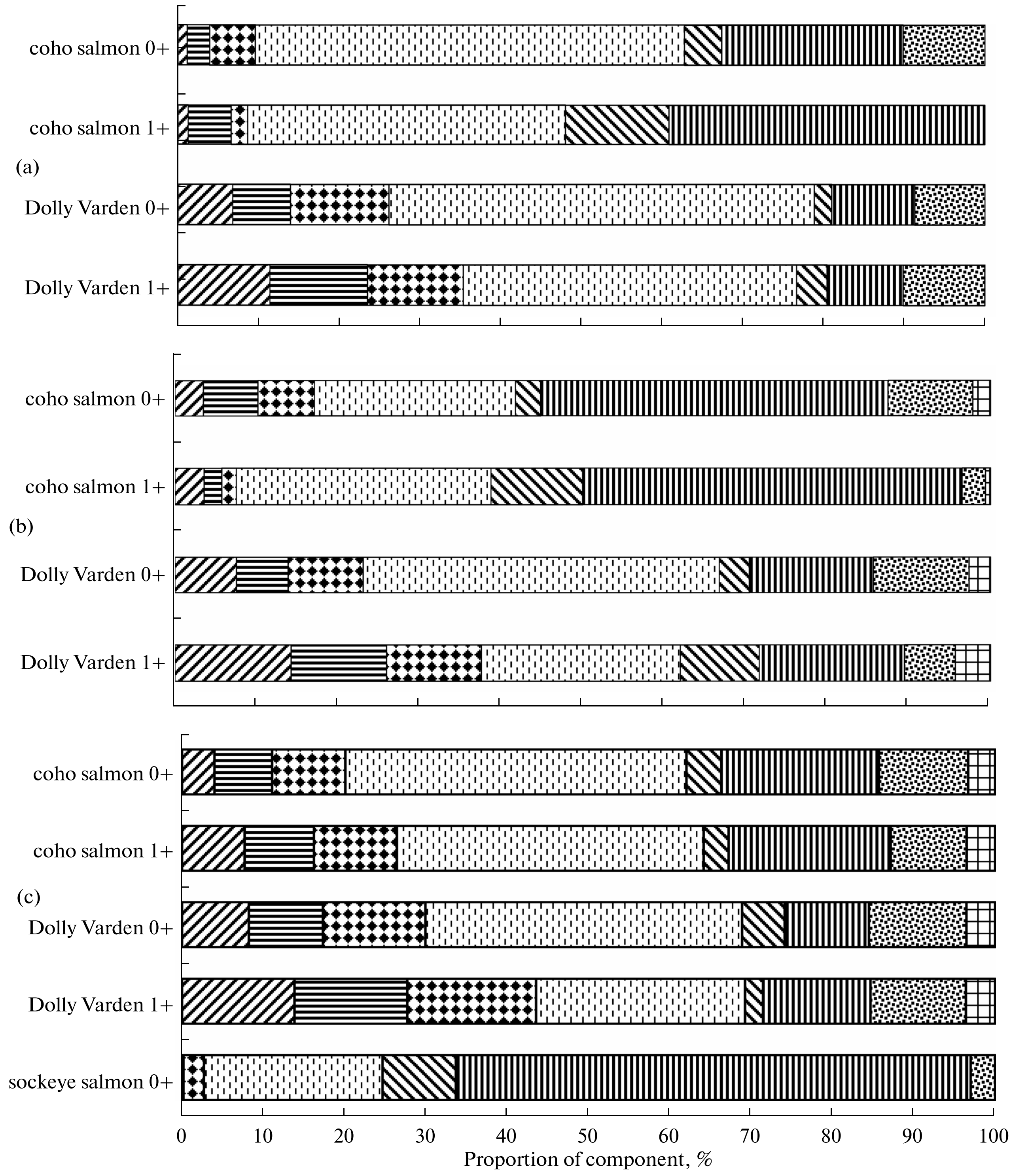

Fig. 4. Spectra of feeding of juveniles of Salmonidae in parafluvial springbrook 1, lower course of the Kol River in different months: (a) July, (b) August, (c) September; designations see in Fig. 2.

to 85.6% in different localities at total biomass of zoobenthos 9480–12340 mg/m^2. In the feeding of juveniles of salmonids, larvae of chironomids Chironominae and Orthocladiinae drastically dominate; Diamesinae and Tanypodinae occur rarely. In the period of observations, the proportion of larvae and pupae of chironomids varies; however, we revealed no distinctly pronounced tendencies related to seasonality. Imago of insects—chironomids and beetles, larvae of weevils and caterpillars, as well as aquatic oligocha-

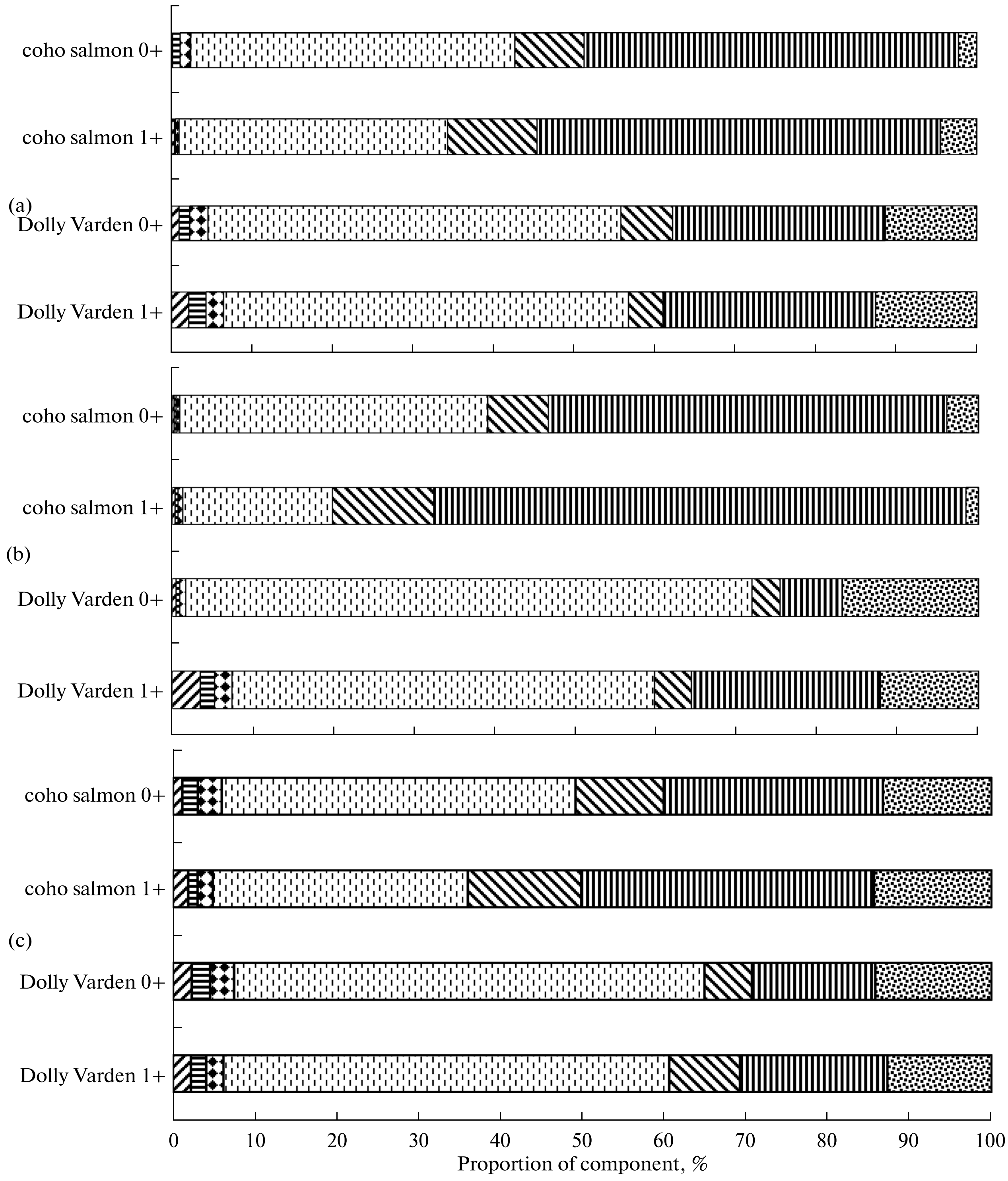

Fig. 5. Spectra of feeding of juveniles of Salmonidae in parafluvial springbrook 2, middle course of the Kol River in different months: (a) July, (b) August, (c) September; designations see in Fig. 2.

etes—have slightly smaller importance in seasonal feeding of juveniles of coho salmon and Dolly Varden. Extremely rarely (2 ind. of coho salmon 1+ in PSS-1 and 1 ind. of coho salmon 1+ and 1 ind. of Dolly Varden 1+ in PSS-2) one very large larvae of weevil (Tipulidae) was found in each stomach. These individuals were excluded from the statistics.

At the same time, despite a considerable similarity in the structure of parafluvial springbrooks, there are some differences in the pattern of feeding of fish juveniles (Figs. 4 and 5). In larger PSS-1, larvae of stone flies, mayflies, and caddis flies play a noticeable role (total proportion 8–10% in juveniles of coho salmon and 25–38% in juveniles of Dolly Varden), while in PSS-2, smaller than the former by sizes and water content, the proportion of organisms of the group EPT is noticeably lower (<8% in juveniles of both species). Besides, in PSS-1 in the period of observations, larvae of mayflies have a noticeably greater importance in the feeding of juveniles, while larvae of weevils dwelling in inflorescences and on willow leaves dominate drastically among larvae of terrestrial insects. In PSS-2 in the feeding of juveniles, caterpillars—larvae of weevils dwelling on leaves of meadowsweet, ragwort, and nettle, as well as imago of beetles dwelling on leaves of alder—dominate. In PSS-1 towards the end of summer, in the composition of benthic organisms, the numbers and biomass of gastropods that are accessible to juveniles due to their habitation among mass of filamentous algae increase. Therefore, in the food bolus of entire Dolly Varden and coho salmon, snails of the family Lymnaeidae are recorded. In PSS-2 where thickets of filamentous alga do not form, the amount of gastropods is negligibly small and fish juveniles do not feed on them.

No considerable change in behavior of fish juveniles in different months was recorded. As a rule, juveniles of both coho salmon and Dolly Varden demonstrate gregarious behavior. Juveniles of coho salmon frequently form temporary aggregations consisting of different-age fish that easily fall apart and get together again. In the light hours of the day, juveniles of coho salmon are located mainly above the surface; at night they are located mainly in the near-bottom water layer. Fingerlings of Dolly Varden stay in schools, but slightly separately from two-year olds. No territorial behavior was recorded in juveniles of Dolly Varden and coho salmon. In September, juveniles of sockeye salmon stay only in a school. Usually in the spring all juveniles of sockeye salmon are grouped into one school that migrates along the springbrook upstream and downstream.

Orthofluvial springbrook. The springbrook selected for study is the spawning area of late chum salmon and coho salmon. Juveniles of chum salmon leave the springbrook up to the end of June; towards July, only juveniles of salmonids with a long freshwater period—Dolly Varden and coho salmon—remain in it. The ratio of these two species in the stream in June and August is nearly equal. In September, their ratio up to 20% is accounted by juveniles of sockeye salmon at an age of 0+. Juveniles of Dolly Varden in the stream are represented by four age classes (0+ to 3+); however, fish of an older age (2+ and 3+) appear only in autumn, in the period of spawning of chum salmon and coho salmon, and represent a temporary contingent. Juveniles of Dolly Varden of an older age were excluded from analysis of feeding of fish since only eggs of salmon were found in the composition of its food bolus. The average density of all fish in July, August, and September is 2.37, 2.88, and 5.74 ind./m^2.

From July to September, an increase in the average length and weight of the body of juveniles of Dolly Varden and coho salmon, as well as of stomach fullness is observed (Table 6). No individuals with empty stomachs were found in the samples. On condition that the temperature mode of the springbrook remains more or less constant during the summer–autumn period, the dynamics of ISF indicates that maximum feeding of juveniles occurs in the second half of summer and at the beginning of autumn.

Food composition of juveniles in the orthofluvial springbrook varies within the summer–autumn period. In *July*, EPT group and chironomids play a considerable role in the feeding of different-age juveniles of Dolly Varden and coho salmon (Fig. 6a). In the aggregate, these organisms comprise more than 50% of the food bolus. Larvae and pupae of chironomids Chitonominae, Orthocladinae, Tanypodinae, and Diamesinae—18–35 and 32–41%, respectively,—have dominant importance in the feeding of coho salmon and Dolly Varden of different age. As in parafluvial springbrooks, in orthofluvial springbrook, chironomids reach very high numbers (8584–12112 ind./m^2) and biomass (235–244 mg/m^2). The remaining proportion is accounted for by allochtonous organisms—ground insects (imago of chironomids and beetles, larvae of weevils, and more seldom, of caterpillars) and aquatic oligochaetes.

In *August*, in the feeding of juveniles of coho salmon, the role of imago of insects considerably increases—their proportion in the food bolus of fingerlings and two-year olds occupies more than 50% (Fig. 6b). The food spectrum of juveniles of Dolly Varden does not change considerably; only in stomachs of two-year olds, gastropods appear.

In *September*, in the feeding of juveniles of Dolly Varden and coho salmon of different age classes, an increase in the role of eggs of chum salmon and larvae of flies is observed (Fig. 6c). In our collections, the proportion of these components is small (no more than 30%), which is determined by the late beginning of spawning of chum salmon in 2008. Material was collected on September 19, there was no mass spawning of chum salmon yet; therefore, the amount of eggs of chum salmon accessible for juveniles was small. The corpses of chum salmon were numerous; correspondingly, the numbers of larvae of flies were also considerably smaller than there could be in the period of mass spawning of chum salmon or after it. Feeding of fingerlings of sockeye salmon that appear in the spring in September is less diverse than of juveniles of coho salmon and Dolly Varden. Sockeye salmon feeds mainly on pupae of chironomids (more than 65%). Unlike juveniles of other species, fingerlings of sockeye salmon do not feed on eggs of chum salmon, since the sizes of their mouth are too small to swallow a large egg.

Table 6. Length and weight of the body, index of stomach fullness in juveniles of Salmonidae in the orthofluvial stream, lower course of the Kol River

Species	Month	Age, years	Length, mm	Weight, g	Index of stomach fullness, ‱	*n*, ind.
Coho salmon	July	0+	33.4 (31–46)	0.45 (0.2–1.1)	88.5 (56–123)	30
		1+	62.1 (51–68)	2.77 (0.7–3.7)	145.7 (113–197)	30
	August	0+	45.6 (32–62)	1.37 (0.4–3.5)	178.4 (136–204)	30
		1+	83.7 (56–98)	8.85 (3.4–12.7)	277.5 (189–397)	30
	September	0+	54.3 (37–72)	2.32 (0.6–5.4)	354.6 (288–496)	30
		1+	96.3 (77–104)	10.8 (7.6–16.3)	679.3 (465–938)	30
Dolly Varden char	July	0+	25.5 (22–33)	0.19 (0.1–0.4)	76.7 (42–103)	30
		1+	81.1 (67–102)	8.12 (2.9–16.8)	112.5 (87–184)	30
	August	0+	48.1 (27–62)	1.18 (0.2–3.1)	195.4 (144–305)	30
		1+	89.5 (80–115)	10.43 (4.1–25.0)	269.4 (212–444)	30
	September	0+	51.5 (37–78)	1.52 (0.5–5.1)	219.6 (168–379)	30
		1+	121.3 (82–130)	12.8 (4.5–31.2)	533.2 (442–887)	30
Sockeye salmon	September	0+	60.5 (45–77)	2.73 (1.0–4.9)	222.3 (166–345)	40

Throughout the entire summer–autumn period, a considerable role in the feeding of juveniles of Dolly Varden and coho salmon is played by larvae of caddis flies (practically only larvae of Apataniidae occur) and mayflies (Ameletidae, Baetidae). This is determined by rather high densities of these organisms in the composition of zoobenthos of orthofluvial springbrook in the basin of the Kol River.

Juveniles of Dolly Varden and coho salmon lead a gregarious mode of life; schools of different species stay separately. In autumn, with the beginning of spawning of chum salmon, juveniles form multispecies schools that are located near spawning salmon. Juveniles of sockeye salmon in September lead a gregarious mode of life; in the daytime, they stay above the surface, separately from schools of coho salmon, while at night they stay near the bottom.

Main channel of the Kol River. In summer in the main channel of the Kol River, the density and biomass of juveniles of salmonids are smaller than in the tributaries and off-channel habitats (Pavlov et al., 2009; Gruzdeva et al., 2011a, 2011b); therefore, specific features of feeding of juveniles were studied in a comparative aspect at one polygon in the river channel (Table 1) according to two samples collected in mid-July and early September. Juveniles of five species of salmonids—coho salmon, Dolly Varden char, cherry salmon, East Siberian char, and king salmon—were found in them. In July and September, juveniles of Dolly Varden and coho salmon dominate (41.5 and 37.4%, respectively); the third place by numbers is occupied by juveniles of king salmon (14.3%), and juveniles of cherry salmon and East Siberian char are scanty. The average density of all fish at the site in July and September are 2.88 and 3.92 ind./m^2, respectively.

In *July*, juveniles in the main channel feed actively; no fish with empty stomachs were found. At the same time, values of ISF on the whole are small (Table 7). The bulk of feeding is formed by larvae of amphibiotic insects (EPT group) and chironomids that account for more than 60% of the food bolus; considerable role is played by larvae of mayflies—their proportion varies from 14 to 46%. The importance of imago of insects and terrestrial larvae of insects (caterpillars and larvae of weevils) is small and comprises a noticeable proportion (34–39%) only in juveniles of coho salmon and cherry salmon.

In *September*, all juveniles continue active feeding, no fish with empty stomachs were found. Average values of ISF comprise 477.3 in juveniles of coho salmon (fingerlings and two-year old), 319.6 in juveniles of Dolly Varden (fingerlings and two-year old), 379.2 in fingerlings of king salmon, 482.2 in two-year olds of cherry salmon, and 345.2 in fingerlings and two-year olds of East Siberian char. All juveniles feed on eggs of pink salmon that at the beginning of September spawns at the site of the main channel in mass. In the overwhelming majority of two-year olds of all species and fingerlings of king salmon, no food except eggs was found in stomachs. Single two-year olds of coho salmon have imago of insects (only adult mayflies) in stomachs, and some two-year olds of cherry salmon have caterpillars. Fingerlings of Dolly Varden feed mainly on eggs of pink salmon (52% of the food bolus), larvae of mayflies (33%), and caddis flies (15%). Fingerlings of coho salmon also mainly consume eggs of pink salmon (67%) and, to a smaller extent, imago of insects—adult mayflies (33%); a similar ratio of food objects was found in fingerlings of cherry salmon (73 and 27%, respectively). The pres-

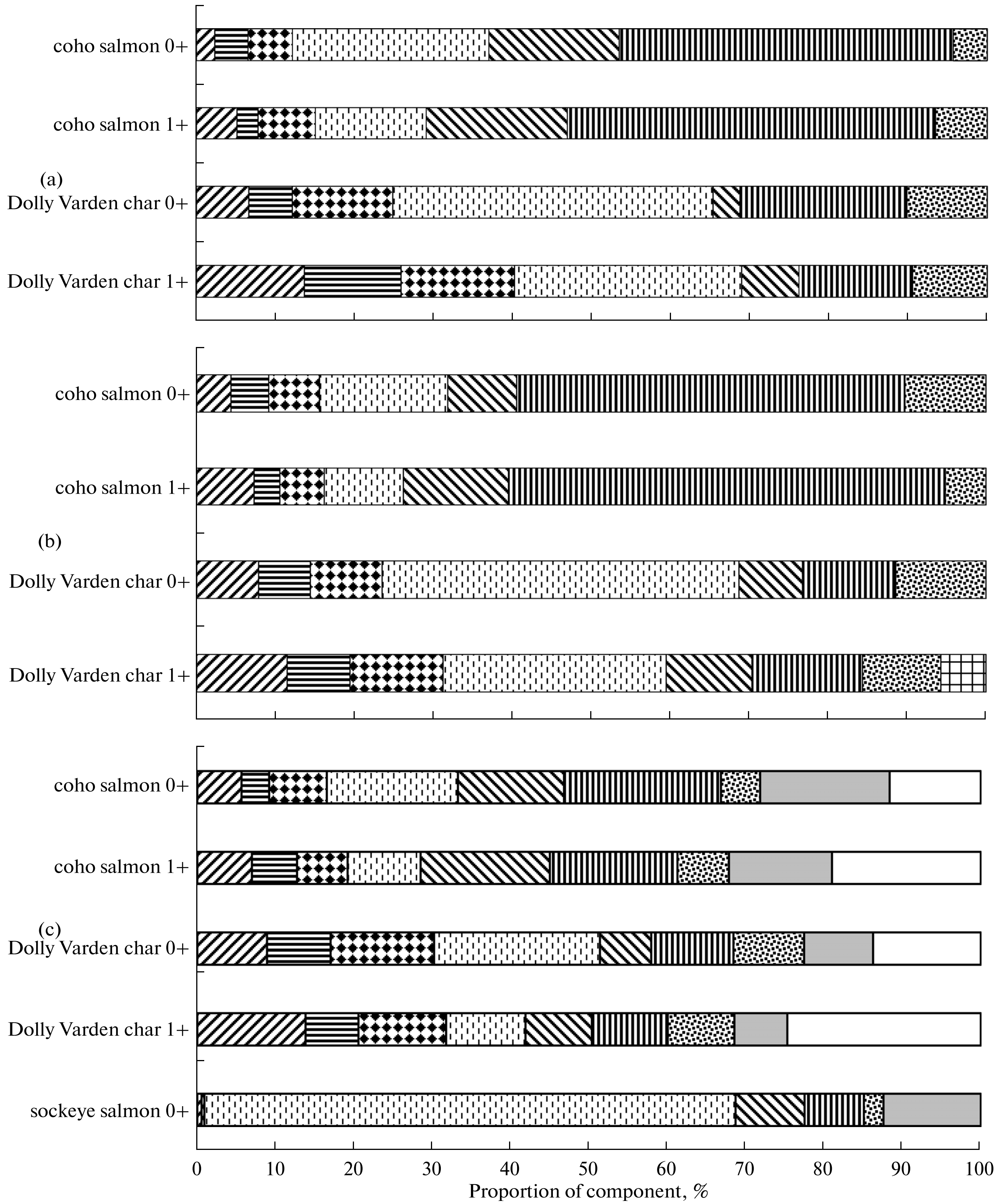

Fig. 6. Spectra of feeding of juveniles of Salmonidae in orthofluvial springbrook, lower course of the Kol River in different months: (a) July, (b) August, (c) September; designations see in Fig. 2.

Table 7. Length and weight of the body, index of stomach fullness and spectra of feeding of juveniles of Salmonidae at the site of the main course of the Kol River, July 20, 2008

Species	Age, years	Length, mm	Weight, g	Index of stomach fullness, ‱	n, ind.	Proportion of food components in the food bolus, %					
						LCF	LSF	LM	LCh	LB	II
Coho salmon	0+	38.1 (28–61)	0.7 (0.2–2.7)	101.2 (65–187)	37	14.2	16.4	17.7	14.2	2.5	35.0
	1+	87.8 (83–97)	9.0 (7.4–11.5)	188.5 (138–316)	33	16.4	17.5	19.1	8.3	4.3	34.4
Dolly Varden char	0+	38.8 (27–61)	0.7 (0.1–2.5)	115.4 (88–179)	36	28.6	18.4	46.3	6.7	0	0
	1+	88.3 (61–119)	10.4 (2.3–46.8)	176.6 (112–221)	40	34.2	29.7	32.5	3.6	0	0
Cherry salmon	0+	71.1 (59–82)	4.8 (2.8–8.5)	195.4 (144–305)	7	12.7	17.3	22.5	10.5	0.8	36.2
	1+	107.3 (96–120)	18.8 (13.8–25.4)	288.4 (176–411)	8	22.4	12.1	16.3	7.4	3.2	38.6
East Siberian char*	1+	130.1 (89–148)	26.9 (8.4–35.9)	189.5 (136–277)	11	47.3	12.7	13.5	4.2	3.9	12.4
King salmon	0+	54.5 (42–73)	2.4 (0.9–5.3)	203.2 (165–313)	29	3.2	33.5	36.4	15.6	2.1	9.2

LCF—larvae of caddis flies, LSF—larvae of stone flies, LM—larvae of mayflies, LCh—larvae of chironomids, LB—larvae of butterflies, II—imago of insects; *—sum of proportions of the listed components of feeding is 94%, of the remaining 6%—fish.

ence of adult mayflies Baetidae in the food bolus of fish is determined by the fact that their mass autumn emergence occurred in the period of sample collection.

In the main channel in *July*, juveniles demonstrate diverse behavior. As a rule, East Siberian char and cherry salmon at an age of 1+ lead a territorial mode of life: each individual strives to occupy a position near any underwater structure (large boulder, part of a tree trunk, piece of sod, etc.). Fingerlings of coho salmon stay in schools. Juveniles of coho salmon at an age of 1+ in the daytime forms small groups, 10–20 individuals each, that sometimes demonstrate coordinated actions. No typical territorial behavior was recorded in juveniles of coho salmon. Juveniles of coho salmon feed on drift particles that it snatches out from the water column or from the surface. Fingerlings of Dolly Varden stay in shallow waters (depth 2–6 cm) and in crevices between particles of bottom pebble. Apparently there is no stable visual contact between separate fingerlings of Dolly Varden. Two-year old Dolly Varden gather into small schools: 15–20 individuals each that pick up food mainly from the bottom surface. The most clearly pronounced territorial behavior is typical of juveniles of king salmon. Each individual occupies its individual site; an individual with a length of 55–60 mm controls a bottom site with a size of approximately 25 × 25 cm. Juveniles of king salmon in the daytime feed only on drift particles and do not seize larvae of invertebrates from the ground surface. In rare cases, juveniles of king salmon seize imago of insects from the surface.

In *September* during mass spawning of pink salmon, all juveniles, including juveniles of king salmon, pass to clearly pronounced gregarious mode of life. In most cases, multispecies schools form. Even juveniles of cherry salmon and East Siberian char lose attachment to underwater objects and become members of the school.

Intra- and Interspecific Relations of Juveniles of Salmonids in the Basin of the Kol River

The data obtained by us indicate a considerable similarity of the spectra of feeding of juveniles of salmonids at all examined sites of the river system of the Kol throughout the summer–autumn period. However, at using of the same kinds of food, there should arise the so-called "exploitation competition" for food resources of the water body. To assess tension within intra- and interspecific relations, formal indices, such as Shorygin index of food similarity (1952) and Schoener index of food overlapping (1970, 1971), were used. The obtained results form a mosaic and extremely complex for interpretation picture of relations between juveniles of different species and size-age groups unique for a concrete site and time of the year (Table 8). For instance, it is difficult to align in any system the relations between two mass and widely occurring species in the Kol River—coho salmon and

Dolly Varden char. In different biotopes and in different seasons of the year, index of degree of food similarity varies within 11–89, and index of food overlapping varies within 0.20–0.89. Both indices are particularly high at comparison of the pattern of feeding of Dolly Varden and coho salmon that dwell in springbrooks. Minimal food similarity between the species is almost uniformly observed in July. At this time of the year juveniles of different species and different size-age groups feed on a multitude of food objects. However, towards the end of summer–beginning of autumn at pair-wise comparison of the spectra of feeding, the degree of food similarity of juveniles increases at all sites of the river system in most cases. Similarity of diets is especially noticeable at those sites of the river basin where spawning of Pacific salmon takes place: increase in the index of food niche overlapping is determined by shift of all juveniles to feeding on eggs and larvae of flies. The increase in the index of food similarity is in full measure typical of two-year olds, while the picture of food preference turns out to be more complex in fingerlings of different species. At some sites of the river system, for instance, in the tundra tributary, divergence by food preferences in fingerlings of cherry salmon and East Siberian char and coho salmon and East Siberian char is observed. Really low values of indices of food similarity in the given pairs of comparison reflect specificity of feeding of fingerlings only of one species—East Siberian char. On the whole throughout the summer–autumn season, an increase in values of Shorygin and Schoener indices occurs, they are particularly high in the autumn time. At the same time, it is difficult to interpret results of comparison of values of these indices in the light of competitive relations. High values of indices seemingly should point to a high level of inter- and intraspecies competition in juveniles. However, in a real nature situation, food relations between species are rather complex, depend on many factors, and are not always amenable to analysis and interpretation. At those sites of the Kol River where spawning grounds of Pacific salmon are located (tributaries, orthofluvial springbrooks), high values of index of food similarity between juveniles of different species in essence only reflect transition of juveniles of all species to feeding on mass kind of food—aborted eggs of salmon and larvae of flies (Tables 2, 3, and 6; Figs. 2, 3, and 6). However, transition of juveniles of different species to the same food occurs simultaneously with an increase in its density and biomass, passing from territorial behavior to gregarious, and formation of multispecies schools consisting of different by size individuals and a drastic increase in stomach fullness of fish. On the contrary, maximum divergence between juveniles of different species and size-weight groups by values of index of food similarity is observed in July, at a pronounced territorial behavior, minimal densities of aggregations of juveniles, and relatively low indices of stomach fullness.

High indices of food similarity between juveniles of different species in parafluvial springbrooks (Table 8) where there are no spawning grounds of salmon have a slightly different nature. Juveniles of Dolly Varden and coho salmon dominant in these water bodies consume similar set of foods in which larvae of amphibiotic insects prevail. According to our observations, in springbrooks, coho salmon and Dolly Varden demonstrate complex means of getting food objects. Dolly Varden stays in a near-bottom water layer, seizes invertebrates from the bottom surface and between gravel particles, and can even displace small ground particles to reach food. Coho salmon more frequently stays in the middle water and under the surface, and it feeds on drift or imago of insects that fell on the water. However, if in springbrooks where the flow is weak and considerable area of the bottom is covered by silt, both coho salmon and Dolly Varden at some moment can get larvae and pupae of chironomids in the near-bottom area, from the surface of silty load or at the border of silt and clean gravel. We observed no cases when schools of Dolly Varden and coho salmon fed simultaneously on the silt surface. We failed to reveal any system in the interaction of juveniles of coho salmon and Dolly Varden in their feeding on chironomids in spring streams. At the same time, even at high values of Shorygin and Schoener indices, indices of stomach fullness of Dolly Varden and coho salmon are high, which indicates an intensive feeding of juveniles of both species.

Thus, indices characterizing overlapping of spectra of feeding of juveniles of salmonids in the given case do not give an objective pattern for assessment of competitive relations. To assess similarity/differences between species and size-age groups of juveniles by the pattern of feeding, cluster analysis of the food bolus composition was performed. The results turned out to be contradictory. For each site of the river, the pattern of clusterization is specific and varies at different time of the year (Fig. 7). For instance, feeding of fingerlings of coho salmon and East Siberian char in the tundra tributary in July (Fig. 7a) and feeding of two-year olds of cherry salmon and Kamchatka steelhead in August turned out to be most similar, whereas fingerlings of coho salmon and East Siberian char got into different clusters (Fig. 7c); in September, a change again occurred in relations and aggregation, and fingerlings of cherry salmon and Kamchatka steelhead were most similar by feeding (Fig. 7e). No less scale changes in the pattern of similarity/differences in feeding are observed in the piedmont tributary (Figs. 7b, 7d, and 7j). Variability in complexes formed by two–three species, as, for instance, in springbrooks is equally considerable (Fig. 8). Only in an orthofluvial springbrook, more or less pronounced clusterization by species principle is retained (Figs. 8b, 8d, and 8j). This is determined by a considerable proportion of caterpillars and imago of insects in the food bolus of juveniles of coho salmon feeding in the water column and from

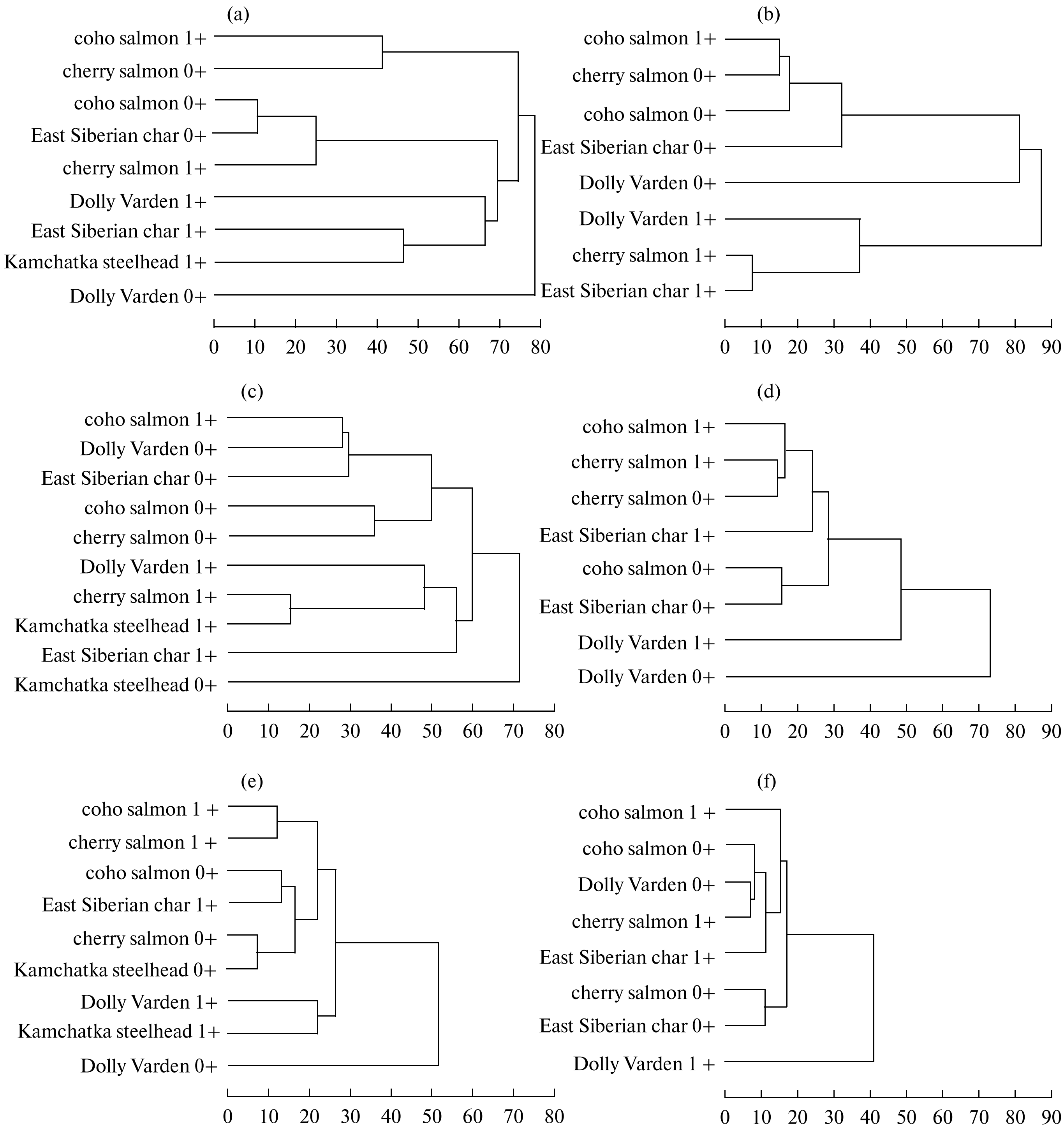

Fig. 7. UPGMA-dendrograms of similarity/differences of the pattern of feeding of juveniles of Salmonidae in streams Skvichik (a, c, e) and Simovyi (b, d, f)—tundra and mountain tributaries of the Kol River in different months. Here and in Fig. 8: (a, b) July, (c, d) August, (e, f) September; along the axis of abscissas—Euclidean distance.

the surface, while Dolly Varden feeds mainly on organisms from the ground surface.

Predation in aggregations of juveniles in the basin of the Kol River is a rather rare phenomenon. Noticeable consumption of fish food is found only in the piedmont tributary in July: almost all two-year olds, except for coho salmon, feed on fish (Fig. 3a). In other biotopes, predation occurs sporadically and is typical only of fingerlings of East Siberian char. Nevertheless, feeding on fish both in the piedmont tributary and at

Table 8. Indices characterizing food relations of juveniles of different species of Salmonidae in water bodies of the tributary system of the Kol River in July-September 2008

Compared species	Water body/date (number, month)								
	tributary of tundra type: Skvichik stream			tributary of mountain type: Simovyi stream			parafluvial spring stream 1		
	18.07	07.08	11.09	17.07	15.08	06.09	10.07	15.08	15.09
Coho salmon-Dolly Varden	18.1 (0.33) / 17.6 (0.20)	48.7 (0.60) / 8.6 (0.21)	86.6 (0.71) / 78.4 (0.75)	10.8 (0.71) / 12.5 (0.26)	36.5 (0.52) / 57.5 (0.54)	72.6 (0.63) / 48.0 (0.47)	65.7 (0.86) / 64.4 (0.64)	75.0 (0.75) / 68.1 (0.68)	89.4 (0.89) / 81.2 (0.81)
Coho salmon-cherry salmon	81.6 (0.65) / 85.9 (0.81)	82.2 (0.82) / 62.3 (0.85)	78.1 (0.71) / 60.4 (0.60)	78.6 (0.78) / 89.9 (0.73)	73.8 (0.72) / 84.6 (0.79)	81.5 (0.76) / 86.2 (0.83)	–	–	–
Coho salmon-East Siberian char	34.6 (0.51) / 59.2 (0.55)	56.6 (0.68) / 51.9 (0.79)	– / 62.4 (0.58)	61.4 (0.71) / 40.8 (0.58)	46.9 (0.64) / 77.5 (0.64)	77.5 (0.65) / 57.3 (0.56)	–	–	–
Coho salmon-Kamchatka steelhead	– / 13.7 (0.33)	24.3 (0.39) / 25.1 (0.51)	77.7 (0.73) / 44.1 (0.39)	–	–	–	–	–	–
Coho salmon-sock-eyed salmon	–	–	–	–	–	–	–	–	– / 46.8 (0.46)
Coho salmon-king salmon	–	–	–	–	–	–	–	–	-
Dolly Varden-cherry salmon	15.4 (0.17) / 28.5 (0.35)	41.1 (0.51) / 41.0 (0.30)	75.6 (0.77) / 57.1 (0.57)	30.6 (0.42) / 18.6 (0.33)	45.9 (0.43) / 62.4 (0.61)	82.1 (0.78) / 79.7 (0.52)	–	–	–
Dolly Varden-East Siberian char	71.3 (0.66) / 30.2 (0.39)	46.5 (0.54) / 36.2 (0.32)	– / 61.2 (0.59)	48.7 (0.58) / 453.9 (0.50)	38.5 (0.60) / 62.8 (0.65)	84.9 (0.87) / 88.0 (0.88)	–	–	–
Dolly Varden-Kamchatka steelhead	– / 64.7 (0.60)	31.3 (0.42) / 83.0 (0.53)	81.3 (0.78) / 49.5 (0.47)	–	–	–	–	–	–
Dolly Varden-sockeye salmon	–	–	–	–	–	–	–	–	39.2 (0.38 / –
Dolly Varden-king salmon	–	–	–	–	–	–	–	–	-
Cherry salmon-East Siberian char	17.8 (0.19) / 56.2 (0.57)	51.8 (0.62) / 71.0 (0.83)	– / 35.3 (0.33)	78.8 (0.81) / 50.2 (0.61)	63.1 (0.63) / 90.6 (0.81)	92.7 (0.87) / 63.9 (0.61)	–	–	–
Cherry salmon-Kamchatka steelhead	– / 53.9 (0.52)	16.5 (0.33) / 55.6 (0.59)	98.3 (0.95) / 18.9 (0.17)	–	–	–	–	–	–
Cherry salmon-king salmon	–	–	–	–	–	–	–	–	–
East Siberian char-Kamchatka steelhead	– / 50.9 (0.43)	13.0 (0.30) / 52.8 (0.62)	– / 80.9 (0.80)	–	–	–	–	–	–

Table 8. (Contd.)

Compared species	Water body/date (number, month)						
	parafluvial spring stream 2			orthofluvial spring stream			main channel
	05.07	12.08	20.07	08.07	10.08	19.09	20.07
Coho salmon-Dolly Varden	82.1 (0.82) / 74.2 (0.74)	52.4 (0.52) / 53.6 (0.53)	83.4 (0.83) / 76.2 (0.76)	70.2 (0.70) / 60.9 (0.61)	67.1 (0.67) / 59.7 (0.59)	75.3 (0.73) / 78.9 (0.79)	59.3 (0.55) / 59.9 (0.56)
Coho salmon-cherry salmon	–	–	–	–	–	–	95.6 (0.93) / 91.3 (0.90)
Coho salmon-East Siberian char	–	–	–	–	–	–	– / 63.4 (0.63)
Coho salmon-Kamchatka steelhead	–	–	–	–	–	–	–
Coho salmon-sockeye salmon	–	–	–	–	–	50.1 (0.50) / –	–
Coho salmon-king salmon	–	–	–	–	–	–	62.9 (0.62) / –
Dolly Varden-cherry salmon	–	–	–	–	–	–	60.7 (0.59) / 57.3 (0.54)
Dolly Varden-East Siberian char	–	–	–	–	–	–	– / 64.9 (0.64)
Dolly Varden-Kamchatka steelhead	–	–	–	–	–	–	–
Dolly Varden-sockeye salmon	–	–	–	–	–	49.2 (0.49) / –	–
Dolly Varden-king salmon	–	–	–	–	–	–	66.4 (0.65) / –
Cherry salmon-East Siberian char	–	–	–	–	–	–	– / 69.7 (0.68)
Cherry salmon-Kamchatka steelhead	–	–	–	–	–	–	–
Cherry salmon-king salmon	–	–	–	–	–	–	64.5 (0.63) / –
East Siberian char-Kamchatka steelhead	–	–	–	–	–	–	–

Beyond parentheses—Shorygin index of food similarity (1952), in parentheses—Schoener index of food overlapping (1970, 1971); above the line—fingerlings (0+), below the line—two-year olds (1+).

other sites is observed at limited time—in July and, rarely, in August. Judging from the data obtained, predation exists at those sites and at that time when juveniles lead a clearly pronounced territorial mode of life.

DISCUSSION

Kol—a typical river of the western coast of Kamchatka represents a dynamic, complex river system with a expanded floodplain and a multitude of diverse aquatic biotopes (Pavlov et al., 2009; Kuzishchin, 2010). Density and biomass and species and size composition of juveniles of salmonids at different sites of the river system are subjected to high variability (Pavlov et al., 2009; Gruzdeva et al., 2011a, 2011b). As it turned out, in the summer–autumn period, active feeding of juveniles occurs at all sites of the river system that we studied: we found no fish with empty stomachs throughout the period of observations. Highest indices of stomach fullness were revealed in juveniles inhabiting springbrooks and the piedmont tributary. High indices of stomach fullness of fish in the autumn time are reached not only at the expense of feeding on eggs of Pacific salmon and larvae of flies in areas of spawning grounds (tributaries and the main river channel). Juveniles of salmonids feed similarly intensively also in parafluvial springbrooks consuming invertebrates (Tables 4 and 5). This indicates a clearly pronounced universal seasonal (early autumn) peak of food consumption by juveniles within the entire basin of the Kol River. It is noteworthy that feeding of juveniles of salmonids in the basin of the Kol River takes place under conditions of their rather high density at all studied sites—on average, approximately 4 ind./m^2, at local sites of springbrooks or tributary density of juveniles at some moments can reach a value of more than 25 ind./m^2. At the same time, aggregations of juveniles at each concrete site of the river system are structured not only by species status. Apparently, ontogenetic stages, i.e., practically size–age groups of species, should be considered as an elementary structural unit at a microscale (site of the tributary or main channel, springbrook, etc.).

In the basin of the Kol River in the summer–autumn period, juveniles of salmons consume a wide spectrum of most diverse food that includes aquatic and aerial components, which is typical of the overwhelming majority of rivers of the northern Pacific (Shapovalov and Taft, 1954; Hartman, 1985; Groot and Margolis, 1991; Chebanova, 1992, 2009; Bogatov, 1994; Zhivoglyadov, 2004). The aquatic component is represented mainly by larvae of amphibiotic insects and, to a smaller extent, by oligochaetes and gastropods; the role of the latter is extremely small. In literature, an aerial component implies mainly adult insects—imago (Gribanov, 1948; Semko, 1954; Levanidov, 1969; Zorbidi, 1970, 1977, 2010; Zhul'kov, 1974). However, the data obtained by us indicate that juveniles of salmonids, besides imago of insects, consume far wider spectrum of food of terrestrial origin—larvae of butterflies, coleopterans (weevils), and flies, as well as ground oligochaetes. In this connection, it would be more correct to use the term "terrestrial component" for allochtonous organisms on which juveniles of fish can feed. A similar picture of a considerable proportion of terrestrial invertebrates in the feeding of juveniles of salmonids was revealed also in several water bodies of North America (Nislow, 2005; Piccolo et al., 2008; Rundio and Lindley, 2008).

The importance of these or other groups of invertebrates in the feeding of juveniles of salmonids depends on the structure of the aquatic site of the river system and adjoining it ground biotopes. For instance, in off-channel habitats, juveniles of different species consume rather small amount of larvae of mayflies, while they comprise a considerable proportion in their feeding in the main channel of the river (Figs. 2–6, Table 6). The role of aerial insects in the feeding of juveniles from the main channel is on the whole small. In the narrow channel of tributaries and in springbrooks over which a canopy of tree and herbaceous vegetation is developed, terrestrial invertebrates come to the foreground in the feeding of juveniles of all salmonids. Precisely here caterpillars and larvae of weevils have dominant importance. In the summer time, they are rather numerous on leaves and inflorescences of willow, alder, nettle, ragwort, and meadowsweet and constantly fall into water because of wind and rain. According to published data, neither caterpillars nor larvae of weevils in the rivers of Kamchatka are mass or have considerable importance in the feeding of juveniles of salmonids (Volovik, 1963, 1964; Gritsenko, 1969; Zorbidi, 1970; Hunt, 1975; Chebanova, 1983; Takami, 1996; Fausch et al., 1997; Zhivoglyadov, 2004; Esin et al., 2009). However, in the basin of the Kol River, precisely these larvae of terrestrial insects are among the main objects of feeding of juveniles in most of-channel habitats of the Kol River.

It is rather difficult to estimate regarding preference for any food objects by different species of salmonids. Practically at each studied site of the Kol River juveniles of salmonids feed mainly on the same food, and only proportions of these or other organisms in the food bolus of different species vary. On the whole, it should be noted that juveniles are not sufficiently scrupulous in selection of objects of feeding and consume the most mass and accessible food present at the given moment in the given biotope. As a rule, the ratio of food objects in stomachs of juveniles more or less correspond to the frequency of their occurrence in the biotope. During the summer–autumn season, a constant and sometimes a very rapid change in the composition of auto- and allochtonous organisms occurs in water bodies related to realization of the life cycle of diverse insects (emergence of mayflies, caddis flies, chironomids, coleopterans) and synoptic phenomena (mass getting into water of ground insects because of strong winds, summer storms or floods). Therefore, throughout the period of observations, juveniles

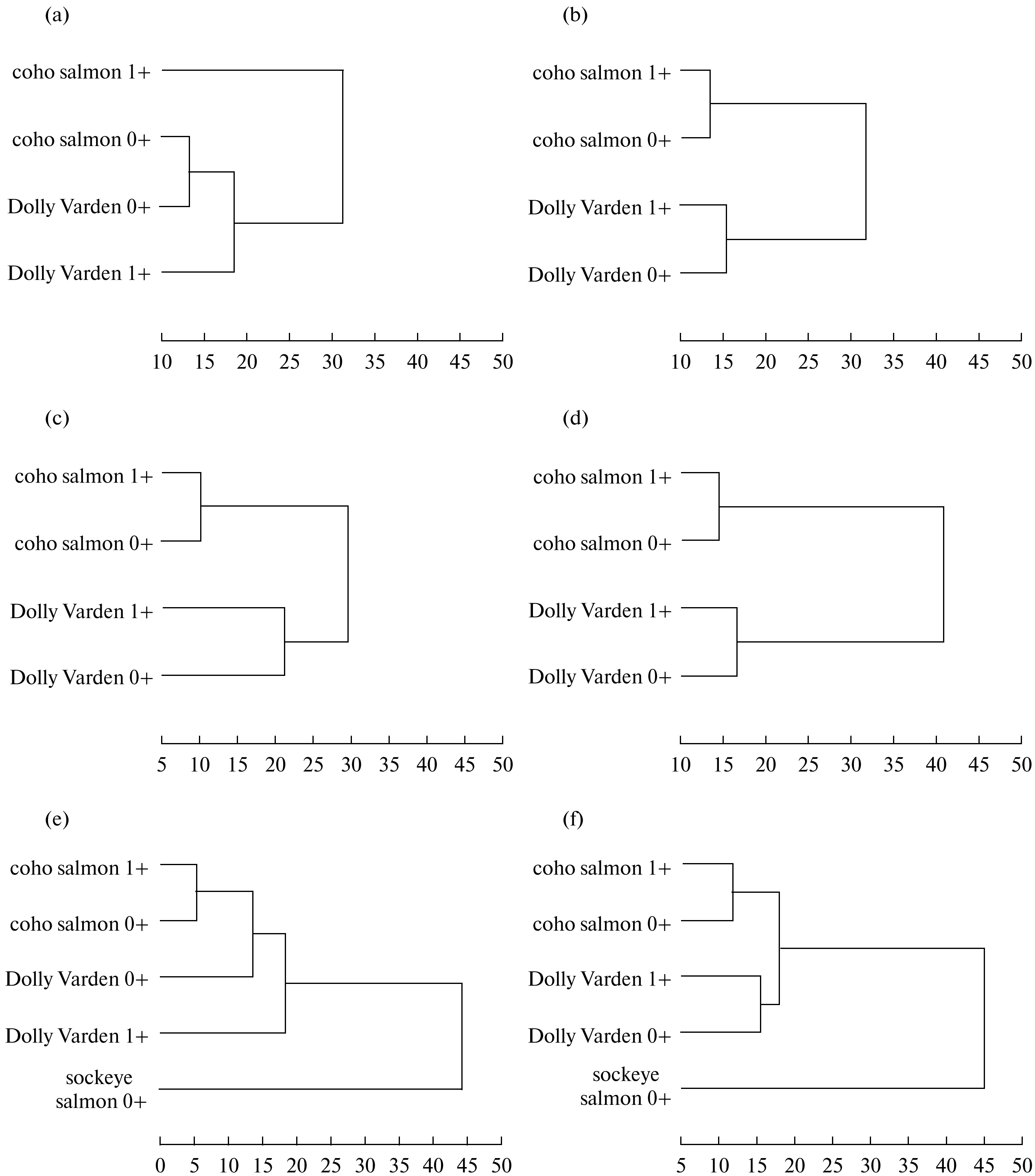

Fig. 8. UPGMA-dendrograms of similarity/differences of the pattern of feeding of juveniles of Salmonidae in parafluvial springbrook 1 (a, c, e) and orthofluvial springbrook (b, d, f) in different months.

repeatedly and rapidly pass from consumption of one group of food to another. No food rejected by juveniles of salmonids was revealed.

A powerful biotic factor drastically changing the pattern of feeding of juveniles of all species and size-age groups of salmonids is spawning of Pacific salmon. In this period, mass transition of practically all juveniles to feeding on eggs of Pacific salmon and associated with their spawning kind of food—larvae of flies—occurs (Kirillova, 2008; Kirillov and Kirillova, 2009; Kirillova et al., 2010). Precisely these two kinds of food dominate at most sites of the basin of the Kol

River at the end of summer–beginning of autumn. It is known that transition of juveniles of salmon to feeding on eggs leads to an increase in the rate of growth of individuals and intensive deposition of fat (Kirillova, 2008; Pavlov et al., 2010). Only small fingerlings of Dolly Varden cannot feed efficiently on eggs, since the width of mouth opening in them at similar body length is smaller than in fingerlings of other species. It is known that the width of mouth opening has key importance when feeding on large prey (Mikheev, 1984, 1994, 2006). The appearance in the water body of accessible and energetically profitable food, such as eggs of Pacific salmon and larvae of flies, leads to considerable changes in the structure of fish population and behavioral responses. As a rule, in the area of the spawning grounds, the numbers of juveniles that pass from the territorial behavior to gregarious increases, and they ignore less caloric and more difficult of access food—larvae of aquatic and ground insects. It is known that salmonids in the course of evolution formed a facultative social strategy at which a rapid change of their behavior motivation occurs in a heterogeneous medium (Mikheev, 1995, 1999, 2000, 2003, 2006).

Thus, at different sites of the Kol River, there exist multispecies aggregations of juveniles with high density of fish that feed intensively in the summer–autumn period. In different species and size-age groups under conditions of joint dwelling, a system of biotic interactions has elaborated that enables them to efficiently colonize food resources of the water body. Food composition of each species and each size-age class depends on the forming situation at each concrete site of the aquatic system. At the same moment of time, the structure of feeding of juveniles of the same species and same size-age class but at different sites of the river system differs considerably. At the same time in the same habitat, composition of the consumed food in juveniles of different species is more similar than in juveniles of the same species but from different habitats. By and large, it would be correct to assert that juveniles of salmonids of different species feed on more mass and most accessible groups of food objects present in the water body at each concrete site of the river system and in each concrete period of time. In the long run, the pattern of feeding of juveniles is affected by a group of factors: (1) gustatory preferences (species status), (2) geomorphological structure of the river site, (3) diversity and abundance of food organisms, and (4) stochastic processes (weather and floods). Of the listed factors, the geomorphological structure of the site of the river system where an aggregation of juveniles dwells at the given moment of time has greatest importance, i.e., practically "biotopic determination" of feeding was revealed. As a result, for the summer–autumn feeding of juveniles, biotopic units, such as ortho- and parafluvial spring streams and river tributaries, have primary importance, while the channel has secondary, subordinated importance. This is supported by data on the density and biomass of juveniles of salmonids that are maximum in water bodies of the tributary system (Pavlov et al., 2009; Gruzdeva et al., 2011a, 2011b). Considering rather high degree of heterogeneity of the habitation environment of juveniles of salmonids in the basin of the Kol River and an active dynamics of composition of benthic and semi-aquatic communities of invertebrates, the general pattern of feeding of juveniles is distinguished by a high degree of mosaicism in space and time.

The pattern of feeding of juveniles of salmonids in the summer–autumn period in the basin of the Kol River indicates dynamic trophic relations in a heterogeneous environment (Mikheev, 2006) and serves as adaptation for dwelling under variable conditions of the alluvial river of a piedmont type (Stanford et al., 2005; Pavlov et al., 2009). In this connection, the situational pattern of feeding of juveniles of salmonids requires special attention at consideration of issues related to the intensity of feeding of fish and determination of the productivity of aquatic ecosystems. The study of trophoecology of ecosystems of salmon rivers is a rather large-scale and multifarious work, and the strategy of studies should necessarily consider the dynamic-mosaic pattern of the feeding of fish. Depending on purposes and concrete tasks and priorities, it is necessary to elaborate optimal methodical approaches. For instance, classical analysis of the food bolus of fish requires great time expenditures, but the obtained result will reflect only a simplified, punctuate (by site and time) ecological situation (Mikheev, 2006). Considering the possibility of an easy transition of fish from one kind of food to other, such fundamental, detailed analyses of the food bolus with separation by groups of organisms or even lower taxa in the light of results obtained by us seem redundant. Possibly for the study of productivity of salmon rivers, express estimates, such as proportion of fish with empty stomachs and indices of stomach fullness, are more suitable as adequate indices of feeding of juveniles. To increase significance of estimates with respect to the river basin, it would be more expedient to increase the number of polygons of collection of primary material.

Thus, in the ecosystem of salmonid Kol River, spatio-temporal dynamic mosaicism of food interactions of juveniles of salmonids at a level of species and biotopes has formed and functions. Thereby, high-effective colonization by salmonids of the spawning and feeding potential of the water body and high productivity of the whole system are provided. The obtained results reveal a high biotopic variation of the pattern of feeding of juveniles of salmonids against the background of constantly varying external environmental conditions and composition of the food resources within one small site of the aquatic system. As it turned out, juveniles of salmonids are well adapted to the dynamic pattern of feeding when an accidental component plays a big role. At the same time, in the basin of the river system, important elements of structure are distinguished, such as spring streams where most favorable conditions for feeding form for juveniles of salmonids; therefore, precisely they should be considered as sites of the river system playing primary role in the summer–autumn feeding of juveniles of salmonids.

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