Proc. Estonian Acad. Sci. Biol., 1995, 44, 1/2, 11-22

https://doi.org/10.3176/biol.1995.1/2.02

THE COMPOSITION AND SEASONAL CHANGES IN THE DIET OF BREAM (ABRAMIS BRAMA) IN THE RELATION TO THE ABUNDANCE AND BIOMASS OF ITS FOOD ITEMS IN LAKE VÕRTSJÄRV

Andu KANGUR and Külli KANGUR

Eesti Teaduste Akadeemia Zooloogia ja Botaanika Instituudi Võrtsjärve Limnoloogiajaam (Võrtsjärv Limnological Station, Institute of Zoology and Botany, Estonian Academy of Sciences), Rannu, EE-2454 Tartumaa, Eesti (Estonia)

Presented by A. Järvekülg

Received June 28, 1994; accepted September 6, 1994

Abstract. From May till August, 1993, the diet of bream was investigated in the shallow eutrophic Lake Võrtsjärv (South-Estonia). 56 breams of standard length of 15—51 cm were examined. Chironomid larvae and pupae made up over 95% of the weight of food, while *Chironomus plumosus* and *Einfeldia carbonaria* had the highest occurrence frequency. The most important food item was *C. plumosus* (about 97% of the chironomid biomass in guts). Smaller breams consume mainly zooplankton.

The total food consumption of bream was estimated and compared with available amounts of food organisms in the lake. The diet of bream was compared with that of eel (*Anguilla anguilla*). Overlap in their diets was discussed.

Key words: bream, diet, seasonal changes, amount of food organisms.

INTRODUCTION

Bream prefers quite large, not very deep eutrophic and hypertrophic lakes in Estonia with moderate water transparency, pH, dichromate oxygen consumption (i. e. the content of organic substances) and fish productivity (Pihu, 1993). In the large eutrophic L. Võrtsjärv bream is the dominating fish species, which made up about 60% of the total commercial catch in 1993 (Fig. 1). The commercial catch of this fish consist of about 112 tons.

According to W. Hoogenboezem et al. (1990), bream appears to have a better chance for survival than other cyprinid species — white bream (*Blicca bjoerkna*) and roach (*Rutilus rutilus*) — because of its more efficient utilization of the available food resources (zooplankton and chironomid larvae) as well as better predation avoidance.

The feeding of bream in L. Võrtsjärv has been repeatedly studied. G. Schneider (1920) investigated the feeding of bream in summer 1911— 1912, presenting a list of its food objects (not identified by species). H. Haberman (1964) studied the seasonal and age related changes in the feeding of bream in 1959—1960 and found out that chironomids



Fig. 1. Composition of fish catches in L. Võrtsjärv in 1993.

predominated in the diet of breams of standard length (S1) over 25 cm. M. Kangur and Ö. Tõlp (Кангур & Тыльп, 1974) examined in 1966— 1967 the food composition of breams with a mean S1 of 58—235 mm. They presented the occurrence frequency (OF) and the number of food objects per individual, as well as the general index of filling and the percentage of fed individuals. However, none of these papers dealt with the biomass of food animals in the diet of bream.

When discussing the diets of bream it is important to know both the type and availability of food organisms. The diet must be related to the size of the fish and to the availability (density, size distribution, . visibility, etc.) of food (Lammens & Hoogenboezem, 1991).

One of the most important benthic food resources of L. Võrtsjärv are larval chironomids, first of all *Chironomus plumosus* (Kangur et al., in press). In particular, bream is specialized for feeding on chironomids in L. Võrtsjärv. In this lake zoobenthos is also actively consumed by eel.

This paper describes the composition and seasonal changes in the diet of bream. An attempt is made to quantify the consumption. The proportion of the number and biomass of food organisms eaten by bream is compared with their abundance and biomass in the bottom substrate. A possible competitive interaction with eel in respect of food organisms is discussed.

STUDY AREA

L. Võrtsjärv is a shallow (mean depth 2.8 m, maximum depth 6 m) eutrophic lake with a surface area of 270 km², surrounded by agricultural lands and forests. The water is practically homothermic and, due to the wind action, very turbid in summer. In winter oxygen deficiency sometimes occurs. Macrophytes cover about 15% of the total area of the lake. Approximately two-thirds of the lake bottom consist of mud lying on marl. The mean macrozoobenthos abundance and biomass $(870\pm70 \text{ ind./m}^2 \text{ and } 6.8\pm1.2 \text{ g/m}^2, \text{ in } 1973-1993)$ were considerably

Table 1

Average abundance and biomass of macrozoobenthos of L. Võrtsjärv in 1973-1993

Main animal groups	ind./m²	%	g/m²	%
Chironomidae, larvae	576 ± 51	66.2	5.68 ± 1.15	83.9
among them C. plumosus	179 ± 40	20.6	4.84 ± 1.14	71.5
Oligochaeta	242 ± 31	27.8	0.45 ± 0.06	6.6
Mollusca	13 ± 1	1.5	0.41 ± 0.04	6.1
Others	39±7	4.5	0.23 ± 0.03	3.4
Total (without big clams)	870±70	100	6.77±1.20	100

lower than in other neighbouring eutrophic lakes. The low quantity of zoobenthos in L. Võrtsjärv is probably caused by its availability to the large number of fishes feeding on benthos (mainly bream, eel and ruff). *Chironomidae* dominated in all zones of the lake; among them *C. plumosus* formed over 70% of the total biomass of macrozoobenthos (Table 1).

According to the fishery typology L. Võrtsjärv belongs to the pikeperch and bream lakes. It has all the qualities characterizing such water bodies (shallow, relatively warm and turbid water, scanty vegetation, favourable spawning and feeding conditions for both fish species).

Bream, eel, pike-perch and pike are the main commercial fishes in the lake. The economic importance of burbot, perch, ide, tench, roach, and asp is quite modest.

MATERIAL AND METHODS

In the period from May to August bream samples were collected once or twice a month with the experimental trawl in the open water of the southern and central parts of the lake.

The collected breams were weighed with an accuracy of 5 g and measured with an accuracy of 5 mm (Table 2). Thereafter the breams were dissected, guts were taken out and frozen. The samples were treated within a month of collection. Before analysing the samples were slowly thawed. The content of 56 stomachs was analysed in detail.

Table 2

		SI, cm		Weight, g		
Month	Number of fishes	average variations		average	variations	
May	16 31		24-39.5	685	270-1430	
June	12	31 15-44 840 30 16-47 731			31 15-44 840	130-1890
July	13				140-2480	
August	15	33	23-51	873	270-2350	

Measurements of examined breams

The prey items or their remains were counted. Food items were identified under the microscope to the lowest possible taxonomic level. The larval instars of *C. plumosus* were identified according to the width of their head capsules (Кангур & Кангур, 1978). The mean live weight of chironomid larvae and pupae was calculated according to the data on macrozoobenthos samples collected monthly in 1993 from a profundal sample station of the lake (Kangur & Tuvikene, in press). The reconstructed weight of the gut content was calculated and expressed as fresh weight (mg) per bream.

RESULTS

1. The composition of the diet

Although none of the cyprinids is strictly monophagous, many species feed on only one type of food organism depending on availability (Lammens & Hoogenboezem, 1991). Young bream feeds efficiently on zooplankton (Хаберман, 1968; Кангур & Тыльп, 1974; Lammens et al., 1987) but is able to consume zooplankton during the whole lifespan (5 mm to 50 cm) (Hoogenboezem et al., 1991). With the increasing size bream turns into a benthos-feeder.

The main food for smaller bream (up to 15—20 cm) in L. Võrtsjärv in winter and early spring is *Copepoda* (mainly *Cyclops kolensis*), in summer-autumn *Cladocera* (particularly *Bosmina coregoni, Chydorus sphaericus* and *Alona affinis*) (Кангур & Тыльп, 1974).

Table 3

Taxon	OF, % *	Mean number per gut
Oligochaeta (indet.)	41	9±3
Mermithidae (indet.)	2	In the period iro
Mollusca		
Gastropoda (indet.)	2	of the +uthern and c
Ostracoda (indet.)	9	The + ollected bre
Malacostraca (indet.)	2	neasurt with an ac
Diptera		
C. plumosus (L.) adult	7	within + month of the
pupae	82	18±3
IV instar	95	165 ± 31
III instar	68	200 ± 39
II instar	11	1±0
Einfeldia carbonaria (Meig.)	77	41 ± 8
Procladius sp.	54	28 ± 9
Microchironomus tener (Kieff.)	21	19±9
Polypedilum tetracrenatum Hirv.	18	1±0
Cladopelma viridula (L.)	4	+
Tanytarsus sp.	2	+
Plants	13	+
Algae	4	the lotal +

Composition of the diet of bream in L. Võrtsjärv in 1993

* OF - occurrence frequency; the guts without food are included.

+ Less than 1 item per gut.

According to the present data young breams in L. Võrtsjärv continue feeding on zooplankton until they are ca. 15 cm long. The gut of bream with a length of 15—16 cm is full of zooplankton or it contains zooplankters and some *Chironomidae* larvae. Larger breams take zooplankters at random.

The diet of larger breams contains chironomids, *Oligochaeta* cocoons, crustaceans, snails, remains of macrophytes and algae (Table 3). Mud is also commonly found in the bream gut.

The larval instars and pupae of chironomids are heavily predated by bream. At present the main food objects for breams over 15 cm SI are the larvae and pupae of *C. plumosus* that are found in all stomachs containing food. The number of swallowed larvae amounts, on an average, to 165 (IV instar) and 200 (III instar) (Table 3). *Einfeldia carbonaria*, too, has a high occurrence frequency in the food of bream.

Unlike eel who takes mainly large fourth instar larvae and pupae of *C. plumosus* (Kangur, 1989a), bream eats abundantly small third and second instar larvae of this species as well as other small chironomids.

Large pupae of *C. plumosus* are heavily predated by bream, which indicates that it feeds chiefly in the surface layer of the bottom substrate of the lake. Obviously, bream takes pupae also during its ascent to water surface. In summer some adult *C. plumosus* specimens were found in the bream gut, which must have been taken from water surface.

Other groups of invertebrate food items have rarely been found in the bream gut (Table 3).

The composition of the diet shows that bream prefers an open water zone with a soft bottom substrate.

2. Seasonal changes of feeding

The food resources in the lake vary continuously. Fishes may shift their diet and feeding modes from day to day when the availability of food changes (Lammens & Hoogenboezem, 1991).

In L. Võrtsjärv the macrozoobenthos abundance and its qualitative composition changes essentially during the year depending on the life cycles and population dynamics of different species (Fig. 2). These changes are reflected on the feeding conditions of bream.

The intensive feeding period for bream in L. Võrtsjärv is summer (Haberman, 1964; Кангур & Тыльп, 1974).

Changes in the feeding of bream in L. Võrtsjärv during summer are in accordance with the peculiarities of life cycles of chironomids, first of all *C. plumosus*. All larval instars and pupae of the chironomids are heavily predated by bream. Their proportion in the stomachs depend on the larval densities in the bottom substrate at a certain time.

The number of eaten chironomids per one bream changes essentially during the vegetation period (Fig. 3). At the beginning of May when the water is yet cold and breams are ready to spawn, they consume *Chironomidae* larvae less intensively. Several guts are empty, containing only slime.

Bream feeds less intensively also in July when the water is too warm.

In June, after spring emergence and hatching of a new generation of C. plumosus, its third-instar larvae are the most numerous food items for bream. As they are small, their proportion in the total weight of food is negligible. The numerical role of small larvae of other chironomid species in the gut varies during summer too. Considering weight, the most important food objects for bream during the whole vegetation period are fourth-instar larvae of C. plumosus.



Fig. 2. Abundance of *Chironomidae* species in the profundal mud bottom of L. Võrtsjärv in 1993.



Fig. 3. Changes in the feeding of bream in L. Vortsjärv during summer 1993.

In summer 1993 more than 95% of the food of breams over 15 cm SI was formed, regarding both the number and biomass, by chironomids. The mean total weight of consumed chironomids was more than 8 g per stomach (Table 4). The estimates of consumption depend on the supposition of a daily ration of the population biomass. Considering the mean weight of the examined breams (Table 2) and assuming that their reconstructed gut content is equal to the daily ration (Nie, 1987), bream takes daily, on the average, at least 1% of the body weight. However, consumption estimates may be higher.

According to our calculation, the biomass of bream over 18 cm S1 made in 1993 at least 6 kg/ha. During the vegetation period (about 150 days) the stock of bream consumes about 9 kg/ha of *C. plumosus* pupae and larvae.

The annual biomass of *C. plumosus* in L. Võrtsjärv was in 1993 on an average, about 8 g/m² or 80 kg/ha. The coefficient P/B of *C. plumosus* ranges from 2.9 to 4.9 in different years (Kahryp, 1977). Consequently, the annual production of the *C. plumosus* population can be calculated as being 230—390 kg/ha. According to our approximate calculation, the stock of bream consumes at least 2-4% of the annual production of *C. plumosus*. The rest is consumed by other benthophagous fishes and remains for the reproduction of the *C. plumosus* population itself.

We compared the proportion of chironomids (number and weight) in the gut with their abundance and biomass in the bottom substrate of the lake (Table 4). Larval densities in the mud bottom of the lake did not correspond to the proportional amounts in the food of bream. The number of *C. plumosus* III instar larvae and *C. plumosus* pupae in the gut was much higher than it was in bottom samples. Free living *Procladius* larvae in the bream gut were scarce in comparison with their occurrence in bottom samples. Probably, *Procladius* is able to avoid predation by fish.

The relative weight of *C. plumosus* in the food of bream over 15 cm SI as well as in the profundal mud bottom of the lake was several times higher than that of all other food items together. *C. plumosus* larvae and pupae made up about 97% of the chironomid biomass in the food of bream and about 98% of the chironomid biomass in the profundal mud bottom. Thus, *C. plumosus* biomass in the bottom substrate corresponds to their proportional amounts in the guts. More than 80% of the weight of consumed chironomids constituted *C. plumosus* fourth-instar larvae.

DISCUSSION

At present, as well as 25-30 years ago, the main food objects for larger bream in L. Võrtsjärv have been *Chironomidae* species predominating among other macrobenthic invertebrates in all zones of the lake bottom. In the 1960s *Procladius, Einfeldia carbonaria, Microchironomus tener* (=*Cryptochironomus* gr. *conjugens*) were prevailing in the food of bream in the central areas of the lake (Kahryp & Tыльп, 1974). Today all these chironomid species are represented in the food of bream, while the highest occurrence frequency, mean number and biomass in the bream guts belong to *C. plumosus* larvae and pupae (Figs. 4, 5). Thus, at present the main food of breams of over 15 cm S1 in L. Võrtsjärv is *C. plumosus*, accounting for about 97% of the chironomid bio-

2 Eesti TA Toimetised. B 1/2 1995

in 1 min 1	M	Mean values	in profundal	*	11年 11年 11日 11日 11日 11日 11日 11日 11日 11日	199 <i>P</i> 1 011	Mean values	values per gut	10
Species	ind./m²	%	g/m²	%	Mean ind. live weight mg	indivi- duals	%		%
Procladius 100 ± 16 C. plumosus pupae 1 ± 1 IV instar 310 ± 54 III instar 33 ± 10 III instar 33 ± 10 III instar 3 ± 2 Einfeldia carbonaria 3 ± 2 Microchironomus tener 0 Other chironomids 0 Total 533 ± 72 * Data of monthly samples (three identical	100±16 1±1 310±54 33±10 3±2 72±13 15±8 0 533±72 hree identica	19 58 6 6 7 13 3 3 3 100 100 100 100	0.18 ± 0.04 0.03 ± 0.03 11.28 ± 2.10 0.06 ± 0.02 < 0.01 0.09 ± 0.02 0.01 ± 0.01 at a time) in	one profession of the profundal station.	3.9 \pm 2.2 42.2 \pm 3.8 39.7 \pm 1.1 2.9 \pm 0.3 <0.1 2.7 \pm 0.6 <1 6 <1	28±9 165±31 200±39 1±0 41±8 19±9 1±0 1±0 473±75	$\begin{array}{c} 6\\ 35\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\$	0.11 0.77 6.56 0.58 0.01 0.11 0.11 0.01 8.14 8.14 8.14	

= Table







Fig. 5. Composition of the diet of bream (mean restored weight of food items per gut) in summer 1993.

mass in the guts. This is in accordance with the general trend of increasing the abundance and biomass of C. plumosus in L. Vortsjärv (Kangur et al., in press). Similarly, C. plumosus is the most important food item for bream in several other eutrophic lakes of Europe, for example in L. Balaton (Tatrai, 1980), L. Peipus (Антипова, 1981), L. Ladoga (Щащаев, 1985).

C. plumosus is available in the profundal and sublittoral mud and marl bottom of the lake, indicating that bream prefers an open-water zone as a feeding place. The available amount of chironomids is inconstant in L. Vortsjärv. The abundance of C. plumosus varies especially greatly from year to year (Kangur, 1989b).

2*



Fig. 6. Composition of the diet of eel (mean restored weight of food items per gut) in 1974-1979.

Chironomidae species, first at all C. plumosus form the most important food resource in L. Võrtsjärv also for eel (Kangur, 1989a). Although 11 fish species (chiefly ruff, roach, young perch, smelt, etc.) have been found among the food items of eel in the lake, the main food objects are still the larvae and pupae of C. plumosus, which made up about 70% of the restored weight of all the food items (Fig. 6).

So, both bream and eel consume a large proportion of the *C. plumosus* production in the lake, which can lead to competition between them. However, bream and eel eat different chironomid instars. Unlike eel who takes mainly large fourth-instar larvae and pupae of *C. plumosus*, bream eats abundantly small third-and second-instar larvae of this species and also other small-size profundal chironomids (Figs. 4, 5).

In the shallow eutrophic lake Tjeukemeer (The Netherlands) chironomids larvae also represent an important food resource for bream and eel. As H. W. de Nie (1987) suggests, eel cannot utilize effectively chironomid larvae burrowed in the bottom substrate. Eel and bream have widely different feeding strategies. Lammens et al. (1985) found that bream takes five times more chironomids than eel does.

Bream is the only commercial fish species in L. Võrtsjärv that may suffer from the food competition arising as a result of the mass introduction of eel. In order to relieve food competition between these two fish species, it is allowed to diminish the abundance of bream in the lake; since 1978 this species is caught without any restrictions.

ACKNOWLEDGEMENTS

We thank our colleague Dr. Ervin Pihu for valuable comments on the manuscript. The English text was kindly checked by Mrs. Ester Jaigma.

REFERENCES

Haberman, H. 1964. Latikas Eesti NSV-s. Manuscript in the Institute of Zoology and Botany, Est. Acad. Sci.

- Hoogenboezem, W., Sibbing, F. A., Osse, J. W. M., Boogaart, J. G. M. v. d., Lammens, E. H. R. R. & Terlouw A. 1990. X-ray measurements of gill-arch movements in filter feeding bream, *Abramis brama (Cyprinidae)*. — J. Fish Biol. 36, 47—58.
- Hoogenboezem, W., Lammens, E. H. R. R., Vugt Y. v., Osse, J. W. M. 1991. A model for switching between particulate-feeding and filter-feeding in the common bream Abramis brama. — In: The Analysis of the Pharyngeal-Sieve Mechanism and the Efficiency of Food Intake in the Bream (Abramis brama, Cyprinidae), 71-98.
- Kangur, A. 1989a. The significance of *Chironomus plumosus* L. on the feeding of eel in Lake Võrtsjärv (Estonian SSR, USSR). — Acta Biol. Debr., Oecol. Hung., 3, 177—187.
- Kangur, K. 1989b. Ecology and population dynamics of *Chironomus plumosus* L. in Lake Võrtsjärv, Estonian S.S.R. — Acta Biol. Debr., Oecol. Hung., 3, 189— 198.
- Kangur, K., Timm, H., Timm, T., Timm, V. Long-term changes in macrozoobenthos of Lake Võrtsjärv. Limnologica. In press.
- Kangur, K. & Tuvikene L. Live wet weight, dry weight and caloricity of some macrobenthic invertebrates of Lake Võrtsjärv. — Limnologica. In press.
- Lammens, E. H. R. R., Geursen, J. & Macgillavry, P. J. 1987. Diet shifts, feeding efficiency and coexistence of bream (Abramis brama), roach (Rutilus rutilus) and white bream (Blicca bjoerkna) in hypertrophic lakes. — Proc. Vth Congress Europ. Ichthyol. Stockholm, 1985, 153—162.
- Lammens, E. H. R. R. & Hoogenboezem, W. 1991. Diets and Feeding Behaviour. In: I. J. Winfield and J. Nelson (ed.). Cyprinid Fishes Systematics, Biology and Exploitation. Chapman and Hall, London, 353-376.
- Lammens, E. H. R. R., Nie, H. W. de, Vijverberg, J. & Densen W. L. T. van 1985. Resource partitioning and niche shifts of bream (Abramis brama) and eel (Anguilla anguilla) mediated by predation of smelt (Osmerus eperlanus) on Daphnia hyalina. — Can. J. Fish. Aquat. Sci. 42 (8), 1342—1351.
- Nie, H. W. de 1987. Food, feeding periodicity and consumption of the eel Anguilla anguilla (L.) in the shallow eutrophic Tjeukemeer (The Netherlands). --Arch. Hydrobiol. 109, 3: 421-443.
- Pihu, E. 1993. Distribution of fish species in Estonian lakes. Proc. Estonian. Acad. Sci. Ecol., 3., 4, 181—186.
- Schneider, G. 1920. Nahrung, Wachstum und Parasiten der Fische des Wirzjerv. Arch. Naturk. d. Ostbalt., 2. Ser., 14 (1), 49—117.
- Tatrai, I. 1980. About feeding conditions of bream (Abramis brama L.) in Lake Balaton. — Hydrobiologia, 3, 81-86.
- Антипова Л. Ф. 1981. Качественная и количественная характеристика питания бентосоядных рыб Псковско-Чудского озера. — Сб. научн. тр. ГосНИОРХ, 162, 181—198.
- Хаберман Х. Х. 1968. О питании и пищевых отношениях леща в озерах Эстонии. Тр. XII научн. конф. по изуч. внутренних водоемов Прибалтики. Вильнюс, 105—107.
- Кангур К. 1977. Продуктивность *Chironomus plumosus* L. в открытой части озера Выртсъярв. In: Исследования по проблемам экологии и рационального использования природных ресурсов. Таллинн, 81—84.
- Кангур К. Э., Кангур А. Э. 1978. Размерно-весовая характеристика личинок *Chironomus plumosus* L. в оз. Выртсъярв. Биология внутренних вод. Информационный бюллетень, 37, 51—55.
- Кангур М., Тыльп Ы. 1974. К питанию рыб озера Выртсъярв. Гидробиологические исследования VI, Тарту, 138—162.
- Щащаев Ю. А. 1985. Возрастная и сезонная характеристика питания леща Ладожского озера. — Сб. научн. тр. ГосНИОРХ, 237, 50—55.

LATIKA (ABRAMIS BRAMA) TOIDU KOOSSEIS JA SELLE SESOONSED MUUTUSED VÕRTSJÄRVES (EESTI)

Andu KANGUR, Külli KANGUR

1993. aasta maist kuni augustini uuriti latika toitumist Võrtsjärves. Kokku analüüsiti 56 15—51 cm pikkuse latika toidu koosseisu. Hironomiidivastsed ja -nukud moodustasid enam kui 95% kasutatud toidu massist, kusjuures suurima esinemissagedusega olid *Chironomus plumosus* ja *Einfeldia carbonaria*. Tähtsaim toiduobjekt oli *C. plumosus* (ligi 97% neelatud hironomiidide biomassist). Latika toidutarbimist võrreldi kättesaadava toidu hulga muutustega järves. Samuti võrreldi latika toidu koosseisu angerja (*Anguilla anguilla*) omaga.

СОСТАВ И СЕЗОННЫЕ ИЗМЕНЕНИЯ ПИЩИ ЛЕЩА (ABRAMIS BRAMA) В СВЯЗИ С ЧИСЛЕННОСТЬЮ И БИОМАССОЙ ПИЩЕВЫХ ОБЪЕКТОВ В ОЗЕРЕ ВЫРТСЪЯРВ (ЭСТОНИЯ)

Анду КАНГУР, Кюлли КАНГУР

С мая по август 1993 г. изучалось питание леща в оз. Выртсъярв. Всего проанализирован состав пищи у 56 лещей длиной 15—51 см. Более 95% массы пищевого комка составляли личинки и куколки хиронимид, причем чаще всего встречались *Chironomus plumosus* и *Einfeldia carbonaria*. Важнейшим объектом питания служил *C. plumosus* (около 97% биомассы хиронимид в желудках). Интенсивность потребления пищи у леща сравнивали с изменениями доступного количества пищи в озере. Также сравнивали между собой состав пищи леща и угря (*Anguilla anguilla*).