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Traits of Biology of European Wels Catfish *Silurus glanis* from the Volga–Ahtuba Water System, the Lower Volga

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Abstract—Seasonal distribution, biology of reproduction, body length/weight composition, age of sexual maturation, and features of feeding in wels catfish *Silurus glanis* from the Volga River channel areas within the Volga–Ahtuba water systems (the lower Volga) have been studied. Within the study region, wels habitats are confined to the system of river-channel pits and to the deep-water sites of the main river channel; the fish roam within the surroundings of the pits. Wels spawns in the waterbodies of the subordinate system of the river: eriks (shallow channels) and branches between the Volga and Ahtuba rivers. In the study region, wels is represented by a long-lived late-maturing group. The fish of different body lengths/weights differ in the feeding modes: the specimens with body weights of <5 kg consume various small-sized prey, including nonfish food; larger individuals feed on large fish prey. Comparative analysis of the structures of wels populations from the Volga River delta and channel areas revealed considerable differences indicating the presence of two spatial groups of the population or subpopulation ranks: deltaic migrant and river channel settled. Development of an optimal strategy for exploitation of this valuable fish necessitates a differentiated approach and detailed analysis of biological traits of this species within the Volga basin. Such analysis should include population-genetic methods.

Keywords: wels catfish *Silurus glanis*, age, body length and weight, distribution, biotope, migration, feeding, Volga–Ahtuba water system

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INTRODUCTION

Wels catfish *Silurus glanis* is the largest freshwater fish of the waterbodies of the European part of Russia. The range of wels covers vast areas, but most numerous populations are confined to lower reaches of large rivers of the Black/Azov and Caspian seas basins. In the past, wels was only a valuable object for commercial fishing but its importance as an object of recreational fishing became paramount by the end of the 20th century to the beginning of the 21st century in Russia and in European countries (Elvira and Almodóvar, 2001; Linhart et al., 2002; Hickley and Chare, 2004; Clarke, 2005; Copp et al., 2009; Barabanov et al., 2016, 2017). At the same time, in spite of considerable interest in this species from the point of view of practical use, this fish is poorly studied in many parts of its range; there are not even basic data for many water systems on the most important parameters of population structure: age composition, body sizes, and growth (Britton et al., 2007; Carol et al., 2007a, 2009; Copp et al., 2009).

The vast majority of knowledge on the catfish wels from the lower Volga concern the river delta and adjacent areas of the Northern Caspian where this fish is subject to commercial fishing (Orlova, 1973, 1987; Kazancheev, 1981; Kushnarenko et al., 2004; Fomichev et al., 2006; Kolosyuk and Tkach, 2014). At the same time, the data on the main traits of biology of wels from the channel parts of the Volga River from Volgograd to the upstream parts of the river delta are extremely fragmentary. The river geomorphology and conditions for dwelling of wels in this region strongly differ from those in the Volga delta, and particularly this species is of great interest for recreational fishing in the former region.

Taking into the account the above noted, the goal of the present paper is the analysis of modern parameters of the population structure (body length/weight, age and sex composition, age of sexual maturation), seasonal distribution, reproduction, and feeding of wels catfish from the parts of the main channel of the lower reaches of the Volga River.

MATERIALS AND METHODS

The studies were carried out in 2009–2017 at the 45-km-long section of the Volga River from

Kopanovka Village to Kapitanskii Island. The study region is situated at the distance of 120–150 km from the beginning of the river delta (distance from the sea of 250–270 km) and at the distance of 290–350 km from the dam of Volgograd hydroelectric power station. Within the study region, the Volga and Ahtuba rivers flow as parallel channels; the width of the floodplain between the channels is 2–4 km. The width of the Volga River at the study region (low water period) is 983–1480 m (1123 m on average), depths at the reaches is 14–16 m, and depth in the channel pits is to 31 m. The structure of the studied river parts did not differ from those lying upstream and downstream and correspond in general to geomorphological features of the Volga and Ahtuba rivers within the borders of the Volga–Ahtuba water systems (Nikolayev, 1962). The materials were collected all year round, except for the period of annual ban for fishing (in Astrakhan oblast: April 20 to June 20; in 2017, it was May 16 to June 20).

Wels was sampled using angling gear whose selection was determined by the efficiency of this gear in the conditions of large depths, presence of sunken trees on the bottom, and complicated structure of the bottom relief. As yet another advantage of this gear is that the same baits allowed for catching the fish with body lengths from 50 to 260 cm. In various years and seasons, a total of 12–26 anglers of the Uspekh fishing-hunting base were participating in the sampling. They actively participated in the field sampling and willingly provided their catches for analysis. During the field studies, variable parts of the river—from shoreline shallows (0.3–0.5 m) to deep water river channel pits—were surveyed. The sum time of catfish wels' targeted catching in 2009–2017 was more than 51000 h. In addition, we used the results of wels by-catches of the fishermen at targeted fishing for sander *Sander lucioperca* (14–22 anglers; sum time 59000 h).

The materials were collected following the developed protocol: registration of location and time of fish catching; the location of catching was mapped using GPS-devices (probable circular error ±3–4 m); the depth at the location where the fish was caught was determined using a depth finder with a precision to 0.2 m. To specify the data on wels distribution, either Lowrance HDS-12 Gen3/Structure Scan or Hummingbird 989cxi HDSI/Side Imaging echo-sounders with side view sensors (space coverage to 36 m to each side; beam width of 55°) were used. Wels with body lengths of more than 80 cm were identified by the strength of the reflected signal (more than 18 dB (Pavlov et al., 2011; Borisenko et al., 2014). The assessment of wels' distribution was based on the localizations of catching of 912 specimens. In addition, we analyzed the data on the visual underwater observations, including the use of scuba diving (single operator; total observation time, 64 h).

In total, 252 wels specimens were subjected to biological analysis following the standard scheme (Pravdin, 1966). The following parameters were measured: total body length (*TL*) from the front part of mandible (at closed jaws) to the posterior edge of the caudal fin, maximal body girth in front of dorsal fin (*Freshwater fishes*..., 1989), and total body weight. The age in fish was determined by two operators independently using two registering structures: saw cut of pectoral fin and vertebrae (Harka, 1984; Harka and Biro, 1990; Horoszewicz and Backiel, 2012); the estimates were reconciled. Where possible, both registering structures were analyzed in each fish, while, in some cases, we registered only vertebrae that, according to some researchers, are a more precise structure fully reflecting the age of European wels catfish (Yilmaz et al., 2007). For the analysis, we used the second and third vertebrae (from the head); the muscles and connective tissues were removed and the vertebrae dried (Alp et al., 2011). The mounts of vertebrae were then preliminary immersed in glycerol or liquid for contact lenses and analyzed under a magnifying glass or an MBS-9 binocular. The saw cuts were prepared using a carpenter fretsaw and immersed into Crystal Bond 509 polymer; the mounts were hand-polished on the tissue abrasive materials with successive change of the grain sizes from 600 to 1200 according to the ANSI-74 system. The preparations polished on both sides were analyzed under an MBS-9 binocular in the drop of liquid for contact lenses.

For analysis of feeding, the amount-weight technique was applied. The materials were processed fresh. The food composition was analyzed by weight proportions of the food items or by recording the number of prey in the predator's stomach in some cases (Fortunatova, 1961). The composition of food was analyzed in 302 individuals.

The materials were processed using the methods of univariant statistical analysis; Statistica v. 10 software package was used for plotting the relevant graphs.

RESULTS

The distribution of wels catfish in the study region is characterized by clearly seasonal and mosaic patterns. Sexually mature specimens are closely associated with deep flow-through pits. Wels winterizes in the 27–31 m deep river channel pits; migration towards wintering pits starts in late autumn following cooling the water to 3°C by the end of November to the beginning of December. By the beginning of complete freezing, at water temperature of 0.2–0.3°C, wels concentrates at the gentle slopes of the pits at depths of 12–25 m (Fig. 1). More or less leveled areas of the bottom at the depths of 15–17 m ("steps") represent typical wintering sites. In such places, the specimens of wels lay on the bottom forming dense, compact groups of several tenths of individuals; according to the data of underwater observations (15 h), the fish lay snuggling next to each other. No full stupor is observed and the fish retreat a few meters towards different sides at

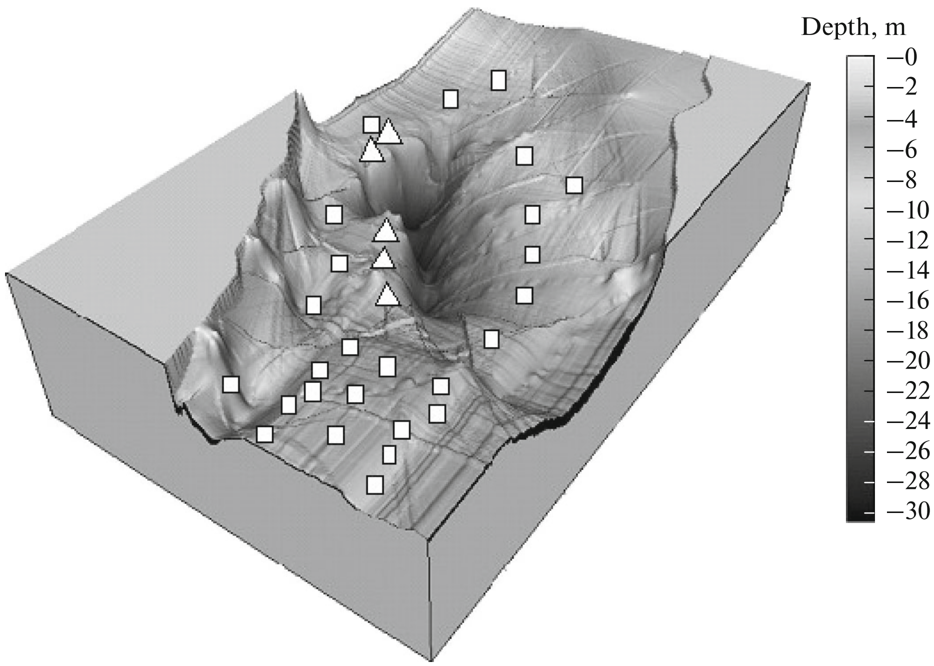

Fig. 1. Distribution of sexually mature wels catfish *Silurus glanis* in summer and winter near the large river channel pit near Ekaterinovka Village (coordinates of the central part: 47°394′ N; 47°032′ E; width, 713–778 m; length, 1020 m; area 81.56 ha); (△) November–March, $n = 82$ ind.; (□) June–October, $n = 331$ ind.

the approach of a diver. The wintering lasts until ice melting, which is as a rule in the third week of March.

Spring activity of wels starts after warming of the water above 2.5°C. From that moment wels distributes over the vicinities of wintering pits at depths of 12–15 m, preferring the site with slow or swirling water currents and avoiding the sites with strong horizontal currents. Wels moves upstream and downstream of the wintering pits a distance of 200–500 m (sum fishing time of ≈6500 h; 14 anglers; number of catches (n) 233 ind.); some fish remain near the wintering biotopes all year round ($n = 112$). Neither catches nor credible strikes by wells were recorded at a long distance from the pits (≈5000 h; 16 anglers). Wells occur at the close vicinities from the pits at the water warming to 7°C; at a temperature from 7 to 12°C, they start to further move upstream and downstream from the pits and distribute at the of pits' edges and at the slopes of deep sites of the reaches usually at the distance of not more than 2 km (≈4000 h; 10 anglers, $n = 275$) (maximal distance, 2.5 km; ≈2500 h; 8 anglers; $n = 4$) from the pit. The edges of slopes at depths of approximately 10–12 m are the typical habitats of wells in early spring. In such places, wels occur until the beginning of the spring flood that starts in the third decade of April in the study region.

The spring flood lasts for approximately 3 weeks during which time the water level varies from +5 to +7.5 m relative to the low water stage. During this period, sexually mature specimens travel from the river channel sites to the waterbodies of the subordinate system of the Volga–Ahtuba interfluve, to spawning grounds. We failed to detect wels in the Volga and Ahtuba channels using sonar devices (12 km long part of the Volga, the area of 963 ha, and 14 km part of the Ahtuba, the area of 403 ha was surveyed).

In mid-June following the peak of the flood, the drop of water level by 2.0–2.5 m and the warming of water in the Volga channel to 17–18°C wels leave the waterbodies of the subordinate system moving down to the river channel. Some fish with $TL \leq 150$ cm and body weight to 25 kg move towards temporal streams to the main river channel from the floodplains and flows from the floodplains (so called "vyteks") in which juvenile and adult cyprinids migrate downstream in mass. Wels situated directly near the flows' mouth at the depths of only 40–50 cm. The water layer is sometimes so thin that it hardly covers the fish body. Wels stay with open mouth opposite the flow and actively swallow juvenile fish moving downstream. This feeding mode of wels in the Volga River delta was described earlier (Fortunatova, 1962; Fortunatova and Popova, 1973). Usually several individuals of wels with TL 100–150 cm line up in a row stretching downstream from the flow's mouth. Following the catch of one specimen remaining directly opposite the flow mouth, the next wels occupies the same location after 25–30 min. Fishing off three "vyteks" (≈750 h; 6 anglers; $n = 64$) revealed that downstream of each of them there may be 12–15 wels individuals with body weight to 25 kg. Downstream the "vyteks," wels individuals behave secretly and move slowly masking at the bottom background.

Following termination of spring flood, from the last week of June at warming of water above 20°C, wels occupy summer habitats that are similar to the late-spring ones: edges of the river channel pits and open deep parts of the reaches with strong horizontal water currents along the edges at depths of 12–15 m. A site situated either slightly upstream or downstream the long edge (longitudinal edge of the river channel with sharp drop of depth) represents typical summer biotope of wels. Some individuals stay at the edges of pits. The areas with cross-wise lamination of the river channel—a series of 1.5–2.5 m high ridges transversal relative to the main river flow—often occur in the Volga River channel at depths to 10–12 m. However, wels occur solitary at such habitats as opposite to other fish species, e.g., sander (Kuzishchin et al., 2016).

In summer time, maximal distance of wels habitats from the wintering pits is 4.5 km (≈7000 h; 18 anglers; n = 21). Even if depths and bottom relief do not change, adult individuals at TL > 150 cm were not detected (≈8500 h; 26 anglers). Short reaches connecting neighboring pits situated at the distance of not more than 10 km are an exception. In summer time, wels individuals spread over the whole area of such reaches at depths of 12–15 m. The distribution of wels remains unchanged during the whole summer until late autumn when water temperature drops to 4°C. Logjams of sunken trees (heaps of snags) in the river channel represent the second type of wels' summer biotopes. At such habitats, wels individuals occur at depths from 4 to 14 m. It is hard to fish off such habitats and we sampled wels using bait (sander with body weights of 500–800 g, frogs *Rana* sp., flesh of bivalve mollusks of gg. *Unio* and *Anodonta*). According to the results of these fishing efforts (≈3500 h; 9 anglers; n = 78), the logjams of sunken trees are inhabited by wels individuals with TL 90–150 cm and body weight of 10–35 kg; solitary specimens with body weights to 48 kg were noted. The sonar survey of a 4.3 km-long logjam area revealed that the fish seldom occur in the dense heaps of sunken trees preferring their external edges at depths of 13–14 m.

Immature and small mature wels individuals with TL ≤ 100 cm exhibit different patterns of distribution. Such fish occur at various depths, from 0.3 to 10–12 m but generally prefer shallow areas at depths of 2–6 m (≈9000 h; 20 anglers; n = 154). As a rule, wels specimens with TL 50–100 cm are widely spread over the reaches and do not have clearly preferable biotopes: they may occur at the edges of pits, at the areas of underwater plateaus at depths of 4–6 m, at areas with transverse ridges, in underwater logjams at depths to 5 m, and at the sites with sharp drop in depths near abrupt shores.

Traits of reproduction. In the study region, wels catfish spawns during the period from the third decade of May to the end of the first week of June. The fish spawns outside the main river channel, in floodplain eriks and lakes, and in flows and branches connecting the Volga and Ahtuba rivers. In the eriks, extended channel-type waterbodies (lengths from 1–2 to 10–12 km), wels individuals ascend from the main river channel for the distance of 300–1200 m. For laying the eggs, they build nests (underwater observations; 25 h). Two types of nests were found. The first type of nests (12 nests) are situated at the sunken meadows at a depth of 1–2 m in the previous year's terrestrial vegetation. At such grounds, small individuals with TL ≤ 110 cm spawn; their nests are roundish, saucer-shaped, in the middle of which the spawners either trample down or partially tear off the plants. The diameter of such nests is approximately 1 m (7 nests). The second type of nests (14 nests) are situated in the channels of eriks at the sites with sandy bottom at depths to 3.5 m. At such grounds, the individuals with TL 120–200 cm spawn. Their nests are cone-shaped with a diameter of approximately 1.5 m and recess to 30 cm (10 nests). According to the data of underwater observations, both parental fish protect laid eggs, and they retreat from the nest but do not exhibit aggressive behavior at the approach of a diver.

We failed to credibly reveal the spawning sites of the individuals with TL > 200 cm. It is quite possible that such fish spawn in the branches connecting the Volga and Ahtuba rivers (Danilovka and Praskov'ya branches). Underwater observations (10 h) in the end of May revealed six large saucer-shaped or cone-shaped pits situated at the sites with sandy bottoms. Their shapes and structures are similar to those found at the bottoms of eriks: they have the shape of an inverse cone with an external edge diameter of approximately 2.5 m and recess to 0.8 m (4 pieces). Due to strong water current and turbidity, it was not possible to record the occurrence of wels individuals at such sites in the end of May to the beginning June.

Body length and weight of wels individuals in the group sample vary within the limits of 55–266 cm and 1.3–114 kg (Table 1). The specimens with body weights of >90 kg were caught at the frequency of 1–2 ind./year; 70–90 kg, 3–5 ind./year; 50–70 kg, 6–8 ind./year. More than 60% of the sampled fish comprised the individuals with TL 80–150 cm and body weights of 3.5–15.0 kg. Fast growth rate is a characteristic of wels catfish from the channel sites of the Volga River: by the age of 10 years, the fish reach TL 120 cm and body weight of >13 kg on average (Fig. 2). Linear and, especially, weight growth are described by S-shaped curves: at the age of 12–20 years, the growth rate is faster than during the period from 3 to 12 years and older than 22 years.

The proportion between body length (TL, mm) and weight (W, g) is described by the following equa-

Table 1. Body length (*TL*) and weight of wels catfish *Silurus glanis* of various ages from the Volga River channel

Age, years	*n*, ind.	*TL*, mm		Body weight, g	
		M	min–max	*M*	min–max
3+	12	561.6	551–601	1363	1120–1580
4+	16	673.3	575–770	2265	1680–3100
5+	19	731.0	619–822	3167	2460–4500
6+	21	858.1	690–910	4749	2980–7000
7+	31	900.3	830–1120	5830	3640–9700
8+	16	1058.1	995–1130	8112	6300–11500
9+	14	1164.1	1001–1290	11806	7800–16600
10+	15	1200.5	1090–1314	13648	10620–18000
11+	13	1370.2	1330–1410	15771	16600–18900
12+	11	1420.1	1220–1575	17564	12670–21100
13+	12	1565.5	1400–1811	25530	18100–36000
14+	10	1653.0	1440–1830	27506	20700–38000
15+	11	1793.5	1625–2000	36250	28100–52200
16+	10	1882.3	1670–2100	43145	31400–60700
17+	12	2044.8	1800–2230	53507	38000–63000
18+	5	2145.2	2090–2190	61900	53500–70000
19+	7	2181.4	2050–2330	74214	71800–78400
20+	4	2247.5	2100–2360	80825	78000–83000
21+	2	2325.0	2300–2350	81950	79800–84100
22+	1	2380	–	83600	–
23+	1	2390	–	85000	–
24+	1	2400	–	89000	–
25+	1	2400	–	88000	–
26+	1	2410	–	91000	–
27+	1	2470	–	93000	–
28+	1	2475	–	93000	–
29+	1	2410	–	96000	–
30+	1	2450	–	103000	–
31+	0	–	–	–	–
32+	1	2560	–	112000	–
33+	1	2660	–	114000	–

M—mean; min–max—limits of parameter variation.

tion: $W = 744.98 \times e^{0.002\,TL}$, $R^2 = 0.9208$, $p < 0.001$, $n = 252$ (Fig. 3). The relation between body length, maximal body girth (G, mm), and body weight is described by the following equation: $W = 1.191TL \times G^2/36323$, $R^2 = 0.8113$, $p < 0.001$, $n = 201$.

Age and sex composition, age of sexual maturation. Maximal age of wels catfish recorded in our study was 33 years (the specimen was caught in April 2011). The fish older than 25 years were caught at the frequency of not more than 1–2 ind./year (<4% of the total group sample) in the beginning of April or in October. The majority of wels harvest consisted of 6–18-year-old individuals (>80% of the total group sample) (Table 1).

The ratio of sexes among the specimens with body weights of <60 kg is approximately equal; females prevail among the individuals with body weights of >60 kg (68%).

Solitary males reach sexual maturity at the age of 4 years; females, 5 years. Mass sexual maturation takes place at the age of 6–7 years and all wels individuals are sexually mature starting from 8 years (Table 2).

Feeding. Wels catfish feeds at the water temperature above 7°C from the end of April to mid-October.

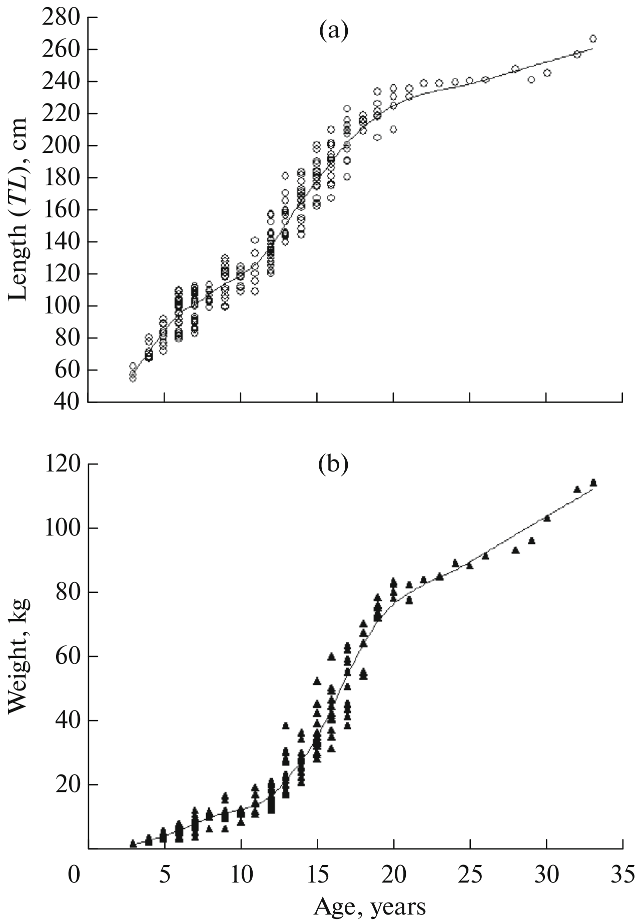

Fig. 2. (a) Linear and (b) weight growths of wels catfish *Silurus glanis* from the channel sites of the Volga River.

Feeding is characterized by pronounced seasonality and differences in food composition in the specimens of various sizes (Table 3). As a rule, with increase in wels size, the size of consumed food increases as well. Small individuals with weights below 5 kg feed on small fish; crayfish (*Astacus* sp.) and frogs represent considerable components of their food especially in the summer time. Presence in the stomach content of frogs, crayfish, roach *Rutilus rutilus*, and perch *Perca fluviatilis* indicate that small wels individuals are confined to shallows and near-shore areas of the river. This fact confirms the data on the fish distribution

Table 2. Shares of sexually mature males and females of wels catfish *Silurus glanis* in various age groups in the catches from the channel sites of the Volga River, %

Sex	*n*, ind.	Age, years				
		4+	5+	6+	7+	8+
Males	58	11.1	27.3	75.0	88.2	100
Females	55	0.0	22.2	75.0	82.3	100

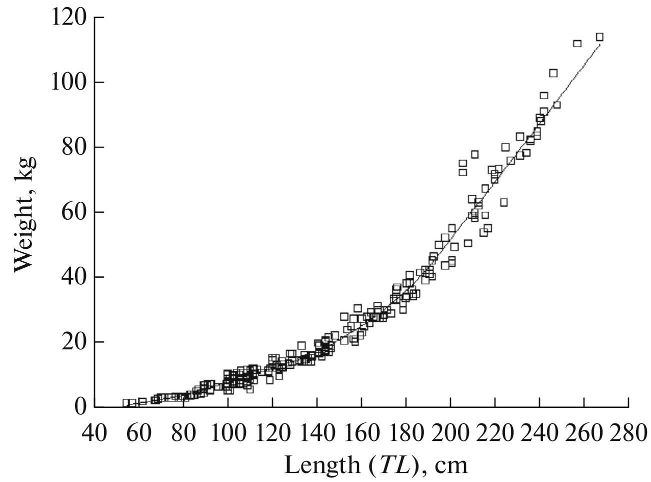

Fig. 3. Dependence between body length and weight of wels catfish *Silurus glanis* from the channel sites of the Volga River.

obtained by the fishing surveys. In the larger wels individuals, food consists of only fish: mass schooling cyprinids prevail. In general, no preferable forage fish species were revealed in the wels individuals at body weight to 30 kg; as a rule, these individuals feed on the mass and most available food items. At reaching the body weight of above 30 kg, the feeding of wels undergoes considerable changes. At such body sizes, wels turns to feeding on large preys: sander, bream *Abramis brama*, and wild common carp *Cyprinus carpio* occurring in the river at deeper parts of the channel.

For instance, occurrence frequency of sander in the food of wels with body weight of above 40 kg reaches 100%. Irrespective of the size of wels individuals, sander with body weights of 800–1200 g was most often found in the stomachs, and sanders with body length of 60–65 cm and weight of 3.5–4.5 kg were sometimes found in the stomachs of wels. As a rule, such large prey were noted in the wels individuals with body weight of 70–80 kg. In the stomachs of wels individuals with body weight of 40–60 kg, we found up to four specimens of bream weighing 1–2 kg. Common carp weighing 2–3 kg occurred in the stomachs of wels with body weights above 50 kg. The share of sander considerably rises in the food of large wels in summer time; the share of asp *Aspius aspius* rises in autumn. These preferences are confirmed by the results of catching wels using live bait (≈4000 h; 54 weighted lines; $n = 81$): in July, wels always selected the lines with sander as bait out of five types of live baits (common carp *TL* 30–35 cm, bream *TL* 25–30 cm, sander *TL* 35–45 cm, roach *TL* 20 cm, asp *TL* 30–35 cm); in September they selected sander and asp in equal shares. These facts indicate that wels catfish exhibits clear seasonal preferences in selection of prey.

During the whole span of the observation period, not one bird was found in wels stomach; a single case

Table 3. Characteristics of feeding of wels catfish *Silurus glanis* of various size groups at the channel sites of the Volga River

Parameter	Months (water temperature, °C)/size groups, kg														
	end of April–beginning of May (8–12)					mid-June* (18–21)					mid-June–mid-July (23–26)				
	1.0–5.0	5.1–10.0	10.1–30.0	30.1–60.0	60.1–100.0	1.0–5.0	5.1–10.0	10.1–30.0	30.1–60.0	60.1–100.0	1.0–5.0	5.1–10.0	10.1–30.0	30.1–60.0	60.1–100.0
Share of component, % of food weight:															
– roach		23	19				21	20			10	11			
– bream		5	11	22	55		12	5				6	9	17	43
– blue bream		31	21	26							11	18	14	4	
– silver bream		32	24	20	5		11	15			12	19	16	6	
– sander			11	15	18							1	18	27	36
– herring											7	28	25	25	
– asp															
– pike			6				7	12			5				
– (wild) common carp				8	17								4	9	15
– crucian carp			8	9	5		22	20			4	3	8	12	6
– rudd							6	9			8				
– sabrefish								5					6		
– perch		9					16	9			12				
– bleak											9				
– crayfish											12	11			
– frog							5	5			10	3			
Sample size, ind.	8	12	18	14			9				14	18	15	16	
Share of fish with empty stomachs, %	100	59	12	8			0				0	0	0	0	

Table 3. (Contd.)

Parameter	Months (water temperature, °C)/size groups, kg									
	mid-July–mid-September (20–25)					mid-September (17–18)–mid-October (8–10)				
	1.0–5.0	5.1–10.0	10.1–30.0	30.1–60.0	60.1–100.0	1.0–5.0	5.1–10.0	10.1–30.0	30.1–60.0	60.1–100.0
Share of component, % of food weight										
– roach	14	11				13	8			
– bream		6	12	20	35	9	12	18	30	32
– blue bream	13	25	17	10		11	32	22		
– silver bream	14	27	18	13		12	36	25		
– sander			26	28	30			13	30	34
– herring										
– asp			3	8	9			10	18	16
– pike	5	6								
– (wild) common carp				9	17			2	11	18
– crucian carp		7	12	12	9	4	1	10	10	
– rudd	10	11	12			10				
– sabrefish										
– perch	12	3				10				
– bleak	10					10				
– crayfish	12	4				12	11			
– frog	10					9				
Sample size, ind.	11	21				12	8	19	12	11
Share of fish with empty stomachs, %	0	0				42	38	11	0	0

* Data on feeding of wels near the flows.

was recorded when a musk rat *Ondatra zibetica* was found in the stomach. Pieces of textile were found twice in the stomachs. In the Volga River channel, adult wels catfish are the clear predators feeding exclusively on fish prey.

Complicated diurnal feeding rhythm is a characteristic of wels catfish inhabiting the river channel. During the iceless period, the wels was caught with artificial baits only in the daytime with 96% of catches (≈42000 h; 24 anglers; $n = 763$) within the period from 8:00 a.m. to 2:00 p.m. At the same time, with the use of weighted line for bottom angling with live baits (≈5500 h; 68 lines; $n = 102$), all wels individuals were caught only in the dark time, which corresponds to experimental data indicating the feeding of wels in the dark time of the day (Girsa, 1981; Boujard, 1995; Pohlmann et al., 2001).

DISCUSSION

Lower reaches of the Volga River represent a geomorphologically complex water system in which two large parts considerably differing in structures and hydrological regimes are defined: the river channel part or the Volga–Ahtuba water system and the Volga delta (Nikolayev, 1962; Zvolinskii et al., 2015). After building of the cascade of dams for hydroelectric power stations, the hydrological regime of the whole lower Volga changed strongly. These changes affected some biological parameters in many fish species, including wels catfish, inhabiting the river channel, delta, and delta front (Orlova and Popova, 1976; Orlova, 1987; Kolosyuk and Tkach, 2014).

Our data allow for the assessment of the modern state of the wels catfish groups inhabiting the Volga River channel areas and for revealing a range of specific features of its biology. The analysis of wels distribution in the study region in various months revealed that wels is settled, its biotopes are confined to the system of river channel pits and deep-water parts of the main river channel with strong horizontal water currents. The fish travel for short distances of hundreds of meters (more seldom, 1–2 km) and these trips are limited by the vicinities of the pits. Spawning migrations are also quite short since, in the study region, numerous variable waterbodies of the subordinate system appropriate for spawning of both small and large wels spawners are situated in direct proximity from the river channel pits in the Volga and Ahtuba floodplain. The analysis of size and age composition of wels population shows that, in the study region, this fish is presented as a long-lived, late-maturing group consisting of large fish. In the channel parts of the Volga River, wels exhibits size-age related differences in feeding: small individuals consume variable small preys, including nonfish food; with age, wels turns to feeding on large fish confined to deep water channel biotopes (sander, wild common carp, and bream).

Comparative analysis of structures of wels populations from the river channel and the Volga delta revealed the presence of pronounced differences between them (Table 4). First of all, this concerns the life expectancy and size of the fish. In the delta, wels population consists predominantly of the fish at the age of 3–6 years, *TL* 68–70 cm, and body weight of 1.3–2.9 kg; specimens weighing 40–50 kg occur solitarily (Orlova, 1987; Kushnarenko et al., 2004; Kolosyuk and Tkach, 2014). In the Volga channel, the population of wels is represented by large individuals $TL >$ 120 cm at the age of 8–20 years, and the presence of especially large individuals weighing to 100 kg is noticeable (Tables 1, 4). In general, our data comply with the data of earlier research on wels catfish from the lower reaches of large plain rivers prior to intensive hydroengineering activity (Berg, 1949; Lysenko, 1978; Harka, 1984). In the Volga delta, wels' growth is fast; its maturation starts at the age of 2 years and mass maturation takes place at the age of 3–4 years (Kazancheev, 1981; Orlova, 1987; Kolosyuk and Tkach, 2014). In the Volga channel, some fish become sexually mature only at the age of 4 years and mature in mass only at 6–7 years (Tables 2, 4). Pronounced differences in wels feeding modes were revealed. It is worth noting that two peaks of fattening in wels are defined in the delta, spring and autumn, which is determined by the mass migration of semianadromous fish from the Northern Caspian for spawning in spring and wintering in fall (Fortunatova, 1962; Fortunatova and Popova, 1973; Orlova and Popova, 1976, 1987; Orlova, 1987). In summer time in the Volga delta, the intensity of wels feeding decreases and it starts to consume resident fish (first of all, rudd *Scardinius erythrophtalmus*), crayfishes and frogs (Orlova and Popova, 1976, 1986, 1987). In the Volga River channel, main fattening falls upon the summer time and large preys are preferred in all months (Tables 3, 4). Only the smallest individuals confined to the shallow areas of the river channel consume nonfish food in some months: crayfishes and frogs. The data on active feeding in summer time revealed in the present study corresponds to the data on the thermal preferences of wels: it starts to feed actively after water warming above 15°C; most intensive feeding is observed at the thermal optimum of 22–28°C (Wysujack and Mehner, 2005; David, 2006; Zaikov et al., 2008).

Most likely, large sizes of wels catfish from the Volga channel are determined by dwelling in the conditions of a large waterbody with deep water, strong water currents, and rich food resources in the form of big reophilic fish species (sander, wild common carp, and asp) that is also a characteristic of wels from other European waterbodies (Davies et al., 2004; Wolter and Freyhof, 2004; Carol et al., 2007a, 2007b; Copp et al., 2009; Horoszewicz and Backiel, 2012).

It is considered that European wels catfish is a species characterized by plasticity with wide limits of tolerance to environmental factors. As a result, the mod-

Table 4. Comparative characteristics of some biological traits of wels catfish *Silurus glanis* from the channel and delta of the Volga River

Parameter	Volga River channel (original data)	Volga River delta
Mode of life	Settled. Undertake short seasonal trips in the vicinities of river channel pits	Migrating. Undertakes distinguishable migration for tens of kilometers between the delta, front delta and open areas of the Northern Caspian (Pavlov, 1979; Orlova, 1987; Kolosyuk and Tkach, 2014)
Biotope	Differs in juvenile and adult fish. Immature fish are confined to shallow areas; adults inhabit channel pits and adjacent deep-water areas of the reaches	As a rule, both juvenile and adult specimens inhabit similar biotopes in the delta and front delta (Orlova, 1973, 1987; Fortunatova and Popova, 1973; Orlova and Popova, 1976; Kazancheev, 1981)
Localization of spawning grounds	In the waterbodies of subordinate system; in lentic or weakly-lotic	In variable delta waterbodies: eriks, branches and floodplain lakes (Koblitskaya, 1963)
Age composition	Fish at ages of 8–20 years prevail; life expectancy to 33 years	Fish at ages of 2–5 prevail; maximal age, 11–12 years (Kazancheev, 1981; Orlova, 1987; Kolosyuk and Tkach, 2014).
Age of sexual maturation	Maturation starts at age of 4 years; mass maturation, at 6–7 years	Maturation starts at age of 2 years; mass maturation at 3–4 years (Kazancheev, 1981; Orlova, 1987; Kolosyuk and Tkach, 2014).
Size composition	*TL* 100–200 cm, body weight 10–60 kg, maximal weight 114 kg	*TL* 68–70 cm, body weight 1.3–2.9 kg, maximal weight 40 kg (Kazancheev, 1981; Orlova, 1987; Kolosyuk and Tkach, 2014).
Feeding mode	Single peak in middle summer. Clear age and size related variability in selection of food items is observed	Two peaks, in spring and autumn; rather strongly depends on abundance of semianadromous fish species (Fortunatova, 1962; Sibirtsev, 1967; Fortunatova and Popova, 1973; Orlova and Popova, 1976, 1986)

ern structure of this species is mosaic and variable at the populational level of organization. This structure strongly depends on geomorphological and hydrological parameters of a waterbody in which wels is dwelling (Hilge, 1985; Bruton, 1996; Alp et al., 2004; Carol et al., 2009; Copp et al., 2009). The mosaic pattern of wels population structure is especially pronounced in the conditions of deep anthropogenic transformation and fragmentation of waterbodies over the whole modern species range (Harka, 1984; Schlumberger et al., 2001; Copp et al., 2007, 2009; Horoszewicz and Backiel, 2012). Our data confirm the conclusion of other researchers: there are good reasons to suggest that two specialized spatial groups of either populational or subpopulational levels are present within the limited part of the wels' range (lower Volga): the deltaic migrating and river channel settled. It is possible that high plasticity of population structure of wels in the lower Volga is also determined by its high genetic variability that is considered to be the highest within the species range (Krieg et al., 2000; Triantafyllidis et al., 2002). The presence of two wels groups in the lower Volga accords well with the concepts of other researchers on the presence in this species of a wide set of specific adaptations. These adaptations concern, first of all, the ability to find appropriate biotopes in any waterbody, to master a wide spectrum of food resources, and to form a unique length/weight and age structure of populations for each waterbody (Harka, 1984; Anthouard et al., 1987; Boujard, 1995; Davies et al., 2004; Copp et al., 2009).

The present study shows that development of an optimal strategy for exploitation of such a valuable biological resource as European wels catfish necessitates a differentiated approach and detailed analysis of the biological traits of the species over the whole Volga basin with application of the methods of population-genetic analysis of spatial and ecological groups. In modern conditions when in the Volga–Ahtuba water system where targeted commercial fishing for wels is absent, the analysis of the results of recreational fishing is nearly the only source of new data on this species appropriate for the purposes of monitoring of its state. The present research points to the perspectives of such approach at adequate organization of studies, preparation and fulfilling of the protocols of sampling and data archiving.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interests. The authors declare that they have no conflict of interest.

Statement on the welfare of animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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