Changes in the Ratio of Rheoreaction Types during Fish Starvation

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Abstract—Changes in the motivational component of rheoreaction (the ratio of rheoreaction types) during starvation in some fish species has been analyzed. The presence of fish motivation to migrate (before starvation) is the major pattern of the future changes in the motivational component of rheoreaction resulting from starvation. All fish of the families Cyprinidae and Salmonidae studied with initially behavior as resident individuals show the same type of response to starvation. Their preference for currentwise movement increases on the 2nd–5th days of starvation, then the preference for movement against the current increases on the 7th–12th days, and the ratio of rheoreaction types approaches the initial one. Juveniles of the Black Sea salmon (*Salmo trutta labrax*) with a motivation to downstream migration, represent a different response to starvation: the downstream movement of individuals monotonically increased from two days after starvation.

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INTRODUCTION

Rheoreaction (the behavior of fish in water current) is an innate reaction associated with fish life in a shifting environment. It is manifested in the selection of a certain part of the reservoir with the optimal (for actual behavior) current velocities and the vector of the fish's individual movements in it. Rheoreaction is one of the main mechanisms of fish behavior in flowing water bodies, including their distribution, and migrations (Pavlov 1979; Pavlov et al., 2007).

The manifestation of rheoreaction is determined by three components: orientational one (perception of a stimulus), motivational (choice of the type of rheoreaction), and locomotor (realization of a selected type of rheoreaction) (Pavlov, 1979; Pavlov et al., 2010, 2020b). The indicators of the motivational component include fish rheopreferendum (choice of a current-free stream or not), selected flow rates in the rheogradient (Pavlov, 1979), and the ratio of rheoreaction types (Maclean and Gee, 1971; Pavlov et al., 2010, 2020b). Three types of rheoreaction are considered: positive (PRT), upstream movement; negative (NRT), currentwise movement; compensatory (CRT), maintaining position relative to fixed landmarks. These types of fish behavior towards the current have also been noted by other authors (Johnston et al., 2017).

Changes in rheoreaction resulting from various environmental factors have different reasons. It is known that the motivational component of rheoreaction during the migration of juveniles from spawning waters to feeding grounds can change rapidly (minutes, hours) and cardinally in action of illumination

(Pavlov et al., 2007, 2019) and the chemical composition of water (Zvezdin, 2016). In these cases, individuals are constantly in a migratory state and a change in rheoreaction is determined by a change in their actual behavior. For example, contranant migration of the juvenile sockeye salmon *Oncorhynchus nerka* changes to a denantant one in the absence of a “lake scent” or a change from resident behavior to migratory during downstream migration in juveniles of many fish species at dusk. In addition, the rheoreaction of juveniles changes with prolonged exposure to unfavorable factors of various nature. In such a case, the change in the rheoreaction in fish, initially with no motivation to migrate, is determined by the formation of migratory state (Pavlov et al., 2010; Ponomareva, 2014).

Under natural conditions, the trophic factor is the most frequent cause of fish migrations (Olsson et al., 2006; Pavlov et al., 2007; Flecker et al., 2010; Ferguson et al., 2019). Fish starvation leads to a rapid (days, weeks) formation of migratory behavior, which changes the fish rheoreaction (Pavlov et al., 2010). All three components of the rheoreaction change. Several special studies have been dedicated to the orientational (Gaffron, 1934; Harden Jones, 1963; Pavlov, 1979) and locomotor (Etingen, 1964; MacLeod, 1967; Laurence, 1972; Saburenkov, 1973; Pavlov, 1979; etc.) components of fish rheoreaction under the influence of starvation. To the best of our knowledge, there is no data on the changes in the quantitative parameters of the motivational component of fish rheoreaction. Some information about its change was obtained in studies of the physiological and behavioral mecha-

nisms of the migratory behavior of fish (Pavlov, 1979; Pavlov et al., 2007, 2010, 2016; etc.).

The purpose of this work is an experimental assessment of the dynamics of the ratio of rheoreaction types during starvation of fish.

MATERIALS AND METHODS

The experiments were carried out in the laboratory of the Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences (IPEE RAS), in 2018. Individuals of four fish species were used: sunbleak (*Leucaspius delineatus*), average body length 31.7 ± 0.25 (28–36) mm; zebrafish (*Danio rerio*), 26.5 ± 0.27 (24–33) mm; Prussian carp (*Carassius auratus*), 94.6 ± 1.14 (78–116) mm; and rainbow trout (*Parasalmo mykiss* = *Oncorhynchus mykiss*), 105.6 ± 0.97 (88–120) mm. The Latin names of the species are given according to Annotated Catalog (*Annotirovannyi katalog...*, 1998). The rainbow trout was taken from a fish farm near Moscow, while the *Danio rerio* (out-bred) were taken from the aquarium of IPEE RAS.

Before the start of the experiments, the fish were fed once a day, given an excess amount of food. Zebrafish and sunbleak were fed with Prodac Tropical Fish Flakes, and rainbow trout and Prussian carp were fed with BioMar artificial food. After the start of the experiments, the feeding was completely stopped; the last time the fish were fed was on the 0th day, one hour before the start of the experiment. Fish were kept in aerated aquariums at a stocking density of 1 ind. per 7 L of water (zebrafish and sunbleak) and 1 ind. per 10 L of water (Prussian carp and rainbow trout). The temperature was maintained with a thermostat at 18°C (Prussian carp, rainbow trout, and sunbleak) and 22°C (zebrafish). Illumination in the laboratory from 10 a.m. to 7 p.m. was 450–500 lux; the rest of the day the artificial lighting was turned off.

To determine the ratio of the rheoreaction types, direct-flow Fishway hydrodynamic devices were used. They allow us to determine three types of rheoreactions: PRT, CRT, and NRT (Pavlov et al., 2010). Such a device is a tray, divided by transverse partitions into nine compartments; the middle compartment (no. 5) was the starting one. Depending on the size of the fish, we used one the devices: for the Prussian carp and rainbow trout, the length of the Fishway device was 200 cm, width, 60 cm; for zebrafish and sunbleak, 110 and 20 cm, respectively.

The experiments were carried out on groups of six fish. At the beginning of the experiment, the fish were placed in the starting compartment (no. 5), previously separated with removable nets. After 20 min of acclimation, the starting compartment nets were removed and the experiment began. After 30 min, the number of fish in the compartments was counted.

For the possibility to compare the results obtained with previous publications, experiments were performed on days 0, 2, 5, 7, 10, and 12 after the last feeding.

Sixty individuals of each fish species were treated in 60 experiments.

Experimental data were used to calculate the frequency of manifestation of each type of rheoreaction:

$$\text{PRT} = \sum n_i / N; \quad \text{CRT} = n_5 / N; \quad \text{NRT} = \sum n_j / N,$$

where N is the number of fish studied, ind.; n_i is the number of fish in compartments 1–4 of the Fishway, ind.; n_5 is the number of fish in the 5th compartment (starting), ind.; n_j is the number of fish in compartments 6–9, ind.; i, j , compartment numbers in the range 1–4 and 6–9, respectively.

In addition to the ratio of rheoreaction types, the index of contranance (I_k) was also calculated. It reflects the ratio of dynamic types of rheoreaction (PRT and NRT). The contranance index assesses the movement of fish relative to the starting compartment, reduced to a scale of $-1 \dots +1$. The calculation of this indicator was carried out according to the formula:

$$I_k = \sum (n_i(\text{No.s} - i)) / N(\text{No.s} - 1),$$

where n_i is the number of fish in the compartment No. i ; No. s , the number of the starting compartment; i , the number of the compartment; and N , the number of all the fish participating in the experiment.

Furthermore, to analyze and summarize the results, we used the initial data on control individuals, obtained by us in studies of the physiological and biochemical mechanisms of migration of the brown trout (*Salmo trutta*), Black Sea trout (*Salmo trutta labrax*), and rainbow trout (Pavlov et al., 2010, 2018, 2020a; Pavlov, E. et al., 2016). These individuals were not subjected to experimental effects (hormonal drugs or denial of access to shelters) either before or during the starvation.

For statistical analysis, we used nonparametric analysis of variance (Kruskal–Wallis H -test) for the results of each treatment and Student's test for fractions (Lakin, 1973), carried out for the summary data for each species. Like any ratio, the ratios of the rheoreaction types differ significantly when the frequencies of manifestations of at least one of the types of rheoreaction are significantly different.

RESULTS

Nonparametric analysis of variance (Kruskal–Wallis H -test) showed that starvation significantly ($p < 0.05$) affects the frequency of manifestations of dynamic types of rheoreaction (PRT, NRT), but not CRT ($p = 0.46$). There was no significant joint influence of two factors (fish species and duration of starvation) on the indicators considered. That is, during

Table 1. Frequency of manifestation of different rheoreaction types in the Fishway device for four fish species during starvation

Fish species	Day of starvation	PRT	CRT	NRT
<i>D. rerio</i>	0	40.0	3.3	56.7
	2	16.7	3.3	80.0
	5	31.7	1.7	66.7
	7	35.0	8.3	56.7
	10	31.7	0.0	68.3
	12	45.0	3.3	51.7
<i>P. mykiss</i> (= <i>O. mykiss</i>)	0	45.0	15.0	40.0
	2	28.7	10.0	61.3
	5	23.3	13.3	63.3
	7	40.0	21.7	38.3
	10	38.3	6.7	55.0
	12	46.7	1.7	51.7
<i>L. delineatus</i>	0	48.3	3.3	48.3
	2	33.3	3.3	63.3
	5	23.3	1.7	75.0
	7	33.3	3.3	63.3
	10	48.3	0.0	51.7
	12	40.0	0.0	60.0
<i>C. auratus</i>	0	43.3	16.7	40.0
	2	45.0	5.0	50.0
	5	36.7	5.0	58.3
	7	66.7	3.3	30.0
	10	51.7	10.0	38.3
	12	46.7	0.0	53.3

NRT frequencies in bold significantly ($p \leq 0.021$) differ from the corresponding PRT frequency, according to Student's test for fractions.

starvation, the nature of the change in the ratio of rheoreaction types is similar in the fish of the species studied.

In nonstarving fish (day 0; Table 1), dynamic types of rheoreaction predominate (83.3–96.7%), while the frequencies of their manifestation (PRT and NRT) are approximately equal ($p > 0.70$, Student's test for fractions). Such a ratio of rheoreaction types is observed in fish with resident behavior using a dynamic method of maintaining location (Ponomareva et al., 2017). This corresponds to the close-to-zero value of the contranance index. Under natural conditions, such a ratio of the types of rheoreaction was observed in nonmigratory fish (Pavlov et al., 2010, 2010a, 2020b). Consequently, before starvation, the experimental fish did not have a migratory state: in the experimental device they manifested resident behavior with a dynamic way of maintaining location.

On the 2nd–5th days of starvation, the frequency of NRT in all studied fish became higher than that of PRT (Table 1). Such a ratio of rheoreaction types in natural conditions indicates the downstream movement (migration) of fish (Pavlov et al., 2010a, 2010b, 2020b; Zvezdin, 2016). Then the motivation to move against the current increased. As a result, on the 7th–

12th days of starvation, the ratio of the rheoreaction types approached its initial value, and the difference in the PRT and NRT frequencies again became insignificant (Table 1).

The contranance index (I_k) represents the most vivid assessment of the dynamics of the migration-associated changes in fish behavior. Table 2 shows the results of both this work and data previously obtained on individuals of the rainbow trout, brown trout, and its subspecies, the Black Sea trout (Pavlov et al., 2010, 2018, 2020a; Pavlov, E. et al., 2016). At the beginning of starvation, all fish are characterized by an increased motivation for currentwise movement, and then, by that against the current. By the end of the experiment, I_k approaches the initial values.

Analysis of variance showed that I_k , as well as the ratio of rheoreaction types depends on (1) the duration of starvation ($p = 0.002$), which indicates a change in the average (by species) value of I_k during the experiment; (2) the fish species ($p = 0.006$), i.e., the average (for the all days of starvation) I_k value is different for different species (Fig. 1a). The combined effect of two factors (fish species and duration of starvation) turned out to be insignificant ($p = 0.26$), which indicates a

Table 2. Average contranatace indices (for the starvation days) in the fish studied

Fish species	Duration of starvation, day					
	0	2	5	7	10	12
<i>L. delineatus</i>	–0.01	–0.28	–0.47	–0.20	0.00	–0.06
<i>D. rerio</i>	–0.14	–0.59	–0.23	–0.15	–0.05	0.00
<i>P. mykiss</i> (= <i>O. mykiss</i>)	0.00	–0.38	–0.21	–0.11	–0.22	0.01
<i>C. auratus</i>	0.10	–0.14	0.03	0.19	0.08	–0.03
<i>P. mykiss</i> (= <i>O. mykiss</i>) (Pavlov et al., 2020a)	–0.14	–0.57	–0.30	–0.23	–0.25	0.05
<i>P. mykiss</i> (= <i>O. mykiss</i>) (Pavlov, E. et al., 2016)	0.13	–0.21	–0.20	–0.03	–0.15	0.00
<i>S. trutta labrax</i> (Pavlov et al., 2010)	–0.08	–0.18	–0.22	–0.09	–0.01	–
<i>S. trutta</i> (Pavlov et al., 2018)	–0.43	–0.62	–0.68	–0.58	–0.42	–

Dash, no data.

similar dynamics of I_k changes in different fish species during starvation (Fig. 1b).

A similar dynamics of I_k is observed in the studied fish on different scales. From the beginning of starvation to days 2–5, the I_k value decreases; this indicates the predominant downstream movement of fish. After reaching the minimum I_k , from days 2–5 to days 7–12 of starvation, the fish begin to move more against the current, and the I_k value approaches its initial value. During this period, the minimum values of the CRT frequency were recorded (Table 1), which indicates a greater mobility of fish on days 7–12 of starvation.

DISCUSSION

The analysis of the materials obtained shows two stages of the behavioral response to starvation in fish with initially resident behavior (without motivation to migrate). At the first stage (days 2–5 of starvation), fish become more motivated to downstream movements, which in natural conditions ensures their downstream migration or drift. That is, at the first stage, the fish's response to starvation is to search for food with minimal energy consumption. It is known that a lack of food motivates juvenile fish toward downstream migrations (Pavlov, 1979; Olsson et al., 2006; Pavlov, E. et al., 2007; Flecker et al., 2010; Ferguson et al., 2019). At the second stage (days 7–12 of fasting), the motivation toward upstream movements increases. This leads to approximately the same movements of fish along and against the current, while their mobility increases. That is, at the second stage, the fish's response to starvation is to seek food in both directions relative to the current.

The duration and nature of changes in the motivational component of rheoreaction in the absence of food correspond to the duration and nature of changes in other components of the rheoreaction. For example, the start of the optomotor reaction in juvenile of the common dace (*Leuciscus leuciscus*), not fed for 48 hours, increased 32 times, and the assessment of the reaction strength decreased significantly. Similar results were obtained for other fish species (Pavlov,

1979). During starvation, the locomotor component of fish rheoreaction also changes. In the experiments, the initial response to a decrease in the diet was an increase in fish activity; individuals more often moved in the stream and less often rested in specific quiet zones (Etingen, 1964; Sogard and Olla, 1996). It was also shown for juvenile fish of various species that their cruising swimming speeds decrease by days 1–6 of starvation (MacLeod, 1967; Laurence, 1972; Pavlov, 1979; Faria et al., 2011). In sturgeon (Acipenseridae), starvation led to a decrease in the number of fish actively resisting the current. For example, in juvenile starry sturgeon (*Acipenser stellatus*) after one day of starvation it decreased down to 49%, after four days, down to 15–25%, and after six days, down to 2% of fish (Pavlov, 1979). The burst (Saburenkov, 1973) and critical (Faria et al., 2011) swimming speeds for juvenile fish do not change during starvation for up to 30 and three days, respectively.

Some authors associate a decrease in the cruising speeds of fish with a decrease in endurance during starvation (Faria et al., 2011); however, in our opinion, this explanation is not always justified. For the larvae of the roach *Rutilus rutilus*, it was shown that the indicators of the swimming ability of fish are significantly influenced by the presence or absence of motivation for downstream migration. In daytime illumination, when there is no roach migration in the river, the swimming ability of migrants was higher than that of residents. And under night-time illumination, when downstream migration occurs in the river, the swimming ability of migrants became lower than that of residents (Pavlov et al., 2007). In roach underyearlings, it was shown that the critical flow rate decreases in fish motivated toward downstream migration (Kostin et al., 2016). Therefore, we believe that a decrease in the experimental indicators of the swimming ability of fish at the beginning of starvation may be caused by the appearance of motivation to currentwise movement, and not only by a change in their physiological capabilities. This is consistent with the literature data; for example, in juvenile Alaska pollock *Theragra chalcogramma*, the transition from active search behavior to

Fig. 1. Changes in the contranance indices (I_k) during starvation of cyprinids and salmonids with initial resident behavior (before starvation). (a) Regression curves for species: 1, *C. auratus*; 2, *P. mykiss* (= *O. mykiss*) (Pavlov, E. et al., 2016); 3, *S. trutta labrax* (Pavlov et al., 2010); 4, *P. mykiss* (= *O. mykiss*); 5, *L. delineatus*; 6, *P. mykiss* (= *O. mykiss*) (Pavlov et al., 2020a); 7, *D. rerio*; 8, *S. trutta* (Pavlov et al., 2018); (b) General diagram of I_k dynamics.

a decrease in motor activity occurred on days 30–54 of starvation (Sogard and Olla, 1996).

Earlier, we obtained data on the effect of starvation on the ratio of rheoreaction types in fish motivated toward downstream migration. Studies of the conditions for the formation of life (migration) strategies were carried out on the Black Sea trout (Pavlov et al., 2010; Ponomareva, 2014). The downstream migration to the sea is genetically determined for some individuals from the population of this species (Jonsson and Jonsson, 2011). Under various unfavorable conditions of life, an increased motivation for downstream migration began to form in the Black Sea trout. In these studies, it was shown that such fish showed a different response to starvation: starting from the second day, the fish's motivation to currentwise movement monotonically increased. Apparently, the response of individuals to starvation is largely determined by their motivation for migration, formed before the start of starvation.

Thus, the revealed changes in the motivational component of the rheoreaction showed that fish with

no migration motivation firstly leave the habitat with minimal energy consumption, and they migrate downstream. With an increase in the duration of starvation, fish begin an active search for food, moving both along and against the current. Individuals motivated to migrate downstream have significantly different behavior—they constantly migrate downstream.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. 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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