
Changes in aggressive behaviour of rainbow trout after starvation and exposure to heavy metal mixture

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Aggressive behaviour of young-of-the-year (y.o.y.) and post-young-of-the-year (p.y.o.y.) rainbow trout (*Oncorhynchus mykiss*) was investigated during the first hour of hierarchy formation. Aggressive encounters were recorded in newly formed social groups of two individuals after 10 days of exposure to a heavy metal mixture (HMM group), after 10 days of starvation (S group), and after 10 days of a combined effect (CE group) of both factors (HMM + S). The following concentration of the heavy metal mixture was used in the study: Cu 0.0005, Zn 0.001, Ni 0.0005, Cr 0.0025, and Fe 0.005 mg/l. Aggressiveness was decreased in all the treated groups of y.o.y. fish. In the HMM and CE groups of p.y.o.y. fish a higher aggressiveness was recorded, while in the S group no significant changes were revealed. No significant interaction of both factors (HMM and S) was detected in any of CE groups. The aggressiveness in the CE groups of y.o.y. fish was caused mainly by the effect of starvation and in the groups of p.y.o.y. fish by the effect of heavy metal mixture.

Key words: rainbow trout, aggressive behaviour, hierarchy formation, starvation, heavy metals

INTRODUCTION

Changes in environmental conditions may evoke various behavioural responses in fish. Behavioural responses in ecotoxicology are usually called integrated functions [7], because they are based on the integration of underlying physiological and biochemical functions. Changes in physiological and biochemical functions may be overlooked, because they are often subtle and not readily observable, but they may be manifested in overt behavioural response [28]. Therefore, behavioural changes respond quickly to changes that arise in the animal's surrounding and may be used as early warning signals about the impaired environmental quality [2, 8, 25, 28]. A lot of external factors such as contaminants, restricted food resources, fluctuating temperature, etc. influence the fish organism and behaviour in nature. It is difficult and sometimes impossible to predict the interaction effects of various unfavourable factors on fish behaviour, because their combined action may to strengthen as well as to mitigate the effects caused separately. It seems more promising to investigate the effects of a few factors and to analyse the mechanism of their interaction under the strictly controlled laboratory conditions.

The combined action of two factors (two stressors) is also used when estimating the chronic toxicity of low concentrations of toxicants for fish [30]. Sometimes it is difficult to reveal the deleterious effects of low concentrations of toxicants, because these effects may occur only after a very long exposure. An additional stressor applied for the animal tested may challenge more rapidly and distinctly the manifestation of stress caused by toxicants. It is assumed that two stressors, when acting simultaneously, can impose a considerable stress response in fish [1, 35]. However, an impaired stress response might be also observed, as have been reported for brown trout exposed to metal-contaminated waters [17]. Thus, the interaction of several stress factors is rather complicate and needs to be studied.

The expression of agonistic behaviour in fish is controlled by several internal factors [14–16; 18, 38–41, 44] and influenced by environmental stimuli. Metal-contaminated waters and food restriction are unfavourable environmental factors that often influence the fish organism. Heavy metals are the most dangerous contaminants for aquatic biota. They cause stress response in fish [31, 32] and change their aggressive behaviour [2; 19–24]. Changes of aggressi-

ve behaviour of fish can be used as an indicator of water quality [2]. However, aggressive behaviour of fish under the influence of toxicants has not been widely studied, most probably for the reason that these studies require much work and take much time to perform.

Food restriction increases aggression, competitive ability and predation risk in rainbow trout [6, 13, 14, 34], while exposure to heavy metals may evoke both an increase and decrease of aggression [21, 23, 24]. The character of the latter changes depends on the metal concentration, on the duration of exposure and on the age of fish. There are no data about a combined effect of toxicants and starvation on aggressive behaviour of fish. Therefore, it is interesting to determine the interaction of both factors and to make some contribution to a better understanding of implication in behavioural modifications.

The aim of the present study was to investigate and to compare changes in the aggressive behaviour of rainbow trout influenced by two stressors: toxicants (heavy metal mixture) and starvation. A low concentration of heavy metal mixture (Cu, Zn, Ni, Cr, and Fe) similar to concentrations found in slightly polluted inland waters of Lithuania was used. Some additional parameters (swimming activity, condition factor, hepatosomatic index) were also studied to compare changes in aggressive behaviour with changes in the physical and physiological state of fish.

MATERIALS AND METHODS

Rainbow trout *Oncorhynchus mykiss* was brought from the State Hatchery Žeimena and kept in big holding tanks (2000-L capacity) under laboratory conditions for 4–5 months before the beginning of experiments. Two age groups of fish were investigated: young-of-the-year (y.o.y.) rainbow trout (11-month-old) and post-young-of-the-year (p.y.o.y.) rainbow trout (13-month-old). The mean body length and weight of y.o.y. rainbow trout were 12 cm and 29 g and those of p.y.o.y. rainbow trout were 16 cm and 56 g, respectively. Fish were kept at 10–11 °C and fed on a mixture of cattle spleen and commercial fish food.

Experiments were carried out in nonchlorinated and aerated still water, but the heavy metal solution and control water was renewed at 24-h intervals. Water specifications were as follows: pH 8.2–8.4, dissolved oxygen 10–11 mg/l, hardness 270–290 mgCaCO₃/l. The following concentrations of heavy metal mixture were used in our study: Cu

0.0005; Zn 0.001; Ni 0.0005; Cr 0.0025, and Fe 0.005 mg/l. It comprises 0.1% of the maximum permissible discharge concentration used in Lithuania for many years.

Four experimental groups of fish of each age were investigated: 1) fish exposed for 10 days to a heavy metal mixture (HMM group) and fed until satiety once a day; 2) starving fish (S group) – kept in clean water and deprived of food for the whole 10-d period; 3) combined effect (CE) group – fish exposed to a heavy metal mixture and deprived of food for all 10-d period; 4) control (C) group – fish kept in clean water and fed until satiety once a day. Experimental fish were kept singly in the 50-L aquariums. Aggressive behaviour was studied after a 10-d treatment in newly formed groups that consisted of 2 individuals. Observations were performed during the first hour immediately after fish were placed together in a new aquarium, *i. e.* during the period of social hierarchy formation. The following parameters of aggressive behaviour were recorded: 1) time of the beginning of threats and attacks, min; 2) total number of aggressive acts (threats, attacks, fighting); 3) continuance of threats and fighting, s; 4) time needed for hierarchy formation (time from the moment fish were placed together into a new group till the moment when only one fish performed aggressive acts), min. The types of aggressive acts recorded were: 1) threat – two fish slowly approach each other expanding their fins and frequently twisting the caudal portion of their body; 2) attack – a rapid approach toward an individual, often finished with a bite; 3) fighting – two fish swim in a close circle and frequently bite each other (for a detailed description, see: [4, 10, 40, 43]). For the convenience of data analysis, the hierarchy formation period was divided into two phases: the initial (first) phase when the aggressive encounters began, and the second phase when such encounters as attacks and fighting were observed. The initial phase was characterized by the following parameters: the beginning of threats and attacks, the number and continuance of threats. The characteristic of the second phase was done using the following parameters: the number of attacks and fighting, continuance of fighting, and the time needed for hierarchy formation.

Additional measured parameters were as follows: swimming activity [25], condition factor, and hepatosomatic index. Swimming activity was recorded four times from 8 to 10 o'clock in the morning during a 3-min observation session (12 min in all) before placing fish to a new aquarium. The condition factor and hepatosomatic index were determined at the very

end of the experiment. There were used 20 fish in each experimental group (in total 80 fish). For statistical analysis, the behavioural data were $\log(x + 1)$ transformed to improve normality and could be analysed using the two-way ANOVA. Multiple comparisons were made using a least significance difference (LSD) test [33].

RESULTS

1. Changes in aggressive behaviour

1.1. Young-of-the-year rainbow trout

The social interactions between the pairs of rainbow trout usually began with threatening and later appeared the more severe acts of aggression such as attacks, fighting [26]. The aggressiveness of fish during the initial phase of hierarchy formation was not significantly changed either by HMM and S alone or by their combined action. The time of the beginning of threats and attacks, the number and continuance of threats were close to the control values (Fig. 1). A two-way ANOVA analysis did not show any interaction of both factors (HMM and S) in any of the CE groups.

There was recorded a marked decrease of the number of attacks in the HMM, S and CE groups as compared with the control group (LSD test: effect of HMM and CE, $p = 0.05$; effect of S, $p = 0.01$). Fighting was completely suppressed in the S and CE groups, while the number of fightings in the HMM group did not significantly differ from

the control level. Therefore, it is possible to suggest that a suppression of fighting behaviour in the CE group is caused mainly by S. Continuance of fighting after exposure to HMM was also not significantly different from the control level. The time needed for hierarchy formation was not significantly different from control in all treated groups. All interactions of both factors in any CE group was revealed by a two-way ANOVA.

1.2. Post-young-of-the-year rainbow trout

The two-way ANOVA showed no interaction of both factors (HMM and S) in any of the CE groups of p.y.o.y. fish.

The time of the beginning of social interactions (threats) was marginally significantly shorter in the S and CE group when compared with the control value (LSD test, $p = 0.07$) (Fig. 2). No significant changes of the number and of the continuance of threats were revealed in either of the treated groups. Attacks began significantly earlier only in the CE group was compared with the control ($p = 0.03$).

A marked increase of the number of attacks was recorded in the HMM group (Fig. 2) (LSD test, $p = 0.02$) as well as in the CE group ($p = 0.03$) as compared to the control value. In the S groups this parameter did not differ from the control group. A comparison of all three treated groups among themselves showed a significantly lower number of attacks in the S than in the HMM group (LSD test, $p = 0.03$) and slightly lower than in the CE group ($p = 0.054$). No significant differences were found

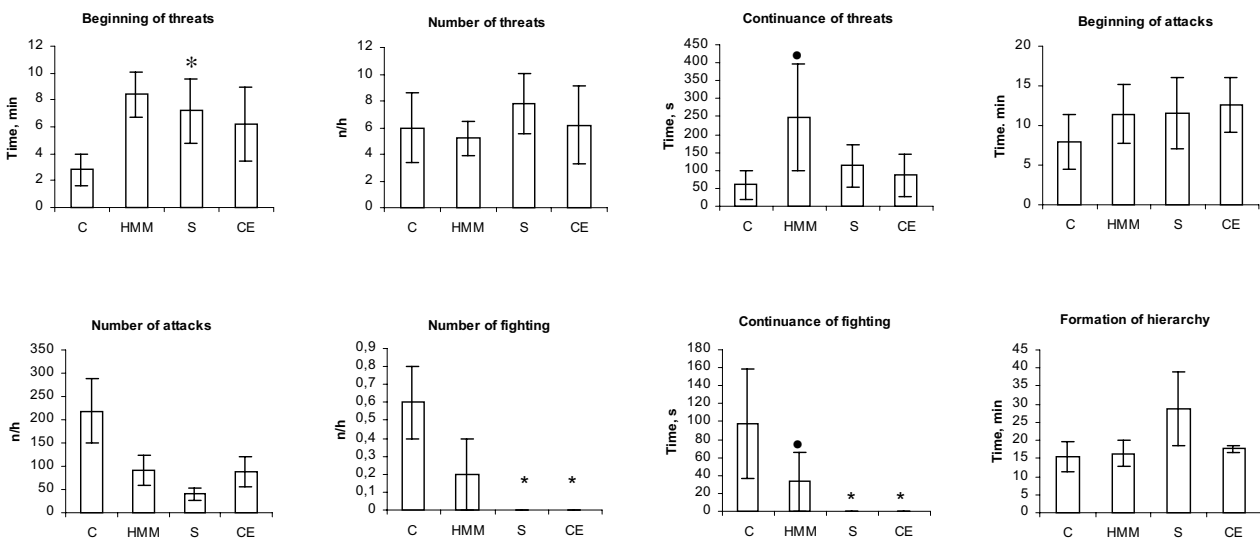


Fig. 1. The impact of heavy metal mixture and starvation on the parameters of aggressive behaviour in young-of-the-year rainbow trout. C – control fish, HMM – fish exposed to heavy metal mixture, S – starving fish, CE – combined effect of heavy metal mixture and starvation on fish. Significant difference from control value: * $p \leq 0.05$, ** $p \leq 0.01$ (LSD test). Other comparisons are given in the text

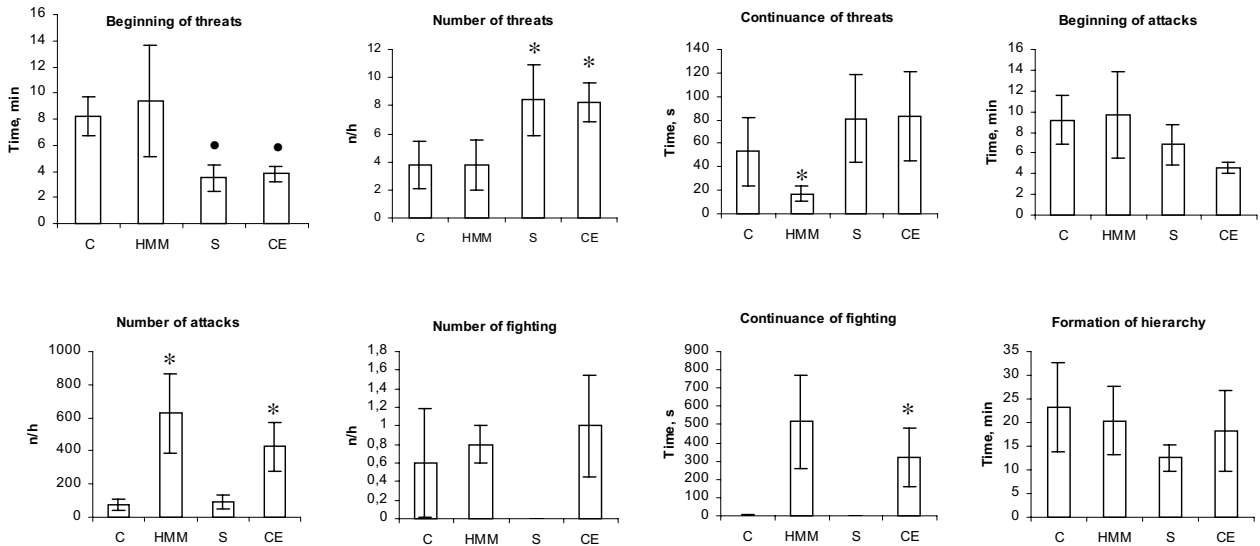


Fig. 2. The impact of heavy metal mixture and starvation on the parameters of aggressive behaviour in post-young-of-the-year rainbow trout. • – marginally significantly differ from control value, $p = 0.07$. Other explanations as in Fig. 1

between the HMM and the CE groups. Thus, it is possible to suggest that the effect of combined action was caused mainly by HMM.

The number of fightings did not significantly differ from the control level in all treated groups. No significant differences in this index were revealed within the treated groups. Continuance of fighting was markedly prolonged after 10 days of exposure to heavy metal mixture (LSD test, $p = 0.01$). The combined action also caused prolongation in the fighting duration when compared with the control level ($p = 0.04$). A comparison within the treated groups revealed significant differences between the S and the HMM groups ($p = 0.01$) and between the S and the CE groups ($p = 0.02$). No significant difference was found between the HMM and CE groups. Therefore, in this case the effect in the CE group is caused mainly by HMM.

The time needed for hierarchy formation was nearly the same in all four experimental groups.

2. Additional parameters

When analysing the interactions of both investigated factors (HMM and S), no significant effects were found in the CE groups on either of the additional parameters studied.

Swimming activity (Fig. 3) was significantly suppressed in all the treated groups, except the HMM group of y.o.y. fish, as compared to the control groups (LSD test, y.o.y. fish: effect of S, $p = 0.04$, effect of CE, $p = 0.05$; p.y.o.y. fish: effect of HMM, $p = 0.02$, effect of S, $p = 0.03$, effect of CE, $p = 0.00$). No significant differences were revealed among the treated groups.

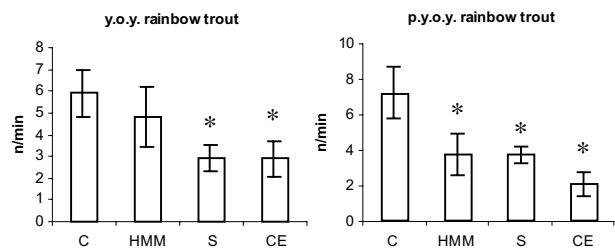


Fig. 3. Changes in swimming activity (frequency of turns, n/min) of young-of-the-year (y.o.y.) and post-young-of-the-year (p.y.o.y.) rainbow trout after exposure to heavy metal mixture and starvation. * – significantly differ from control value, $p = 0.00$. Other explanations as in Fig. 1

Condition factor (Fig. 4) was significantly lower ($p = 0.05$) only in the CE group of y.o.y. fish as compared to the control value. A comparison within the treated groups showed that the effect of S in p.y.o.y. fish was significantly stronger than that of HMM ($p = 0.03$).

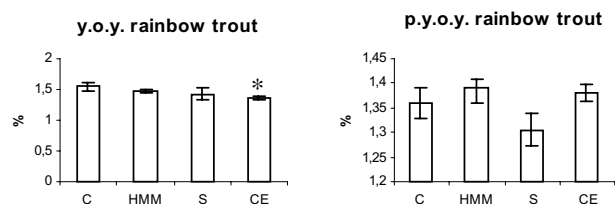


Fig. 4. Condition factor of young-of-the-year (y.o.y.) and post-young-of-the-year (p.y.o.y.) rainbow trout after exposure to heavy metal mixture and starvation. Explanations as in Fig. 1

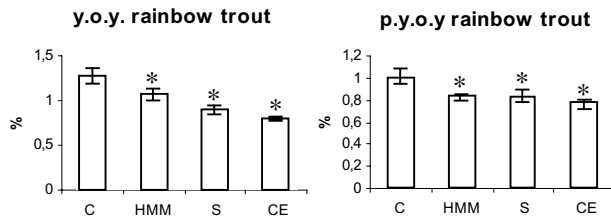


Fig. 5. Hepatosomatic index of young-of-the-year (y.o.y.) and post-young-of-the-year (p.y.o.y.) rainbow trout after exposure to heavy metal mixture and starvation. Explanations as in Figs. 1 and 3

Hepatosomatic index (Fig. 5) was decreased in all three treated groups of both ages of fish (LSD test, y.o.y. fish: effect of HMM, $p = 0.02$, effect of S, $p = 0.00$, effect of CE, $p = 0.00$; p.y.o.y. fish: $p = 0.02$, $p = 0.01$ and $p = 0.00$, respectively). While comparing effects of HMM and S, significant differences were revealed only in the treated groups of y.o.y. fish: a decrease of this index was more pronounced after starvation than after exposure to HMM ($p = 0.03$) and after the combined effect of both factors than after the effect of HMM alone ($p = 0.00$). The difference between the S and CE groups was not significant. Thus, the contribution of S to the CE effect in y.o.y. fish was more considerable than that of HMM.

DISCUSSION

The parameters of aggressive behaviour that characterized the initial phase of hierarchy formation in rainbow trout (time of the beginning of threats and attacks, number and continuance of threats) were not a sensitive indicator of the impact of HMM, S and CE on fish. The changes were most remarkable in some parameters that characterized the second phase of hierarchy formation: in the number of attacks and in the duration of fighting.

A low concentration of HMM caused different changes in the aggressive behaviour of the y.o.y. and p.y.o.y. fish. HMM caused an increased aggressiveness in the post-young-of-the-year rainbow trout, while in the young-of-the-year rainbow trout, on the contrary, it caused a decrease of aggressiveness. Depressive effects caused by heavy metals and other toxicants are usually observed at high concentrations of toxicants (or at low concentrations but after long exposures), while low and intermediate concentrations (or high concentrations but short exposures) cause stimulation effects [8, 11, 12, 21, 23, 24]. Lethal concentrations of toxicants completely suppress aggressiveness in rainbow trout [23]. Consistently, the impact of HMM on the rainbow trout in the

present study was more deleterious on y.o.y. than on p.y.o.y. fish.

Two-phase changes (increasing \rightarrow decreasing) in behavioural responses are known for many toxicants [8]. There are no data elucidating the physiological mechanisms of biphasic changes in the agonistic behaviour of fish exposed to toxicants. As far as heavy metals and other toxicants cause stress response in fish [31, 32], it seems possible to suggest that the increasing phase of response reflects the alarm stage of stress, while the decreasing phase shows the exhaustion stage. On the other hand, social interactions *per se* evoke severe stress in rainbow trout, especially during hierarchy formation, which can end even in the death of subordinate fish [19, 22, 36]. The increased aggressiveness under the influence of HMM recorded in our study might be considered as enhanced stress response in fish (response to a new neighbour and fight for a new territory). The decreased aggressiveness under the influence of HMM might be considered as an impaired stress response. The latter suggestion is based on studies of Norris et al. [17] who found that acute stress response of brown trout chronically exposed to heavy metals was depressed when compared with fish living in uncontaminated waters. Impaired stress response indicates the impaired adaptation abilities of fish.

Starvation caused depressive effects in aggressiveness of y.o.y. fish during the second phase of hierarchy formation (decreased number of attacks, suppressed fighting behaviour). No significant changes were revealed in the parameters of aggressiveness of p.y.o.y. fish, however, disappearance of fighting behaviour after starvation indicates a tendency of the decreased aggressiveness.

According to the literature data [6, 13, 34], deprivation of food causes an increase of aggressiveness in salmonids by increasing the number of aggressive encounters. It is known that hunger increases the concentration of the growth hormone in fish organism [37]. The growth hormone increases metabolic demands, feeding motivation, competitive ability and aggression in fish [14, 15]. Starvation also causes a liver glycogen depletion and reduction of the liver lipid fraction as well as down-regulation of the hormone metabolism [3, 27, 29]. The latter alterations result in a reduction of the levels of plasma thyroid hormones that are responsible for the metabolic rate regulation in the organism. Differences in standard metabolic rate may contribute to differences in aggression between individuals of the juvenile Atlantic salmon: aggression is highest in fish with the highest standard metabolic rate and lowest

in fish with the low standard metabolic rate [5]. The high metabolic rate raises the dominance status in masu salmon [44]. Agonistic behaviour, in turn, raises the standard metabolic rate in fish [9]. Thus, on the one hand, food deprivation increases aggression in fish, elevating feeding demands and increasing motivation for encounters, on the other hand, the reduced metabolic rate and impaired energetic state of fish reduce aggression. Final response of fish should be determined by the interaction of several physiological processes going on in fish organism. Such encounters as prolonged attacking or fighting, demanding great energetic costs might be “too expensive” for starving fish. It is quite natural that y.o.y. fish is more sensitive to prolonged starvation than p.y.o.y. fish: the energetic resources in younger and smaller fish are lower than in larger ones.

The combined impact of HMM and S on rainbow trout did not show significant interactions of both factors in any of the CE groups in our study. A suppression of fighting behaviour in the CE groups of y.o.y. fish was caused mainly by S. On the contrary, a marked increase of the number of attacks and of the continuance of fighting was caused mainly by the impact of HMM on p.y.o.y. fish.

No significant interactions of HMM and S were determined when investigating the additional parameters, either. While comparing changes caused by HMM and S in all the additional parameters, it is evident that in some cases the effect of S was stronger than the effect of HMM. No one case was revealed when the influence of HMM was significantly stronger than the influence of S.

It is known that a higher swimming activity increases aggression in rainbow trout [15], while in subordinate and artificially stressed fish swimming activity is reduced [41, 42]. A comparison of changes in swimming activity and in aggressive behaviour observed in our study allow to suggest that the lower aggressiveness in y.o.y. rainbow trout might result from the decreased level of swimming activity. However, this suggestion is absolutely not valid in case of p. y.o.y. fish: the swimming activity in the HMM and CE groups is reduced, while aggressiveness is increased.

In conclusion, the results of the present study indicate that a heavy metal mixture and 10-day starvation caused changes in the aggression of rainbow trout, however, the both factors did not show a significant interaction. It was starvation that mainly contributed to the combined effects in the groups of y.o.y. fish, while in the groups of p.y.o.y. fish it was a heavy metal mixture.

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**VAIVORYKŠTINIO UPĖTAKIO AGRESYVAUS
ELGESIO POKYČIAI BADAUJANT IR VEIKIANT
SUNKIŪJŲ METALŲ MIŠINIUI**

S a n t r a u k a

Vaivorykštinio upėtakio (*Oncorhynchus mykiss*) šiųmetukų ir metinukų agresyvus elgesys tirtas socialinės hierarchijos formavimosi pradžioje (pirmąją valandą) naujai suformuotoje socialinėje grupėje, susidedančioje iš 2 individų. Agresyvūs veiksmai registruoti po 10 d. poveikio sunkiųjų metalų mišiniu (HMM grupė), po 10 d. badavimo (S grupė) bei po 10 d. abiejų veiksnių poveikio (badavimas +

sunkiųjų metalų mišinys), pastaroji grupė vadinta CE grupe. Sunkiųjų metalų mišinio koncentracija buvo šios sudėties: Cu – 0,0005, Zn – 0,001, Ni – 0,0005, Cr – 0,0025, Fe – 0,005 mg/l. Šiųmetukų agresyvumas sumažėjo visose trijose grupėse. Metinukų agresyvumas HMM ir CE grupėse buvo padidėjęs, o S grupėje patikimų pokyčių nerasta. Nė vienoje CE grupėje neaptikta patikimos sąveikos tarp abiejų tirtų veiksnių (badavimo ir sunkiųjų metalų mišinio). Šiųmetukų CE grupėse agresyvumo pokyčiai atsiradavo dėl badavimo, o metinukų CE grupėse – dėl sunkiųjų metalų mišinio poveikio.

Raktažodžiai: vaivorykštinis upėtakis, agresyvus elgesys, hierarchijos formavimasis, badavimas, sunkieji metalai