Electrical Activity of the Broadhead Catfish *Clarias macrocephalus* during Paired Aggressive–Defensive Interactions: Effects of Illumination and Chemical Alarm Signal

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Abstract—We studied the effects of illumination and alarm pheromone on emition of specialized electric discharges in the broadhead catfish *Clarias macrocephalus* (Clariidae, Siluriformes) during aggressive–defensive interactions. The discharges were recorded with a special hardware in two adult fish of a similar size placed into an aquarium, during a period of 24 h, under alternating 30-min-long light (700 lx) and dark periods. The electrical activity of the broadhead catfish was found to be higher in the dark than under the light; by the end of the trial, the frequency of electrical discharges gradually decreased. The overall number of discharges recorded in different pairs of the fish was significantly different, which is evidence of individual variability in the electrical activity. Changes in the illumination regime in many cases increased the emition of electrical discharges, which could be a result of a stress-response. However, the stimulation of the fish by alarm pheromone (extract of the skin, 0.5 g/l) caused no pronounced changes in the electrical activity. It is supposed that aggressive motivation caused in the broadhead catfish by the presence of another individual of the same species dominated over the defensive response initiated by the alarm pheromone and, thus, dominated in the development of the electrical response.

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Intraspecies aggressive–defensive responses are characteristic of many fish species. Most often, such a behavior is observed in territorial fishes with solitary mode of life that defend their personal areas and in social fishes with complex intra-group structure based on hierarchical relationships between individuals. In many fishes, intraspecies aggression is revealed only in certain periods of their life cycle or in some particular situations, for example, during spawning or under unfavorable trophic conditions, at high density of natural populations, at certain particular age, as a result of maintenance together, in one aquarium, etc. (Wootton, 1984; Bakker, 1986; Brown and Brown, 1993; Blanchet et al., 2006, Osório et al., 2006; Moretz et al., 2007; Magellan and Kaiser, 2010; Paull et al., 2010).

The manifestation of direct aggressive contacts between individuals is usually preceded by exchange of threat or warning signals between the interacting individuals (Lorents, 1994). In fish, such signals could be different locomotory demonstrations perceived visually or, to some extent, by the lateral line, special sounds perceived aurally, or touches and other forms of tactile stimulation (Bres, 1993; Wysocki and Ladich, 2001; Kasumyan, 2011). In catfishes of the family Clariidae, a high level of intraspecies aggression is a characteristic behavioral feature (Carter and Davies, 2003; Fatollahi and Kasumyan, 2006; Martins et al., 2006a; Van de Nieuwegiessen et al., 2008a) and the aggressive–defensive interactions correspond with emition of specialized electrical discharges (Baron et al., 1994a, 1994b). Signal functions of such discharges and their role in the regulation of aggressive–defensive behavior in these fishes still remains uncertain (Olshanskii et al., 2002, 2009, 2011; Olshansky, 2010).

Complex forms of fish behavior, including manifestations of aggression, are of a polysensory nature (Manteifel', 1987). The presence of numerous sense systems makes the sensory base of behavior highly adaptive, plastic, and reliable and allows fishes to perform signalization and communication in a changing environment (von der Emde and Bleckmann, 1998). One of the external factors that is among the most powerful in terms of effects on behavior and conditions of fishes is light (Pavlov, 1959, 1962, 1979; Manteifel' et al., 1965; Girsa, 1981; Helfman, 1993;

McMahon and Holanov, 1995; Mazura and Beauchamp, 2003; Richmond et al., 2004; Ljunggren and Sandström, 2007; Pekcan-Hekim and Horpilla, 2007; Stephenson et al., 2011). Daily fluctuations of light level change signal activity of fishes and cause redistribution of sensory canals in obtaining biologically significant information. Limitation or total loss of visual reception during the nighttime can involve or enhance other abilities for communication compensating the appearing deficiency of information (Connaughton and Taylor, 1995; Mann et al., 1997; Parzefall, 2001; Poulson, 2001; Thorson and Fine, 2002; Kasumyan, 2004, 2009). Visual and other forms of sensory deprivation are major and the traditional approaches in experimental investigations of the role of sense systems and signal importance of the stimuli of different nature in the life and behavior of fishes.

Broadhead catfishes and other members of the order Siluriformes possess a well-developed electroreception system (Lissmann and Machin, 1963; Finger, 1986). Loss of vision in these fishes could be compensated by electroreception, which, as well as vision, belongs to distant sensory systems, thus allowing of perceiving signals from remote sources (Moller, 1995). In this connection, the main target of our study was to investigate the correlation between the emition of specialized electrical discharges by broadhead catfish and the conditions of illumination. Changes in electrical activity of broadhead catfish in response to artificially initiated visual deprivation would allow us to corroborate the signal function of electrical discharges emited by the fish in the case of paired aggressive–defensive interactions and understand in more detail the behavior of these fish that still remain poorly studied. Among other targets, we also planned to study some other peculiarities of electrogeneration in broadhead catfish and the effects of alarm pheromone on the latter; this pheromone is a natural signal of danger.

MATERIALS AND METHODS

Trials were performed on 20 adult specimens of broadhead catfish *Clarias macrocephalus* (Clariidae, Siluriformes) with absolute length *TL* 27–33 cm and body weight 150–280 g. The catfish were captured in natural water bodies of southern Vietnam (Ca Mau Province) and delivered to the laboratory of Primorye Department of Russian–Vietnam Tropical Scientific and Technological Center (the city of Nha Trang), where the trials were carried out. The catfish were kept in a common aquarium (120 × 60 × 50 cm in size; water level 15 cm), supplied with an external biofilter, at water temperature 25–28°C and a natural regime of illumination; the fish were fed regularly. During the period of trials (2 months) we revealed no damages that the fish could do to each other.

For each trial, two fish were taken from the common aquarium and placed individually into polystyrene boxes filled with settled water and covered with a lid. One day later, the fish were placed together into a glass experimental aquarium (60 × 60 cm in size; water level 25 cm) installed in a dark room. The experimental fish in most pairs differed from each other by no more than 1–2 cm in length (i.e., by 5–6%) and 30–40 g in weight (i.e., by 10–15%). In 10 experiments, the fish in the pairs were of different sexes; in 5 trials, the fish were of the same sex, either females (4 trials) or males (1 trial). Carbon electrodes (20 × 1 × 1 cm in size) wrapped in foam rubber to prevent direct contact with the experimental fish were installed at the angles of the aquarium and along the vertical midline of lateral walls using vacuum caps. The electrodes were connected (pairwise) to two dual-channel autonomous microprocessor units that recorded all electric events in the aquarium and stored them in their built-in flash-memory. In some experiments, we used three units; in these cases, we placed four supplementary electrodes designed as 20 mm in diameter and 10 mm high brass cylinders into the aquarium; they were also fixed on the walls of the aquarium using the vacuum caps (Fig. 1).

The units recorded all electrical events if their amplitude at even one the electrode exceeded the taken threshold of 1/16 of the maximum amplitude of specialized electrical discharges which were recorded in the above described experimental aquarium. At such a susceptibility level (which was the same in all trials), the units recorded all specialized electrical discharges and even some nonspecialized discharges whose amplitude exceeded the threshold. Such nonspecialized discharges included miograms associated with rapid swimming and sharp rushes of the fish (attack, pursuit, etc.), respiratory behavior (strong air discharges from the epibranchial organ), fragments of low-frequency or constant electrical fields emited by the fish and recorded during their movements at the close vicinity of the electrodes, and different kinds of electrical noise. Flash-memory of the units recorded the form, size, and time (accurate to 1 ms) of each registered electrical event. Among all the electrical events recorded during the trials, we chose for subsequent analysis only specialized discharges using the specially designed viewer software (worked out by S.V. Volkov). Data about the discharges, including the precise time, were exported into a Microsoft Excel file formed by the viewer. To average the shape, all discharges were transformed to positive polarity, rated to the same amplitude, and aligned by front edge; the median values were calculated against the time scale for each data point. Detailed description of the equipment and the method of data analysis have been provided elsewhere (Olshansky, 2010).

The aquarium and recording units were installed in a shielded chamber. After the experimental fish were placed into the aquarium, the latter was covered with a transparent glass lid; an LED plastic panel comprising four 50-cm-long pieces of RT-5000-12V LED band was placed onto the lid; each piece contained 30 smd
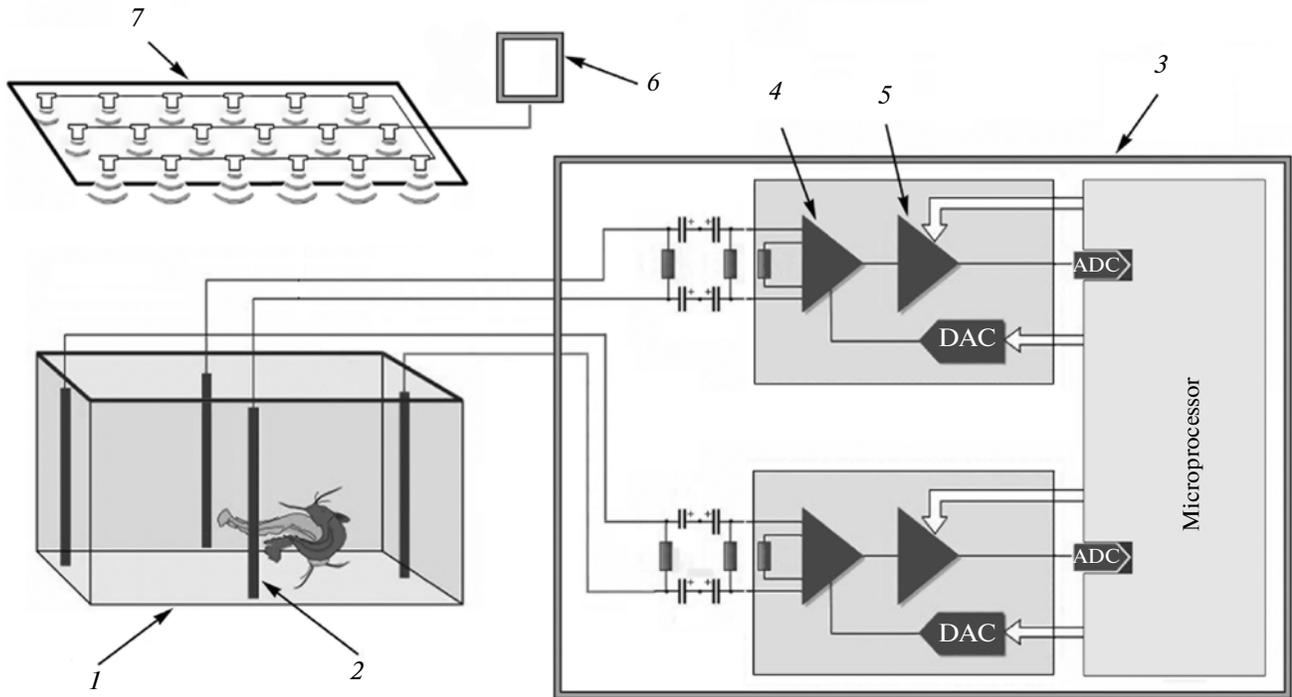
Fig. 1. Scheme of the experimental equipment: (*1*) aquarium with experimental fish, (*2*) recording electrode, (*3*) dual-channel recording unit, (*4*) input amplifier, (*5*) amplifier with programmed gain, (*6*) microprocessor unit driving the LED panel, (*7*) LED panel, and (8) digital-to-analog converter (DAC). Only one of two simultaneously used identical recording units is shown on the scheme; four electrodes of the second unit were located at the angles of the aquarium.

3528 (Airlight) LED units. The nominal luminous flux produced by one LED unit at 12 V is 4 lm. The LED panel was located at approximately 10 cm from the water surface in the aquarium and provided the illumination of approximately 700 lx at this level. The illumination was measured using a PCE-174 luxometer.

When the fish were placed into the aquarium, the LED panel was turned on immediately and the units for electrical discharge recording were also turned on. During the following 1—2 min, the experimenter left the dark room, closed the door, and isolated the latter by a piece of hard dark tissue to prevent the penetration of light through the doorway. The functioning of the light panel was driven by a particular microprocessor unit, which was programmed as follows: 10 min after the turning on (the prestart regime) the panel was turned off; then it was alternatively turned on and off every 30 min; the illumination was changed gradually for 5 s. Each trial lasted for 24 h, including 24 dark and 24 light 30-min-long periods. Most trials were started during daytime (11:00 a.m.—6:00 p.m.).

After each experiment, the data from the flash-memory of the recording units were transferred into a computer; the experimental fish were individually placed into a small glass chamber with low water level and a measuring band laid under the transparent bottom for photographing from above and beneath. Then, using the obtained photos, we identified the length of

the fish and their sex (by the presence of urogenital papilla, which is present only in males) (Fig. 2). Some of the fish were used in the trials for the second time, but that was 10—15 days after the first test. Some fish were dissected and showed that the experimental specimens had gonads at the fourth stage of maturity (large gonads and easily noticeable eggs in females).

In the series of trials with alarm pheromone, the water extract of catfish skin was introduced into the experimental aquarium. For this series of trials, a plastic tube approximately 3 m long with an inner diameter 4 mm was connected with the aquarium, and its outlet was fixed on the bottom and at the center of the aquarium using two vacuum caps. The other end of the tube was, through a narrow hole in the wall, extended outside the dark room and connected with a glass funnel fixed at a level of 1.3 m above the water level in the aquarium. Several hours after the beginning of the experiment, we injected clean settled water (800 ml) 1—2 times into the aquarium (2—3 min each time) followed by freshly made solution of skin extract (800 ml, with the concentration 0.5 g of wet weight/l). The injection was usually performed in the middle of dark periods, 8—10 h after the beginning of the trial. The interval between the injections of clean water and skin extract was 1—2 h. To prepare the extract, a sample of fresh or fresh-frozen skin of bighead catfish (a male with *TL* of 21 cm and weight of 67 g) was homogenized

(a)

(b)
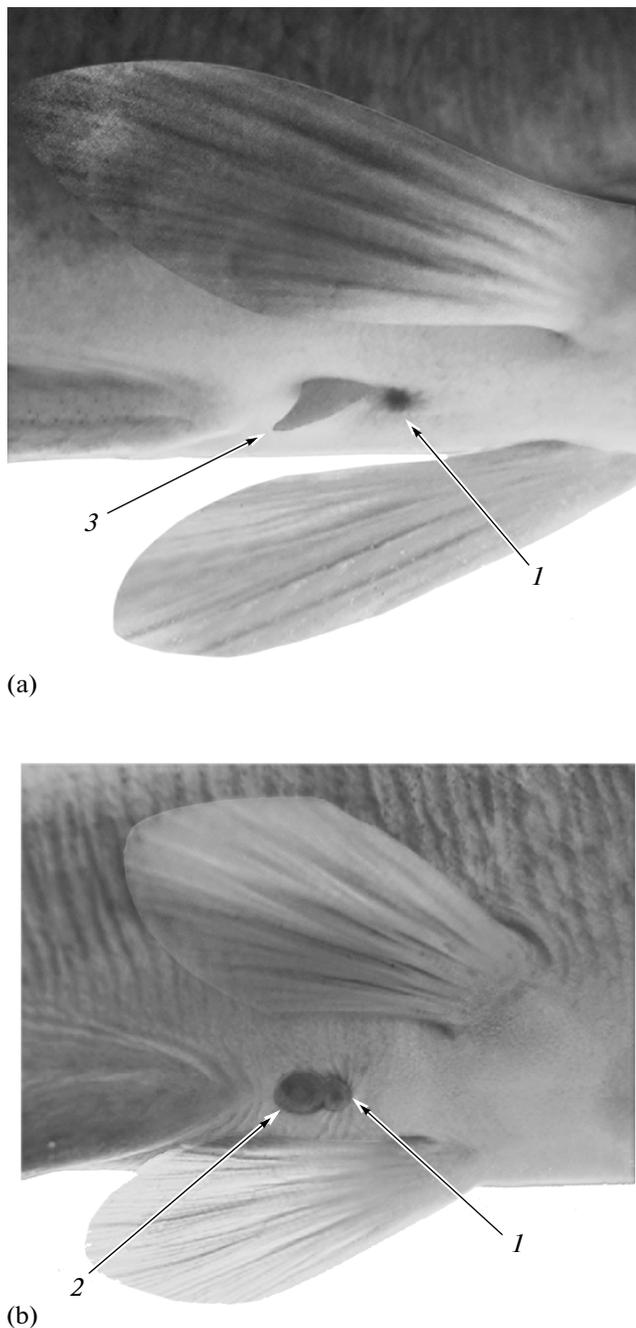
Fig. 2. (a) Male and (b) female of the broadhead catfish *Clarias macrocephalus* (a view from beneath): (*1*) anal opening, (*2*) female urogenital opening, (*3*) male urogenital papilla.

in a marble mortar; the obtained homogenate was diluted by water down to the required concentration stored for 3 h and filtered. The skin for preparation of the extracts was stored in a deep fridge ($-18°C$).

After each trial, the water was removed from the experimental aquarium, and it was carefully rinsed several times and filled with clean water. Temperature

and electric conductivity of water was recorded using an Expert-002 conductometer prior to the beginning and at the end of each the trial. In different trial, the water temperature ranged within $24.5-27.9°C$; during each trial, the temperature fluctuations were the smallest, no more than $0.5°C$. Water conductivity equaled $65-75$ µS/cm; by the end of trial it raised, on average, $5-10$ µS/cm, owing to excretion of waste by the experimental fish.

Altogether, 15 24-h-long trials were performed, including 10 in clean water (exp. nos. 1–10), and 5 using the skin extract (exp. nos. 11–15). Statistical analysis of the obtained results was made using Wilcoxon test, Spearman correlation test (r_s), and two-way analysis of variance (ANOVA).

RESULTS

In all 15 performed trial, we recorded electrical discharges of broadhead catfish, i.e., after the placement into the experimental aquarium, the fish in all pairs showed electrical interactions. A visual inspection of the fish by the end of trials revealed no pronounced traces of fight, like fresh wounds on the body or damaged fins. The total number of recorded discharges in different trials ranges from 29 to 1097, i.e., it was strikingly different (Tables 1, 2).

Electrical Activity of Fish in Trials without Alarm Pheromone Stimulation

In trials where no alarm pheromone stimulation of fish was performed (nos. 1–10), the mean total number of electrical discharges equaled 463 (the value ranged within 147–1097). The mean total number of electrical discharges in trials with fish of the same sex (746) was more than twice higher than that recorded in trials with fish of different sex (342 discharges).

A dispersion analysis of the obtained results revealed highly reliable differences in electrogeneratory activity of the fish in the light and in the dark ($p < 0.001$). In eight of ten trials, the total number of discharges recorded in dark periods was greater than that in light periods and these differences were statistically significant in six trials. The differences were most pronounced in trial nos. 1, 7, and 9 (the total number of discharges in the dark was greater than that recorded in the light 12, 57, and 9 times, respectively). The smallest differences were recorded in trials 2 and 10 (1.30 and 1.04 times, respectively). The results of trials 4, 6, and 8 occupied an intermediate position (Table 1). The total number of discharges was greater in light time in only two trials, but the difference was statistically significant only in one trials (trial no. 5; $p < 0.05$). On average, the total number of discharges in the trials equaled approximately 281 (110–658) and 182 (5–475) for dark and light periods, respectively. The electrical activity in fish pairs of the same sex (nos. 2, 3, 6) and in most pairs of different sex (nos. 1, 4 and 7–9)

Table 1. Electrical activity of the broadhead catfish *Clarias macrocephalus* during paired maintenance under the regime of alternating 30-min-long dark and light periods

Number of trial	Time of the beginning of trial	Experimental fish			Total number of discharges for 24 h (relative percentage proportion)			Number of discharges during first 5 min of each respective period (their percentage proportion in the total number of discharges recorded during the respective period)	
		sex	*TL*, cm	weight, g	Light periods	Dark periods	Total	Light periods	Dark periods
1	16 h 50 min	Female / Mal	28.0 / 27.5	210 / 187	15	176*** (92.1)	191	2 (13.3)	45** (25.6)
2	10 h 30 min	Female / As above	28.0 / 32.0	200 / 268	475	622 (56.7)	1097	104 (21.9)	97 (15.6)
3	14 h 00 min	Mal / As above	29.0 / 30.0	199 / 208	398	247* (38.3)	645	143 (35.9)	85 (34.4)
4	17 h 30 min	Female / Mal	29.0 / 30.0	197 / 231	29	118* (80.3)	147	2 (6.9)	10 (8.5)
5	19 h 20 min	Female / Mal	29.0 / 30.0	197 / 231	326	142*** (30.3)	468	98 (30.1)	42 (29.6)
6	21 h 30 min	Female / As above	27.3 / 27.8	173 / 166	176	320*** (64.5)	496	64 (36.4)	56 (17.5)
7	9 h 20 min	Female / Mal	29.0 / 28.5	203 / 179	5	285*** (98.3)	290	3 (60.0)	60*** (21.1)
8	11 h 10 min	Female / Mal	31.0 / 33.0	241 / 279	274	658*** (70.6)	932	157 (57.2)	148 (22.5)
9	15 h 10 min	Female / Mal	30.0 / 28.0	206 / 157	15	136*** (90.1)	151	2 (13.3)	52 (38.2)
10	15 h 00 min	Female / Mal	28.5 / 28.0	183 / 155	106	110 (50.9)	216	88 (83.0)	19* (17.3)

Note: Here and in Table 2, the electrical discharges recorded during the prestart 10-min-long periods are not recorded; the beginning of the trial is shown as local time in Nha Trang (Vietnam); the differences are statistically significant as follows: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Table 2. Electrical activity of the broadhead catfish *Clarias macrocephalus* during paired maintenance under the regime of alternating 30-min-long dark and light periods and stimulation by skin extract (0.5 g/l)

| Number of trial	Time of the beginning of trial	Experimental fish			Total number of discharges for 24 h (relative percentage proportion)			Number of discharges during first 5 min of each respective period (their percentage proportion in the total number of discharges recorded during the respective period)	
		sex	TL, cm	weight, g	Light periods	Dark periods	Total	Light periods	Dark periods
11	9 h 10 min	Female Male	28.5 27.5	187 156	53	53 (50.0)	106	20 (37.7)	9 (17.0)
12	12 h 10 min	Female As above	28.5 29.5	181 175	89	47 (34.6)	136	13 (14.6)	7 (14.9)
13	16 h 30 min	Female As above	18.0 18.0	40 58	13	16 (55.2)	29	3 (23.1)	3 (18.6)
14	10 h 20 min	Female Male	30.0 30.5	208 248	429	610* (58.7)	1039	91 (21.2)	116 (19.0)
15	17 h 10 min	Female Male	28.0 29.5	166 169	386	435 (53.0)	821	55 (14.2)	97 (22.2)

was greater in the dark than in the light. Dispersion analysis showed also the presence of individual variations in this index value between different experimental fish pairs ($p < 0.001$).

Dynamics of electrical activity. In most trials, the fish already produced first electric discharges during the first dark period (nos. 1–6, 9) or even earlier, in the prestart period (nos. 1–4), i.e., soon after they were placed into the experimental aquarium. The electrical activity of the fish in that time could be fairly high and exceed or be comparable with the number of emited discharges in the following 30-min-long intervals (nos. 1, 2, 4). However, in some trials, first discharges were recorded only 1–2 h after the beginning (nos. 7, 10) or even 3 h after the beginning of the trial (no. 8). In some trials, the electrical activity of fish enhanced during the first hours, but then remained constant (no. 7), decreased (nos. 1–3) or showed even more complicated dynamics in discharge frequency emition (nos. 4, 5, 8, 9). In many trials, the electrical activity of the fish by the end of the trial was significantly lower than at the beginning; such a trend is well pronounced in trial nos. 1–2, 5, 6, and 10 and totally for all the trials, including both dark and light periods (Figs. 3a–d, 4). However, when the recording period was extended for an extra 12 or 24 h (nos. 1 and 2, respectively), the

electrical activity still was not suppressed entirely and remained at the level of 40–60% of the initial one.

In all trials, the number of discharges recorded in the neighboring or chronologically close 30-min-long period could be significantly different, often manifold, in both dark and light periods. The emition of discharges during the trial could strikingly decrease for a certain period of time (nos. 8, 9) or entirely die out for 1–2 h or even more (nos. 1, 3–5). In some trials (nos. 4, 5, 8, 9), the enhancement of electrical activity was observed during morning hours (7:00 a.m.– 9:00 a.m.). Trials 3, 5, 6, and 8 revealed reliable positive correlation between the number of electric discharges emited by the fish in dark and light periods (r_s, $p < 0.05$). In other trials, the correlation was positive, but did not reach the reliable level (r_s, $p < 0.05$).

Response to changes in illumination. The switching of light regime affects the frequency of electrical discharge emition by the fish (Fig. 5). During the first 5 min after sharp changes in illumination, the total number of discharges in most trials significantly exceeded the value that could be expected in the case of monotonous emition. Enhanced emition is more pronounced in response to light switching on; in three trials (nos. 3, 5, 6), approximately 1/3 of all discharges recorded during light periods fell into the period of the first 5 minutes; in two trials (nos. 7, 8), approximately
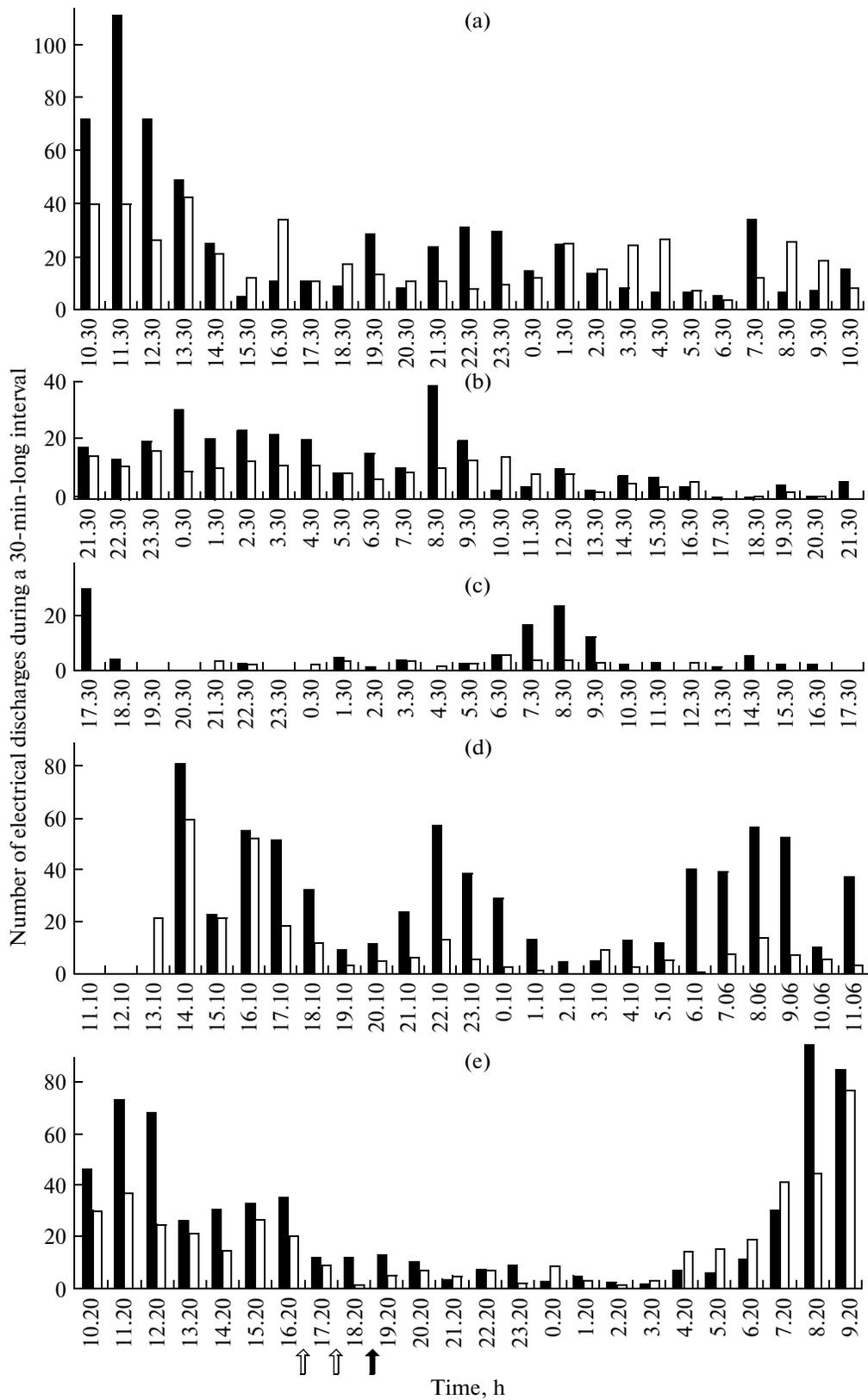
Fig. 3. Variants of changes in electrical activity of broadhead catfish *Clarias macrocephalus* in the dark (■) and light (□), when they were maintained together for 24 h in clean water (a−d, trial nos. 2, 4, 6, 8) and at stimulation of the fish with alarm phero−mone (e, trial no. 14); (⇑) moment of injection of clean water into the aquarium; (⬆) moment of injection of skin extract (0.5 g/l).
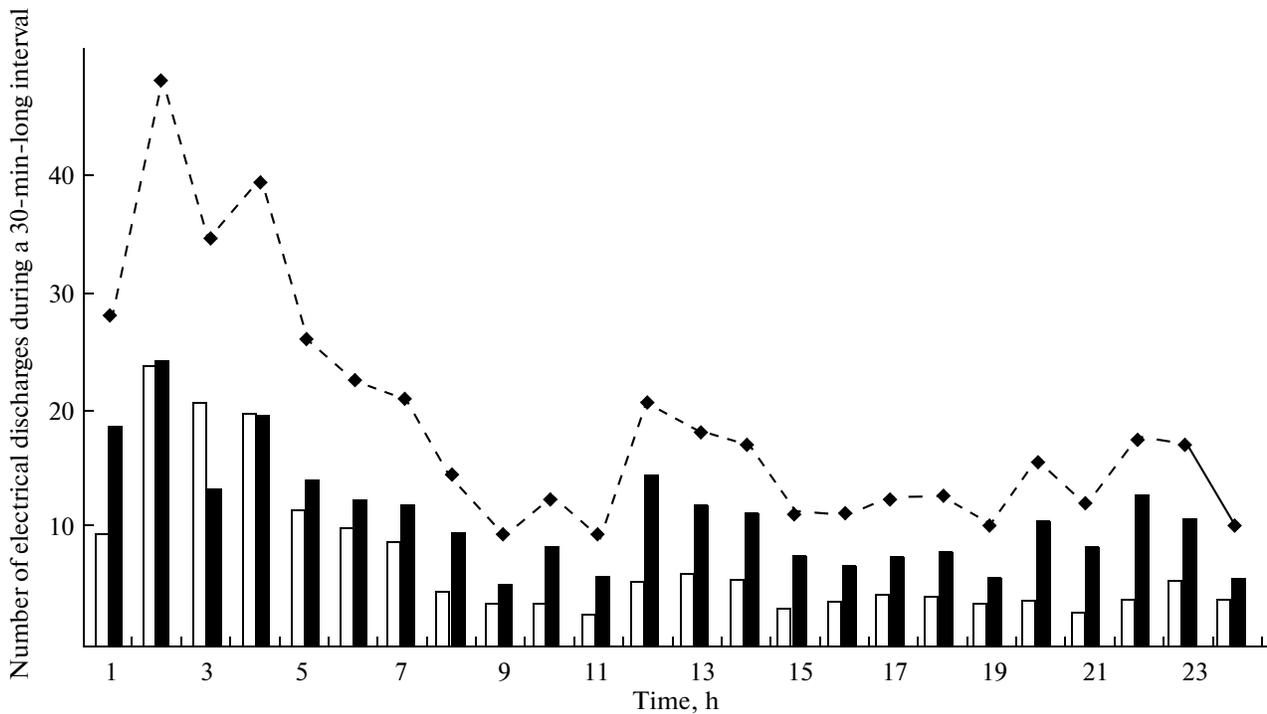
Fig. 4. Changes in electrical activity of broadhead catfish *Clarias macrocephalus,* when they were maintained together for 24 h, under regime of alternating 30-min-long dark (■) and light (□) intervals and as a total for 1 h-long periods, according the results of trial nos. 1−10.
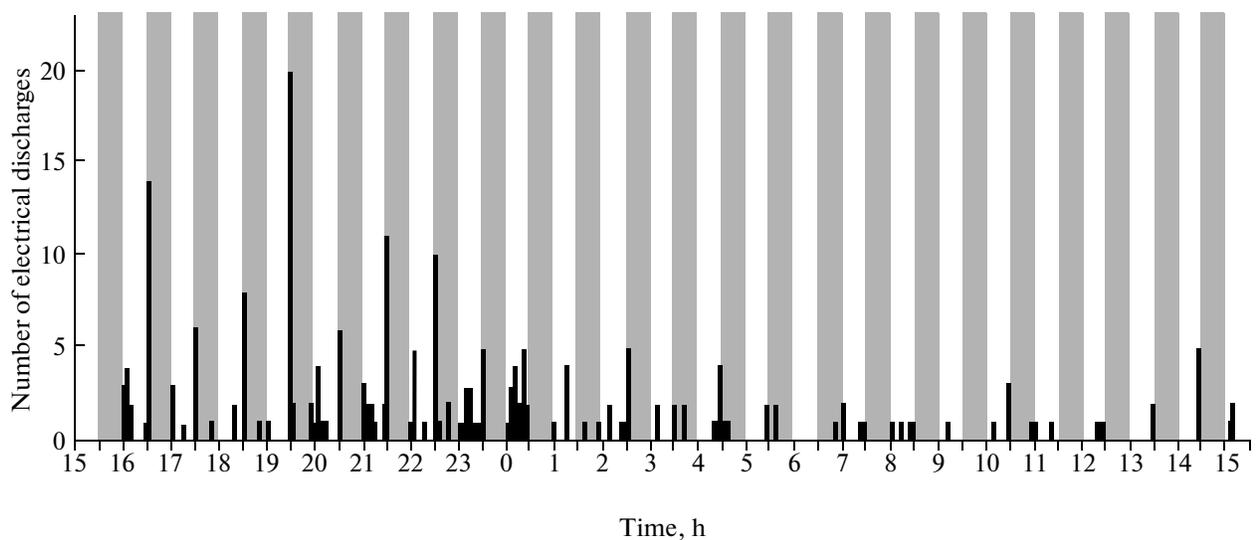
Fig. 5. Changes in electrical activity of broadhead catfish *Clarias macrocephalus*, after beginning of dark (light zone) and light (grey zone) periods, according the results of trial no. 10.

2/3 of the discharges were recorded during the first 5 min and the proportion of such discharges reached 83% in one trial (no. 10). In dark periods, such a response was weaker pronounced; approximately 1/3 of all discharges were recorded during the first 5 min of the trial in only two periods (nos. 3, 9); in other trials, this proportion was significantly lower (Table 1). A statistical comparison of the total number of discharges emited by the fish during the first 5 min of both dark and light periods revealed reliable differences in only four trials; in two of them (nos. 7, 9), this value was greater for the dark periods, whereas it was greater for light periods in the other two (nos. 1, 10). The response of the fish to light switching on or off could be observed throughout

the trial; however, during the first hours of the trial, it was usually stronger pronounced.

Electrical Aactivity of Fish in Trials with Stimulation by Alarm Pheromone

In the trials using skin extract, we revealed no pronounced changes in the electrical activity of the fish in response to injection of the chemical stimulus to the aquarium. However, in some trials, we recorded long-term decrease in the frequency of electrical discharge emition after the injection of the extract. In trial no. 11, only one discharge was recorded during the following 8.5 h; in trial no. 12, five discharges were observed during the following 7 h, and the injection of the extract was followed by a long-term period of low electrical activity in trial no. 14. In all these trials, a prolonged decrease in the emition of electrical activity was followed by a period of sharp increase of the latter (Fig. 3e).

In trials with skin extract, as well as in the previous series of trials, the total number of discharges and number of electrical discharges in light and dark periods ranged in wide limits, 29–1039, 16–610, and 13–429, respectively. In three of five trials, the fish produced more discharges in the dark than in the light, but the difference was statistically significant in only one case (trials no. 14; Table 2).

Characteristics of Specialized Electrical Discharges

Specialized electrical discharges, whose emition by broadhead catfish was studied within this project were unipolar impulses. Their amplitude did not exceed 5–7 mV if recorded by electrodes fixed onto the opposite wall of the aquarium. The shape of discharges was variable and changed even during one particular trial (i.e., in one pair of experimental fish). The oscillograms are indented owing to different in amplitude and time local maximums and minimums on the top and leading and trailing edges of the respective oscillogram. The oscillograms differ from each other in position, width, and amplitude of main peaks. The length of a single discharge usually ranged within 20–30 ms. The shape and length of discharges that were simultaneously recorded by two independent recording units were similar (Fig. 6). The averaged shape of electrical discharges recorded in the dark and light was also fairly similar. Averaging was performed for 22 dark and 12 light discharges from trial no. 2, where the electrical activity of fish was similar under different conditions of illumination (Fig. 7).

DISCUSSION

Effects of Illumination on Electrogeneration and Electrocommunication

The performed studies showed that the emition of specialized electrical discharges associated with aggressive–defensive behavior of broadhead catfish takes places under different conditions of illumination. However, in the dark, electrical activity in these fish increases and can manifold exceed the level observed in the light. Similar correlations between the elecrogeneratory activity and illumination level is also observed in other examined species of fishes with weakly and strongly pronounced capabilities for electrogeneration, for example, in thornback ray *Raja clavata* (Baron et al., 1994c), *Gymnotus carapo* and *G. mamirauma* (Gymnotidae) (Crampton, Hopkins, 2005), *Brachyhypopomus punnicaudatus* (Hypopomidae) (Silva et al., 2007), and electric catfish *Malapterurus electricus* (Malapteruridae) (Belbenoit et al., 1979). Pronounced correlation between dark time of the day and the period of the maximum electrical activity is observed in water bodies inhabited by several species of "weakly electric" fishes (Baron et al., 2001). All these facts allow us to conclude that the enhancement of electrogeneratory activity under decreased illumination conditions is a common feature characteristic not only of the broadhead catfish but all other electrical fishes as well. The adaptive significance of the enhanced electrogeneratory activity of fish under low illumination is obvious. It can compensate the loss of information perceived through the visual channel owing to enhanced electrical signalization providing successful orientation, location, and communication of the fishes in changing environmental conditions. Thus, the idea about the signal function of specialized electrical discharges produced by broadhead catfish is well grounded and casts no doubt.

The electrical discharges recorded in our experiments (in terms of their main characteristics, such as unipolarity, shape, and length) agree well with those associated in broadhead catfish with aggressive–defensive behavior (Ol'shanskii et al., 2002, 2009, 2011; Ol'shansky, 2010). It is supposed that the generation of such discharges is related to regulation of hierarchical relationships within a group of fish (Baron et al., 1994a, 1994b). Thus, the frequency of emition of electrical discharges obviously reflects the dynamics and intensity of aggressive contacts between the fish. High electrical activity manifested in the dark is an unambiguous evidence of sharp activation of fish behavior in the dark, which allows for considering these conditions (the dark) as the most adequate for broadhead catfish. However, in the light, the electrogeneration in broadhead catfish is not inhibited entirely and remains at a fairly high level, which reaches, on average, 70–80% of the respective dark level. Thus, illumination is indeed the factor regulating behavior and signalization in broadhead catfish but not driving these activities entirely. In natural water bodies, *C. macrocephalus* could obviously be active also during daytime; they could search for food, move within the water body, or migrate but not necessarily stay for all this time in refuges. Such behavior is characteristic, for example, of a closely related species, the
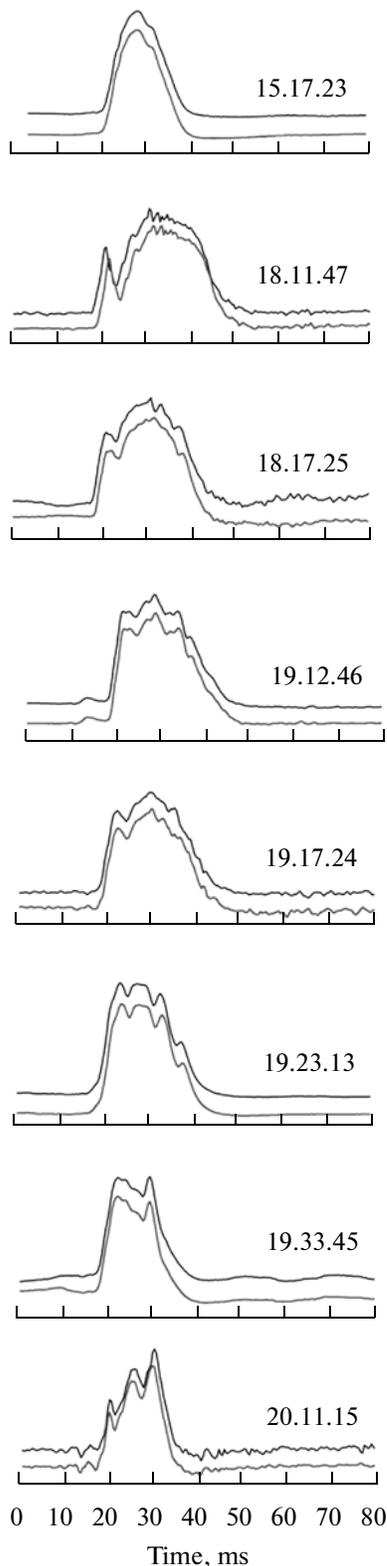
Fig. 6. Diversity in the shape of electrical discharges in broadhead catfish *Clarias macrocephalus*, according the results of trial no. 2; oscillograms of discharges recorded simultaneously by two independent recording units; the discharges were normalized to amplitude; the numbers in the upper right corners of the oscillograms mean the moments of the registration of the respective discharge (h: min: s).

African sharptooth catfish *C. gariepinus* (Bruton, 1979).

The absence of strict correlation between aggressive–defensive relationships and illumination in broadhead catfish could also be corroborated by similar averaged shape of electrical discharges that the catfish emit in the light and dark. The electrical discharges emited by the fish under different illumination conditions most likely have the same function and are used for communication. In some of weakly electric fish, for example, *Marcusenius altisambesi* (Mormyridae) and *Brachyhypopomus punnicaudatus* (Hypopomidae), the differences between dark and light electrical discharges indeed has been revealed (Franchina and Stoddard, 1998; Franchina et al., 2001; Salazar and Stoddard, 2008; Machnik and Kramer, 2011).

A characteristic feature of electrical activity in broadhead catfish is sharp fluctuations in its intensity. Instability and fluctuations of electrical activity were observed in most trials, both in the dark and light. This peculiarity is most likely due to the general behavioral pattern (syndrome of behavior) in broadhead catfish, the alteration of long periods of rest, when the fish are almost motionless, with shorter (usually no longer than 1 min) periods of fast swimming. In our data, the catfish demonstrate such a behavioral pattern irrespective of social conditions, when maintained both individually or in groups of different size. The alternation of the periods of rest and active swimming is irregular, but, evidently, is not accidental and, in turn, could be due to more prolonged changes in the inner motivation condition of the fish. This is corroborated by the fact of statistically significant positive correlation between fish activity in dark and light periods (trial nos. 3, 5, 6, 8, 11, 14). This correlation could be related to circadian rhythms of behavior or the general activity of the fish. The rhythms that were not dependent on the real illumination regime and thus considered as circadian ones, were revealed during the emition of electrical discharges in adult specimens of *B. pimmicaudatus* (Stoddard et al., 2003). It is still dubious whether the electrogeneration in broadhead catfish follows the circadian rhythms. It is fairly difficult to reveal the circadian rhythms under conditions of sharp and frequent changes of illumination, as was the case in our rather short-term (24-h-long) trials. The solution of this problem requires different design of the trials and was not among the targets of our project.

Stress

Broadhead catfishes belong to stress-labile fishes, i.e., they are vulnerable to such effects as population density and handling (Van de Nieuwegiessen et al., 2008a). However, in most our trials, electrical discharges were recorded already at the beginning of the first dark period or, in some trials, even during the pre-start 10-min-long interval, i.e., almost immediately
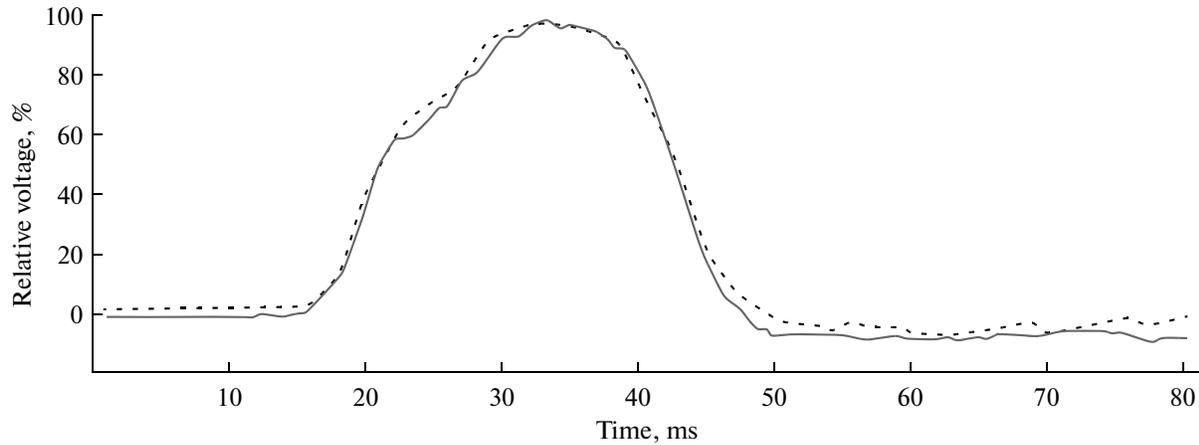
Fig. 7. Averaged shape of electrical discharges in broadhead catfish *Clarias macrocephalus*, emited in the dark (—) and light (- - -), according the results of trial no. 2; the discharges were normalized to amplitude.

after the fish were transferred into the new conditions. This is evidence that the aggression and the associated electrogeneration in the broadhead catfish is weakly affected by manipulator stress that could suppress numerous behavioral manifestations in fishes (Schreck, 1990; Schreck et al., 1997; Conte, 2004; Portz et al., 2006). It is possible that the presence of a fish of the same species in the direct vicinity can be a strong releasing stimulus for the broadhead catfish, which is capable to initiate stereotypic aggressive behavior and emition of specialized electrical discharges irrespective of the stress suffered by the fish during capturing and transfer to the experimental aquarium.

This speculation is corroborated by results of trials with alarm pheromone, a natural chemical signal of danger. The alarm pheromone is released into water from damaged skin, is perceived by olfactory receptors, and causes an inherent defensive response in the fish, i.e., fear, withdrawal, and concealment (Malyukina et al., 1977; Kasumyan and Pashchenko, 1982; Døving et al., 2005). The primary (physiological) effect of the signal includes a typical stress syndrome that develops in the recipients (Malyukina et al., 1982; Lebedeva and Golovkina, 1988). Alarm pheromone is present in many fish species, including broadhead catfishes (Smith, 1992; Brown et al., 2003; Van de Nieuwegiessen et al., 2008b, 2009). In our experiments, no pronounced effects on the generation of electrical discharges by fish were revealed. We recorded temporarily decreasing electrogeneration only in some trials after the injection of the extract into the aquarium that was observed against the background of the general high fluctuation of electrical activity. The absence of any pronounced effect of the pheromone was not due to the concentration of skin extract (0.5 g/l), which significantly exceeded the threshold level of fish for this signal (10^{-7} g/l) (Malyukina et al., 1977; Døving et al., 2005). Obviously, the aggressive motivation caused by

the presence of a specimen of the same species was significantly stronger than the defensive one, developing under the effect of the alarm pheromone, which finally determined the result of contradiction (conflict) between these two oppositely directed motivations.

A stressor or excitation factor for the fish, whose effects, unlike those of the alarm pheromone, were more obvious, was the fluctuation of illumination. At the beginning of the 30-min-long periods, the emition of electrical discharges was higher, but then decreased. More characteristic is increasing of electrical activity in response to switching the light on, whereas switching the light off more rarely caused a stress response. The latter fact could be considered as more evidence in favor of the adaptation of broadhead catfishes for night or twilight mode of life.

In some trials, we observed increased electrical activity of the fish in morning hours (7:00 a.m.–9:00 a.m.), i.e., at the beginning of working hours, and associated noise and vibrations caused by city transport and by electrical noise (trial nos. 4, 6, 8, 9). We cannot exclude the idea that the "industrial" stimuli, exceeding the threshold level for these fish, caused certain discomfort for the experimental specimens, thus affecting their motivation condition. Additional stressors can initiate aggression in fishes, as has been shown for the catfish *C. gariepinus* (Van de Nieewegiessen et al., 2008a), thus enhancing the generation of electrical discharges.

Adaptation

The increasing of electrical activity in response to light switching on or off goes out fairly quickly, which is evidence of fast adaptation of the fish to the new, strikingly different, conditions of illumination. The electrical activity of fish usually comes down also during the entire trial, i.e., as long as the experimental fish stay together in the aquarium. This trend is well
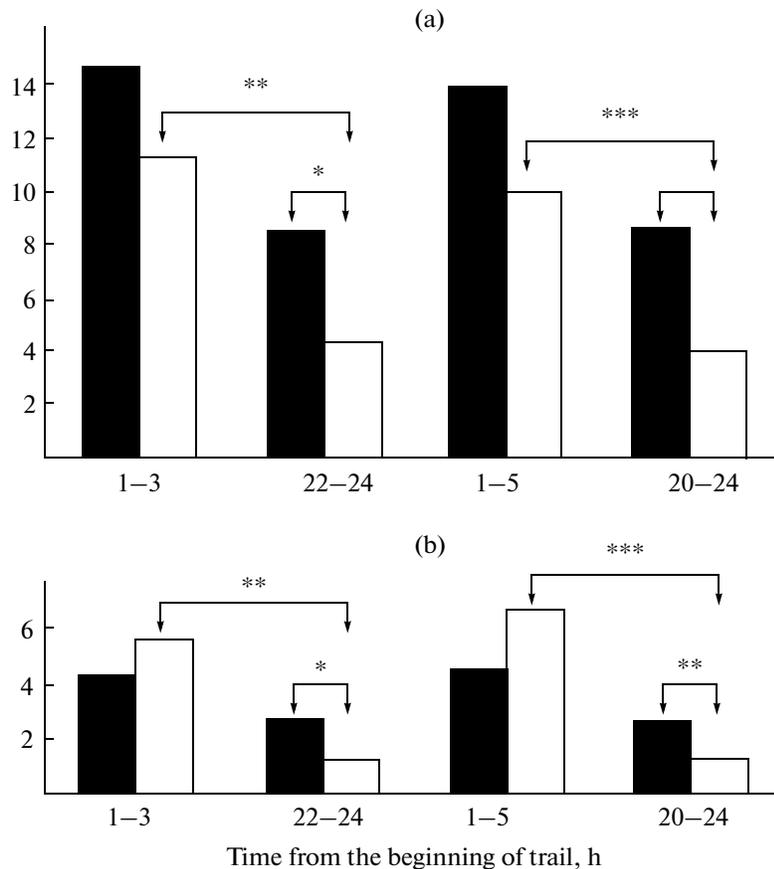
Fig. 8. Electrical activity of broadhead catfish *Clarias macrocephalus*, in the dark (■) and light (□) at the beginning and by the end of being kept together during the trial: (a) mean number of electrical discharges emited during 30-min-long dark and light intervals (the ordinate), (b) mean number of discharges emited during the first 5 min of 30-min-long dark and light periods (the ordinate); according the results of trial nos. 1–10. Differences are statistically significant as follows: (*) $p < 0.05$, (**) $p < 0.01$, (***) $p < 0.001$.

noticeable if we compare the number of electrical discharges recorded during the first and the last hours of exposition; in all the trial, the latter was smaller than the former (including both dark and light periods) (Fig. 8). It is pertinent to note that this trend is revealed irrespective of the dynamics of electrical activity of the fish in the course of the trial. By the end of the trial, the intensity of discharge emition was always smaller compared with the level that was observed at the beginning of the trial.

The frequency of electric discharge emition is an indirect index of the manifestation of aggressive interactions by the fish. The decrease of this index by the end of the first day of observations could be evidence of dominant–subdominant relationships that could develop in the experimental fish pairs by that time. It is known that broadhead catfish in small groups develop nonlinear hierarchy, with a dominant leader and subdominant specimens that do not differ from each other in their social status (Carter and Davies, 2004). In *C. gariepinus*, in groups of four specimens, such a hierarchy appears already by the end of the first

day of the experiment (Fatollahi and Kasumyan, 2006). Gradually decreasing aggression level in broadhead catfish maintained together was emphasized in several publications (Martins et al., 2006a; Van de Nieuwegiessen et al., 2008a). During this study, we did not plan to reveal whether the long-term maintainance of the fish together could result in total disappearance of electrical interactions between the fishes. According to our preliminary results, it remains for a significantly longer period (no less than several days or weeks). In the specimens of *C. gariepinus* maintained together, the aggressive behavior, despite the fact of its significant decrease, remained for approximately a month (Martins et al., 2006a; Van de Nieuwegiessen et al., 2008a). Proceeding from these facts, we could conclude that broadhead catfishes in natural water bodies prefer staying in sparse populations or individually and try to avoid each other if gathering together. Similar behavior is revealed in *C. gariepinus*, as was revealed in experiments with tracing of movements and distribution of radio tagged fish in natural water bodies (Hocutt, 1989). However, in some cases, *C. gariepinus* can hold together, for example for group

hunting or mutual migration to spawning grounds (Bruton, 1979; Merron, 1993). The mechanisms that suppress the aggression in the catfish and allow them to develop temporary assemblages still remain unclear.

Individual Variability

The fish that were united into experimental pairs to use in our experiments were captured in one water body; they were maintained together in the laboratory and were similar in size and physiological condition. Most the experimental pairs were also composed of fish of the same sex. Despite this fact, the electrical activity of fish in the trials varied significantly; the total number of electrical discharges could differ by an order of magnitude or even greater. For example, the minimum and maximum number of discharges recorded during the trial equaled 29 and 1097, respectively (Tables 1, 2). The main reason for so great of differences could be individual variability of specimens by stress-lability, behavior, and other important features. Differences between certain individuals in the strength of response for different stress stimuli were revealed in several fish species (Barton and Iwama, 1991; Pottinger and Carrick, 1999), including broadhead catfishes (Martins et al., 2005, 2006b). Variability is a characteristic feature of fish behavior (McLaughlin et al., 1992; Magurran, 1993; Biro and Ridgway, 1995; Kasumyan, 2000; Kasumyan and Sidorov, 2002; Lee and Bereijikian, 2008); it is considered as a manifestation of variability, i.e., a complex of patterns and features of behavior that are characteristic of a single particular individual and determine its personality. This aspect of fish behavior has attracted the growing interest of scientists in recent years (Gosling, 2001; Sih et al., 2004a, 2004b; Huntingford and Adams, 2005; Budaev and Brown, 2011).

The individual variability of electrocommunication activity in electrical fishes still remains poorly studied. The variability in shape and length of specialized electrical discharges is a characteristic feature of broadhead catfish during paired aggressive—defensive interactions. The mechanism of emition of these unipolar impulses still remains unknown (Olshansky, 2010). Their shape cannot be described quantitatively using the approach that is applied for analysis of shape of stable discharges in the members of Mormyriformes or Gymnotiformes (Arnegard and Hopkins, 2003; Lavoué et al., 2008). It is most likely that the indentation of oscillograms and variability in the length of electrical discharges in broadhead catfishes is due to asynchronously functioning elements of the electrical organ, as is the case in a weakly electric Uranoscopidae, where unipolar discharges are emited at the expense of consecutive initiation of individual units that constitute the electrical organ (Baron et al., 2002).

CONCLUSIONS

Our knowledge about the behavior and development of sensory systems in broadhead catfishes are mostly based on the information obtained for the African sharptooth catfish *C. gariepinus* that is the most well-studied species of the family Clariidae that has a wide geographical range and is used as an object of aquaculture in many countries (Bruton, 1979; Huisman and Richter, 1987; Alves et al., 1999). On the other hand, there are little data about the broadhead catfish inhabiting water bodies of Southeastern Asia that are widely cultivated there. The results of this study allow us to consider that the broadhead catfish is active in twilight or in the nighttime and prefers to stay in refuges during the daytime, significantly decreasing the motility in this period. This is corroborated by the results of our study; these fish were more electrically active in the dark than in the light; switching a light on causes more anxiety that turning a light off. However, the electrical activity in this species of catfishes is not entirely suppressed during the daytime, but is retained; it is retained not only during paired aggressive—defensive relationships but also during spawning and hunting for highly motile preys (Ol'shansky et al., 2009, 2011; Ol'shansky, 2010). One may suppose that the sensory specialization of the broadhead catfish for twilight—nocturnal mode of life is weaker pronounced compared with that in other weakly electric fishes. It is known that visual reception allows the broadhead catfish to search for food successfully and to perform selective choice of artificial food objects by their color (Fattolahi and Kasumyan, 2006). Broadhead fishes are capable of feeding during daytime also in natural circumstances (Bruton, 1979) and their movements within the respective water bodies, as was shown in experiments with tagged fish, are not confined only to the dark time (Hocutt, 1989). Broadhead catfish possess a well developed olfactory system (Resink et al., 1987, 1989; Van Weerd et al., 1991). Obviously, in different natural conditions, different sense organs can play the role of the main sensory system. Such a peculiarity anticipates a high level of development of many sensory systems and the capability to use these patterns of orientation and communication, which are the most appropriate for certain particular conditions. As was shown in our study, in broadhead catfish, the loss of ability to use visual reception is compensated by enhanced electrical emition and signalization.

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