

Research Article

The effect of brackish water on the movement patterns of non-native armoured catfish (Loricariidae)

Efim D. Pavlov¹, Tran Duc Dien², Ekaterina V. Ganzha¹¹ Institute of Ecology and Evolution A.N. Severtsov of the Russian Academy of Sciences, Moscow, Russia² Coastal Branch of Joint Vietnam-Russia Tropical Science and Technology Research Center, Nha Trang, VietnamCorresponding authors: Efim D. Pavlov (p-a-v@nxt.ru); Tran Duc Dien (mrtran_cnvb@yahoo.com)

Abstract

Non-native suckermouth armoured catfish *Pterygoplichthys* spp. have spread extensively across many river systems in Vietnam. It is possible that their expanded distribution occurred through the brackish waters of estuaries and coastal zones, facilitating movement from one river system to another. It has been previously hypothesized that, for successful dispersal through brackish water, armoured catfish can tolerate changes in water salinity and are capable of avoiding high salinity levels that threaten their survival. In this study, we experimentally estimated the movements and the directions of juvenile and adult wild loricariids in fresh and brackish water. Our results showed that juveniles exhibit a circadian rhythm of locomotor activity similar to that of adults. However, juveniles display a more pronounced reaction to increasing water salinity – at 5 PSU – while adults respond at 15 PSU. This likely explains the absence of juveniles in natural brackish water environments and their reduced potential to spread through brackish waters compared to adults. Adult loricariids are likely capable of recognizing and avoiding high-salinity zones (>10 PSU) by increasing locomotor activity, predominantly directed toward the surface. Their ability to grasp air helps maintain positive buoyancy, allowing them to remain in the surface layer of freshwater over extended periods of time. Variability in salinity tolerance among adults (ranging from 2 to 16 hours in 15 PSU) may enable some individuals to be more successful in dispersing through estuaries and along coastlines.



Academic editor: Charles Martin

Received: 29 March 2025

Accepted: 13 June 2025

Published: 3 September 2025

Citation: Pavlov ED, Dien TD, Ganzha EV (2025) The effect of brackish water on the movement patterns of non-native armoured catfish (Loricariidae). *Aquatic Invasions* 20(3): 371–390. <https://doi.org/10.3391/ai.2025.20.3.162564>

Copyright: © Efim D. Pavlov et al. This is an open access article distributed under terms of the Creative Commons Attribution License ([Attribution 4.0 International – CC BY 4.0](https://creativecommons.org/licenses/by/4.0/)).

Key words: Fish spread, locomotor activity, non-native fish, *Pterygoplichthys* spp., salinity gradient, water salinity

Introduction

South American suckermouth armoured catfishes (Siluriformes: Loricariidae: *Pterygoplichthys*) are globally popular as ornamental species (Novák et al. 2022). These fish are transported worldwide in substantial quantities and have become invasive in tropical and subtropical aquatic ecosystems, primarily through the ornamental fish trade (Orfinger and Gooding 2018; Saba et al. 2020). Unlike many other freshwater fish, armoured catfish have a highly protected body with dermal plates

and various protective mechanisms (Ebenstein et al. 2015), which likely reduce predation risk, especially in new aquatic environments. In regions with favorable climatic conditions, loricariids can establish new populations, reproduce extensively, and spread rapidly (Orfinger and Goodding 2018; Zworykin and Dinh 2023; Marr et al. 2024). Armoured catfish exhibit parental care, nest-building behavior, the production of large eggs, and high fecundity rates (Gibbs et al. 2017; Orfinger and Goodding 2018; Araujo and Langeani 2020), all of which contribute to their reproductive success. These features are the reason why catfish have a potential to spread in new bodies of water and successfully compete with native fish. Climate change and global warming may further accelerate the spread of more adaptive non-native species, posing significant threats to native fish populations (Alix et al. 2020).

Possibly, non-native loricariids could have a significant negative impact on natural water ecosystems and human economic activities, also indicated by decision-support tools for Vietnam (Ruykys et al. 2021; Zworykin and Dinh 2023). Adverse effects have also been associated with their burrowing activities, which contribute to bank instability and erosion (Nico et al. 2012). It has been experimentally shown that invasive *Pterygoplichthys* spp. impact the trophic ecology of native fish (Quintana et al. 2023), with their diet remaining stable across different density treatments. However, the diet of native fish deviated increasingly from control values as catfish density increased (Parvez et al. 2023). The widespread presence of armoured catfish in the Vietnamese Suoi Trau Reservoir likely reduced native species diversity and biomass (Dien et al. 2025). Armoured catfish also cause significant damage to fishing nets after capture (Pavlov et al. 2023b), resulting in increased time and financial resources required for fishermen to check and repair their gear. The spread of suckermouth armoured catfish to cultured ponds decreases the productivity of carp aquaculture in India (Seshagiri et al. 2021). Conversely, a single mesocosm study showed that the catfish appeared to have a positive impact on the growth of wild rice (*Zizania texana*), likely due to their consumption of algae on and around the plants (Norris 2017).

In the bodies of water of South Vietnam, *Pterygoplichthys* spp. was initially recorded in 2003–2004 (Welcomme and Vidthayanom 2003; Serov 2004). By 2010, they rapidly spread to Central Vietnam (Zworykin and Budaev 2013) and Northern Vietnam (Levin et al. 2008). One alternative pathway for the spread of non-native loricariids in lotic water bodies involves traversing brackish waters (estuaries and coastlines) to reach new river systems (Capps et al. 2011; Pavlov et al. 2023a). The availability of this pathway aligns well with the rapid expansion of armoured catfish into Vietnamese rivers.

Loricariids are considered a strictly freshwater family of fish in their native range throughout the Neotropics (Myers 1949). Nonetheless, there are several reasons to consider the possible spread of loricariids through brackish waters. Our earlier field studies (Pavlov et al. 2023a) revealed that loricariids inhabited riverine estuaries in Vietnam with water salinity levels of up to 18 PSU. The genus *Pterygoplichthys* is known to tolerate salinity levels of 15–16 PSU (Capps et al. 2011). Additionally, some individuals can survive in high-salinity water (up to 15 PSU) for up to two days (Dien et al. 2022). Salinity tolerance is one of several important physiological features that determine expansion success and the pattern of dispersal of introduced aquatic organisms between freshwater bodies through brackish waters (Cognetti and Maltagliati 2000; Schofield et al. 2009). Specific environmental conditions, such as seawater desalination and the presence of single river estuaries in Vietnam, could further increase the likelihood of fish spreading through brackish waters (Pavlov et al. 2023a). For example, approximately 30% of freshwater fish in Vietnam occupy brackish waters in estuaries and desalted coastal zones (Zworykin 2016).

However, the availability of specific features of armoured catfishes that could facilitate their successful spread through brackish waters remains uncertain. In the original study, we focused on behavioral and physiological features that are likely to increase the chances of armoured catfish rapid and successful dispersal through brackish waters: the capacity for long-term directed movements and survival in water of varying salinity. Our previous field studies (Pavlov et al. 2023a, b) showed that adult armoured catfish can avoid increased salinity by horizontal and vertical movements towards the water surface in estuaries. However, there is no evidence to determine whether loricariids recognize changes in water salinity or whether their movements are associated with other environmental conditions. If loricariids can detect increasing salinity, how do they react, and how quickly? Additionally, we did not find any juvenile loricariids in natural Vietnamese brackish waters (Pavlov et al. 2023a, b). This observation is consistent with findings that juveniles of *Pterygoplichthys* spp. rarely occur in waters with salinity greater than 10 PSU (Capps et al. 2011). The phenomenon suggests that juveniles and adults differ in their tolerance to water salinity and that age may influence the likelihood of successful dispersal.

The study aimed to experimentally assess changes in movement patterns and directionality of juveniles and adults of the armoured catfish genus *Pterygoplichthys* under the influence of brackish water.

Materials and methods

The study was conducted from February to March 2023 and was focused on the suckermouth armoured catfish genus *Pterygoplichthys* (Siluriformes: Loricariidae). For species identification, we used systematic keys (Armbruster and Page 2006), which are based on the number of dorsal-fin rays and body color patterns. In the study, most of the fish were identified as *P. disjunctivus*, with some identified as *P. pardalis*. However, it is possible that these fish were hybrids, as suggested by Godwin et al. (2016).

Fish catching and transfer to laboratory

Wild fish were captured in the Am Chua canal (12°17'26"N, 109°06'00"E) and the Da Rang River (13°00'50"N, 109°11'35"E). The irrigation Am Chua canal is isolated from the Cai River by small dams that control the water supply to the rice fields. These dams block armoured catfish movements from the Am Chua canal to the Cai River and prevent their contact with brackish waters. The Da Rang River is one of the largest river systems in Central Vietnam, with a length of 374 km and a basin area of 13900 km². This river forms a wide and extended estuary and flows into the Eastern Sea. In the Da Rang River, armoured catfish can move downstream and come into contact with brackish waters in the estuary. Previously, fish have been found in both the freshwater and brackish water of the Da Rang River (Pavlov et al. 2023a).

In the Am Chua canal, we caught forty juvenile armoured catfish using a bottom trawl (5 × 5 m with a mesh size of 10 mm) and transferred them to the laboratory. In the freshwater zone of the Da Rang River, we used two types of fishing gear to catch adult fish: ten sectional net traps and one vertical gillnet. The sectional net traps, with a mesh size of 10 mm, were placed on the bottom. Each trap measured 9 meters in length and consisted of rectangular metal frames (0.3 × 0.2 m) positioned 0.3 meters apart. The traps were connected in a single line spanning 90 meters. The vertical gillnet was 320 meters long, 2.5 meters high, with a mesh size of 22 mm. Both fishing gears were set along the river banks (Suppl. material 1) once in the afternoon (16:00, GMT+7) and checked five hours later (21:00, GMT+7). A total of two hundred adult fish were transferred to the laboratory in two 50 L tanks.

Fish maintenance

In the laboratory, one tank with a water volume of 50 liters was used to maintain the juvenile fish stock. Adult fish were separated into 60 L tanks, each containing 40–50 fish. The tap freshwater (mineralization of 300 ppm) used in the laboratory was conditioned by settling and aeration for two weeks in two 2000 L basins. The water in the stock tanks was aerated and replenished once daily. The level of dissolved oxygen in the water ranged from 7.0 to 7.2 mg/L, measured with a Pro Dissolved Oxygen Meter MW600 (Milwaukee, USA). The water temperature was maintained between 25.5 and 26.5 °C. Illumination in the tanks was natural, passing through laboratory windows, and varied throughout the 24 hours from 0.1 lx to 100 lx, measured with a Lutron LX-1102 Lux Meter (Lutron Electronic, Taiwan). The illumination conditions in the stock tanks resembled the natural conditions of the Am Chua canal (Suppl. material 2). Juvenile and adult fish were fed once daily at 16:00 (GMT+7) with Pro's Choice Bottom Feeders tablets (Fwusow Industry, Taiwan) for demersal fish. Behavioral tests began after one week, once cumulative fish mortality did not exceed 5%.

Estimating locomotor activity

The protocol described in this article is published on protocols.io <https://www.protocols.io/private/94E6B54D66A711EE9EF90A58A9FEAC02> and has been verified (Pavlov et al. 2023b).

Three test apparatuses (Type 1) were used to evaluate the locomotor activity of armoured catfish and their stress response in brackish water. Each apparatus consisted of four 10 L glass aquaria, each measuring 20 × 22 × 20 cm (width × height × depth). To minimize the risk of fish jumping out during the trial, each aquarium was filled with 5 L of water. Video cameras (SjCam A10, China) equipped with infrared lights were positioned above each apparatus at a distance of 0.7 meters from the bottom (Suppl. material 3). For preparing water with the required salinity, seawater (32 practical salinity unit, PSU) was collected from Nha Trang Bay (12°13'03"N, 109°12'47"E), conditioned by settling and aeration for two weeks. The dissolved oxygen level in the seawater ranged from 7.0 to 7.2 mg/L. The seawater was mixed with freshwater in appropriate proportions to achieve the desired salinity. Trials were conducted during daytime hours, from 8:00 to 16:00 (GMT+7). At the start of the trial, one random individual from fish stock was transferred into each apparatus. After the trial, the fish were transferred into a recovery tank. Each fish was used only once for testing. The water in the aquaria was replaced after each trial to remove fish metabolites.

The time duration of fish locomotor activity (LA) during each second of the trial was estimated from video recordings using DVR-Scan v1.5.1 (Python Software Foundation) for movement detection with consistent settings. The programming module did not account for short-term twitches of the fish and interpreted them as motionless. Based on the trial duration, individual locomotor activity during each ten minute, one-hour or two-hour interval of the trial was assessed using normalized values, calculated with the following formula:

$$LA = t_i \times 100/T$$

Where: *LA* – locomotor activity during a specified time interval of the trial, expressed as a percentage of ten minutes, one or two hours, *t_i* – duration of fish movements during *ith* time unit of the trial, *T* – total time of fish movements during the entire trial.

The circadian activity of juveniles was estimated to exclude its influence on the experimental design and to determine the optimal timing for the initiation and

duration of the main behavioral tests involving brackish water exposure. We used 55 juveniles from Am Chua canal, with a standard body length of 8.4 cm (range: 6.3–11.8 cm) and a body weight of 11.8 g (range: 4.2–36.0 g). The tests were conducted between 8:00 and 16:00 using test apparatus Type 1. Each trial lasted 25 hours and was recorded on video. Based on our previous data (Pavlov et al. 2023b), the first hour was excluded from analysis because the fish were still experiencing manipulation stress from transfer to the test apparatus. In total, 55 trials and 1320 hours of video recordings were analyzed.

To evaluate the effect of brackish water on juveniles, we transferred one randomly selected individual from the fish stock to each Type 1 apparatus containing either freshwater (0 PSU, control) or brackish water (5 PSU). The control group was necessary to differentiate possible effects of manipulation stress from osmotic stress (Fiol and Kultz 2007) during the trial. We used 39 juveniles from Am Chua canal, with a standard body length of 8.7 cm (range: 6.6–11.2 cm) and a body weight of 13.0 g (range: 4.7–30.6 g). Eighteen fish were transferred to freshwater, and twenty-one to brackish water. The fish subjected to different water conditions had similar length or weight (Student's *t*-test: $p > 0.7$). Experiments were conducted from 8:00 to 14:00, with each trial lasting 6 hours and recorded via video. In total, 39 trials and 234 hours of video recordings were analyzed. To evaluate the effects of osmotic stress, we compared juvenile's locomotor activity during six-hour exposures at water salinity 0 PSU and 5 PSU.

To assess the influence of osmotic stress on locomotor activity and survival of adult fish, we transferred one randomly selected individual from the fish stock to each Type 1 apparatus containing either freshwater (0 PSU, control) or brackish water at 5 PSU, 10 PSU, and 15 PSU. A total of one hundred fish from the Da Rang River were used, with a standard body length of 15 cm (range: 9–23 cm) and a body weight of 60 g (range: 15–134 g). Twenty fish were used in each of the experiments at 0 PSU, 5 PSU, and 10 PSU, while forty fish were tested at 15 PSU to evaluate individual survival time at high salinity. The fish across the different exposure groups had similar length and weight (Student's *t*-test: $p > 0.16$). Experiments began between 8:00 and 14:00. Each trial lasted 24 hours and was recorded. In total, 100 trials and 2400 hours of video recordings were analyzed. To evaluate the effects of osmotic stress, we compared locomotor activity of adult fish during six-hour exposures at different salinity levels.

Assessment of fish perception and avoidance of water salinity

Another three test apparatuses (Type 2) were used to assess armoured catfish perception of water salinity and their navigation within a salinity gradient. Each apparatus consisted of two paired 10 L glass aquaria (see Figure 1). Three external side walls of the apparatus (excluding the long front wall) were covered with semi-transparent white film. Each aquarium had a 22 mm hole in the center of its bottom for freshwater or seawater inflow (32 PSU). The 22 mm tubes (internal diameter 18 mm) were mounted through these holes, extending 30 mm above the bottom of the aquaria and sealed with hermetic covers at the ends. Water inflow was provided through six 3 mm holes evenly spaced around the perimeter of the tubes, located 10 mm from the bottom. This hole placement minimized mixing between seawater and freshwater. The other ends of the tubes were connected to each other using 10 mm hoses via special fittings. The hoses were connected to an aquarium pump (Eheim Bio-Flow 1000, placed in a 100-liter tank), which supplied water to the paired aquariums. The discharge rate was regulated using a water tap. To record fish behavior during the trials, GoPro Hero 8 cameras (GoPro Inc., USA) were positioned at the front of each apparatus.

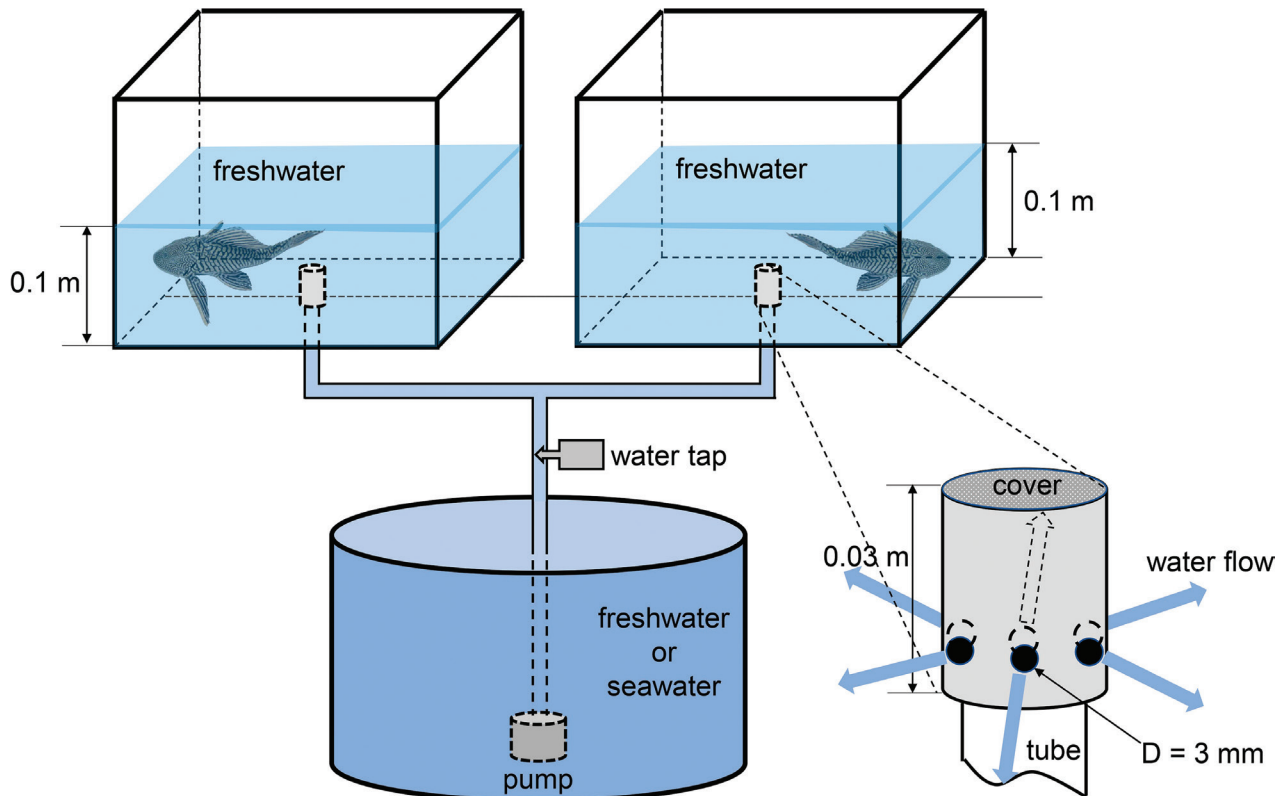


Figure 1. Scheme of test apparatus Type 2.

Using apparatus Type 2, we aimed to maintain water salinity stratification – enabled by weak mixing between freshwater and seawater – within the apparatus, thereby mimicking the natural stratification observed in the Da Rang River estuary: seawater near the bottom and freshwater near the surface (Pavlov et al. 2023a). We believe that this experimental design could provide valuable insights into the movement patterns of wild armoured catfish under the influence of brackish water in estuarine environments. To assess water salinity stratification, 4 liters of seawater were supplied to the aquaria at a discharge rate of 6.7×10^{-3} L/s over a ten-minute period (Suppl. material 4). This test was performed without fish in the apparatus. Following Miyanishi and Uchida (2021), methylene blue was added to the seawater for coloration and visual detection within the aquaria. Water samples were collected from different depths, spaced at 2.5 cm intervals, using a glass pipette to assess salinity changes during seawater inflow throughout the trial. Salinity measurements were performed using an optical refractometer (RHS-10ATC, Kelilong Electron, China). It was observed that, during ten minutes of seawater inflow in apparatus Type 2, seawater near the bottom exhibited weak mixing with freshwater (Suppl. material 5).

The experiments assessing fish perception and avoidance of seawater were conducted during the daytime when adult armoured catfish exhibited lower locomotor activity (Pavlov et al. 2023b). Therefore, the onset of increased locomotor activity following seawater inflow was primarily attributed to the individual's response to changes in water salinity rather than to circadian rhythm. Laboratory illumination during the experiment (from 7:00 to 14:00, GMT+7) was 100 lx. At the beginning of each trial, one randomly selected individual was transferred from the fish stock to each Type 2 apparatus containing 4 L of freshwater. The limited water volume was used because loricariids are facultative air-breathers and often dwell in shallow water for aerial respiration (Gibbs et al. 2021) or for algae feeding (Power 1984). Fish were acclimated in the apparatuses for thirty minutes before cameras were switched on. Ten minutes

later, the pumps and water tap were activated to initiate inflow of freshwater or seawater into the apparatus. After an additional ten minutes of water inflow, the trial and video recording were stopped. Fish body length and weight were then measured, and individuals were transferred to a recovery tank with freshwater and aeration. In the experiment, eighty adult armoured catfish from the Da Rang River were used: forty fish subjected to freshwater inflow and forty to seawater inflow. The fish had a standard body length of 15 cm (range: 10–19 cm) and a body weight of 61 g (range: 24–134 g). In total, 40 trials with 27 hours of video recordings were analyzed.

We used DVR-Scan v1.5.1 to measure the duration of fish locomotor activity during the ten minutes before and during the ten minutes after water inflow, based on video recordings. To evaluate the influence of water salinity on fish movement behavior, we compared locomotor activity values during freshwater and seawater inflow. The analysis included the number and duration of fish movements in two directions: near the bottom and vertical movements toward the water surface. Additionally, we assessed the number and timing of aerial respiration events (Armbruster 1998; Gibbs and Groff 2014; Gibbs et al. 2021) associated with vertical movements to the water surface. We also recorded the number and duration (more than one minute) of events when fish remained motionless in a vertical position along the wall of the aquarium.

Statistical data analysis

Statistical data analysis was conducted using Minitab 18.1. The Shapiro-Wilk test was employed to assess the normality of the sample distributions. Parametric statistics (Student's *t*-test, Chi-Square test) were used when the *p*-value was greater than 0.05, indicating a normal distribution of the data set. Non-parametric statistics (Kruskal-Wallis *H* test, Spearman's rank correlation, Mann-Whitney *U* test) were applied when the *p*-value was less than 0.05, indicating that the data set did not follow a normal distribution. *P*-values less than 0.05 were considered indicative of statistically significant differences between data sets, with multiple comparisons corrected using Holm's sequential Bonferroni procedure.

To analyze changes in locomotor activity of armoured catfishes, we used several statistical tests. The distribution of individual diurnal locomotor activity during a specified time interval of the trial did not follow a normal distribution (Shapiro-Wilk test: $p < 0.05$). To evaluate the circadian rhythm (differences in locomotor activity between two consecutive hours or trial intervals) of catfish, the Mann-Whitney *U* test was used. Spearman's rank correlation examined the relationships between average diel locomotor activity (minutes of fish diel activity per hour) and fish length and weight. The Kruskal-Wallis *H* test was applied to assess changes in locomotor activity of fish in freshwater and brackish water. The similarity of circadian rhythm trends between juveniles and adults was assessed using the Chi-Square test.

To compare movement patterns and the duration of behavioral events of armoured catfish in freshwater and brackish water, Student's *t*-test was conducted. The Chi-Square test was used to analyze differences in the timing distributions of aerial respiration movements of fish in freshwater and brackish water.

Results

Circadian rhythm of locomotor activity of juveniles

Armoured catfish remained motionless on the bottom of the stock tank with freshwater during the daylight period. After the fish were transferred to test apparatus Type 1, periods of locomotor activity alternated with inactivity.

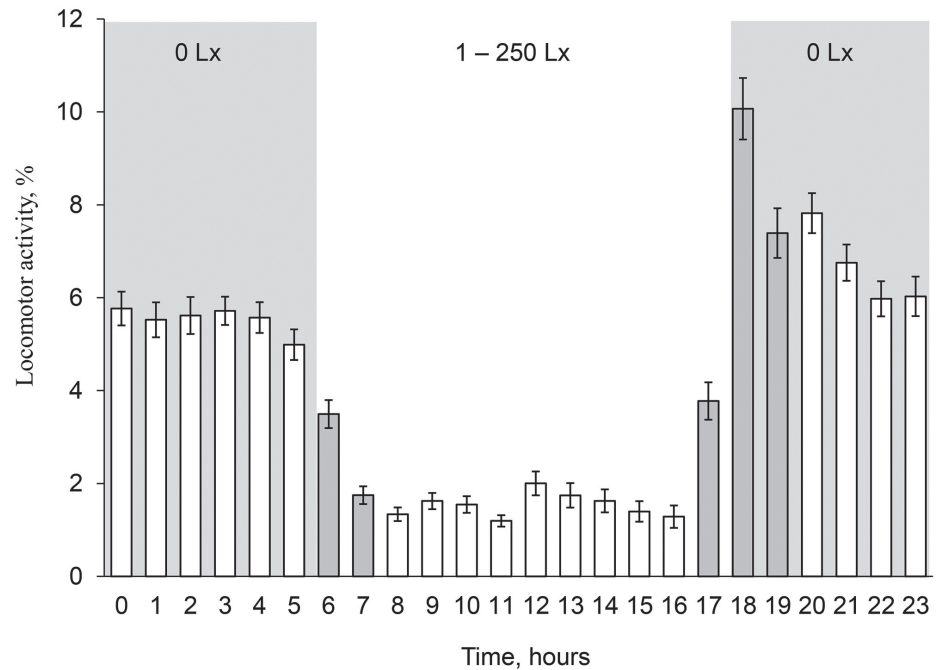


Figure 2. Locomotor activity (% of the one hour) of armoured catfish *Pterygoplichthys* spp. juveniles from Am Chua canal. Numbers on the top of the graph indicate illumination of the time periods. Gray color column indicates significant differences (Mann–Whitney U test (5 vs 6; 6 vs 7; 16 vs 17; 17 vs 18 and 18 vs 19): $p = 0.0020$; $p < 0.0001$; $p < 0.0001$; $p < 0.0001$ and $p = 0.0067$, $n = 55$) with the previous column. Standard error (\pm).

Juveniles from Am Chua canal had an average diel locomotor activity 9.7 ± 0.50 (3.0–17.8) minutes per hour (here and after before the brackets are the mean value and its error; in the brackets are min and max). The diel changes of this parameter did not correlate with length and weight (Spearman correlation: $r_s = 0.16$, $p > 0.27$). The fish were mostly active at nighttime (18:00–6:00) with 0 lx illumination, contributing to 77% of the total locomotor activity, compared to daytime (6:00–18:00) (Mann–Whitney U test: $p < 0.0001$, $n = 55$) (Figure 2). Locomotor activity (LA, % of the one hour) decreased by half (1.8 ± 0.19 (0.3–5.9) %) during the first two hours after dawn (6:00–8:00) (Mann–Whitney U test: $p < 0.0001$, $n = 55$). This parameter in juveniles increased by 2.9 times (3.8 ± 0.40 (0.1–12.3) %) during the hour before sunset (17:00–18:00) and reached its maximum values (10.1 ± 0.66 (1.9–22.9) %) during 18:00–19:00 period, coinciding with sharp changes in illumination. After that (19:00–20:00), LA gradually decreased to 7.4 ± 0.54 (0.1–15.8) %.

Manipulation stress and salinity stress in juveniles

After juveniles were transferred to the test apparatus Type 1, their locomotor activity (LA, % of the one hour) was similar in freshwater (0 PSU) and brackish water (5 PSU) during the first hour: 7.9 ± 1.74 (0.9–29.0) % and 10.0 ± 1.41 (0.2–20.5) %, respectively (Figure 3). In freshwater, fish locomotor activity decreased by 2.2 times during the second hour of exposure, reaching 3.6 ± 0.79 (0.2–11.1) % (Mann–Whitney U test: $p = 0.0237$, $n = 18$). Despite this, at the second hour, the locomotor activity of juveniles in brackish water remained stable at 10.1 ± 1.39 (0.6–23.2) % and was 2.8 times higher compared to fish in freshwater. During the following hour, the locomotor activity of fish in brackish water was more than 2.5 times higher than in freshwater: 5.9 ± 0.89 (0.9–20.1) % and 2.4 ± 0.45 (0.1–7.0) %, respectively. From the fourth to the sixth hour, locomotor activity in fish from both 0 PSU and 5 PSU remained similar.

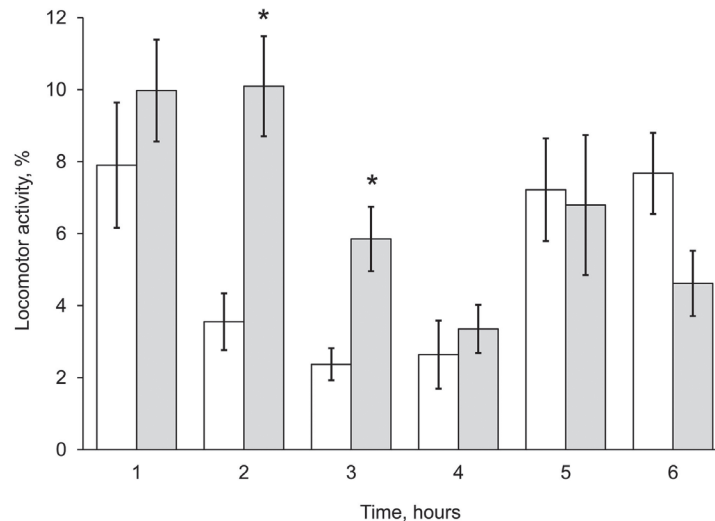


Figure 3. Locomotor activity (% of the interval timing) of armoured catfish juveniles *Pterygoplichthys* spp. under freshwater 0 PSU (white columns, n = 18) and brackish water 5 PSU (gray columns, n = 21) exposure for six hours. * – indicate significant differences between intervals timing. Standard error (()).

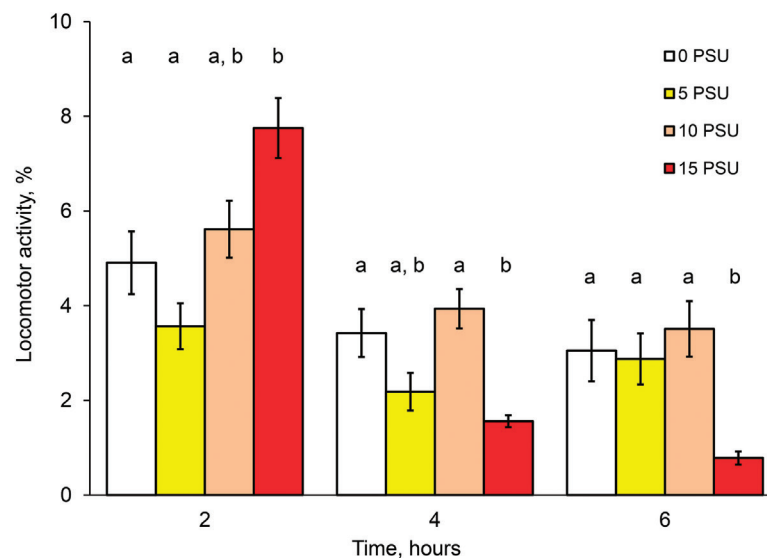


Figure 4. Locomotor activity (% of the two-hour interval) of adult armoured catfish *Pterygoplichthys* spp. from the Da Rang River during six hours after transfer to test apparatus Type 1 with different water salinities (0 PSU, 5 PSU, 10 PSU, 15 PSU). Different letters (a vs b) indicate statistical differences by Mann–Whitney U test between two values of locomotor activities during two hours. Standard error (()).

Effect of different salinity water on osmotic stress and survival time of adult fish

All tested adult fish survived after 24 hours of exposure to water salinity levels of 0 PSU and 5 PSU. One fish died in water salinity of 10 PSU. Fish remained alive in water salinity of 15 PSU on average for 5.6 ± 0.37 (3.0–16.0) hours. Sixty-five percent of the fish died between 3 and 6 hours of exposure at 15 PSU. Some fish (12.5%) died between 2 and 3 hours, and 20% died between 6 and 12 hours. One fish (2.5%) remained alive for 16 hours. The timing of fish survival showed a weak correlation with fish weight (Spearman correlation: $r_s = 0.32$, $p = 0.047$, $n = 40$).

After adult fish were transferred to the test apparatus (Type 1), their locomotor activity (LA, % of the two-hour interval) remained consistent in freshwater, 5 PSU, and 10 PSU water salinity over six hours of exposure (Figure 4). During

the first two hours, LA of fish in water salinity of 15 PSU was higher (7.8 ± 0.63 (0.6–26.7) %) than in freshwater (4.9 ± 0.66 (0.1–15.6) %) and water salinity of 5 PSU (3.6 ± 0.48 (0.3–12.8) %), by 1.6 and 2.2 times respectively (Mann–Whitney U test: $p = 0.0052$, $n = 40$; $p < 0.0001$, $n = 40$). During the subsequent two hours, LA in fish from 15 PSU decreased (1.6 ± 0.13 (0–5.1) %) by 2.2 times compared with freshwater (3.4 ± 0.51 (0.1–12.3) %) and by 2.5 times compared to water salinity of 10 PSU (3.9 ± 0.42 (0.5–11.4) %) (Mann–Whitney U test: $p = 0.0094$, $n = 40$; $p < 0.0001$, $n = 36$). This trend persisted during the last two hours of observation: locomotor activity of fish from 15 PSU decreased to 0.8 ± 0.14 (0–5.3) %, which was 3.9 and 4.5 times lower than in freshwater (3.1 ± 0.65 (0.2–13.9) %) and 10 PSU water (3.5 ± 0.59 (0.6–14.0) %) respectively (Mann–Whitney U test: $p < 0.0001$, $n = 40$; $p < 0.0001$, $n = 36$).

Fish movement patterns in salinity gradient

Armoured catfish alternated periods of movement and inactivity during ten minutes before water inflow into test apparatus Type 2. We observed various behaviors: predominantly lying motionless on the bottom or rarely pressing vertically against the aquarium wall; moving horizontally along the walls; or rising towards the water surface. In some cases, fish surfaced for aerial respiration, breathing out air bubbles and then taking in new air from the surface. Prior to freshwater or seawater inflow, the fish exhibited similar levels of locomotor activity (Kruskal–Wallis H test: $H_{3,40} = 0.3$; adjusted $p = 0.6$) (Table 1). The average duration of a single locomotor activity event was 3 ± 0.1 (1–9) seconds. We did not find any influence of movement type on the duration of events before or during freshwater or seawater inflow (Student's t -test: $p > 0.05$, $n = 40$).

Fish locomotor activity decreased by 2.9 times ten minutes after freshwater inflow compared to their activity during the ten minutes before water inflow (Kruskal–Wallis H test: $H_{3,40} = 9$; adjusted $p = 0.0010$) (Table 1). During the freshwater inflow period, 80% of the fish remained motionless. The remaining 20% moved in horizontal and vertical directions; two fish remained in a vertical position along the aquarium walls. Only one instance of aerial respiration behavior was observed during freshwater inflow.

The value of fish locomotor activity before and during seawater inflow was similar (Kruskal–Wallis H test: $H_{4,5,40} = 0.2$; adjusted $p = 0.6$) (Table 1). During the period of increasing seawater in the aquarium, only 22.5% of the fish were inactive. The remaining 87.5% primarily moved horizontally. Seventeen fish alternated between periods of movement and inactivity while positioned vertically against the aquarium wall. The average duration of inactivity was more than three minutes. When positioned vertically, the fish's gill slits were in the freshwater zone (Suppl. material 6). Vertically, the fish predominantly moved toward the water surface for aerial respiration. A total of 22 aerial respiration events were recorded during seawater inflow.

Fish in seawater inflow spent 1.6 times more time performing aerial respiration movements compared to fish in freshwater (Student's t -test: $p > 0.05$, $n = 40$) (Table 1). Additionally, the timing distributions of aerial respiration movements did not match between the two groups (Chi-Square test: $p < 0.0001$, $n = 40$). Some fish exhibited neutral or positive buoyancy of the body or only the tail part during seawater inflow (Suppl. material 7). This buoyancy effect was typically observed after their aerial respiration movements.

Table 1. Behavioral patterns of armoured catfish *Pterygoplichthys* spp. under freshwater and seawater exposure.

Pattern	Freshwater exposure		Seawater exposure	
	Before freshwater inflow	During freshwater inflow	Before seawater inflow	During seawater inflow
Nonactive fish, %	40.0	80.0	35.0	22.5
Locomotor activity, %	7.5 ± 1.48 (0–31.0)	2.6 ± 1.15 (0–34.0)	9.4 ± 1.84 (0–40.0)	8.2 ± 1.23 (0–27.0)
Number of horizontal movements	33	16	45	51
Total duration of horizontal movements, seconds	90	48	113	150
Number of vertical movements ¹	51	10	77	11
Total duration of vertical movements, seconds	145	32	207	33
Number of aerial respiration events	12	1	6	22
Aerial respiration time of one event, seconds	4.3 ± 0.64 (1.0–9.3)			6.9 ± 0.39 (3.8–10.0)
Percentage of fish in vertical position, %		5		43
Beginning of fish vertical position, minutes		6.5 ± 1.50 (5.0–8.0)		4.9 ± 0.43 (2.0–7.0)
Duration of fish vertical position		3.5 ± 1.50 (2.0–5.0)		3.4 ± 0.42 (1.0–7.5)

Note. Number and duration of fish vertical movements exclude aerial respiration movements.

Discussion

Our laboratory mesocosm experiments offer a straightforward method of evaluating behavioral responses (movement) of non-native armoured catfish when exposed to elevated salinity level, providing insights into trends observed in our previous field and experimental studies (Pavlov et al. 2023a, b). Particularly, the results of these studies showed that *Pterygoplichthys* spp. occur in Vietnamese river estuaries, including in brackish water, and they move horizontally and vertically through zones with varying water salinity. In the present study, we assessed the range of movement reactions and survival of the fish across different salinity levels of brackish water. Overall, the results indicated that wild armoured catfish can recognize brackish water habitats, which likely allows them to avoid zones with high salinity. Further in the article, we focus on the investigated data, which provide insights into the possibilities and risks of non-native armoured catfish spreading through brackish waters to new aquatic environments.

Locomotor activity of juveniles in freshwater and brackish water

Juvenile loricatoriids from Am Chua canal were predominantly active (77% of total diel locomotor activity) during nighttime (18:00–6:00, GMT+7). Our previous data (Pavlov et al. 2023b) also showed that adult armoured catfish from this canal were mostly active at night, accounting for 77% of their total diel locomotor activity. Overall, the diel activity patterns of juveniles and adults from the same body of water were similar. This suggests that both age groups have comparable locomotor activity rates in the same water volume (10 L) and that this does not cause stress to the fish. We hypothesize that the circadian rhythm of *Pterygoplichthys* spp. locomotor activity remains largely unchanged during ontogeny, provided environmental conditions are predominantly stable. Our findings align with Lloyd et al. (2023) hypothesis that the total locomotor activity and duration of rest are robust across life stages, while the timing of rest-activity patterns is influenced by ontogeny.

Typically, fish circadian rhythms are strongly regulated by natural light cycles. However, other environmental factors such as water temperature, chemistry, food availability, social interactions, or predation risk can also act as potential synchronizers (Reebs 2002; Zhdanova and Reebs 2006). For example, food availability has been shown to regulate armoured catfish movement patterns (Nico 2010). Additionally, saline water inflow during high tide altered the timing of armoured catfish locomotor activity in the estuary (Pavlov et al. 2023b). This further indicates that in new habitats, armoured catfish are capable of adapting to various adverse environmental factors, which explains their successful spread across different types of Vietnamese water bodies (Zworykin and Budaev 2013; Dien et al. 2023; Dien et al. 2025). Possibly, in homogeneous habitats, the species exhibits similar biological rhythms, as observed for juveniles and adults from Am Chua canal.

When juveniles were transferred to water salinity of 5 PSU (test apparatus Type 1), they experienced two types of stress: manipulation stress and osmotic stress. During the first hour of exposure, the locomotor activity of fish in freshwater and brackish water was similar. However, during the second hour, locomotor activity of fish in freshwater significantly decreased compared to the first hour of the trial. This is consistent with results obtained for adult armoured catfish, whose manipulation stress noticeably diminished during the second hour after transfer from a freshwater stock tank to a freshwater test aquarium (Pavlov et al. 2023b). Nonetheless, juveniles in water salinity of 5 PSU displayed higher activity values during the second and third hours after transfer compared to fish kept in freshwater. During the subsequent three hours (4th–6th hours), locomotor activity in fish in both freshwater and brackish water remained stable. Therefore, the duration of osmotic stress (exposure to 5 PSU) in juveniles was approximately three times longer than manipulation stress. This suggests that salinity levels up to 5 PSU are sufficient for juvenile armoured catfish to recognize and attempt to escape from such conditions.

Influence of water salinity levels on the locomotor activity and survival time of adult fish

We exposed adult fish to four water salinity concentrations (0 PSU, 5 PSU, 10 PSU, 15 PSU) to evaluate osmotic stress. During the six-hour experiment, there was no significant difference in locomotor activity among fish from water salinity of 0 PSU, 5 PSU, and 10 PSU. We propose that salinity levels below 10 PSU exert only a weak influence on adult fish locomotor activity. It remains unclear whether adults are capable of recognizing water salinity up to 10 PSU. However, this ability may not be critically important for their survival, as they exhibited a low mortality rate (13.9%) during prolonged (two-day) exposure to water salinity of 10 PSU (Dien et al. 2022). Our results indicate that adult armoured catfish have greater tolerance to brackish water than juveniles, which become stressed at a water salinity of 5 PSU. The high sensitivity of juveniles to saline water and their elevated locomotor activity may enable them to avoid such habitats, explaining their absence in estuaries compared to adults. For example, armoured catfish with standard lengths over 11 cm were captured (using bottom net traps with a 10 mm mesh size) in the Da Rang River estuary (Central Vietnam), where water salinity exceeded 4 PSU (Pavlov et al. 2023a). Similar patterns were observed in brackish-water habitats (4–8 PSU) of rivers in southeastern Mexico, where juveniles of *Pterygoplichthys* spp., with standard lengths of 5.0–9.9 cm, were found only in waters with salinity \leq 4 PSU (Capps et al. 2011).

During the first two hours of our experiment with different water salinity exposures, the locomotor activity of adult fish in water salinity of 15 PSU was significantly higher compared to that of fish in lower salinity concentrations. This indicates

that the osmotic stress at 15 PSU surpassed the effects of manipulation stress. By the third hour, locomotor activity in fish from 15 PSU water significantly decreased compared to adults in lower salinities. But the decline in activity at 15 PSU was likely associated with respiratory failure and subsequent mortality. According to Armbruster (1998), loricariid catfishes have evolved several adaptive modifications of the digestive tract (enlarged stomach and thinning its wall, U-shaped or ringlike diverticulum), that appear to function as accessory respiratory organs. Possibly, the water salinity of 15 PSU impairs both gill respiration and facultative aerial respiration in fish, leading to mortality after sixteen hours of exposure. However, some adult *Pterygoplichthys* spp. can survive in water salinity of up to 15 PSU for two days if they are pre-acclimated through a gradual increase in salinity (Dien et al. 2022). The short survival time observed in our study may be due to the lack of preliminary acclimatization. Prolonged exposure to high salinity over generations can lead to adaptive changes that increase salinity tolerance in freshwater macroinvertebrates (Kay et al. 2001; Kefford et al. 2004). Additionally, the brief survival period could be explained by the fact that fish from Am Chua canal have not had contact with brackish waters during their ontogeny. Additionally, armoured catfish in estuaries may tolerate higher salinities than fish from permanent freshwater environments.

The individual survival time of adult fish at water salinity of 15 PSU varied significantly, ranging from two to sixteen hours. Notably, 65% of the fish died between 3 and 6 hours of exposure. Our results align with findings that armoured catfish can survive in water salinity up to 16 PSU for a few hours (Capps et al. 2011; Kumar et al. 2018). The high variability in survival times indicates a broad range of individual adaptive potential to high salinity. This variability may cause some individuals to remain in high-salinity water for significantly longer periods than others. We highlight salinity tolerance and high locomotor activity as a key factor underlying the successful expansion of armoured catfish into various natural water ecosystems. Based on the “restricted movement paradigm” (Gowan et al. 1994), which likely applies to armoured catfish (Hay et al. 2022), populations composed of heterogeneous mixes of a large number of stationary fish and a small number of mobile fish. Although the proportion of adults possessing these advantageous traits may be small, they are likely primarily responsible for facilitating the species’ dispersal.

Obviously, several environmental factors could facilitate the successful spread of armoured catfish through estuaries and coastlines. For example, the mouths of new rivers are often located in areas where salinity is lower due to the mixing of freshwater and seawater. Additionally, fish tend to move along the surface freshwater plume, which is common in estuarine systems dominated by freshwater (Pavlov et al. 2023a). Such conditions are observed in Nha Trang Bay (Central Vietnam), situated between the estuaries of the Cai River and Be River, where surface water salinity varied noticeably from 0.5 PSU to 27.0 PSU (Nezdolii et al. 2014). Based on our findings, non-native adult armoured catfish may spread to new rivers via brackish water, facilitated by their high salinity tolerance and favorable environmental conditions. Moreover, the likelihood of their successful dispersal increases if they are capable of recognizing and avoiding high-salinity zones during such movement.

Fish movement pattern in water salinity gradient

Many studies on loricariids salinity tolerance have been conducted through experiments (Brion et al. 2013; Kumar et al. 2018; Dien et al. 2022; Pavlov et al. 2023a) and field observations (Capps et al. 2011; Lai et al. 2020; Pavlov et al. 2023a). Typically, in field studies, the salinity tolerance range of catfish was inferred from their occurrence in different types of fishing gear. While this approach is valuable, it provides only an

approximate estimate due to the influence of complex and dynamic factors present in natural environments. In contrast, experimental studies involve controlled exposure of armoured catfish to water with specific salinity levels, with each solution maintained for a defined time period during the trial. However, in estuarine habitats, fish respond not to stable conditions but to fluctuating salinity gradients (Hartog 1974; Mateus et al. 2008; Geyer 2010). Clearly, in the wild, fish can move in various directions and encounter a range of habitat conditions, unlike the static conditions in an aquarium. Based on this conception, we developed and utilized test apparatus Type 2 to assess armoured catfish movement patterns in water with a dynamic salinity gradient.

In this study, we simulated a rapid (ten-minute) increase in water salinity near the bottom of the test chamber. Such conditions can occur in stratified estuaries with wide salinity ranges influenced by the ebb and flow of tides. For example, armoured catfish have been found in the brackish waters of the Da Rang River estuary in Central Vietnam, where high salinity stratification occurs with water salinity ranging from 4 to 25 PSU near the bottom (Pavlov et al. 2023a). Similar salinity conditions were recreated in our experiment. Two main factors influenced fish locomotor activity in the test apparatus: the level of water and changes in water salinity. Fish exhibited significantly higher locomotor activity prior to water inflow. After freshwater inflow, the percentage of active fish and their total locomotor activity decreased, coinciding with the increase in water level in the aquarium from 10 cm to 20 cm (Table 1). The high activity levels observed at low water levels at the beginning of the test may be related to the fact that adult armoured catfish naturally inhabit deeper habitats than those simulated in our experimental conditions.

The inflow of seawater altered the movement patterns of armoured catfish. Specifically, the species exhibited several responses to increasing water salinity: a shift from a static horizontal position to a static vertical position (observed in 43% of fish), an increase in the number of active fish (82.5%), and a rise in both the number (by 3.7 times) and duration (by 1.6 times) of aerial respiration movements. These behavioral responses varied among individuals. The high locomotor activity observed may be related to a behavioral strategy aimed at avoiding high salinity water. However, fish in the vertical static position did not engage in active movement, likely because their gill slits remained in the freshwater zone during the trial.

Our results demonstrated that fish engaged in aerial respiration more frequently during seawater inflow than during freshwater inflow. We hypothesize that this is due to the blocking of gill respiration caused by high water salinity (>15 PSU), prompting fish to compensate through facultative breathing. In natural conditions, surfacing to the water surface may help fish avoid high salinity at the bottom. In the wild, armoured catfish often swim near the surface in both freshwater and brackish water (Pavlov et al. 2023b). In natural conditions, the lower reaches of rivers often exhibit strong stratification between freshwater and higher salinity layers, which enables armoured catfish to access surface areas without exposure to elevated salinity levels. Our data also indicate that aerial respiration can occasionally lead to changes in buoyancy, shifting from negative to neutral or positive, especially in brackish water. This phenomenon is likely due to morphological modifications of the digestive tract in loricariid catfish, which facilitates holding air (Armbruster 1998). We hypothesize that this trait helps maintain the fish within the low-salinity surface layer.

Conclusions

Our results confirmed that juvenile armoured catfish exhibit a circadian rhythm of locomotor activity similar to that of adults; however, juveniles display a more pronounced reaction to increasing water salinity – at 5 PSU – whereas adults respond

at 15 PSU. This likely explains the absence of juveniles in natural brackish water environments. Additionally, juveniles appear to have a reduced capacity for dispersal through brackish waters compared to adults. Adult loriciids are likely able to recognize and avoid high-salinity zones (>10 PSU) by increasing locomotor activity, mainly directed toward the surface. Their ability to grasp air facilitates the maintenance of positive buoyancy, enabling them to remain in the surface layer of freshwater for extended periods without significant energy expenditure. Variability in salinity tolerance among individual adults (ranging from 2 to 16 hours in 15 PSU) may allow some individuals to be more successful in spreading through estuaries and coastlines. We hypothesize that the risk of non-native loriciid invasion depends on a combination of species-specific traits (such as facultative breathing and body buoyancy regulation), individual characteristics (including rapid recognition of high salinity, high salinity tolerance, and elevated locomotor activity), and environmental conditions—particularly the proximity of freshwater zones or the presence of areas with reduced salinity along dispersal pathways.

Funding

Field work and experiments were supported by Joint Vietnam – Russia Tropical Science and Technology Research Center (Ecolan 3.2 “Taxonomic diversity, ecology and behavior of freshwater hydrobionts”, Mission 1).

Author's Contributions

EP and EG contributed to the study conception and experimental design. DT carried out equipment provision and controlled wild fish capture and transfer. EG and EP performed experimental work and analyzed data. First draft of the manuscript was written by EP and all authors edited the manuscript. All authors read and approved the final manuscript.

Ethics and permits

All experimental procedures with fish were carried out according to the guidelines and following the laws and ethics of Socialist Republic of Vietnam and approved by the ethics committee of the Institute of Ecology and Evolution, Russian Academy of Sciences.

Acknowledgments

Authors would like to thank the administration and staff of Coastal Branch of Joint Vietnam – Russia Tropical Science and Technology Research Center for their help in organizing field sample collection and for kindly allowing us to use their laboratories and experimental facilities. We are grateful to D.D. Zworykin, and anonymous reviewers for valuable comments on the manuscript's text.

References

- Alix M, Kjesbu OS, Anderson KC (2020) From gametogenesis to spawning: How climate driven warming affects teleost reproductive biology. *Journal of Fish Biology* 97: 607–632. <https://doi.org/10.1111/jfb.14439>
- Araujo RB, Langeani FB (2020) Ontogenetic development related to parental care of a neotropical fish, *Pterygoplichthys ambrosettii* (Siluriformes: Loricariidae). *Zoological Studies* 59(56): 1–21. <https://doi.org/10.6620/ZS.2020.59-56>

- Armbruster JW (1998) Modifications of the digestive tract for holding air in loricariid and scoloplacoid catfishes. *Copeia* 3: 663–675. <https://doi.org/10.2307/1447796>
- Armbruster JW, Page LM (2006) Redescription of *Pterygoplichthys punctatus* and description of a new species of *Pterygoplichthys* (Siluriformes: Loricariidae). *Neotropical Ichthyology* 4: 401–409. <https://doi.org/10.1590/S1679-62252006000400003>
- Brion MA, Gil Guillermo Jr J, Uy C, Chavez J, Carandang IV JS (2013) Salinity tolerance of introduced South American sailfin catfishes (Loricariidae: *Pterygoplichthys* Gill 1858). *Philippine Journal of Science* 142(1): 13–19. https://animorepository.dlsu.edu.ph/faculty_research/11201
- Capps KA, Nico LG, Mendoza-Carranza M, Arévalo-Frías W, Ropicki AJ, Heilpern SA, Rodiles-Hernández R (2011) Salinity tolerance of non-native suckermouth armoured catfish (Loricariidae: *Pterygoplichthys*) in South-Eastern Mexico: Implications for invasion and dispersal. *Aquatic Conservation: Marine and Freshwater Ecosystems* 21(6): 528–540. <https://doi.org/10.1002/aqc.1210>
- Cognetti G, Maltagliati F (2000) Biodiversity and adaptive mechanisms in brackish water fauna. *Marine Pollution Bulletin* 40(1): 7–14. [https://doi.org/10.1016/S0025-326X\(99\)00173-3](https://doi.org/10.1016/S0025-326X(99)00173-3)
- Dien TD, Ganzha EV, Pavlov ED, Samoïlov KYu, Pavlov DS (2022) Survival and level of thyroid hormones and ions in armored catfish (Loricariidae) during increasing water salinity. *Journal of Ichthyology* 6: 1201–1207. <https://doi.org/10.1134/S0032945222060054>
- Dien TD, Ha VT, Dang M, Sang HM, Hieu NTD, Stolbunov IA (2023) Phenotypic divergences in growth and reproduction underpin the invasion of suckermouth armored catfish *Pterygoplichthys disjunctivus* (Loricariidae) into lotic and lentic habitats in Vietnam. *Water* 15: 3616. <https://doi.org/10.3390/w15203616>
- Dien TD, Ganzha EV, Hieu NTD, Pavlov ED (2025) Non-native and native fish occurrence and distribution in the Suoi Trau reservoir (Central Vietnam). *BioInvasions Records* 14(1): 123–139. <https://doi.org/10.3391/bir.2025.14.1.11>
- Ebenstein D, Calderon C, Troncoso OP, Torres FG (2015) Characterization of dermal plates from armored catfish *Pterygoplichthys pardalis* reveals sandwich-like nanocomposite structure. *Journal of the Mechanical Behavior of Biomedical Materials* 45: 175–182. <https://doi.org/10.1016/j.jmbbm.2015.02.002>
- Hay A, Riggins CL, Heard T, Garoutte C, Rodriguez Y, Fillipone F, Smith KK, Menchaca N, Williamson J, Perkin JS (2022) Movement and mortality of invasive suckermouth armored catfish during a spearfishing control experiment. *Biological Invasions* 24: 3119–3131. <https://doi.org/10.1007/s10530-022-02834-2>
- Fiol DE, Kültz D (2007) Osmotic stress sensing and signaling in fishes. *The FEBS Journal* 274(22): 5790–5798. <https://doi.org/10.1111/j.1742-4658.2007.06099.x>
- Geyer WR (2010) Estuarine salinity structure and circulation. In: Valle-Levinson A (Ed.) *Contemporary Issues in Estuarine Physics*. 1st ed. Cambridge University Press, 12–26. <https://doi.org/10.1017/CBO9780511676567.003>
- Gibbs MA, Groff BW (2014) Patterns of aerial respiration by *Pterygoplichthys disjunctivus* (Loricariidae) in Volusia Blue Spring, Florida. *Florida Academy of Sciences* 77: 53–68. <https://www.jstor.org/stable/24321983>
- Gibbs MA, Watson P, Johnson-Sapp K, Lind C (2017) Reproduction revisited – a decade of changes in the reproductive strategies of an invasive catfish, *Pterygoplichthys disjunctivus* (Weber, 1991), in Volusia Blue Spring, Florida. *Aquatic Invasions* 12(2): 225–239. <https://doi.org/10.3391/ai.2017.12.2.10>
- Gibbs MA, Thornton A, Pasko S, Crater A (2021) Patterns of air-breathing behavior in juvenile armored catfish, *Pterygoplichthys* sp. (Gill 1858). *Environmental Biology of Fishes* 104(2): 171–180. <https://doi.org/10.1007/s10641-021-01068-w>
- Godwin JC, Steen DA, Werneke D, Armbruster JW (2016) Two significant records of exotic tropical freshwater fishes in southern Alabama. *Southeastern Naturalist* 15(4): 57–60. <https://doi.org/10.1656/058.015.0401>

- Gowan C, Young MK, Fausch KD, Riley SC (1994) Restricted movement in resident stream salmonids: a paradigm lost? *Canadian Journal of Fisheries and Aquatic Sciences* 51: 2626–2637. <https://doi.org/10.1139/f94-262>
- Hartog C (1974) Brackish-water classification, its development and problems. *Hydrobiological Bulletin* 8(1–2): 15–28. <https://doi.org/10.1007/BF02254902>
- Kay WR, Halse SA, Scanlon MD, Smith MJ (2001) Distribution and environmental tolerances of aquatic macroinvertebrate families in the agricultural zone of southwestern Australia. *Journal of the North American Benthological Society* 20(2): 182–199. <https://doi.org/10.2307/1468314>
- Kefford BJ, Papas PJ, Metzeling L, Nugegoda D (2004) Do laboratory salinity tolerances of freshwater animals correspond with their field salinity? *Environmental Pollution* 129(3): 355–362. <https://doi.org/10.1016/j.envpol.2003.12.005>
- Kumar B, Schofield P, Raj S, Satheesh S (2018) Salinity tolerance of non-native suckermouth armoured catfish (Loricariidae: *Pterygoplichthys* sp.) from Kerala, India. *Management of Biological Invasions* 9(1): 49–57. <https://doi.org/10.3391/mbi.2018.9.1.05>
- Lai QT, Orfinger AB, Tran TT, Le NK (2020) Distribution of suckermouth armoured catfishes (Siluriformes, Loricariidae) across the salinity gradient of the Mekong Delta, Vietnam. *Asian Fisheries Society* 33: 300–306. <https://doi.org/10.33997/j.afs.2020.33.3.011>
- Levin BA, Phuong PH, Pavlov DS (2008) Discovery of the Amazon sailfin catfish *Pterygoplichthys pardalis* (Castelnau, 1855) (Teleostei: Loricariidae) in Vietnam: Discovery of *Pterygoplichthys* in Vietnam. *Journal of Applied Ichthyology* 24(6): 715–717. <https://doi.org/10.1111/j.1439-0426.2008.01185.x>
- Lloyd E, Rastogi A, Holtz N, Aaronson B, Albertson RC, Keene AC (2023) Ontogeny and social context regulate the circadian activity patterns of Lake Malawi cichlids. *Journal of Comparative Physiology B* 194: 299–313. <https://doi.org/10.1007/s00360-023-01523-3>
- Marr SM, Patoka J, Zworykin DD (2024) Estimating the potential distribution range of the invasive South American suckermouth armoured catfishes *Pterygoplichthys* spp. in the Indo-Burma biodiversity hotspot using MaxEnt. *Aquatic Conservation: Marine and Freshwater Ecosystems* 34(5): e4173. <https://doi.org/10.1002/aqc.4173>
- Mateus M, Mateus S, Baretta JW (2008) Basic concepts of estuarine ecology: Estuarine systems: the land-ocean link.
- Miyanishi H, Uchida K (2021) Establishment of a simplified system to evaluate salinity preference and validation of behavioral salinity selection in the Japanese medaka, *Oryzias latipes*. *Fishes* 6(2): 18. <https://doi.org/10.3390/fishes6020018>
- Myers GS (1949) Salt-tolerance of freshwater fish groups in relation to zoogeographical problems. *Bijdragen tot de Dierkunde* 28(1): 315–322. <https://doi.org/10.1163/26660644-02801038>
- Nico LG (2010) Nocturnal and diurnal activity of armored suckermouth catfish (Loricariidae: *Pterygoplichthys*) associated with wintering Florida manatees (*Trichechus manatus latirostris*). *Neotropical Ichthyology* 8(4): 893–898. <https://doi.org/10.1590/S1679-62252010005000014>
- Nico LG, Butt PL, Johnston GR, Jelks HL, Kail M, Walsh SJ (2012) Discovery of South American suckermouth armored catfishes (Loricariidae, *Pterygoplichthys* spp.) in the Santa Fe River drainage, Suwannee River basin, USA. *BioInvasions Records* 1(3): 179–200. <https://doi.org/10.3391/bir.2012.1.3.04>
- Nezdolii VK, Pavlov DS, Ngo CT, Nguen DT, Nguen QT (2014) Downstream migration of juvenile fish in the Cai River. In: Pavlov D, Zworykin D (Eds) *Ecology of inland waters of Vietnam*. KMK, Moscow, 298–319. [In Russian]
- Norris A (2017) A Mesocosm Study of the Impact of Invasive Armored Catfish (*Pterygoplichthys* sp.) on Endangered Texas Wild Rice (*Zizania texana*) in the San Marcos River. University of Houston-Clear Lake, Houston. <https://www.uhcl.edu/environmental-institute/research/publications/documents/norris-2017-ms-thesis.pdf>
- Novák J, Hofmann J, Hohl D, Magalhães ALB, Patoka J (2022) Enigmatic armoured catfishes (Siluriformes: Callichthyidae and Loricariidae) in ornamental aquaculture: a new insight into neotropical fish diversity. *Aquaculture* 547: 737460. <https://doi.org/10.1016/j.aquaculture.2021.737460>

- Orfinger AB, Gooding DD (2018) The global invasion of the suckermouth armored catfish genus *Pterygoplichthys* (Siluriformes: Loricariidae): annotated list of species, distributional summary, and assessment of impacts. *Zoological Studies* 57: e7. <https://doi.org/10.6620/ZS.2018.57-07>
- Parvez MT, Lucas MC, Hossain MI, Chaki N, Mohsin ABM, Sun J, Galib SM (2023) Invasive vermiculated sailfin catfish (*Pterygoplichthys disjunctivus*) has an impact on highly valued native fish species. *Biological Invasions* 25: 1795–1809. <https://doi.org/10.1007/s10530-023-03012-8>
- Pavlov ED, Dien TD, Ganzha EK (2023a) Distribution in the estuary and salinity tolerance of armoured catfish (Loricariidae) in central Vietnam. *Aquatic Invasions* 18(3): 401–414. <https://doi.org/10.3391/ai.2023.18.3.104066>
- Pavlov ED, Dien TD, Ganzha EK (2023b) Spatial distribution and circadian locomotor activity of invasive armoured catfish (Loricariidae) in the freshwater and brackish water. *PLOS ONE* 18(12): e0296222. <https://doi.org/10.1371/journal.pone.0296222>
- Power ME (1984) Depth distributions of armored catfish: predator-induced resource avoidance? *Ecology* 65(2): 523–528. <https://doi.org/10.2307/1941414>
- Quintana Y, Keppeler FW, Winemiller KO (2023) Does invasion by armored catfish shift trophic ecology of native fishes? Evidence from stable isotope analysis. *Ecology* 104: e4024. <https://doi.org/10.1002/ecy.4024>
- Reebs SG (2002) Plasticity of diel and circadian activity rhythms in fishes. *Reviews in Fish Biology and Fisheries* 12: 349–371. <https://doi.org/10.1023/A:1025371804611>
- Ruykys L, Ta KAT, Bui TD, Vilizzi L, Copp GH (2021) Risk screening of the potential invasiveness of non-native aquatic species in Vietnam. *Biological Invasions* 23: 2047–2060. <https://doi.org/10.1007/s10530-020-02430-2>
- Saba AO, Ismail A, Zulkifli SZ, Halim MRA, Wahid NAA, Amal MNA (2020) Species composition and invasion risks of alien ornamental freshwater fishes from pet stores in Klang Valley, Malaysia. *Scientific Reports* 10: 17205. <https://doi.org/10.1038/s41598-020-74168-9>
- Schofield PJ, Loftus WF, Fontaine JA (2009) Salinity effects on behavioural response to hypoxia in the non-native Mayan cichlid *Cichlasoma urophthalmus* from Florida Everglades wetlands. *Journal of Fish Biology* 74(6): 1245–1258. <https://doi.org/10.1111/j.1095-8649.2009.02192.x>
- Serov DV (2004) Harnischwelse in Südostasien. *Die Aquarium- und Terrariumzeitschrift* 2: 18–19.
- Seshagiri B, Swain SK, Pillai BR, Satyavati C, Sravanti Y, Rangacharyulu PV, Rathod R, Ratnaprakash V (2021) Suckermouth armoured catfish (*Pterygoplichthys* spp.) menace in freshwater aquaculture and natural aquatic systems in Andhra Pradesh, India. *International Journal of Fisheries and Aquatic Studies* 9(1): 375–384. <https://doi.org/10.22271/fish.2021.v9.i1e.2423>
- Welcomme RL, Vidthayanon C (2003) The impacts of introductions and stocking of exotic species in the Mekong Basin and policies for their control. *MRC Tech Paper* 9.
- Zhdanova IV, Reebs SG (2005) Circadian rhythms in fish. *Fish physiology* 24: 197–238. [https://doi.org/10.1016/S1546-5098\(05\)24006-2](https://doi.org/10.1016/S1546-5098(05)24006-2)
- Zworykin D, Dinh THY (2023) Risk screening of non-native suckermouth armoured catfishes *Pterygoplichthys* spp. in the River Dinh (Vietnam) using two related decision-support tools. *Biological Communications* 68(2): 122–131. <https://doi.org/10.21638/spbu03.2023.206>
- Zworykin D (2016) Marine, freshwater and brackish water fishes of Vietnam. Is there always a critical salinity barrier? *Marine Biological Research: Achievements and Perspectives* 2: 69–72. [In Russian]
- Zworykin DD, Budaev SV (2013) Non-indigenous armoured catfish in Vietnam: invasion and systematics. *Ichthyological Research* 60(4): 327–333. <https://doi.org/10.1007/s10228-013-0356-9>

Supplementary material 1

Scheme of fishing gears mounting in the Da Rang River

Authors: Efim D. Pavlov, Tran Duc Dien, Ekaterina V. Ganzha

Data type: jpg

Explanation note: **figure S1**. Scheme of fishing gears mounting in the Da Rang River. n – vertical gillnet along the shores, nt – net traps near shore. Arrow (→) indicates the water flow direction.

Copyright notice: This dataset is made available under the Open Database License (<http://opendata-commons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3391/ai.2025.20.3.162564.suppl1>

Supplementary material 2

Illumination in the mid-water and near the bottom of Am Chua canal

Authors: Efim D. Pavlov, Tran Duc Dien, Ekaterina V. Ganzha

Data type: jpg

Explanation note: **figure S2**. Illumination (lx) in the mid-water (depth 0.5–0.6 m) and near the bottom (depth 1.2 m) of Am Chua canal at 12:00 (GMT+7); the surface illumination was 100000 lx.

Copyright notice: This dataset is made available under the Open Database License (<http://opendata-commons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3391/ai.2025.20.3.162564.suppl2>

Supplementary material 3

Scheme of test apparatus Type 1

Authors: Efim D. Pavlov, Tran Duc Dien, Ekaterina V. Ganzha

Data type: jpg

Explanation note: **figure S3**. Scheme of test apparatus Type 1.

Copyright notice: This dataset is made available under the Open Database License (<http://opendata-commons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3391/ai.2025.20.3.162564.suppl3>

Supplementary material 4

Dynamic of water salinity increasing during seawater inflow in the test apparatus type 2 during the trial

Authors: Efim D. Pavlov, Tran Duc Dien, Ekaterina V. Ganzha

Data type: jpg

Explanation note: **figure S4**. Dynamic of water salinity increasing during seawater inflow (numbers on the graph, PSU) in the test apparatus Type 2 during the trial.

Copyright notice: This dataset is made available under the Open Database License (<http://opendata-commons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3391/ai.2025.20.3.162564.suppl4>

Supplementary material 5

Seawater inflow on 6th minute of the trial in the test apparatus

Authors: Efim D. Pavlov, Tran Duc Dien, Ekaterina V. Ganzha

Data type: jpg

Explanation note: **figure S5**. Seawater inflow (blue color) on 6th minute of the trial in the test apparatus Type 2.

Copyright notice: This dataset is made available under the Open Database License (<http://opendata-commons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3391/ai.2025.20.3.162564.suppl5>

Supplementary material 6

Fish moved to vertical positions in aquaria during seawater inflow

Authors: Efim D. Pavlov, Tran Duc Dien, Ekaterina V. Ganzha

Data type: mp4

Copyright notice: This dataset is made available under the Open Database License (<http://opendata-commons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3391/ai.2025.20.3.162564.suppl6>

Supplementary material 7

Positive buoyancy of the fish body under seawater inflow. The playback speed is set to 4x

Authors: Efim D. Pavlov, Tran Duc Dien, Ekaterina V. Ganzha

Data type: mp4

Copyright notice: This dataset is made available under the Open Database License (<http://opendata-commons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3391/ai.2025.20.3.162564.suppl7>