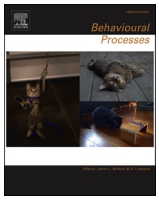
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Understanding feeding competition under laboratory conditions: Rohu (*Labeo rohita)* versus Amazon sailfin catfish (*Pterygoplichthys* spp.)

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ABSTRACT

Competitive interactions between species is widely prevalent within the animal world. In this manuscript, we attempted to understand feeding competitions between the Amazon sailfin catfish, an invasive species introduced globally, and rohu, a keystone species native to several countries within southeast Asia. We used two different size classes of each species, large-size having total length (TL, from snout tip to caudal fin) of 15–20 cm and fingerling having TL<6 cm, and feeding duration was used as a proxy to understand competition. Our results demonstrated that feeding durations of large-size rohu were either similar or significantly ($P<0.05$) higher in presence of catfish when compared to trials in presence of conspecifics, indicating that large-size rohu is not a weak competitor. However, feeding durations of fingerling rohu was significantly ($P<0.05$) reduced in presence of both large-size and fingerling catfish, when compared to trials in presence of conspecifics. Moreover, fingerling rohu also displayed freeze (alarm) behavior in presence of the catfish. Interestingly, presence of rohu had no significant ($P>0.05$) impact on feeding durations of catfish. Overall, the study demonstrated that invasive catfish may behaviorally outcompete fingerling rohu, thus, threatening the sustenance of a species that is native to several freshwaters around the globe.

1. Introduction

The competitive exclusion principle by Gause (1934), spurred a lot of interest among ecologists and ethologists to test the theory under varied laboratory and field conditions. Subsequent studies following Gause's work demonstrated that competition between any two species may vary over both temporal and spatial scales. Temporal scales may possibly compare interactions across different developmental stages (Brenden and Murphy, 2004) or across different seasons (Borcherding et al., 2019). Similarly spatial scales may look at competitive interactions across habitats with different levels of anthropogenic disturbances (Carrete et al., 2010) or with varying levels of resources (Rudolf and McCrory, 2018). Fate of the interactions greatly depend upon the competitive ability of the interacting species (Birch, 1957; Bowers and Brown, 1982). For example, Gause showed *Paramoecium aurelia* outcompeted (in terms of population size) *P. caudatum* in combined cultures, however, the latter was the winner while competing with *P. bursaria* (Gause, 1934). Further, Gause's experiments (1934) also demonstrated that due to competitive interactions for resources, for example, food and space, one of the interacting species may outcompete the other and eventually may lead the poorer competitor towards exclusion from the system or a given habitat. Such exclusions are of great concern if the species is a native one for a given habitat, and may lose out to a highly competitive exotic or alien species (Beisner et al., 2003), thus, impacting the stability of a given ecosystem (Janssen et al., 2014).

In this paper, we aim to understand competitive interactions in the context of feeding between two freshwater fish species, the Amazon sailfin catfish and rohu *Labeo rohita*, that have been reported to co-occur in different countries across Asia. The catfish is native to the Amazon basin, and has been tagged as one of the invasive species in several countries, Mexico (Wakida-Kusunoki et al., 2007), Florida (Ludlow and Walsh, 1991) and Texas (Edwards, 2001) states within USA, Malaysia (Saba et al., 2020), Iraq (Qasim and Jawad, 2022), Vietnam (Levin et al., 2008), Philippines (Jumawan et al., 2011), Sri Lanka (Herath et al., 2020), Italy (Piazzini et al., 2010), Bangladesh (Hossain et al., 2018), and the Indian freshwaters (Bijukumar et al., 2015; Rao and Sunchu, 2017; Hussan et al., 2019; Das et al., 2020; 2023). Catfish is a benthic forager with hard armor and spines, belonging to the Loriicariidae family, known for their aggressive and territorial nature (Hossain et al.,

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2018; Umar and Ramayani, 2021). Moreover, several species of catfish, for example, "*multiradiatus*", "*pardalis*", "*disjunctivus*", belonging to the genus *Pterygoplichthys* have been introduced in different freshwater habitats across the globe (Singh and Lakra, 2011; Sumanasinghe and Amarasinghe, 2014; Tarkan et al., 2017). Due to high rate of hybridization among the different species of sailfin catfish, and due to difficulty in detecting hybrids using physical features, most studies refer to Amazon sailfin catfish using the genus name, *Pterygoplichthys* spp. (Jumawan et al., 2011).

Catfish is a voracious algae eater and have been shown to have a huge dietary overlap with several native species in the introduced habitats (Gestring et al., 2010; Parvez et al., 2023). One such native species belonging to the Indian freshwaters is rohu (Suresh et al., 2019). Rohu is a natural inhabitant of the Indian freshwaters (Das et al., 2013) and widely distributed in different rivers, for example, Cauvery, Narmada (Bhaumik et al., 2017), Tapti and Mahanadi (Mohanta et al., 2008). Rohu is considered as a keystone (Dwivedi et al., 2020) and an ecological indicator species (Mahamood et al., 2021), and is also economically valuable (Modeel et al., 2023). India is the second largest producer (9.59 million tonnes) of rohu (Seshagiri et al., 2022) contributing to 1.07 % of national GDP along with an export income generation of 31,000 million, as reported in 2018–19 (Ngasotter et al., 2020). Using mesocosm-based approach, several studies have shown that catfish negatively impacted the growth of fingerling rohu [fingerling defined in terms of total length (TL, from snout to tip of caudal fin) of <15 cm, Munilkumar and Nandeesha, (2007)], when both the species were reared together under similar experimental conditions (Parvez et al., 2023; Mallick et al., 2023). However, the catfish had no significant impact on different abiotic (water quality and soil C/N profiles) and biotic (zoo- and phytoplankton abundance) measures of the given experimental condition (Seshagiri et al., 2021; Parvez et al., 2023; Mallick et al., 2023). Based on the findings, the studies have speculated that the observed negative impact on rohu fingerlings can be mediated via feeding competitions with the catfish (Mallick et al., 2023), and thus, warrants further investigations. Since, to the best of our knowledge, there has been no studies on feeding behaviors of catfish, in this manuscript we aimed to define and characterize such behaviors in the context of feeding. Though feeding behavior of rohu has been studied in detail (Mookerji and Rao, 1993; Rahman et al., 2008; Rahman, 2015), nonetheless, we still included objectives on characterizing feeding behavior of rohu to justify its inclusion in competition trials with catfish under our laboratory conditions. Further, we attempted to investigate if there is any impact on feeding behaviors of rohu in presence of the catfish. We also aimed to assess if the impact was due to the body size (TL, as a proxy for age, Raphael et al., 2016) of both the species. We used the feeding duration of each species as a proxy to understand competition.

The purpose of the study is to understand feeding competitions between catfish and rohu to help understand any potential impact of the invasive catfish (Parvez et al., 2023; Wakida-Kusunoki et al., 2007) on the keystone and commercially valuable species, rohu (Dwivedi and Nautiyal, 2012; Dwivedi et al., 2020; Rabbane et al., 2022; Mallick et al., 2023). Such understanding may help in assessing the threats associated with several ecosystems across the globe, where the native rohu now co-occur with the invasive catfish (Wakida-Kusunoki et al., 2007; Saba et al., 2020; Seshagiri et al., 2021; Parvez et al., 2023).

2. Materials and methods

2.1. Study animals

Catfish and rohu were divided into two size classes based on TL: large (TL=15–20 cm) and fingerlings (TL<6 cm). In fishes, length is used as a proxy for age, where younger fish have shorter length when compared to older fish (Raphael et al., 2016). Body weights were kept similar for both the species proportional to their respective size classes. Details on length and weight of study animals are mentioned in Table 1. Catfish were procured from the local pet store whereas rohu were obtained from commercial aquaculture farms. Catfish and rohu were stocked separately (including separate tanks for large and fingerling classes) in 70 L glass tanks (53 ×37×37 cm) and were fed daily with algal wafer having a mixture of algae, shrimp meal, and fish oil (Red China, Guangzhou, China) for four months before the start of the experimental trials. Both the species had no prior exposure to each other before the experimental trials. Fishes were housed under laboratory conditions with a photoperiod of 14:10 light:dark cycle at 24–26°C. There were no observed mortality of the fishes during the entire experimental duration (6 months).

2.2. Pilot study to standardize experimental protocol

Trials were conducted with algal wafer (Red China, Guangzhou, China) in food bags that were made by wrapping 100 mg of food in a fine mesh and stitched on all the sides. From here onwards, we refer to algal wafer as 'home food' that was used during housing and during pilot trials. Our pilot trials with catfish and rohu (N=4 trials for each species per size class, fingerling and large-size; each for 3 h) indicated that both the species were able to access food via the mesh, and the bags were found empty (food was eaten completely) after the said duration of the trials. Based on the results of the pilot trials, the following experimental protocol was designed.

2.3. Experimental protocol

A uniform protocol was followed for all the experiments across different trial types. Experiments were conducted under low light and low sound conditions. All the trials were conducted in 70 L glass tanks, and the individuals were starved for 48 h prior to the experiment. Trials were initiated with the introduction of food bags. Trials were conducted for a period of three hours and were recorded using a handycam (VIXIA HF R800, Canon, China). Experimental trials were conducted during the day (any three-hour slot between 09:00–13:00), and different behaviors in the context of feeding were identified, scored and defined during the playback of the recorded videos. With regards to mixed-species trials, behaviors were scored from the perspective of both the species.

2.4. Single-species trials to characterize feeding behavior of the catfish

Feeding trials for large-size catfish are abbreviated as 'C' from now onwards, and that of fingerling catfish trials are abbreviated as 'SC' (Fig. 1). C trials were conducted with four different food items, 'home food', spirulina (composed of blue-green algae, Parry Limited, Tamil Nadu, India), chlorella (composed of single celled green algae, Parry Limited, Tamil Nadu, India), and flake (composed of fish meal, Taiyo Feed Mill Pvt. Ltd., Tamil Nadu, India) added separately to the tanks. Since catfish is known to be an algae eater (Gestring et al., 2010; Parvez

Table 1
Details on group composition of each trial type and length and weight of experimental animals.

Trial Type		Group composition	Weight (g) (Mean ±SE)	Length (cm) (Mean ±SE)
I	C	2	18.1±0.66	17.76±0.31
	SC[b]	8	2.18±0.08	5.85±0.10
II	R	2	18.04±5.09	18.9±0.20
	SR[b]	8	2.36±0.05	4±0.12
III	C/R	2 (1 catfish + 1 rohu)	Same as above	Same as above
	SC/SR	16 (8 catfish + 8 rohu)	Same as above	Same as above
	C/SR	9 (1 catfish + 8 rohu)	Same as above	Same as above

[b] Multiple individuals of fingerling were used instead of a single individual as fingerling *(young) fish usually show reduced feeding when occurring under solitary conditions (*Boujard, 1995*)*.

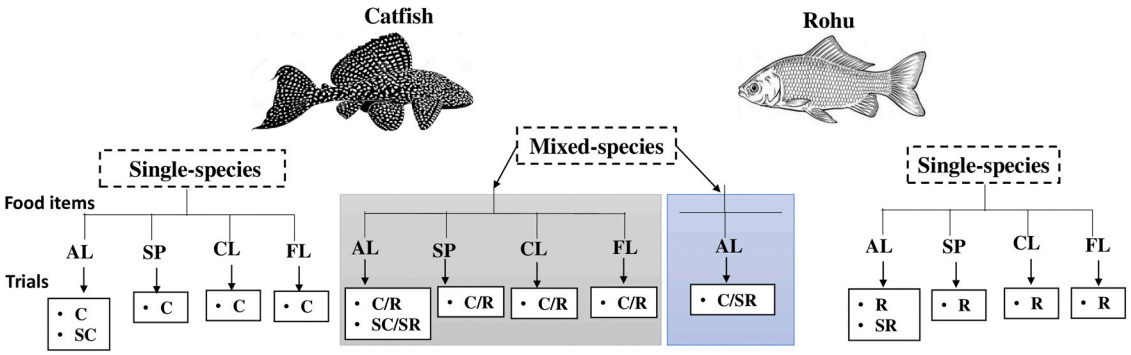


Fig. 1. Schematic representation of the experimental design for assessing feeding competition between catfish and rohu. Experimental trials were classified as single-species and mixed-species, while the latter was further divided into size-matched ( ) and size-unmatched ( ) classes. Food items used during the trials were algal wafer (AL), spirulina (SP), chlorella (CL), and flake (FL). All large-size, single species trials were denoted as C and R, all fingerling trials as SC and SR, for catfish and rohu respectively. Mixed species trials for size-matched category were C/R for large-size class and SC/SR for fingerlings, and for size-unmatched having large-size catfish and fingerling rohu, was C/SR.

et al., 2023), most of the selected food items were algae-based. However, SC trials were conducted only using the 'home food'.

2.5. Single-species trials to characterize feeding behavior of rohu

Feeding trials for large-size rohu are abbreviated as 'R' from now onwards, and that of fingerling rohu trials are abbreviated as 'SR (Fig. 1)'. R trials were conducted with the same four food items, 'home food', spirulina, chlorella and flake, as described above for C trials, and previous studies have shown these items to be preferred by rohu (Rahman, 2015). SR trials were conducted with only the 'home food'.

2.6. Mixed-species trials to characterize interspecific interactions between the catfish and rohu

Mixed-species trials were categorized into size-matched and size-unmatched setups. Size-matched trials were conducted using individuals of equal body size (TL) and body weights for both the species, rohu and catfish. Size matched trials were of two types, large-size catfish with large-size rohu, abbreviated as C/R from now on; and fingerling catfish with rohu fingerling, abbreviated as SC/SR from now on (Fig. 1). C/R trials were conducted for all the four food items, 'home food', spirulina, chlorella and flake, as mentioned above for C and R trials. SC/SR trials were conducted only on the 'home food'.

With regards to the size-unmatched category, trials were conducted by including large-size catfish with rohu fingerlings, abbreviated as C/SR trials from now on. For size-unmatched trials (C/SR), biomass (weight) matching (de Lourdes Ruiz-Gomez et al., 2008) was taken into consideration (Table 1). C/SR trials were conducted only on the 'home food'.

2.7. Behavioral characterization

We defined, characterized and quantified three behaviors for our study, namely feeding, push and aggressive attack. Feeding is defined as placing suckers (for catfish) or mouth (for rohu) over a food item accompanied by bucco-pharyngeal pumping (BPP) (Claus and Sorensen, 2017). We measured catfish to be having BPP at a frequency of 2.09 ±0.038 BPP/min (N=180 incidents of feeding across all trial types) and that of rohu at 1.36±0.034 BPP/min (N=180 incidents of feeding across all trial types) during feeding. For push and aggressive attack, we calculated speed by measuring the distance covered by an individual from start to end point over a given time. We used ImageJ software (Audira et al., 2019) to calculate the distance on screen. Both push and aggressive attack were dyadic interactions involving two individuals, sender, who initiates the behavior, and receiver, who is at the receiving end of the intended behavior. We defined push behavior as the sender swimming towards the receiver at a certain speed, calculated (N=100 recorded incidents of push behavior) as 5.2±0.39 cm/s for large-size catfish, 2.25±0.15 cm/s for fingerling catfish and 7.56±0.51 cm/s for large-size rohu, and then striking the receiver with snout (for rohu and catfish) or pectoral fin (for catfish), which results in displacement of the receiver from food. The aggressive attack is defined as the sender swimming towards the receiver at a speed of 6.2±0.42 cm/s (N=100 recorded incidents of aggressive attacks for large-size catfish), and then striking the receiver with an erected dorsal fin, which also results in displacement of the receiver from food. Both push and aggressive attacks are displayed by the sender only when the receiver is feeding on the food.

Feeding behavior was displayed by both the species, catfish and rohu, and both the size classes of each species, fingerling and large-size. Large-size catfish displayed both aggressive attack and push behaviors, whereas fingerling catfish displayed only push behaviors. For rohu, push behavior was displayed by large-size class only, however, fingerling rohu neither showed push or aggressive attacks. From here onwards, we pooled the durations of aggressive attack (only for large-size catfish) and push behaviors to represent aggressive interactions. In addition to these behaviors, freeze behavior was also displayed by fingerling rohu. We defined freeze behavior as cessation of movement and swimming activity for ≤10 sec, and fingerling rohu showed this behavior only in mixed species trials (C/SR and SC/SR).

2.8. Sample size for trials

For each type of single (C, SC, R and SR, Table 1) and mixed species trials (C/R, SC/SR, C/SR, Table 1), three tanks with defined group compositions (Table 1) were set up as biological replicates, and three trials (each of 3 h duration) were conducted on each tank (N=9 trials for each trial type). However, C, R and C/R trials were conducted on four different food items, and each food item had 9 trials. Each replicate tank was reused for trials after a gap of 48 h to provide a rest period to the experimental fishes. Fish reuse was limited only for a given trial type, and not across different types (C, SC, R, SR, C/R, SC/SR, and C/SR). Pooling all the trials (N=144), a total of 432 h of video recordings were analyzed and the entire duration of the experiment was for six months.

2.9. Statistical analysis

All the behavioral durations are expressed as Mean±Standard Error (SE) per individual per trial for both mixed and single species' trials. Behavioral data (durations) was tested for normality by conducting Shapiro-Wilk test, and F-test was performed to check for equal or

unequal variances.

Since for a given trial type (C, SC, R, SR, C/R, SC/SR, and C/SR), tanks (individuals) were repeated over time (trials), this would have given rise to pseudoreplication (temporal pseudoreplicates) error. To account for this, we conducted repeated measures ANOVA separately for each trial type to assess if feeding durations changed over time (from first to second to third rounds of experiment).

Additionally, we also applied the Linear mixed effect (LME) model to C and R trials. Separate LME analyses was conducted for feeding and aggressive interactions data of C and R trials, to assess if behavioral (feeding or aggressive interaction) duration varied with regards to food type ('home food', spirulina, chlorella and flake food) including tank (repeated over time) as the random effect. Significant results obtained from the LME model were followed up with post-hoc analyses using Student's t-test to check for pairwise comparisons between any two given food items.

To understand competitive interactions, only pairwise comparisons were conducted. For all the mixed-species trials (C/R, SC/SR and C/SR), duration of different behaviors (feeding and aggressive interactions) displayed by a species was compared with durations in their respective single species' trials (C, R, SC, SR). Following normality assumptions, either Student's t-test was applied to data to compare between two groups of treatment that had equal variances and Welch's t-test was applied to compare groups having unequal variances. Mann-Whitney U test was performed to compare two groups that followed non-normal distribution. The level of significance was kept at $P \leq 0.05$. All the statistical analyses were done on the R program (Crawley, 2014), version 4.2.3 using 'nlme', and 'ggplot2' packages.

3. Results

Repeated measures ANOVA showed that feeding duration did not change significantly ($P>0.05$; Supplementary Table 1) over time (from first to second to third rounds of experiment), and this pattern was similar for all the trial types (C, SC, R, SR, C/R, SC/SR, and C/SR).

3.1. Single species trials to characterize feeding behavior of the catfish

Overall, the feeding durations of large-size catfish (in C trials) were significantly different across the four tested food items, 'home food' (1185.61±262.97 s), flake (771.05±109.43 s), chlorella (627.72 ±135.99 s), spirulina (648.77±59.40 s) (LME model, $P<0.05$; Supplementary Table 2 and Supplementary Fig. 1a), however, post-hoc pairwise comparisons were not significant ($P>0.05$). Duration of aggressive interactions of large-size catfish for the four tested food items were 78.5 ±23.15 s for 'home food', 165.22±43.85 s for flake, 65.94±28.81 s for chlorella, and 197.22±50.42 s for spirulina (Supplementary Fig. 2a). The duration of aggressive interactions of large-size catfish differed significantly (LME model, $P<0.05$; Supplementary Table 2) across the four tested food items (Supplementary Fig. 2a), and a post-hoc test showed significant differences ($P<0.05$) between chlorella and spirulina ($t=2.57$, $P=0.02$), and between chlorella and flake ($t=2.46$, $P=0.03$).

Feeding duration of fingerling catfish (in SC trials) was 1654.13 ±131.29 s for 'home food' and duration of aggressive interactions was 76.66±20.51 s.

3.2. Single species trials to characterize feeding behavior of rohu

Feeding durations for large-size rohu was 448.75±95.33 s for 'home food', 496.5±130.67 s for flake, 1437.33±349.84 s for chlorella, and 1863.83±439.10 s for spirulina. Feeding durations of large-size rohu were significantly different (LME model, $P<0.05$; Supplementary Table 2) across the tested food items (Supplementary Fig. 1b), and post-hoc tests showed significant differences in feeding durations between 'home food' and chlorella ($t=2.72$, $P=0.03$), 'home food' and spirulina ($t=3.14$, $P=0.02$), flake and chlorella ($t=2.51$, $P=0.04$) and flake and spirulina ($t=2.98$, $P=0.02$) (Supplementary Fig. 1b). Duration of aggressive interactions for large-size rohu was 190.58±127.80 s when presented with 'home food', 32.83±28.57 s with flake food, 44.25 ±29.23 s with chlorella, and 14.75±6.81 s with spirulina. Significant differences (LME model, $P<0.05$; Supplementary Table 2) were obtained across the tested food items in the duration of aggressive interactions by large-size rohu in R trials (Supplementary Fig. 2b), however, post-hoc pairwise comparisons were not significant ($P>0.05$).

Feeding duration of fingerling rohu (in SR trials) was 525.9±77.82 s for 'home food' and no aggressive interactions were displayed by fingerling rohu.

3.3. Mixed-species trials to characterize interspecific interactions between catfish and rohu

In absolute terms, large-size catfish showed higher durations of feeding in mixed-species C/R trials when compared to single-species C trials. The feeding durations of large-size catfish in C/R trials were 2677.66±697.51 s for 'home food', 1318±460.83 s for spirulina, 2581± 271.50 s for chlorella, 2692.5±852.61 s for flake. Significant increase was observed in feeding duration of large-size catfish in C/R trials when compared to duration in C trials for three of the food items, 'home food' (Student's t-test; $t=-2.30$; $P=0.03$) (Fig. 2a), spirulina (Mann-Whitney U test, $W=0$, $P=0.0003$) (Fig. 2b) and chlorella (Student's t-test; $t=-7.09$; $P=8.061e-06$) (Fig. 2c). No significant differences were obtained for feeding durations of large-size catfish between C/R and C trials for flake food (Welch t-test; $t=-2.23$; $P=0.07$) (Fig. 2d).

Similarly, the average feeding duration of large-size rohu, in absolute terms, was either higher or equal when compared to durations in R trials (Fig. 2a-d). Feeding durations of rohu in C/R trials were 1696±336.03 s for 'home food', 1801.16±460.83 s for spirulina, 1678.5±267.88 s for chlorella and 1275.66±293.14 s for flake. Significantly higher feeding durations were observed in large-size rohu during C/R trials for 'home food' (Welch's t-test; $t=3.57$; $P=0.01$) (Fig. 2a) and flake (Student's t-test; $t=2.42$; $P=0.03$) (Fig. 2d) when compared to R trials for the given food items. No significant differences were obtained in feeding durations of large-size rohu between C/R and R trials for spirulina (Student's t-test; $t=-0.09$; $P=0.92$) (Fig. 2b) and chlorella (Student's t-test; $t=0.54$; $P=0.59$) (Fig. 2c) items.

Duration of aggressive interactions of large-size catfish in C/R trials for four tested food items (Fig. 3) were 150.66±27.86 s for 'home food', 137.16±22.87 s for spirulina, 62±13.98 s for chlorella, 127.83±31.75 s for flake. There were no significant differences in the duration of aggressive interactions of large-size catfish between C and C/R trials for spirulina (Welch's t test, $t=0.21$; $P=0.83$) (Fig. 3b), chlorella (Welch's t test, $t=-1.36$; $P=0.20$) (Fig. 3c) and flake (Welch's t test, $t=0.69$, $P=0.50$) (Fig. 3d). However, there was a significant increase (Student's t-test; $t=-3.89$; $P=0.003$) in the duration of aggressive interactions of catfish in C/R trials for 'home food' (Fig. 3a) when compared to C trials. The duration of aggressive interactions of large-size rohu in C/R trials were 60.16±22.73 s for 'home food', 26.5±13.66 s for spirulina, 4 ±2.04 s for chlorella, 30.5±13.09 s for flake. There were no significant differences (Student's t-test for 'home food' [$t=0.82$, $P=0.42$] and spirulina [$t=0.76$, $P=0.45$]; Mann-whitney U test for chlorella [$W=20$, $P= 0.79$] and flake [$W=26$, $P=0.22$]) in the duration of aggressive interactions of large-size rohu between R and C/R trials for all the tested food items (Fig. 3a-d).

In SC/SR trials, fingerling catfish showed no significant (Student's t-test; $t=-1.99$; $P=0.07$) differences in feeding duration (1979.20 ±148.49 s) in presence of fingerling rohu in SC/SR trials when compared to single-species SC trials (1654.13±131.29 s) (Fig. 4). In contrast, fingerling rohu showed significantly (Welch's t-test; $t=6.70$; $P=0.001$) reduced feeding duration (85.34±33.28 s) in presence of fingerling catfish when compared to single-species SR trials (525.96 ±77.82 s) (Fig. 4). In size-unmatched mixed-species C/SR trials, there were no significant (Welch's t-test; $t=-1.86$; $P=0.11$) differences in

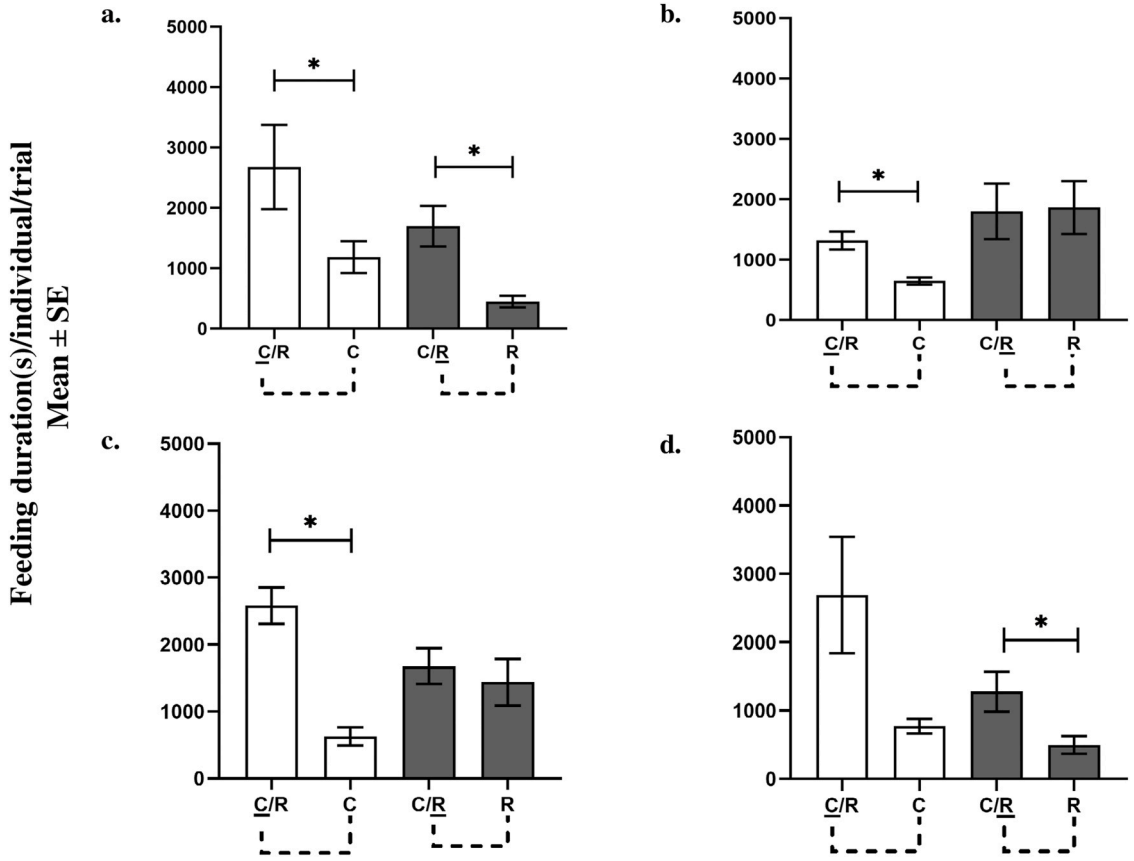


Fig. 2. Feeding durations (Mean±SE per individual per trial) of large-size catfish in C trials, large-size rohu in R trials, and large sizes of both catfish and rohu in size-matched, mixed-species C/R trials for different food items, panel a: algal wafer; panel b: spirulina; panel c: chlorella; and panel d: flake food. The underlined C and R represent feeding durations of large-size catfish and large-size rohu in C/R trials, respectively. Dotted line indicates species included for appropriate pairwise comparisons. *indicates significant differences (P≤0.05).

feeding duration (3670.5±1308.18 s) of large-size catfish between C/SR and C trials (Fig. 5). In fact, in absolute terms, the average feeding duration of large-size catfish was higher in C/SR when compared to C trials (Fig. 5). However, feeding duration of fingerling rohu (192.02 ±36.16 s) significantly (Welch's t-test; t=-3.89; P=0.003) reduced when compared to SR trials (Fig. 5).

For size unmatched C/SR trials, duration of aggressive interactions of large-size catfish (16±4.65 s) reduced significantly (Welch's t-test; t=-3.89; P= 0.005) when compared to C trials (Fig. 6). Similarly, for fingerling catfish, duration of aggressive interactions (23.33±4.69 s) reduced significantly (Welch's t-test; t=2.76; P=0.03) (Fig. 6) in SC/SR trials when compared to SC trials. Since fingerling rohu did not show any aggressive behavior, no comparisons could be made. Freeze behavior was displayed only by fingerling rohu both in C/SR and SC/SR trials (Fig. 7) The frequency of freeze behavior in C/SR trials was 52.12±3.71 and in SC/SR trials was 12.18±2.77. A significant (Student's t-test; t=8.60; P=6.155e-06) difference was observed in freeze behavior between C/SR and SC/SR trials, wherein fingerling rohu showed increased freeze behavior in presence of large-size catfish when compared to fingerling catfish.

4. Discussion

The study, for the first time, described feeding behavior of catfish under laboratory conditions showing that the feeding interactions in catfish is frequently associated with aggression. Our results demonstrated that rohu fingerlings were weak competitors in presence of catfish, and showed a significant reduction in feeding duration when compared to durations in presence of the conspecifics. This reduction in feeding durations of fingerling rohu was independent of the size of the catfish, and occurred in presence of both fingerling and large-size catfish. Rohu fingerlings also showed freeze behavior in presence of the catfish, which could be a sort of alarm response towards a hard-armor, aggressive species. Contrastingly, large-size rohu and large-size catfish had comparable or even higher feeding durations in presence of each other when compared to durations in presence of their conspecifics for a given food item. Thus, both the species of the large-size category appeared to be equal in terms of their competitive abilities in the context of feeding. However, whether the dynamics of feeding competition between the two species change in relation to varying levels of resources (from low to high food availability), and across temporal (breeding versus non-breeding seasons) and spatial (different habitats) scales warrants further investigations (Glova, 1986; Balshine et al., 2005; Grabowska et al., 2016).

Our study demonstrated that feeding behavior of catfish is mostly associated with aggression (Hossain et al., 2018; Umar and Ramayani, 2021), which is characteristic of both fingerling and large-size classes, and is displayed towards conspecifics and hetero species, as well. We also showed that large-size rohu was not a weak competitor in presence of the large-size catfish and this pattern was consistent, in terms of both feeding and aggressive interactions, across different food items. Similar results, where different fish species compete equally in a given habitat and had no significant impact on each other, were demonstrated in several studies by Paszkowski (1985), Savino and Kolar (1996) and Fullerton et al. (2000). However, contrasting results were also demonstrated by Mills et al. (2004) showing that both large- and small-size classes of least chub (*Iotichthys phlegethontis*), a native fish to Bonneville basin of Utah, were behaviorally submissive in presence of

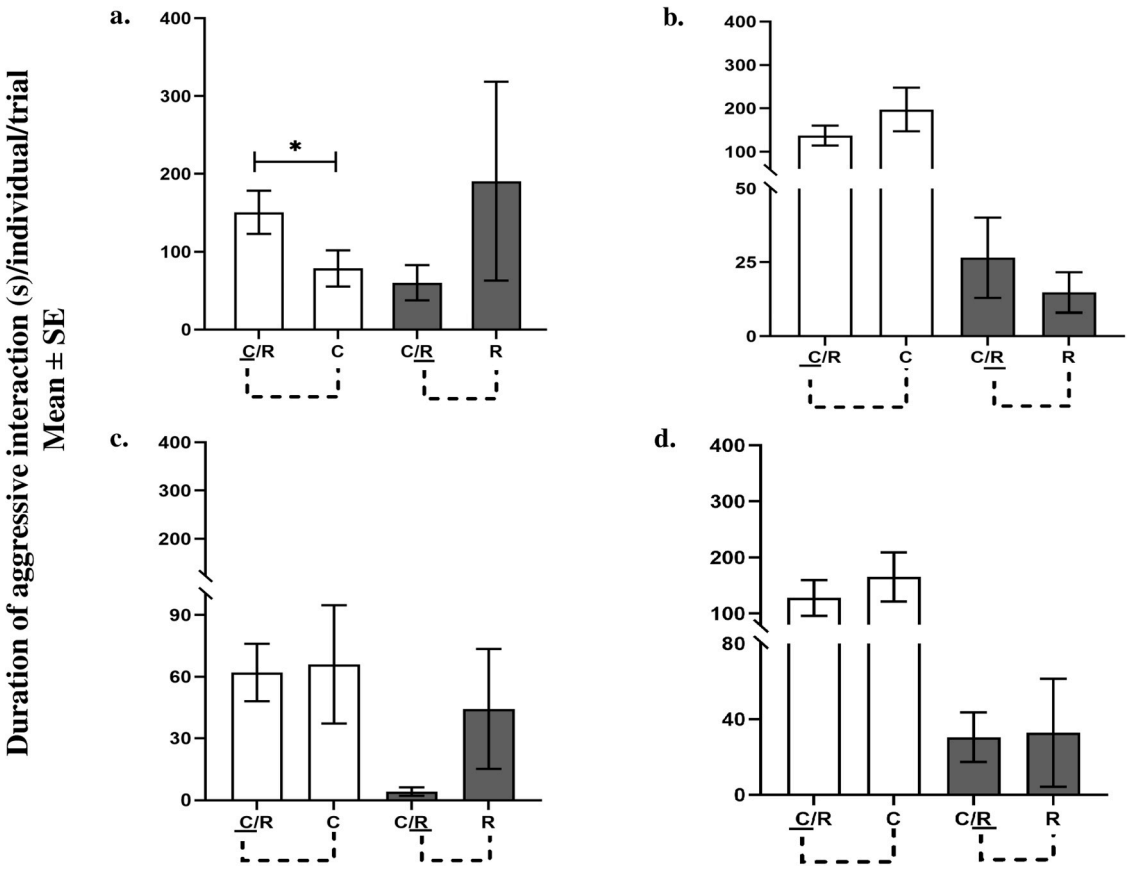


Fig. 3. Duration of aggressive interactions (Mean±SE per individual per trial) of large-size catfish in C trials, large-size rohu in R trials and large-size of both catfish and rohu in size-matched, mixed-species C/R trials for different food items, panel a: algal wafer; panel b: spirulina; panel c: chlorella; and panel d: flake food. The underlined C and R represent durations of aggressive interactions of large-size catfish and large-size rohu in C/R trials, respectively. Dotted line indicates species included for appropriate pairwise comparisons. *indicates significant differences (P≤0.05).

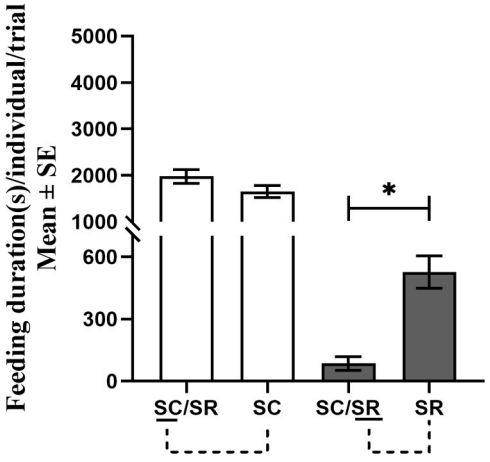


Fig. 4. Feeding durations (Mean±SE per individual per trial) of fingerling catfish in SC trials, fingerling rohu in SR trials and fingerlings of both catfish and rohu in size-matched, mixed-species SC/SR trials. The underlined SC and SR represent feeding durations of fingerling catfish and fingerling rohu in SC/SR trials, respectively. Dotted line indicates species included for appropriate pairwise comparisons. *indicates significant differences (P≤0.05).

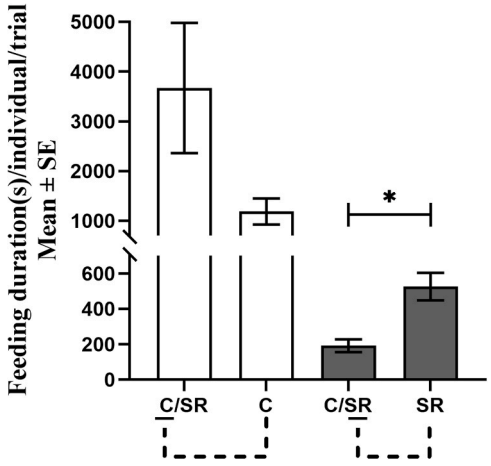


Fig. 5. Feeding durations (Mean±SE per individual per trial) of large-size catfish and fingerling rohu in size-unmatched, mixed-species C/SR trials. The underlined C and SR represent the feeding durations of large-size catfish and fingerling rohu in C/SR trials, respectively. Feeding durations of large-size catfish and fingerling rohu in C and SR trials are repeated from Fig. 2 and Fig. 4, respectively for comparison purposes only. Dotted line indicates species included for appropriate pairwise comparisons.*indicates significant differences (P≤0.05).

mosquitofish (*Gambusia affinis*), an invasive fish within the same habitat. Thus, feeding competitions between species may vary depending on the competitive ability of the interacting partner, and needs thorough investigations under different environmental and ecological conditions.

The results for large-size rohu are in contrast to the findings observed for the fingerling rohu, which was outcompeted, in terms of feeding durations, in presence of both size-matched and large-size catfish.

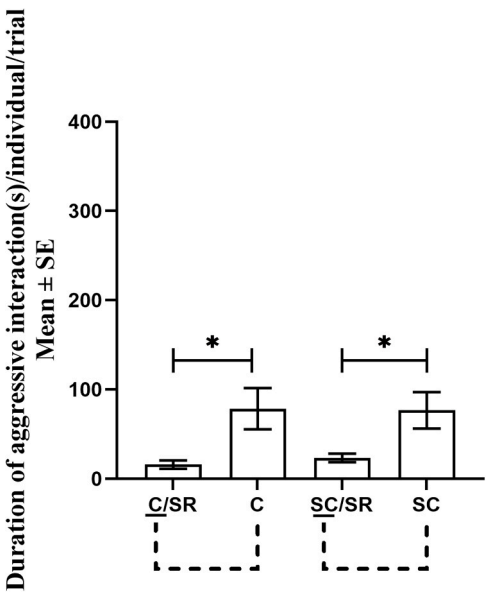


Fig. 6. Duration of aggressive interactions (Mean±SE per individual per trial) of large-size catfish in size-unmatched, mixed species C/SR trials, fingerling catfish in size-matched, mixed-species SC/SR trials, and fingerling catfish in single-species SC trials. The underlined C and SC represent durations of aggressive interactions of large-size and fingerling catfish in C/SR and SC/SR trials, respectively. Duration of aggressive interactions of large-size catfish in C trials is repeated from Fig. 3 for comparison purposes only. Dotted line indicates species included for appropriate pairwise comparisons.*indicates significant differences (P≤0.05).

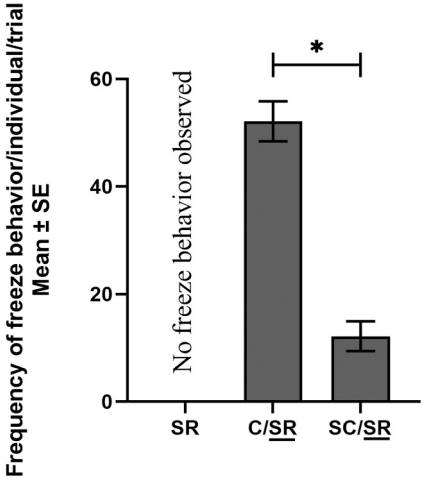


Fig. 7. Frequency of freeze behavior (Mean±SE per individual per trial) of fingerling rohu (represented as underlined SR) in size-unmatched and size-matched, mixed-species C/SR and SC/SR trials. *indicates significant differences (P≤0.05).

Similar results, where young individuals are poorer competitors than older ones, have been obtained by Winemiller and Taylor (1987), Persson and Greenberg (1990), and Byström and García-Berthou (1999) using different species of fishes. The authors showed that differences in competitive abilities of young versus old individuals could be due to experience or in relation to health or physiological characteristics of a particular developmental stage (Winemiller and Taylor, 1987; Nol and Smith, 1987; Persson and Greenberg, 1990; Byström and García-Berthou, 1999; Šárová et al., 2013). Significant negative impact of the catfish on feeding durations of the fingerling rohu clearly draws parallels between the current work under laboratory conditions, and previous field-based studies (Mallick et al., 2023; Parvez et al., 2023), which also showed that growth of only fingerling rohu (and not larger than fingerling size class) got severely impaired in presence of the catfish within a given mesocosm setup. Similar impact of an exotic species, exclusively targeting young-age individuals of the native fish species, has been widely documented in several studies by Mills et al. (2004) and Bašić et al. (2019). Additionally, we demonstrated that both the fingerling and large-size catfish were significantly impactful in terms of reducing feeding durations of rohu fingerlings. This is highly concerning in the field of invasion ecology and fisheries sciences, as catfish species has now spread in several Asian (Bijukumar et al., 2015; Parvez et al., 2023) and Southeast Asian countries (Jumawan et al., 2011; Chaichana et al., 2011), where Rohu is an important economically valuable, native species (Rasal and Sundaray, 2020; Modeel et al., 2023).

Though catfish are known to be aggressive, we found that the species was less aggressive towards rohu fingerlings when compared to trials with conspecifics (in C and SC trials) or large-size rohu (in C/R trials). This was not surprising as rohu fingerling was a weak competitor (in terms of reduced feeding duration) in presence of catfish, and thus, received less aggression from the catfish (Franco and Arce, 2022). Contrary to this, in C/R trials, both species of large-size classes showed comparable feeding durations, and thus, received similar or even higher levels of aggression from each other (Miyai et al., 2011; McCarthy et al., 1999) when compared to their respective conspecific (C or R) trials. Poorer competitive ability of the fingerling rohu was further supported by display of freeze behavior in presence of the catfish. Fingerling rohu displayed higher frequency of freeze behavior in presence of large-size catfish when compared to fingerling catfish, and such contrast might be obvious due to sheer size differences (Templeton et al., 2005). Freeze behavior has been widely documented in several fish species, mostly displayed in the context of alarm or anti-predatory behavior (Brown et al., 1999; Bass and Gerlai, 2008; Näslund et al., 2016). The results of this study are in agreement with the study on zebrafish (*Danio rerio*) (Bass and Gerlai, 2008), where the authors documented a significant difference in freeze behavior of zebrafish between test, in presence of an exotic swordtail fish (*Xiphophorus helleri*), and control, in presence of conspecifics, groups. Our study clearly demonstrates that the presence of the exotic catfish not only impedes the feeding duration of the fingerling rohu but also has a significant impact on the behavioral expressions of the rohu, which in turn may negatively influence the growth and development of the keystone species.

5. Conclusion

Our results suggest that the fate of interspecies competition may depend on the size or age of the fish species (Munday et al., 2001; Byström and García-Berthou, 1999), and expressions of different behaviors (freeze or aggressive behaviors) may vary depending on the competitive ability of the interacting partner (Persson, 1983; Grether et al., 2009). Overall, the survival of a species greatly depends on the nature of its interactions within a given environment, and thus, exotic invasions to an ecosystem may not always be ecologically or environmentally threatening but also may impede the behavioral interactions of the natives within the introduced system.

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CRediT authorship contribution statement

RATNA Ghosal: Writing – review & editing, Supervision, Project administration, Investigation, Funding acquisition, Data curation,

Conceptualization. **Jitendra Kumar Sundaray:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Suman Mallick:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Conflict of Interest

None.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.beproc.2024.105029.

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