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Chub movement is attracted by the collision sounds associated with spawning activities

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Abstract

Cyprinids (carps, chubs and minnows) possess well-developed hearing and high sensitivity to sound pressure. The sensitive hearing may assist cyprinids with searching for food, territory defense, and mating behavior. Many paired fishes violently shake in sand and gravel while spawning in rivers. However, no study has examined the ecological importance of the collision sound made by the behavior. This study examined whether cohabitated chubs (*Opsariichthys evolans* and *Zacco platypus*) use the collision sound as a signal to locate spawning events so they can be a male satellite or egg eater. Three types of sounds (i.e., collision sound, music noise and ambient noise) were played with or without jerkbaits at the midstream of the Keelung River, Taiwan during the spawning season in 2018 and 2019. Generalized linear mixed models were then built to examine the effects of the sound types and the presence of jerkbaits on the number of individuals that the two chubs attracted. Results showed significantly different levels of attractiveness among the three sound types, with the collision sound attracting most fishes, including both females and males, followed by music noise and ambient noise. The presence of jerkbaits increased the number of fishes attracted, but the effect was only statistically marginally significant. These results suggest that the collision sound as an acoustic signal may be more important than a visual signal for the chubs to locate spawning events of other mating pairs, probably because of the longer transmission distance of the former. The present study demonstrates the ecological meanings of the collision sounds made in association with spawning activities of the chubs and implies that the native chub's spawning activities may be affected by the introduced *Z. platypus*. More studies on the interactions between these cohabitated chubs will benefit the conservation of native chubs.

Key words: Spawning behavior, egg eater, environmental sound, *Opsariichthys*, *Zacco*

Introduction

Males and females of many freshwater fishes, including chubs, form mating pairs, and their sperm and eggs are deposited in a redd or gravel nest. Before spawning eggs, members of a mating pair remain close to each other and look for a suitable redd, usually with a sandy bottom and gravel. Once the female stops around the redd, the male tries to find the right position, at which time both continually shake their caudal fins. The male subsequently leans to one side of the female and pushes the female close to the redd to lay eggs into the redd while both male and female violently shake their tails (Katano 1992b; Wang *et al.* 1995; Yan *et al.* 1995; Chuang *et al.* 2006). Such violent shaking movements often disturb sand and gravel, helping bury the eggs in the redd to protect them from

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cohabited or conspecific egg eaters. The behavior of egg cannibalism is believed to be accompanied by spawning behavior, and has been reported in the Japanese chub *Zacco temminckii* (Katano 1992a, 1992b, 1998; Katano & Maekawa 1995). One can easily observe many cohabitated male and female Japanese chubs and/or other cyprinids swimming straight toward the redd, being spawned satellites or egg eaters, during or after spawning (Katano 1992a, 1992b). Herein, we also observed that mating pairs of Taiwanese chubs violently shake their tails in sand and gravel for 10-30 seconds at a time during spawning and other individuals quickly swim toward the spawning events to eat eggs or perform spawning-like actions (FIGURE 1a). However, while this spawning behavior and the accompanied satellites or egg cannibalism are well known, it remains unclear how fishes locate the spawning locations of mating pairs nearby so they can quickly swim toward the redds.

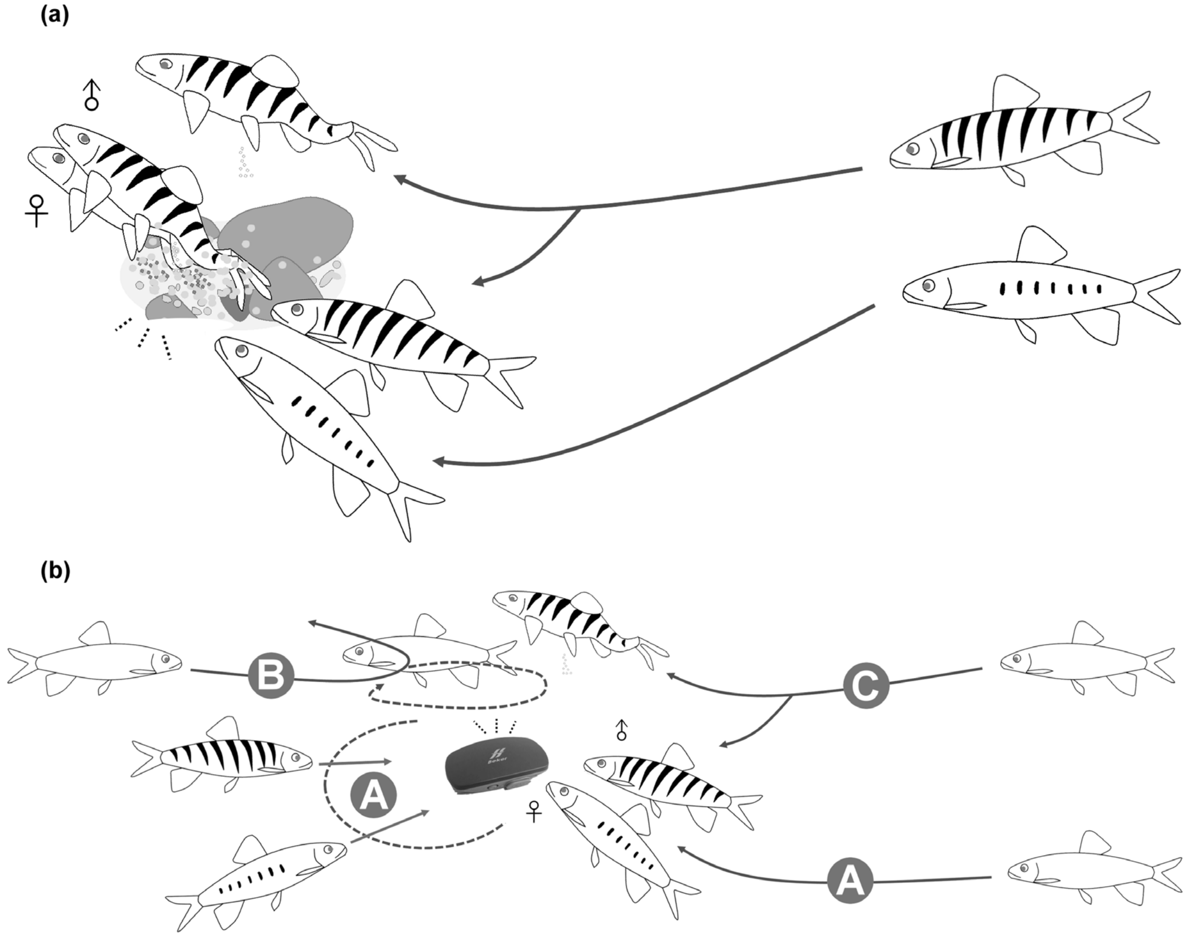

FIGURE 1. Observational and experimental design of this study. (a) Collision sounds associated with spawning activities may attract egg eaters and/or male satellites and (b) description of three movement behaviors. A fish was considered as being attracted if it performed any of the following three movement behaviors: (A) swimming close to the Beker at a distance shorter than the length of the Beker; (B) swimming straight toward the Beker and suddenly stopping and returning, staying nearby, or circling around the Beker; and (C) swimming straight toward the Beker and biting and/or performing spawning-like actions.

There are at least six species of chubs in the genera *Candidia*, *Opsariichthys* and *Zacco* in Taiwan (Chen *et al.* 2008; Chen *et al.* 2009; Ma *et al.* 2006a; Ma *et al.* 2006b; Wang *et al.* 1997). Ma *et al.* (2006a) discovered four synonymous subtypes of *Z. platypus* (A1, A2, L1, L2) and found that the subtype L2 shares the same haplotypes with Japanese *Z. platypus* from Lake Biwa. Chen *et al.* (2009) reclassified subtype A1 as *O. pachycephalus*, A2 as *O. kaopingensis*, L1 as *O. evolans,* and L2 as *Z. platypus*. Based on the above literatures and Taiwanese museum records, Japanese *Z. platypus* was introduced in the 1980s and its distribution is restricted to upstream of the Tamsui drainage, especially in Hsintein and Keelung Rivers (Huang *et al.* 2017; Liao *et al.* 2020; Ma *et al.* 2006b). Although the taxonomic status of these chubs is confirmed, their basic ecological information and their interactions remain poorly known.

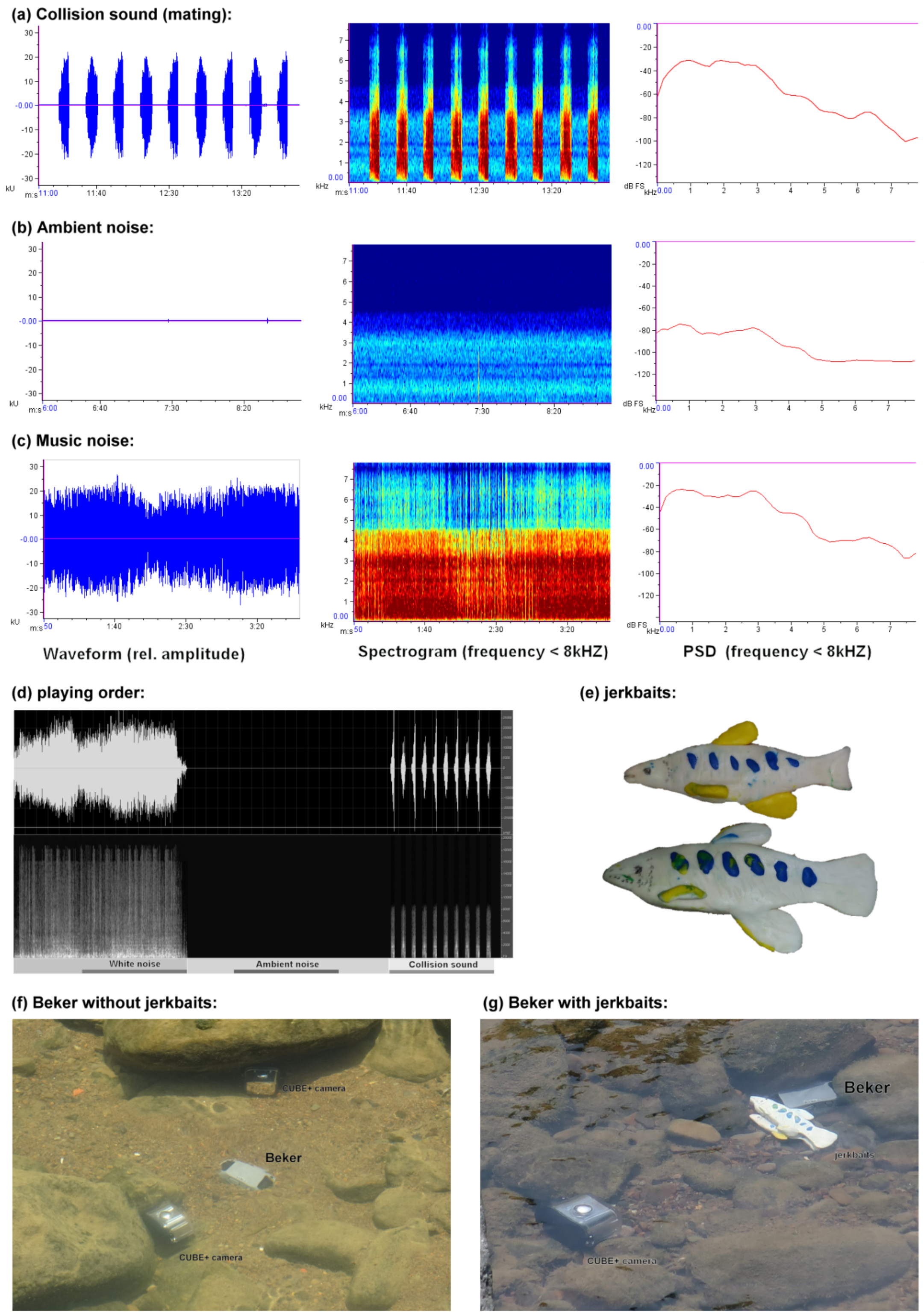

FIGURE 2. Sound profiles and field experiments. Waveform (rel. amplitude [kUnit] = proportional to the sound pressure of the recording), spectrogram (frequency [kHz]) and power spectral density (PSD, [dB]) of (a) the 3-minutes collision sound, (b) ambient noise and (c) music noise. The right two diagrams highlight the three sounds that fish may sense, including the frequency lower than 8 kHz. (d) Fixed playing order of sound profiles as example for each time of experiment, 5 minutes of music noise; 6 minutes of ambient noise; 3 minutes of collision sound (mating). The bar regions represent 3 minutes of sound for further statistics. Two field experiments with underwater sound player on a putative redd and home-make jerkbaits (e) based on the mature chub's coloration-- (f) Beker without chub-like jerkbaits; (g) Beker with chub-like jerkbaits.

A better understanding of how these chubs sense and interact with other species and cohabitated environment, especially during their spawning season, would clarify their ecological roles and assess the potential impact of introduced species during the spawning activities. For examples, a previous study suggested that two Taiwanese chubs (*O. pachycephalus* and *Candidia barbatus*) have specific color vision and might allow them to identify different nuptial coloration between species (Wang *et al.* 2008). However, the introduced *Z. platypus* and native *O. evolans* cohabitat in the same river section of the Keelung River and may mis-identify each other, leading to hybridization during the mating season (Liao *et al.* 2020). This implies that the latter two chubs may not visually identify each other well.

On the other hand, Cyprinids (carps, chubs and minnows) possess well-developed hearing (200-8000 Hz) and high sensitivity to sound pressure (~60 decibels) due to their Weberian apparatus, which mechanically connects the swim bladder and inner ears (Ladich & Fay 2013). The sensitive hearing could help the fishes search for food, defend territory, mate, etc. (Hawkins & Popper 2018; Sisneros & Rogers 2016). Because sands and gravels disturbed by the violent shaking movements associated with the spawning activities make collision sounds, it is possible that nearby chubs can hear the sound and swim directly toward the redd. This study aims to clarifying whether chubs can locate spawning activities of cohabitated chubs using hearing or vision. Specifically, we examined whether the collision sound associated with spawning activities (i.e., acoustic signals) and/or the presence of chub-like jerkbaits (i.e., visual signals) can attract chubs.

Materials and methods

Study areas. The study area (25°06'22.9"N 121°48'32.2"E) is at the midstream of the Keelung River, a major tributary of the Tamsui River, and located in Ruifang District, Keelung in northern Taiwan. There are two major chubs (introduced *Z. platypus* and native *O. evolans*) in the study area. The water temperature, measured in 1-minute intervals with the HOBO Pendant® Temperature/Light 64K Data Logger, ranged between 24 and 34°C during the experiments conducted in July and August in 2018 and 2019 (see below).

Collision sound collection. We put a waterproof Polaroid CUBE+ camera nearby spawning redds without disturbing mating pairs and recorded the sounds, including the collision sound, during the spawning of paired chubs. We then extracted a 10-second clip of the collision sound from the video when the paired chubs performed the most violent shaking movements. A 3-minute recording was made by repeating the 10-second collision sound followed by 10 seconds of silence nine times (FIGURE 2).

Experimental design. The entire sound track for each trial of the experiment (FIGURE 2d) was composed of:

(1) 5 minutes of music noise representing non-related acoustic signals,
(2) 6 minutes of ambient noise recorded in the studied river without collision sounds, and
(3) 3 minutes of the collision sound mentioned above.

These sounds were loaded into a waterproof player (74 mm L x 41 mm W x 18 mm H, hi Beker, Happy Island Co., Ltd., Taiwan). The sound player, Beker, was then put on a putative redd to play the three periods of sounds (FIGURE 2f). Meanwhile, a digital camera (Sony FDR-AXP55) was used to record any fishes attracted by the sounds. To examine if a vision signal can attract fishes or enhance the attraction of collision sounds, the experiment was conducted with and without homemade chub-like jerkbaits (FIGURE 2e) placed next to the Beker (FIGURE 2g). For either with or without the jerkbaits, twenty trials of the experiment with a fixed order of sounds (music noise-ambient noise-collision sound) were conducted from 9:00 to 12:00 during 9 days of the spawning season in July-August 2018. To ensure that the results were not affected by the playing order of the three types of sounds, we conducted an additional without-jerkbaits experiment with a random playing order for 30 trials during 11 days of the spawning season in July-August 2019.

Data analysis. The videos taken in the field were brought back to the lab and the number of fishes attracted during each type of the sounds being played was counted. For each type of sound, we only counted the fishes attracted within 3 minutes, then separated them from other periods to avoid confusion among the different sound types (bar regions shown in FIGURE 2d, for example). A fish was considered as being attracted if it performed any of the following three types of movement behaviors: (A) swimming close to the Beker at a distance shorter than the length of the Beker; (B) swimming straight toward the Beker and suddenly stopping and returning, staying nearby or circling around the Beker; and (C) swimming straight toward the Beker and biting and/or performing spawning-like actions (FIGURE 1b). We counted males and females separately, but did not distinguish between the two species (*Z. platypus* and *O. evolans*) since they may have hybridized with each other (Liao *et al.* 2020). Although during our experiments, the collision sound also attracted other cohabitated cyprinids (*Acrossocheilus paradoxus* and *Hemibarbus labeo*), goby (*Rhinogobius* sp.) and tilapia (*Oreochromis* sp.), only a few individuals of those species were attracted (data not shown). In addition, while the hearing sensibility in cyprinids and mating and reproductive behaviors of the target chubs are similar (Katano 1985, 1990a, 1990b, 1992b, 1994, 1998; Wang *et al.* 1995; Yan *et al.* 1995), they are different from those of the other species. Therefore, we excluded the other species from the analyses. In addition, if there were any paired chubs spawning near the redd, then the trial was also excluded from the analyses.

Generalized linear mixed models (GLMMs) with Poisson distribution were built to examine the effects of the presence of jerkbaits (visual signals) and the sounds (acoustic signals) on the number of fishes attracted. Because the numbers of male and female fishes attracted were not significantly different among the trials (TABLE 1), we used the total number of fishes as the dependent variable in the models. We considered the presence/absence of jerkbaits and the three sound types as fixed effects and the trials as a random effect in the model for the first-year experiment. To further examine whether the attraction of different sound types was affected by the presence/absence of jerkbaits, we also built a model with the interaction between the sound types and presence/absence of jerkbaits as additional fixed effects. Because the second-year experiment was conducted only without jerkbaits, only the sound type was included as a fixed effect. To further examine whether the chubs would respond to different sounds with different behaviors, we built additional GLMM models with the number of each of the three types of behaviors (FIGURE 1b) as a dependent variable and the sound type as a fixed effect for the second-year experiment.

TABLE 1. Results of the GLMM examining the difference in the number of fishes attracted between sexes.

Fixed effect	Coefficient	SE	*p*-value	N	# of trails
Intercept	1.078	0.101	**< 0.001**	240	40
Sex (male vs. female)	-0.057	0.071	0.426		

TABLE 2. Results of the GLMMs for examining the effects of the presence of jerkbaits and the sound type on the total number of fishes attracted.

Fixed effect	Coefficient	SE	*p*-value	N	# of trails
Without interaction between jerkbaits & sound					
Intercept	1.654	0.136	**< 0.001**	120	40
Jerkbaits (presence vs. absence)	0.331	0.176	0.060		
Sound (ambient noise vs. music noise)	-0.634	0.101	**< 0.001**		
Sound (collision sound vs. music noise)	0.312	0.078	**< 0.001**		
With interaction between jerkbaits & sound					
Intercept	1.666	0.147	**< 0.001**	120	40
Jerkbaits (presence vs. absence)	0.310	0.201	0.122		
Sound (ambient noise vs. music noise)	-0.685	0.154	**< 0.001**		
Sound (collision sound vs. music noise)	0.306	0.118	**0.009**		
Jerkbaits x ambient noise	0.090	0.204	0.661		
Jerbaits x collision sound	0.010	0.157	0.948		

Results

During our experiments, we found that more fishes were attracted when the collision sound was played (10.7±4.4 and 8.4±6.0 for with and without jerkbaits, respectively) than when music noise (7.8±4.4 and 6.2±4.9) or ambient noise (4.3±2.7 and 3.1±2.4) was played, no matter whether jerkbaits were present or not (FIGURE 3). Our model indicated that the number of fishes attracted by the collision sound was significantly higher than that attracted by music noise, which in turn was significantly higher than that attracted by ambient noise (TABLE 2). Although we also found that more fishes were attracted when jerkbaits were placed near the Beker (FIGURE 3), the effect of the presence of jerkbaits was only marginally significant (TABLE 2). When we included the interaction terms between the sound type and the presence/absence of jerkbaits in a model, none of the interaction terms were significant (TABLE 2), suggesting that the presence of jerkbaits did not change how the sound types attracted the fishes.

When the three sounds were played in a random order, the results were consistent. After excluding the trials that interfered by other spawning events nearby, our model also showed that the collision sound attracted the most fishes, followed by music noise and ambient noise (FIGURE 3 and TABLE 3). Further examination of the numbers of different response behaviors performed by the attracted fishes, we found no difference among the three types of movement behaviors. Three types of movement behaviors were observed when each type of sound was played and were all observed most frequently when the collision sound was played and least frequently when ambient noise was played (FIGURE 4). Except for the behavior type C, which was observed only a few times during the experiment, the differences in the observation frequency were significant among the sound types (TABLE 3). These results suggest that, while the three types of sounds had different levels of attractiveness to the chubs, they triggered similar behaviors.

Discussion

Previous studies have reported that fish may make calls (sexual signals) associated with reproduction behavior, such as the Gulf corvina (Erisman & Rowell 2017) and the hamlet and striped parrotfish (Lobel 1992). However, none of them reported the sounds made from the behaviors associated with reproduction—at least not by the fish itself—or examined the ecological importance of those sounds. This study showed that the collision sound made when a spawning pair or chubs shake their tails and disturb sand and gravel can attract both females and males of the two chub species (*Z. platypus* and *O. evolans*), as significantly more fishes were attracted by the collision sound than by ambient noise (FIGURE 3 and TABLE 2). We also found that music noise attracted significantly more fishes than ambient noise did, indicating that the two chub species can also be attracted by other non-background acoustic signals. The similarities in power spectral densities (PSD), which demonstrated the energy in each frequency band, between the collision sounds and music noise (FIGURE 5) may be the reason why chubs were also attracted by the music noise.

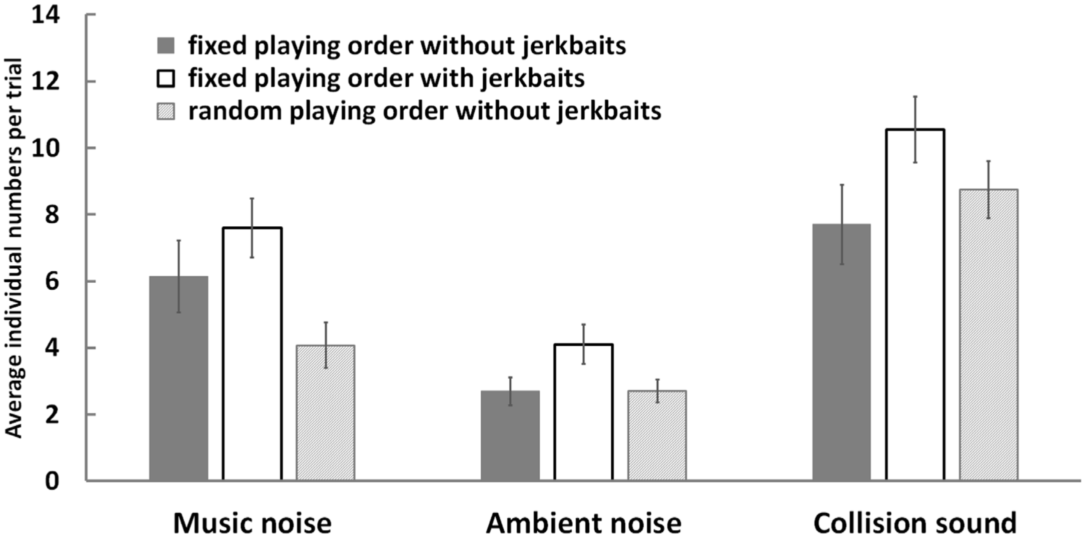

FIGURE 3. Average individual numbers of cohabitated chubs attracted by three sounds with/without playing order and jerkbaits.

TABLE 3. Results of the GLMMs for examining the effects of sound type on the total number of fishes attracted and on the number of each behavior type observed. The experiment was conducted with a random playing order of the three types of sounds and without jerkbaits. See FIGURE 1b for the three movement behavior types.

Fixed effect	Coefficient	SE	*p*-value	N	# of trails
Number of fishes attracted					
Intercept	1.373	0.162	**< 0.001**	62	24
Sound (ambient noise vs. music noise)	-0.458	0.185	**0.014**		
Sound (collision sound vs. music noise)	0.715	0.155	**< 0.001**		
Number of behavior A observed					
Intercept	1.841	0.160	**< 0.001**	62	24
Sound (ambient noise vs. music noise)	-0.574	0.144	**< 0.001**		
Sound (collision sound vs. music noise)	0.608	0.118	**< 0.001**		
Number of behavior B observed					
Intercept	1.232	0.167	**< 0.001**	62	24
Sound (ambient noise vs. music noise)	-0.643	0.203	**0.002**		
Sound (collision sound vs. music noise)	0.765	0.160	**< 0.001**		
Number of behavior C observed					
Intercept	-4.672	2.253	**0.038**	62	24
Sound (ambient noise vs. music noise)	-0.001	0.780	0.999		
Sound (collision sound vs. music noise)	0.558	0.708	0.430		

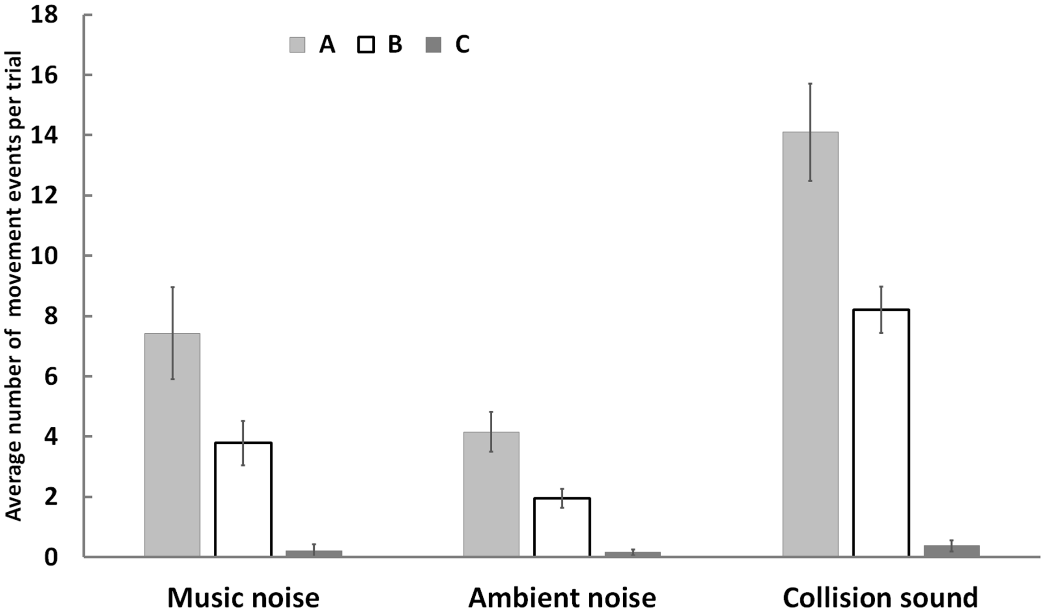

FIGURE 4. Average numbers of three movement behaviors counted in three sounds, with radom playing order per trial. See FIGURE 1b for the description of three movement behavior types.

However, our finding that chubs responded significantly stronger to the collision sound than to music noise suggests that the collision sound may convey an important message to chubs. Egg cannibalism and satellite spawning are common in chubs (Katano 1992a, 1992b, 1998; Katano & Maekawa 1995) and we observed that some chubs attracted by the collision sound performed spawning-like actions during our experiments (FIGURE 4). Therefore, we believe that the collision sound indicates where a spawning event is happening and surrounding chubs use it to locate the event so that they can either eat eggs and/or release their own sperm onto the eggs.

The results showed that the collision sound can attract both females and males of the two chub species, and that its attractiveness to both sexes is similar. However, although females and males may respond similarly to the acoustic signal (i.e., swimming toward the sound source), their purposes should be different. Unpaired, matured male adults (or satellite males) may swim straight toward the redd to seek an opportunity for mate to proliferate offspring (FIGURE 1a). In contrast, females and/or immature chubs (or young adults) swim straight toward the redd to eat eggs (Katano 1992a, 1992b; Katano & Maekawa 1995). Cannibalism is a particularly common behavior in teleost fishes, usually attributed to food scarcity, but low food quality may also encourage it (Katano 1992a; Manica 2002). In addition, we found that the collision sound attracted other cohabitated cyprinids, goby and tilapia. These fishes might also be putative heterospecific egg eaters.

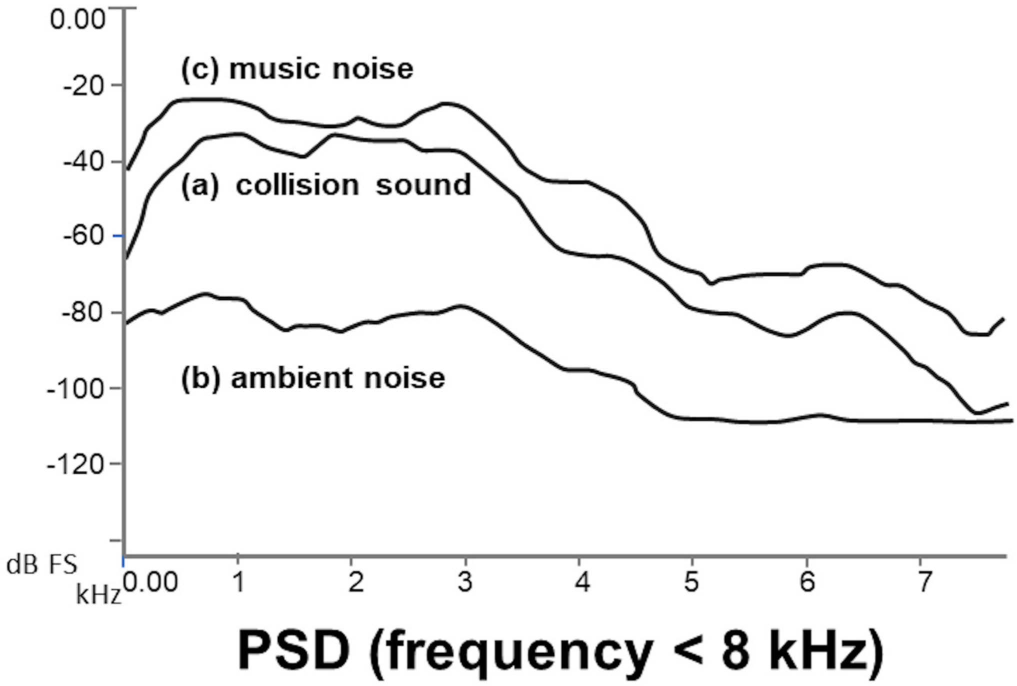

FIGURE 5. Similar power spectral density (PSD, [dB]) of 3 minutes of collision sound and music noise, compared to ambient noise in FIGURE 2. The PSD demonstrates the energy in each frequency band. If two curves have a similar pattern, it means that those curves have a similar sound frequency composition.

The results also showed that more fishes were attracted by the sounds when jerkbaits were placed near the Beker than when no jerkbait was presence (FIGURE 3), although the difference was only marginally significant (TABLE 2). This suggests that acoustic signals are more important than visual signals for the chubs to locate the spawning events of other mating pairs. Turbidity or complex substrates may inhibit visual detection while sounds can be transmitted over large distances underwater, even in a low photic environment (Hawkins & Myrberg 1983). The underwater predators could locate the fishes mainly based on olfactory and/or acoustic signals, and minor to visual signals during the breeding season (Holt & Johnston 2009; White *et al.* 2022). For example, a water snake (*Nerodia sipedon pleuralis*) is a fish predator that preys on small minnow species (such as *Cyprinella*) mainly by acoustic signals from the minnows and visual cues (Holt & Johnston 2009). Because acoustic signals may transmit further than visual signals in the fish's habitat, sensing the collision sound allows the chubs to detect a spawning event from a longer distance. The marginal but consistent effect of the visual signal on attracting the chubs suggests that the visual signal may help confirm whether the sounds are actually made by mating pairs, especially when the fishes are close to the sound source. While our analysis on the recorded number of response behaviors of the chubs did not show any significant difference among different behavior types, further studies with more defined behaviors are needed to clarify the importance of visual signals for detecting spawning events.

This study shows that chubs can sense the collision sound made by spawning events of other mating pairs, distinguish it from other sounds and use it to locate those spawning events. It also demonstrates the ecological importance of the collision sound as it may be associated with satellite spawning and egg cannibalism. These findings have important conservation implications because the spawning activities of the native chubs in the Keelung River may be negatively affected by the introduced chubs due to enhanced egg cannibalism and interspecific misidentification (Liao *et al.* 2020). To evaluate the impact of introduced *Z. platypus* on native species conservation, further comparisons of these cohabitated chub's genomes, reproductive isolation, body color patterns, interspecific hybridization and mating behaviors are necessary in the future.

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Authors' contributions

TYW and MNT designed the study and prepared the manuscript. CYL, YLW, SPH and TYW performed the field work. YLW and CYL performed video analysis. All authors participated in revising the manuscript and approved the final manuscript.

Competing interests

All authors declare that they have no conflict of interest. TYW have received research grants from the MOST, Taiwan.

Availability of data and materials

Not applicable.

Consent for publication

All authors have approved the manuscript and agree with its submission to Zootaxa.

Ethics approval consent to participate

Not applicable.

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