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A comparative study of predation rhythms on cladocerans by juvenile invasive crayfish and native shrimp

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The red swamp crayfish *Procambarus clarkii* is one of the most widely distributed invasive species in the world. Effects of juvenile crayfish (< 5 cm in body length) in lake ecosystems remain largely unknown, despite that they have a great potential of preying upon zooplankton. The shrimp *Exopalaemon modestus* is one of the most abundant native shrimps in China and also predate on zooplankton. The predation rhythm of juvenile crayfish on zooplankton and how it differs from native shrimps remain to be studied. We elucidated the predation rhythms of juvenile and sub-adult crayfish and shrimps on *Simocephalus mixtus*, a common Cladocera in the littoral region of freshwater lakes. Predation rates during the day or at night were measured for juvenile crayfish (~3.75 cm in body length), sub-adult crayfish (~6.68 cm) and juvenile shrimp (~3.88 cm) at different zooplankton densities (18, 54, 108 ind./L representing low, medium and high natural densities, respectively). The results showed that (1) juvenile crayfish predated slightly more at night than during the day, and with significantly higher predation rates than sub-adult crayfish; (2) Juvenile shrimp predated significantly more at night than during the day, as predation was almost absent during the day; (3) Juvenile shrimp had slightly higher night-time predation rates than juvenile crayfish, however, their daytime predation rates were significantly lower at medium and high zooplankton densities. Juvenile crayfish fed for a longer period than shrimp of similar length, exhibiting higher feeding capacity on zooplankton which supports the inherent superiority hypothesis that invasive species possess advantages over native species in feeding capacity. Our study provides information about the predation rhythms on Cladocera of early stages of crayfish and of shrimp, that may help in explaining, in part, the invasion success of red swamp crayfish.

KEYWORDS

feeding rhythms, native shrimp, predation rates, red swamp crayfish, zooplankton

1 Introduction

Red swamp crayfish *Procambarus clarkii* is one of the most important invasive species worldwide, the only alien freshwater crayfish introduced in China since 1930s (Chen et al., 2017; Oficialdegui et al., 2020). It is a popular aquatic product in China and is cultured in more than 20 provinces with an area larger than 1.46 million hectares (Yuan et al., 2022). Red swamp crayfish is also widely distributed in lakes, rivers, ditches, sloughs, and elsewhere (Yi et al., 2018; Yue et al., 2021). Crayfish have been found to disrupt the clear water state of lakes through physical disturbances and direct consumption of macrophytes (van der Wal et al., 2013; Dercksen et al., 2025). They also negatively impact native species such as amphibians, gastropods, and insect larvae through predation or competition for food (Souty-Grosset et al., 2016; Huang et al., 2025). However, most research on the impacts of crayfish has focused on macrophytes and benthic animals (Ruokonen et al., 2016), while little attention has been paid to other taxa within the freshwater food web.

Crayfish are generally omnivores and their diet varies according to life stage (Correia, 2003; Geiger et al., 2005). The diet of adult crayfish (>8 cm in total length) consists of macrophytes, insect larvae, gastropods, and detritus (van der Wal et al., 2013; Wu et al., 2022), while little is known about the diet of juveniles and sub-adults. Adult female crayfish lay eggs and incubate them on their pleopods until hatching. By the third instar stage, juveniles become free-living (Hamasaki et al., 2023). Juvenile crayfish (<5 cm) are primarily carnivorous, feeding on zooplankton or small benthic animals (Correia, 2003; Weber and Traunspurger, 2017). They are capable of capturing planktonic organisms, giving them great potential to influence the littoral food web (Alcorlo et al., 2004; Geiger et al., 2005). The total length of sub-adult crayfish is 5~8 cm and they share trophic niches with both juvenile and adult crayfish (Correia and Anastácio, 2008; Veselý et al., 2020). In the field, 30% ~80% of individuals are juveniles or sub-adults (Dorn et al., 2005), highlighting the importance of investigating their impacts on the food web to understand their effect on the stability of freshwater ecosystems.

Zooplankton play an important role in freshwater ecosystems and are the main food source for many kinds of fish and macroinvertebrates (Li et al., 2022; Neale and Rudolf, 2025). High densities of white leg shrimps *Litopenaeus vannamei* significantly reduce zooplankton abundance and diversity (Tran et al., 2023). The presence of juvenile and sub-adult crayfish *P. clarkii* has been shown to greatly reduce the abundances of the crustaceans *Daphnia* and *Cyclops* (Correia and Anastácio, 2008), indicating that crayfish have strong potential to feed on and influence zooplankton community.

Aquatic animals including fish, macroinvertebrates, and zooplankton exhibit diurnal feeding rhythms that vary among species and habitats (Williamson et al., 2011; Krylov et al., 2021; Viccon-Pale, 2022). Light intensity influences the circadian rhythm of crustaceans which is regulated by putative pacemakers such as the brain (López-Becerril et al., 2025). The juvenile shrimp *L. vannamei* exhibit higher feeding rates in light than in darkness (Sanudin et al., 2014). Crayfish *P. clarkii* often hide in burrows to avoid predators such as fish or waterbirds, which mainly feed during the day (Haubrock et al., 2019). The feeding activity of crayfish follows rhythmic patterns (Viccon-Pale, 2022), some studies reported peak feeding time in the morning from 8:00 to 10:00 and at night from 19:00 to 22:00 (Xu et al., 2012), while others suggested continuous feeding during the day and at night (Zhou and Zhao, 2007). Most studies on feeding rhythms focus on adult crayfish, while little is known about the behavior of the juveniles.

Invasive crayfish have significant impacts on native crustaceans due to their advantages in growth, reproduction and locomotion (Lodge et al., 2012; Guareschi et al., 2024). Native freshwater shrimps in China are generally omnivorous, feeding on zooplankton, dipteran larvae, periphyton and detritus (Tiffan and Hurst, 2016; Zhu et al., 2022). Presence of shrimp may reduce periphyton biomass and increase macrophyte biomass in freshwater lakes (Ye et al., 2019). Shrimps prefer to feed on cladocerans, leading to changes in zooplankton community structure (Mamani et al., 2019). The shrimp *Exopalaemon modestus* is one of the most abundant and common native shrimp in lakes in the lower reaches of the Yangtze River (Zhao et al., 2023). *E. modestus* predate on various zooplankton species (He et al., 2021), with cladocerans and copepods constituting a high percentage in their diets (Zhu et al., 2022). This shrimp is generally active at night, with feeding activity peaked near 22:00 (Wen and Xie, 2013). Co-occurrences of *P. clarkii* and *E. modestus* have been reported in natural lakes in China (Wu et al., 2022; Zhao et al., 2023). Although field observations indicate a similar trophic niche between the invasive *P. clarkii* and the native *E. modestus* (Wu et al., 2022), their differential predation rhythms on zooplankton remain unclear.

In this study, we hypothesized that there is a circadian rhythm difference between invasive juvenile crayfish and native shrimp in their predation of zooplankton, which might lead to a higher zooplankton feeding intensity in juvenile crayfish than in shrimp. To test this hypothesis, we compared the predation intensity and efficiency of crayfish and shrimp on cladoceran *Simocephalus mixtus*, one of the most common cladocerans in the littoral regions of freshwater lakes (Huang, 2014), at different prey densities under both daytime and night-time conditions. Our results provide insights into the mechanisms through which invasive species adversely affect native ones and partly help explain the invasion success of crayfish.

2 Materials and methods

2.1 Pre-culturing of the animals

Juvenile and sub-adult crayfish were obtained from a rice-crayfish field in Qianjiang, China (112°59”6’ E, 30°11”1’ N) in April 2024. *Simocephalus mixtus*, was collected from a natural pond in Wuhan, China (114°18”24’ E, 30°29”4’ N). Shrimps were collected from Lake Taihu, China (120°13”36’ E, 31°24”05’ N). All organisms were obtained in April 2024 and cultured in the lab for a month prior to the experiment. One day before the experiment, individuals were placed in BG11 medium to evacuate their guts.

The experiments were conducted in cylindrical glass beakers (diameter 15 cm, height 8 cm, volume 1.4 L) with black tape applied under the bottom to mimic natural conditions (Figure 1). Culture medium (500 mL BG11) was added to each beaker as well as shelters (tiles) to mimic crayfish burrows (Haubrock et al., 2019). The beakers were placed in an incubator (PGx-60013) at 25°C, with a light intensity of 1000lx and a light:dark cycle of 12:12 h.

2.2 Predation experiment

The densities of zooplankton were set at 18 ind./L in the low-density treatment, 54 ind./L in the medium-density treatment, and 108 ind./L in the high-density treatment. The density gradients were set based on field observations of cladocerans (Choi and Kim, 2020; Chen et al., 2021). The predation experiments included all three zooplankton densities, with three replicates per treatment. The average body length of *S. mixtus* used in the experiments was 1.57 ± 0.29 mm in body length and 0.24 ± 0.15 mg in wet weight. The number of living zooplankton in each beaker was counted at the end of the experiment, and potential leftovers under the bottom of beakers were checked. A control experiment containing only zooplankton was included to determine the natural mortality rate of zooplankton.

The experiment was conducted with the five treatments at the three zooplankton densities mentioned above, with one predator per beaker. Each treatment has three replicates, and the set-ups are listed in the table (Table 1). The first and second treatments tested the predation of juvenile crayfish on zooplankton during the day and at night, respectively. The third treatment tested the predation of sub-adult crayfish on zooplankton at night. The fourth and fifth treatments tested the predation of juvenile shrimp on zooplankton during the day and at night, respectively.

2.3 Data analysis

Predation rates were estimated based on differences in the biomass of zooplankton between the start and end of the experiment, taking predator biomass into account (Vucic-Pestic et al., 2010):

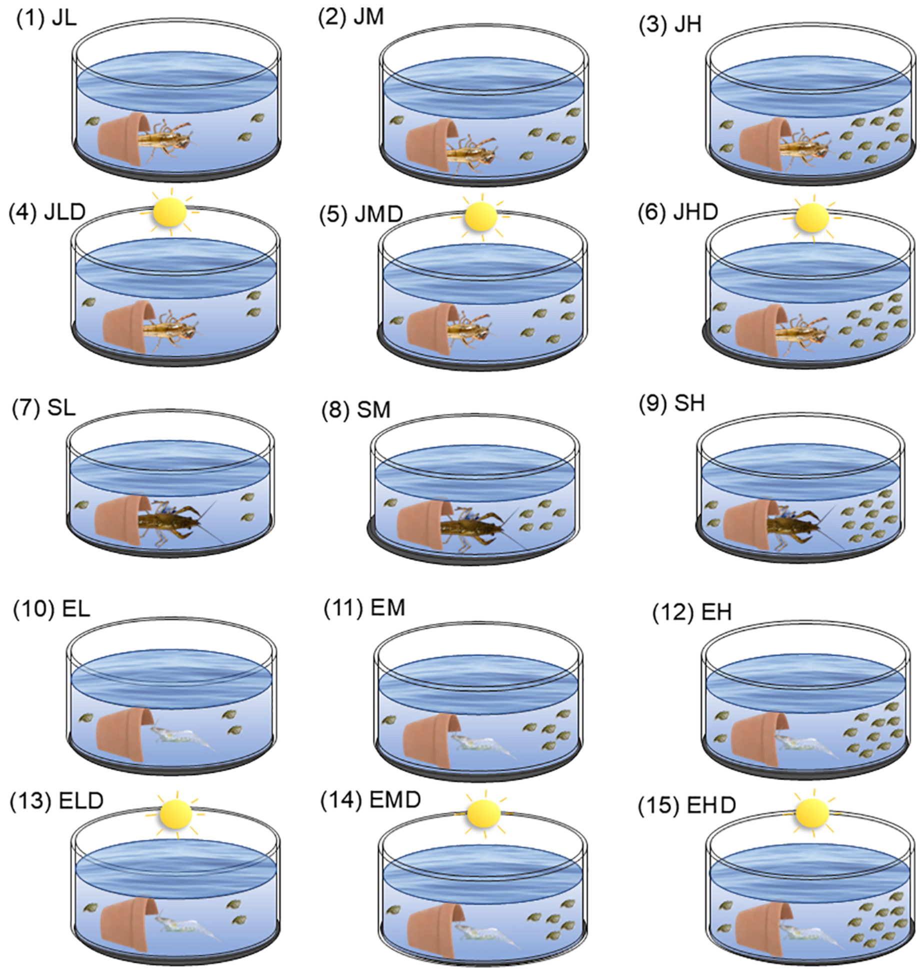

FIGURE 1
Schematic overview of the experimental beakers. (1) Juvenile crayfish *procambarus clarkii* (J) + low density of zooplankton (L); (2) J + medium density of zooplankton (M); (3) J + high density of zooplankton (H); (4) J + L + light during the day (D); (5) J + M + D; (6) J + H + D; (7) Sub-adult crayfish (S) + L; (8) S + M; (9) S + H; (10) shrimp *Exopalaemon modestus* (E) + L; (11) E + M; (12) E + H; (13) E + L + D; (14) E + M + D; (15) E + H + D.

TABLE 1 Experimental set-up for predation experiment.

Number	Predator	Length (cm, mean±SE)	Wet weight (g, mean±SE)	Period	Duration
1	Juvenile crayfish	3.75±0.037	1.10±0.041	Daytime	10:00~18:00
2	Juvenile crayfish	3.74±0.033	1.07±0.028	Night-time	0:00~8:00
3	Sub-adult crayfish	6.68±0.026	8.35±0.034	Night-time	0:00~8:00
4	Juvenile shrimp	3.88±0.073	0.40±0.026	Daytime	10:00~18:00
5	Juvenile shrimp	3.87±0.067	0.40±0.030	Night-time	0:00~8:00

$$r = {}^{(m_t - m_0)}\Big/_{(M \cdot T)}$$

where r is the predation rates (mg/(g·h)), m_0 is the initial biomass of zooplankton (mg), m_t is the final biomass of zooplankton (mg); M is the biomass of predator (g) and T is the duration of experimental period (h). For each treatment, predation rates at different zooplankton densities were analyzed using one-way ANOVA, and the LSD test was used for pairwise comparisons. Differences in predation rates between juvenile crayfish and shrimp during the day or at night were assessed using Student's T-test. All analyses were performed using R (R core Team, 2023).

3 Results

3.1 Predation rates of juvenile crayfish on zooplankton

Predation rates of juvenile crayfish on cladoceran *S. mixtus* increased with increasing prey density (Figure 2). In the control treatments with only zooplankton, no dead individual was observed during the 8 hour-experimental period. At the initial high zooplankton density of 108 ind./L, the night-time predation rate (1.3 mg/(g·h)) was significantly higher than at medium zooplankton density (p < 0.001).

For juvenile crayfish, the daytime predation rate at the high zooplankton density was significantly higher than at medium zooplankton density (p < 0.05; Figure 2A). Mean predation rates tended to be lower during the day than at night, though the differences were not significant at any zooplankton density (Supplementary Table S1).

For sub-adult crayfish, predation rate was significantly higher at the high zooplankton density than at medium zooplankton density (p < 0.05; Figure 3). Juvenile crayfish (length< 5 cm) showed higher predation rates than sub-adult crayfish (length 5~8 cm) at all densities (p < 0.05; Supplementary Table S2).

3.2 Predation rates of juvenile shrimps on zooplankton

For juvenile shrimps, the predation rate was significantly higher at the high zooplankton density than at medium zooplankton

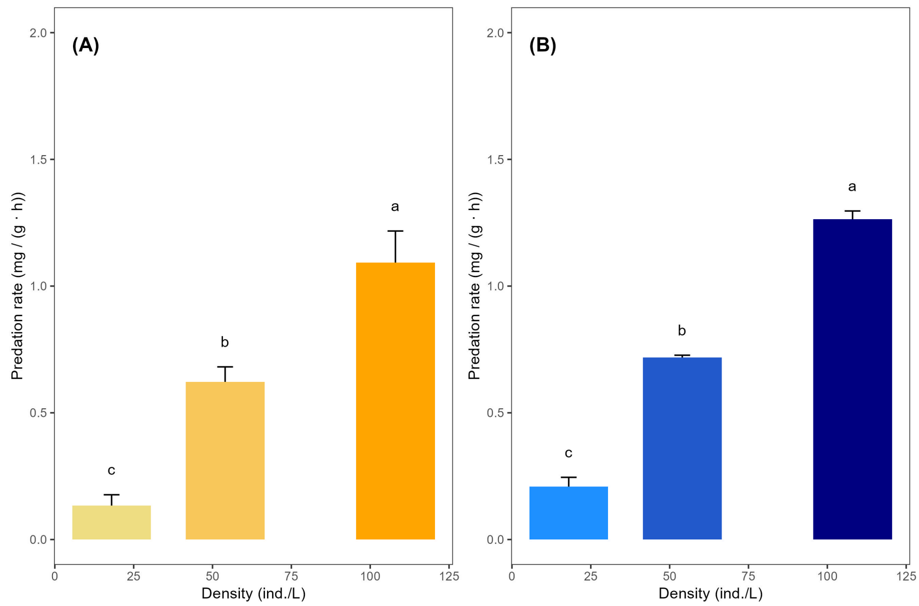

FIGURE 2
Daytime **(A)** and night-time **(B)** predation rates of juvenile crayfish *procambarus clarkii* on different densities (18, 54 and 108 ind./L) of zooplankton. Different letters indicate significant differences in the LSD test by ranks.

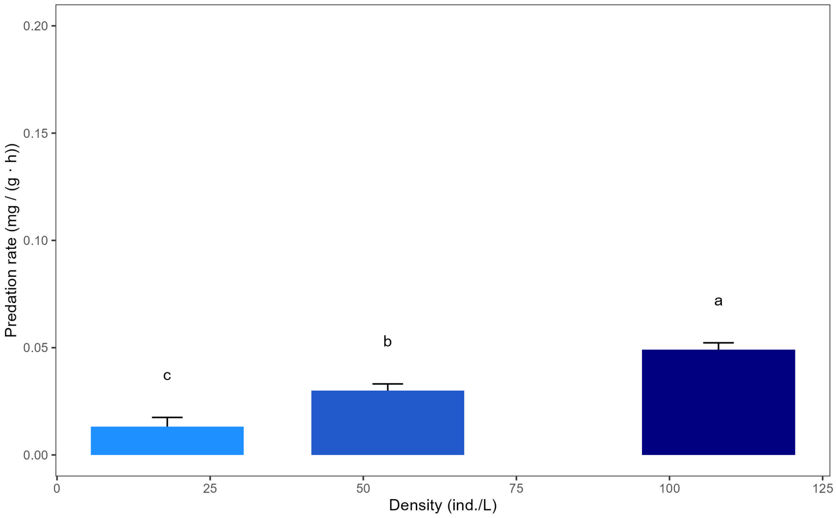

FIGURE 3
Night-time predation rates of sub-adult crayfish *procambarus clarkii* on different densities of zooplankton (18, 54 and 108 ind./L). Different letters indicate significant differences in the LSD test by ranks.

density ($p < 0.05$; Figure 4). Night-time predation rates of juvenile shrimps on zooplankton tended to be higher than those of juvenile crayfish at all zooplankton densities, though the differences were not significant (Table 2).

For juvenile shrimps, the daytime predation rates were similar at all three zooplankton densities, being close to 0 at low and medium densities (Figure 4). Mean predation rates on zooplankton during the day were significantly lower than at night at medium and high zooplankton densities ($p < 0.01$; Supplementary Table S3), with no significant difference at the low zooplankton density.

Predation rates of juvenile shrimp on zooplankton during the day were significantly lower than for juvenile crayfish at medium and high zooplankton densities ($p < 0.05$; Table 2), with no significant difference being found at the low zooplankton density.

4 Discussion

Invasive species generally have higher feeding efficiency, faster growth rate and/or higher fecundity than native species (Vila-

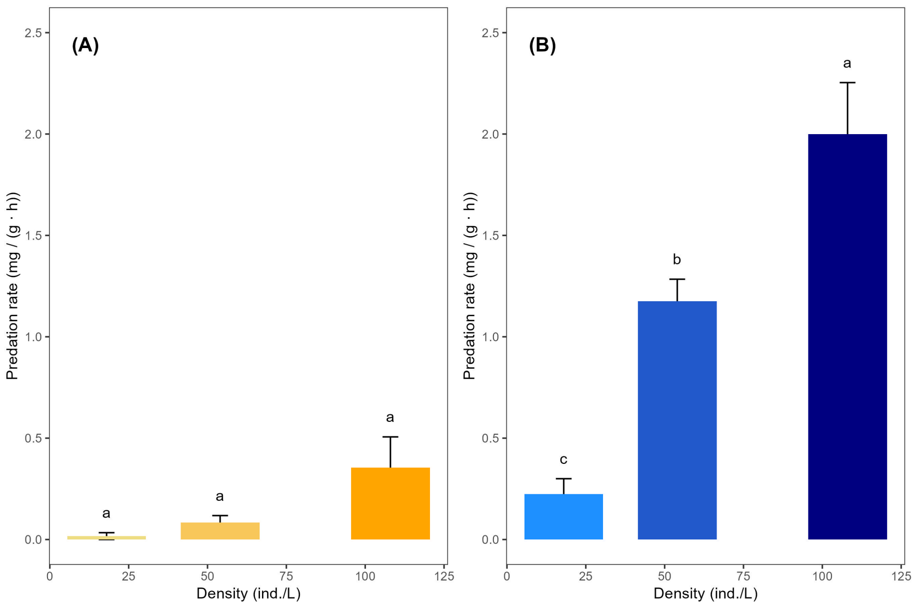

FIGURE 4
Predation rates of shrimps *exopalaemon modestus* during the day **(A)** and at night **(B)** on different densities of zooplankton (18, 54 and 108 ind./L). Different letters indicate significant differences in the LSD test by ranks.

TABLE 2 Daytime and night-time predation rates of juvenile crayfish and shrimp.

Number	Density (ind./L)	Period	Predator	Mean predation rate (mg/(g·h))	*p* value
1	18	Daytime	Crayfish	0.135 ± 0.073	0.0922
		Daytime	Shrimp	0.017 ± 0.029	
		Night-time	Crayfish	0.209 ± 0.063	0.8612
		Night-time	Shrimp	0.225 ± 0.130	
2	54	Daytime	Crayfish	0.622 ± 0.102	0.0034**
		Daytime	Shrimp	0.084 ± 0.058	
		Night-time	Crayfish	0.718 ± 0.016	0.0516
		Night-time	Shrimp	1.175 ± 0.189	
3	108	Daytime	Crayfish	1.093 ± 0.215	0.0210*
		Daytime	Shrimp	0.354 ± 0.263	
		Night-time	Crayfish	1.264 ± 0.057	0.0987
		Night-time	Shrimp	2.000 ± 0.439	

Significant results of *p* values are indicated as follows: $p \le 0.05$ and $p \le 0.01$ are marked with * and **, respectively.

gispert et al., 2005; Van Kleunen et al., 2010). In our study, juvenile crayfish exhibited higher zooplankton feeding intensity than shrimp. The results confirmed the hypothesis that the invasive crayfish and native shrimp differ in circadian rhythm of predation on cladocerans. Invasive juvenile crayfish fed continuously throughout the day and night, while native shrimp showed low feeding activity during the day.

Predation rates of crayfish increased with increasing zooplankton densities in all experiments. As prey abundance rises, encounter and predation rates normally increase (Turesson and Brönmark, 2007). Functional responses describe the relationship between predation rate and prey density (Faria et al., 2023). Juvenile crayfish shows a Type II functional responses when feeding on another cladoceran *Daphnia magana*, maintaining high feeding rates at low prey densities (South et al., 2019). Prey density also affects the defense of cladocerans against handling of predators, which tends to be stronger at higher prey densities (Jeschke and Tollrian, 2000). We found that feeding rates of juvenile crayfish on cladocerans increased as prey density increased, however, density gradient of zooplankton was not high enough to fit the Type I, Type II or Type III functional responses. Further studies are needed to explore the functional responses of juvenile crayfish and shrimp to variations in density of *S. mixtus* and other zooplankton species.

We found that the larger sub-adult crayfish predated less on zooplankton than juvenile crayfish at all zooplankton densities. Furthermore, one individual of sub-adult crayfish also predated less on zooplankton than one juvenile crayfish (1.71 versus 4.88 ind./h under high zooplankton density). This aligns with the fact that juvenile crayfish tend to be carnivores, while sub-adult and adult crayfish shift toward higher degree of herbivory (Correia, 2003). Moreover, juvenile crayfish are capable swimmers (Geiger et al., 2005; Kato et al., 2018), whereas the swimming ability of sub-adult crayfish is limited, resulting in low possibility of catching cladocerans (Barbaresi et al., 2004). Predation of juvenile and sub-adult crayfish on cladocerans will influence zooplankton community structure, with potential cascading effects on phytoplankton abundance and water clarity (Jeppesen et al., 2004). Crayfish influence the zooplankton community not only through predation but also by increasing water turbidity (Correia and Anastácio, 2008), and their influence on zooplankton is more complicated under natural conditions. Differences in eyesight between juvenile and sub-adult crayfish also contribute to variations in their catching ability (Fanjul-Moles and Prieto-Sagredo, 2003). As sensitivity to light varies between juvenile and adult crayfish (Ou and Liang, 2017), further studies are needed to explore how light influences their predation rhythms.

Juvenile crayfish showed similar feeding rate but a longer feeding period on *S. mixtus* compared to shrimps of similar length, indicating higher feeding capacity of this invasive species. In our study, the feeding rate of juvenile crayfish tended to be slightly lower during the day than at night. Shrimp *E. modestus* mainly fed at night, which aligns with findings of other studies of diurnal variation in the feeding activity of another shrimp of the same genus (*E. carinicauda*) (Wang et al., 2023). For shrimp *L. vannamei*, the circadian rhythm of nocturnal feeding is driven by an endogenous clock and persist under different conditions (Santos et al., 2016). Juvenile crayfish fed continuously during the day and at night, showing no apparent circadian rhythm, which might be linked to the fact that crayfish rely on both eyesight and smell for foraging (Zhou and Zhao, 2007). The night-time feeding rates of juvenile crayfish were close to that of shrimp, indicating that juvenile crayfish has high catching ability on cladocerans (South et al., 2019). Cladocerans can identify predators with different feeding habitats and behaviors (Ekvall et al., 2020; Lee and Hansson, 2024). Juvenile crayfish are ambush predators, while shrimp swim at relatively constant speeds at night (Hu et al., 2001; Renai and Gherardi, 2004), which may also explain the observed differences in their predation rhythms on *S. mixtus*. Size of the predator influence the enzyme digestive activities, which indirectly influence the predation rates and frequency (Gilannejad et al., 2021). Juvenile shrimp at weight 0.4 g showed relatively lower enzyme digestive activities than shrimp at weight 0.1-0.3 g (Wang et al., 2010). For juvenile crayfish, enzyme digestive activities increase steadily through 42 days of development and remain high at weight 0.6 g (Hammer et al., 2000). Our study on early stages of invasive crayfish and native shrimp supports the inherent superiority hypothesis that invasive species possess advantages over native species in feeding behaviors and capacity (Ju et al., 2013). Presence of crayfish has also been found to cause shift in the trophic niche of shrimp (Baudry et al., 2024). Moreover, adult and sub-adult crayfish have the potential to prey on shrimps (Banha and Anastácio, 2011), adding to their invasion success.

To conclude, juvenile crayfish and shrimp were found to consume cladocerans efficiently. Juvenile crayfish fed more at night than during the day and at a faster rate than sub-adult crayfish. Juvenile crayfish also fed for longer periods than shrimp, showing higher feeding capacity for invasive species than their native counterparts (Faria et al., 2025). Future studies are needed to investigate the differences between invasive crayfish and native shrimps in natural lakes, and to explore the overall impacts of decapods on the zooplankton community and the entire freshwater ecosystem.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

HZ: Conceptualization, Data curation, Formal Analysis, Funding acquisition, Methodology, Resources, Software, Supervision, Visualization, Writing – original draft, Writing – review & editing. YL: Writing – original draft, Formal Analysis, Investigation, Methodology, Resources. JG: Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Validation, Writing – review & editing. ML: Investigation, Methodology, Resources, Writing – review & editing. HW: Investigation, Methodology, Resources, Writing – review & editing. YcJ: Investigation, Resources, Writing – review & editing. YyJ: Visualization, Writing – review & editing. LW: Investigation, Resources, Writing – review & editing. XZ: Investigation, Resources, Writing – review & editing. EJ: Supervision, Visualization, Writing – review & editing. FC: Supervision, Visualization, Writing – review & editing.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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