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RESEARCH ARTICLE

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Predatory decapods for biological control of pest snails: Ecological, behavioural and mechanical aspects

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Abstract

1. Integrated pest management (IPM) is invaluable in fighting parasitic diseases carried by freshwater snails as disease-transmitting vectors. Here, we studied the effectiveness of two non-GMO monosex decapods, the giant freshwater prawn *Macrobrachium rosenbergii* and the Australian redclaw crayfish *Cherax quadricarinatus*, as biocontrol agents against such disease-transmitting snails, namely, *Melanoides tuberculata*, *Thiara scabra*, *Tarebia granifera* and *Haita acuta*, found in fishponds.
2. In food-choice experiments, the two decapods preferred snails which had thinner, weaker shells, with this feeding selectivity being stronger for the prawns than for the crayfish, which demonstrated more opportunistic feeding behavior. Notably, the crayfish were more efficient in snail predation than the prawns, displaying both shorter handling times and lower encounter rates.
3. Subsequent physical–mechanical tests on the snails revealed that the snail species least preferred by the prawns had significantly 2.5 times thicker shells, which required 8 N more force to initially break.
4. Practical implication: our findings suggest that the two monosex decapods could provide sustainable biocontrol solutions, potentially enhancing IPM strategies in aquaculture and offering win-win-win sustainable polyculture for fish farmers, with the biocontrol agent, which could be tailored to farmers' preferences, doubling as a valuable polyculture-produced protein.

KEYWORDS
Cherax quadricarinatus, encounter rate, food choice, functional response, handling time, integrated pest management (IPM), *Macrobrachium rosenbergii*

1 | INTRODUCTION

Integrated pest management (IPM) approaches to reducing pesticide use for pest control may incorporate nature-based solutions, such as natural enemies of the target pests (Haggerty et al., 2021; Halstead et al., 2018). In agricultural environments, where elimination (or more realistically, near elimination) of the pest is the goal, a predator that can collapse the pest population is preferred, for example, barn owls, nematodes and parasitoids (Azmi et al., 2022; Meyrom et al., 2009; Stiling & Cornelissen, 2005). Pests that are particularly damaging in freshwater environments are freshwater snails, since they serve as intermediate hosts for infectious parasites. Diseases caused by such snail-borne parasites include schistosomiasis in humans (Eyre et al., 2020; Pennance et al., 2022; Prichard et al., 2012) and an array of diseases in farmed fish, which cause havoc in aquaculture industries. The best-known way to remedy snail-borne diseases is prevention (Ozretich et al., 2022) through eradication of the snails, which reduces the parasite load in the water and hence the chance of infection and transmission. In aquaculture, such solutions usually involve chemical pesticides (Al-Akel & Suliman, 2012; Mitchell et al., 2007; Sokolow et al., 2016). In general terms, snail predators might include competitors and predatory insects (Turner & Chislock, 2007), fish and leeches (Ahlgren & Bronmark, 2012). Specifically for aquaculture, nature-based IPM solutions for the eradication of snails include snail predators, such as black carp (Ben-Ami & Heller, 2001), catfish (Ledford & Kelly, 2006; Monde et al., 2016, 2017) and some decapod crustaceans (Haggerty et al., 2020; Hoover et al., 2019; Monde et al., 2017; Savaya-Alkalay et al., 2014; Savaya, Glassner, et al., 2020; Savaya-Alkalay, Ovadia, et al., 2018; Sokolow et al., 2016; Swartz et al., 2015).

Among the decapod predators that have been used as biocontrol agents against snails is the giant freshwater prawn, *Macrobrachium rosenbergii* (Palaemonidae). This predator has been used as a biocontrol agent against snails that transmit human diseases (Hoover et al., 2019; Sokolow et al., 2014) and against apple snails in rice paddies (Azmi et al., 2022; Savaya-Alkalay, Ovadia, et al., 2018; Wang et al., 2023). Since 2017, it has also been used as a biocontrol agent in aquacultural practices in Northern Israel (Savaya, Glassner, et al., 2020). *Macrobrachium rosenbergii* is itself a highly valuable aquacultural product, amounting to an annual production of 337 tons and grossing 2.5 million USD (FAO, 2025). Ecologically—as an opportunistic omnivore with carnivorous tendencies (Dusci et al., 2022; Lima et al., 2014)—it has been shown to be a voracious predator of snails (Savaya, Glassner, et al., 2020; Savaya-Alkalay, Ovadia, et al., 2018; Sokolow et al., 2014; Swartz et al., 2015). However, before releasing this species into the environment as a biocontrol agent, assurances must be obtained that *M. rosenbergii* will not become invasive. The solution is rooted in the introduction of biotechnologically produced monosex populations, either all-female or all-male (Savaya, Glassner, et al., 2020; Shaked et al., 2024; Ventura & Sagi, 2012), that cannot reproduce if there are no wild individuals of the species in the area.

Another decapod crustacean with excellent potential as a biocontrol agent against snails is the Australian redclaw crayfish, *Cherax quadricarinatus* (Parastacidae). A monosex all-female technology has recently been established for this species (Shaked et al., 2024). Like *M. rosenbergii*, this omnivorous crayfish is also a valuable aquaculture product, popular as a food in Southeast Asia and Australia (FAO, 2011; Haubrock et al., 2021; Marufu et al., 2018).

In the current study, the efficacy of these two non-GMO biocontrol species was tested against four species of pest snail—*Melanoides tuberculata* (Thiaridae), *Thiara scabra* (Thiaridae), *Tarebia granifera* (Thiaridae) and *Haita acuta* (Physidae)—that are prevalent in fish ponds in Northern Israel [as mapped in aquacultural fishponds and their environment in Northern Israel (Moscovitz et al., 2024)]. These snails are known globally as successful invaders when introduced into non-endemic areas (Ben-Ami & Heller, 2001; Dillon et al., 2002; Facon & David, 2006; Heller et al., 2014; Okumura & Rocha, 2020; Quintana et al., 2001; Thompson et al., 2009; Tolley-Jordan & Chadwick, 2019; Tolley-Jordan & Owen, 2008). Indeed, after accidental introduction into Northern Israel, they have been found in massive numbers on the bottoms of fishponds (reaching thousands of snails per 0.25 m^2), where they act as hosts for vectors of diseases harming the farmed fish (Leventer, 1981; Moscovitz et al., 2024; Savaya, Glassner, et al., 2020).

Since the above four species of pest snail have different external morphological traits, it is expected that, for the same snail size grade, the handling times of the predators may vary between snail species, as has previously been found for decapods (Dumas et al., 2013; Mascaró & Seed, 2000; Savaya, Glassner, et al., 2020); for example, in contrast to the species of the Thiaridae family, *H. acuta* has a smooth thin shell, which should be easy to crack open on the one hand, but could be difficult to hold on the other. The apparently thicker, conical shells of Thiaridae species have unevenly patterned (*Tarebia granifera*, *M. tuberculata*) or spiny (*Thiara scabra*) surfaces, which could either make them easier to hold or more difficult to break. In general, it is common for predators (both vertebrates and crustaceans) to prefer food that is easier to handle, since it increases the overall ratio of gained energy to time spent foraging (Dumas et al., 2013; Mascaró & Seed, 2000; Rudolf, 2008; Savaya-Alkalay, Ovadia, et al., 2018). Recent studies on functional responses in two- or three-prey systems have focused on adaptive foraging, in which a predator essentially shows opportunistic behaviour for similarly perceived prey species, while predators that perceive prey species as very different from each other generally display more selective feeding behaviour, tending to focus on a single prey species (Lehtinen et al., 2024; Van Baalen et al., 2001; Van Leeuwen et al., 2013).

In this study, we hypothesized that predators' perceptions of different snail species would be reflected in prey preference. Therefore, we compared the two crustacean predators in a food-choice experiment in which the prey comprised the above four disease-transmitting snail species. By quantifying the differences in foraging traits, that is, prey encounter rates and handling times, between the two predator species, we could offer another IPM tool against snails in aquaculture. Such as with apple snails (Wang et al., 2023) or schistosoma spreading snails (Ozretich et al., 2022; Sokolow et al., 2014; Swartz et al., 2015), this study could therefore have implications for other pest or disease-spreading snails beyond the four snail species investigated here.

2 | METHODS

2.1 | Food-choice experiments

The prey for the food-choice experiments comprised snails collected from fishponds in Emek HaMa'ayanot, Northern Israel, namely, from the Tirat Zvi farm (N 32.400784, E 35.530227), the Ein HaNaziv farm (N 32.471151, E 35.507449) and a drainage trench near Kibbutz Shlukhot (N 32.476060, E 35.486404), based on mapping from a previous study (Moscovitz et al., 2024). A uniform shell width of 4–6 mm at the snail widest point in the shell was determined by using a set of sieves, one with holes of 6 mm and the second of 4 mm, thus snails which were trapped between them after rigorous washing were used for the experiment, as previously described (Savaya-Alkalay, Ovadia, et al., 2018; Savaya, Glassner, et al., 2020). This size grade was chosen because it is the smallest size at which snails reach sexual maturity, and thus the smallest size capable of disease-causing trematode transmission (Livshits & Fishelson, 1983; Pinto et al., 2018; Pointier et al., 1992). Snails were tested for vitality by placing them in a water-filled container and choosing those that climbed up the walls.

Two mirroring food-choice experiments were conducted, one with *M. rosenbergii* prawns as the predator and the other with *C. quadricarinatus* crayfish, using 30 medium-sized (±15–20 g) naïve female decapods of each species, as previously described (Savaya, Glassner, et al., 2020; Shaked et al., 2024). A similar body mass was used instead of body or body-part length, since medium-sized adults of both species would have very different lengths, with *M. rosenbergii* being longer and having long, thin claws. At the same time, *C. quadricarinatus* is more stout and has shorter, thicker claws when compared side by side (see exemplary pictures in Figure 1); thus, body mass was used as a standard for predator size. Female (rather than male) decapods were chosen because all-female monosex technology is available for both species, and all-female populations can be stocked at higher densities than all-male populations in aquaculture systems (Levy et al., 2017; Rahman et al., 2022; Wahl et al., 2023, 2025). Each predator was presented with five snails of each species of size grade of 4–6 mm (a total of 20 snails per predator). Predation on snails was monitored for one week. Before the crayfish experiment, each individual was checked for its moult stage using X-ray-assisted measurement of its gastroliths to avoid using crayfish at a far-advanced moult stage, which can alter feeding behaviour (Shaked et al., 2024).

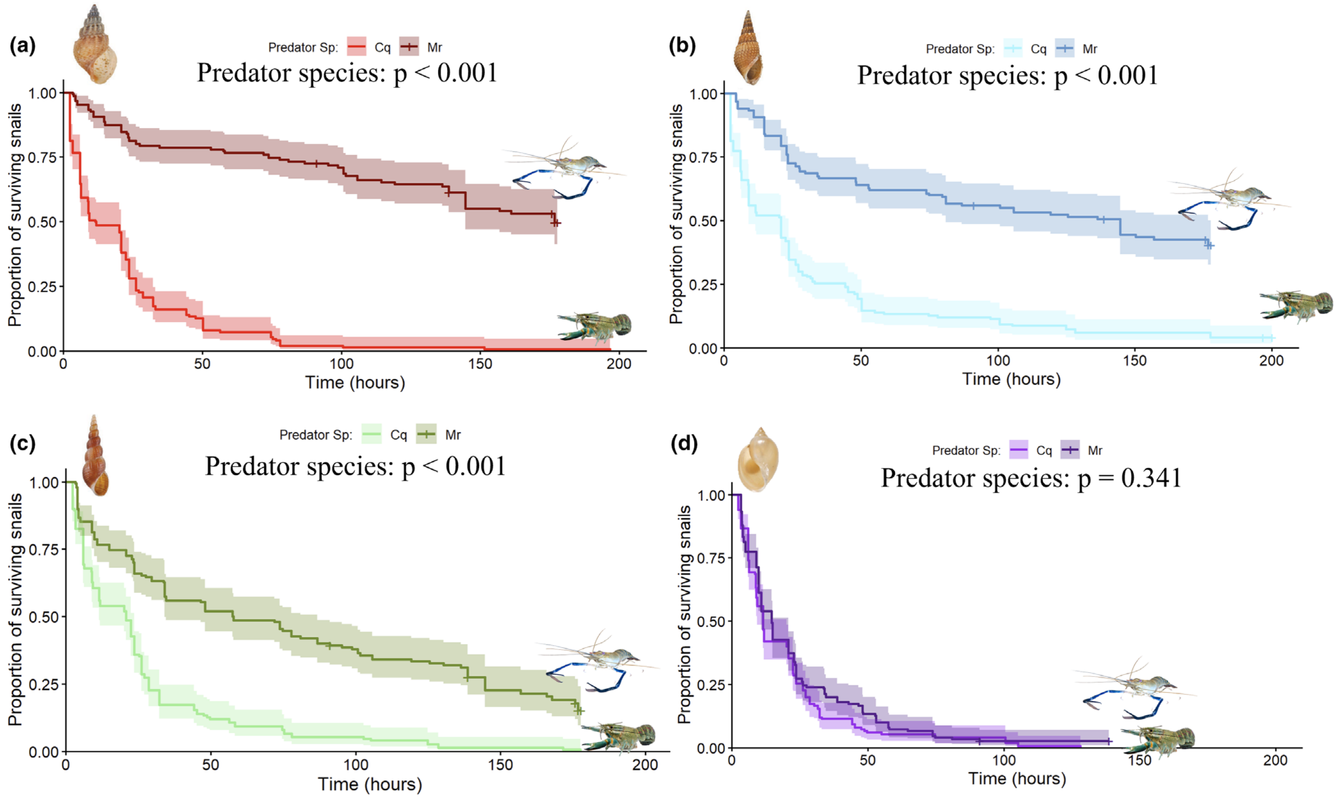

FIGURE 1 Comparison of Kaplan–Meier curves for survival of each snail species, (a) *Thiara scabra*, (b) *Tarebia granifera*, (c) *M. tuberculata tuberculata* and (d) *H. acuta*, in the presence of the predator, either the crayfish (Cq) or the prawn (Mr). Lighter hues represent snail survival in the presence of a crayfish, and darker hues represent snail survival in the presence of a prawn. The ending + sign is the censor ending for the surviving snails. Shading represents the 95% confidence interval. *p* values correspond to Table S2. For snail survival comparison with the control tanks, see Figure S3.

Each decapod was held in a covered 130-L experimental tank with an independent internal water filtration-aeration system, under a 12:12 light/dark photoperiod and at 27 ± 1°C. The decapods were fed dry pellets ad libitum. On the first day of the experiment, they were given an additional feed (frozen bloodworms, artemia, cyclops) about half an hour before the snails were introduced into the tank. The feeding regimen was intended to ensure that predation was due to preference and not to starvation.

For each predator species, the experiment was conducted in six rounds, each comprising five experimental tanks and one control tank (snails alone, no predator). This resulted in 30 experimental tanks and six control tanks per experiment, for a total of 72 tanks across the two experiments. In each round, two GoPro cameras were placed in randomly selected tanks during the light hours. A camera was moved to a different tank if the initially chosen predator had predated all the snails in its tank, but there were still snails in the other tanks. Snails were checked for vitality three times a day during the first three days of the experiment, and once a day on the remaining four days. A snail was considered alive if its operculum was in place, and dead if the shell was empty or in pieces, or if there was no shell at all.

In practice, for the prawn experiment, there were only five control tanks instead of the planned six. For the crayfish experiment, in the first two blocks (10 experimental and two control tanks), most of the snails had been predated by the first snail vitality check, 6 h after the food choice experiment began. Thus, the predators' preferences could not be determined. Therefore, for the remainder of the crayfish rounds, on the first day, the tanks were examined every 3 h for 12 h (e.g. at 9:00 AM, 12:00 PM, 3:00 PM, 6:00 PM and 9:00 PM) to pinpoint crayfish preferences. On the following days, the tanks were examined as planned. The first two blocks were omitted from the food-choice analysis and functional response quantification. However, they were used for the video analysis, while two blocks were added to the food-choice experiment to achieve 30 crayfish repetitions and match the prawn experiment. Lastly, three crayfish died for unknown reasons at the beginning of the experiment and were immediately replaced. The replacement crayfish were not X-rayed; however, none moulted during the experiment or the following week.

2.2 | Functional response traits

Foraging traits were quantified using the random-predator equation, developed to analyse the functional response of predators facing prey depletion (Ovadia et al., 2001; Rogers, 1972). Specifically, we used the following linearized form of the random predator equation [which has been used successfully in many empirical studies (Islam et al., 2022; Ovadia et al., 2001; Toscano et al., 2014)] to estimate the prey encounter rate a (in units of 1/h) and the handling time h (in units of hours/snail) for each predator species foraging on snails:

$$t_h = \left(\frac{1}{a}\right) \cdot \left(\frac{N_0}{N_f}\right) + h \cdot (N_0 - N_f)$$

where t_h (in hours) is the total time spent foraging in the tank, N_0 is the initial number of snails in the tank and N_f is the final number of live snails in the tank. The first term in the equation represents the total time spent searching for/encountering snails, and the second term is the total time spent handling the captured snails. If all the snails had been predated, and N_f was 0, N_f was taken as 0.01 to avoid mathematically invalid results.

To capture the entire predation rate spectrum, the data were divided into time blocks within the experiment (up to 5 h, up to 10 h, up to 15 h and so on), and the number of live snails remaining in any time block was recorded as the N_f of that block. We first estimated the encounter rate and handling time for all 20 snails together, and thereafter, for each snail species separately.

2.3 | Predation behaviour

As proof of snail predation, video recordings were made for eight *M. rosenbergii* prawns and six *C. quadricarinatus* crayfish during the food-choice experiment. Inspection of the videos revealed that important insights could indeed be obtained by comparing the predation behaviour of the two predator species. Thus, partially based on previous ethograms of *M. rosenbergii* and *C. quadricarinatus* (Barki et al., 1992; Barki & Karplus, 1999; Dos Santos et al., 2018; Dos Santos & Pontes, 2016), behavioural variables were defined as follows to compare between the two predator species: (1) counts of the use of appendages (claws, walking legs or mandibles) during predation; (2) number of prey encounters with the different snail species (or grouping of species when identification was visually impossible), defined as the number of times the crustacean picked up a snail and placed it in its mouth; (3) ingestion duration, defined as starting with the placing of a snail in the crustacean's mouth and ending when the snail had been fully predated or dropped half-eaten and (4) direct handling time (in minutes/snail), measured in cases where a predator ingested a snail entirely and the event was continuously caught on camera.

In practice, two of the prawns were excluded from these analyses owing to inactivity throughout the entire recording period (which would have biased the findings). Due to marked variations in video time per animal (Supporting Information, Section S3. Behaviour), we standardized encounter counts to total video time for each predator. The use of an appendage was standardized for each predator by the total use of all appendages. These standardizations enabled the presentation of the proportions of encountered snails and of used appendages.

2.4 | Physicochemical properties of the snail shells

2.4.1 | Shell thickness of the snail species most and least preferred by *M. rosenbergii* prawns

Shell thickness is a trait likely to influence feeding preferences, as it would take more effort to crack or crush a thicker shell initially. Thus, we investigated the difference in shell thickness of the snail species most (*H. acuta*) and least (*Thiara scabra*) preferred by *M. rosenbergii* prawn. Thirty empty snail shells of size grade 4–6 mm for each of the two species were washed with soap and water to remove possible soft-tissue remnants and then air-dried. The empty shells were sliced longitudinally using a razor. The shell slice was attached, with the hollowed side facing up, to a scanning electron microscopy (SEM) plate using double-sided carbon tape. Shell thickness was measured twice in the same location, that is, on the left side of the sliced shell on the first shell whorl, using SEM (HRSEM, Gemini 300, Zeiss), and then averaged for a shell thickness for each snail (total of 60 measurements per species).

2.4.2 | Compression testing of the snails most and least preferred by *M. rosenbergii* prawns

A total of 50 live most preferred (*H. acuta*) and 70 live least preferred (*Thiara scabra*) snails of size grade 4–6 mm were tested in a LabVIEW program-controlled compression tester (Portnikov et al., 2013; Portnikov & Kalman, 2018). The experimental set-up, originally designed for single-particle compression testing, is illustrated and detailed in Figure S1 and in the above-cited literature, with the experimental particle being a snail. A representative force–displacement curve for a compression test of a *Thiara scabra* snail is shown in Figure S2. Each compression test was conducted independently for a first and a second breakage event, with a breakage point identified by a sudden drop of more than 20% in the measured force (Figure S2). The first and second breakage points were measured to investigate whether a predator requires less or similar force to prey on a previously encountered snail. Before testing, all snails were euthanized in ice water.

2.4.3 | Physicochemical properties of the main shell components

The main constituents of the shells and their grain sizes are presented in the Supporting Information, Section S4.

2.5 | Statistical analysis

2.5.1 | Predation preferences

Predation preferences based on snail mortality rate caused by predation were analysed using the Cox proportional hazards model (Hosmer et al., 2008), with treatment (control = 0, predator = 1) and snail species as covariates; for this analysis, the 'Survival' (Therneau et al., 2024) and 'Survminer' (Kassambara et al., 2024) packages in R were used. The categorical variable 'snail species' was converted into a set of binary predictor variables, with *H. acuta* as the reference group. Due to very low snail death events in the control (no predator) tanks, the mean survival of the snails was calculated using the 'survRM2' package (Uno et al., 2022) in R. For comparison between the predators, the predator species was added as a covariate.

This time-to-event data allows evaluation of the different predictors (such as snail species) on snail mortality rate due to predation, allowing comparison of the two predators' preferences and the chances of a death event occurring for each snail species in the presence of either the prawn or the crayfish predator. To control for repeated measurements in the same tank and with the same predator, we used a robust variance estimator grouped (clustering by ID) by observations per tank (Lin & Wei, 1989).

2.5.2 | Functional response traits: Handling time and encounter rate

The estimation of handling times and encounter rates for all snails together and for each snail species separately was performed using the linearized form of the random predator equation presented above (Ovadia et al., 2001) with the 'hglm' package (Alam et al., 2019) in R software. To test for differences in foraging traits between the two predator species, we included in the model a dummy/binary variable with *M. rosenbergii* = 1 and *C. quadricarinatus* = 0. To control for repeated measurements on the same individual predators, predator ID was included as a random factor in the statistical model.

2.5.3 | Predation behaviour

Differences between the predators regarding the proportional time spent ingesting prey, the direct encounter rate with each snail species or grouping of species, the proportional use of appendages and the direct measurement of handling time were tested using multivariate repeated measures ANOVA (RMANOVA), followed by post-hoc contrasts performed using the 'emmeans' package (Lenth et al., 2025) in R software. The proportions of direct encounters and used appendages were arcsin(sqrt(x)) transformed due to violations of assumptions. The proportion of ingestion time was tested using the Kruskal–Wallis test due to a violation of the normality assumption and the small sample size. The direct ingestion times were compared using the Welch two-sample *t*-test due to unequal variances.

2.5.4 | Shell thickness

The differences between species in the mean shell thickness of the first body whorl of empty snail shells were tested with the Welch *t*-test for unequal variances using the 'rstatix' (Kassambara, 2023), 'emmeans' (Lenth et al., 2025) and 'afex' (Singmann et al., 2024) packages in R software for $\log_{10}$-transformed data (to meet the test assumptions).

2.5.5 | Compression tests

As previously noted, compression tests were performed for a total of 50 *H. acuta* and 70 *Thiara scabra* snails. The sample sizes were determined using a previously published convergence-based result method (Portnikov et al., 2013; Portnikov & Kalman, 2014), as detailed in Figure S2. Based on this criterion, 38 *H. acuta* and 63 *Thiara scabra* snails were selected for the final statistical analysis. The results were subsequently analysed using a multivariate RMANOVA with 'afex' (Singmann et al., 2024) and 'emmeans' (Lenth et al., 2025) packages in R software, testing for differences in breakage force required for the first and second breakage points within and between species. Breakage force data were log10-transformed due to an assumption violation.

3 | RESULTS

3.1 | Food choice

Two mirroring food-choice experiments were conducted, one with *M. rosenbergii* prawn as the predator and the other with *C. quadricarinatus* crayfish as the predator. Analysis of the combined data for the two predator species (Whole model: Wald test = 376.4, df = 5, $p < 0.001$, Table S1) revealed that their presence significantly increased the snails' mortality rate by 14.3-fold ($e^{\beta} = 14.30$, $z = 18.298$, $p < 0.001$; Table S1). Notably, the snail mortality rate was 2.8-fold higher when caused by the crayfish compared to the prawn ($e^{-\beta} = 2.86$, $z = -6.649$, $p < 0.001$; Table S1).

The mortality rate of *Thiara scabra* was 8.3-fold higher in the presence of the crayfish than in the presence of the prawn ($e^{-\beta} = 8.349$, $z = -7.373$, $p < 0.001$; Figure 1a, Table S2). The mortality rate of *Tarebia granifera* was 3.5-fold higher in the presence of the crayfish than in the presence of the prawn ($e^{-\beta} = 3.56$, $z = -5.014$, $p < 0.001$; Figure 1b, Table S2). The mortality rate of *M. tuberculata* was threefold higher in the presence of crayfish than in the presence of prawns ($e^{-\beta} = 2.95$, $z = -5.074$, $p < 0.001$; Figure 1c, Table S2). However, the mortality rate of the most preferred snail species, *H. acuta*, did not differ significantly between the two predator species; both had almost eliminated the *H. acuta* snails by the 80-h mark and had eliminated them by the end of the experiment ($e^{-\beta} = 1.198$, $z = -0.953$, $p = 0.341$; Figure 1d, Table S2).

A complete description and in-depth analysis of each experiment is presented in the Supporting Information (Section S2 and Tables S3 and S4 for *M. rosenbergii* prawn and *C. quadricarinatus* crayfish, respectively). Additional evidence of predation by the two predators is presented in the videos (Videos 1 and 2, Supporting Information).

During the experiments, cracked shells and partially consumed snails were found (Figure S4) as proof that snails were indeed predated. Furthermore, the partially consumed still-alive snails indicated that the decapods could attempt to prey on a snail but 'give up' after some time, likely returning to it after a while since most snails were indeed eventually predated (see examples in Supporting Information, Videos 3 and 4 and Figure S4).

3.2 | Predation behaviour: Handling time (*h*) and encounter rate (*a*)

The total recording times for the *C. quadricarinatus* crayfish and the *M. rosenbergii* prawns were 26.95 h (1617 min), and 30.93 h (1856 min), respectively (for complete information regarding the video analyses, see Table S5). From the video data, the crayfish ($N = 6$ recorded predators, $n = 100$ videos) spent 11.7% ± 22.7% (mean ± 1SD) of the time ingesting prey. In comparison, the prawns ($N = 6$ recorded predators, $n = 110$ videos) spent 7.7% ± 23.6% of the time ingesting prey, that is, significantly less time than the crayfish (Kruskal–Wallis, predator species: $\chi^2_1 = 8.37$, $p = 0.003$). Some individual predators were significantly more active, while others were less active (Kruskal–Wallis, predator ID: $\chi^2_{11} = 41.422$, $p < 0.001$).

Due to the small sample size of videos in which predator–prey encounters were recorded and due to difficulties in identifying the snail species in many of the video recordings, there was not sufficient statistical power to compare the proportion of encounters with each snail species (see Supporting Information, Figure S5). Only a very few videos recorded direct handling time (Figure S6), but nonetheless we observed interesting trends in appendage use (Figure S7). There was a marginally significant difference between crayfish and prawns regarding the appendages used for handling the snails (RMANOVA Appendages: Wilks $\Lambda = 0.529$, $F_{2,9} = 3.992$, $p = 0.057$) in that the crayfish used their claws significantly less frequently than the prawns [3% ± 4% vs. 37% ± 35% use of claws (mean ± 1 SD), respectively; Figure S7] (claws contrast: $t_{20.8} = -3.17$, $p = 0.004$). There were no significant differences for the other behavioural traits (for complete information, see Supporting Information, Figure S7).

In the *M. rosenbergii* prawn experiment (Table 1), the shortest handling time was 8 h for *H. acuta* ($t = 3.123$, $p = 0.0019$), followed by 27 h for *M. tuberculata* ($t = 10.326$, $p < 0.001$), 36 h for *Tarebia granifera* ($t = 10.32$, $p < 0.001$) and, lastly, 58 h for *Thiara scabra* ($t = 14.074$, $p < 0.001$). When considering all four snail species together, the average handling time was 10 h (All: $t = 16.267$, $p < 0.001$). The encounter rate (*a*) for *H. acuta* was 0.08 1/h ($t = 5.51$, $p < 0.001$), followed by 0.17 1/h for *M. tuberculata* ($t = 2.417$, $p = 0.016$). The encounter rate for *Tarebia granifera* was negative, being −0.67 1/h and not significantly different from zero ($t = -0.45$, $p = 0.653$), and that for *Thiara scabra* was also negative, being −0.04 1/h, but significantly different from zero ($t = -4.148$, $p < 0.001$). Across all snail species, the average encounter rate was 0.36 1/h, and this value did not differ significantly from zero ($t = 0.679$, $p = 0.498$). Thus, when all the snails were present, and the results for the most and least preferred species were pooled together, the encounter rate was very low.

In the *C. quadricarinatus* crayfish experiment (Table 1), the shortest handling time was 0.3 h for *H. acuta* (not significantly different from zero, $t = 0.132$, $p = 0.895$), followed by 5.5 h for *Thiara scabra*

TABLE 1 Encounter rates (*a*) in units of 1/h and handling time (*h*) in units of hours for all the snails together and for each snail species separately.

		M. rosenbergii **prawn**				***C. quadricarinatus*** **crayfish**			
Snail species	**Factor**	**Estimate**	**SE**	***t*-value$_{df}$**	***p* value**	**Estimate**	**SE**	***t*-value$_{df}$**	***p* value**
All	*a*	0.364	4.042	0.679_{301}	0.498	0.074	1.293	10.370_{306}	**<0.001**
	h	10.878	0.668	16.267_{301}	**<0.001**	1.709	0.491	3.478_{306}	**0.0005**
H. acuta	*a*	0.082	2.206	5.510_{314}	**<0.001**	0.054	1.949	9.538_{325}	**<0.001**
	h	8.320	2.664	3.123_{314}	**0.002**	0.301	2.277	0.132_{325}	0.895
M. tuberculata	*a*	0.178	2.313	2.417_{302}	**0.016**	0.072	2.300	5.991_{312}	**<0.001**
	h	27.351	2.649	10.326_{302}	**<0.001**	6.366	2.842	2.240_{312}	**0.026**
Thiara scabra	*a*	−0.045	5.254	-4.148_{301}	**<0.001**	0.075	2.683	4.930_{316}	**<0.001**
	h	58.288	4.142	14.074_{301}	**<0.001**	5.451	3.269	1.668_{316}	0.096
Tarebia granifera	*a*	−0.668	3.326	-0.45_{298}	0.653	0.089	2.683	4.191_{307}	**<0.001**
	h	36.251	3.512	10.32_{298}	**<0.001**	9.705	3.385	2.867_{307}	**0.004**

Note: Significant results are indicated in bold.

(also not differing significantly from zero, $t=1.668$, $p=0.096$) and then by 6.3 h for *M. tuberculata* ($t=2.240$, $p=0.0258$). Finally, the longest handling time was that for *Tarebia granifera*, being ~10 h ($t=2.867$, $p=0.0044$). For all the snail species together, the average handling time was 1.7 h ($t=3.478$, $p<0.001$). The encounter rate with *H. acuta* was 0.053 1/h ($t=9.538$, $p<0.001$), and the encounter rates for *M. tuberculata* and *Thiara scabra* were 0.072 1/h ($t=5.991$, $p<0.001$) and 0.075 1/h ($t=4.930$, $p<0.001$), respectively. Finally, the encounter rate with *Tarebia granifera* was 0.088 1/h ($t=4.191$, $p<0.001$). For all four snail species taken together, the average encounter rate was 0.074 1/h ($t=10.370$, $p<0.001$).

In summary, the crayfish displayed significantly shorter handling times and higher encounter rates than the prawn for all four snail species, taken separately or together (Table S6).

3.3 | Physical properties of the snail shells

3.3.1 | Shell thickness of the snails most (*H. acuta*) and least (*Thiara scabra*) preferred by *M. rosenbergii* prawn

For the inspected location, namely, the first whorl extending from the operculum, the *Thiara scabra* shell, with an average thickness of 131.16 μm, was significantly, nearly 2.5 times thicker than the *H. acuta* shell, which was 55.04 μm thick on average ($t_{0.228}=-14.368$, $df=48.054$, $p<0.001$; Figure 2).

3.3.2 | Compression test of the snails most and least preferred by *M. rosenbergii* prawn

Significantly less force was required to create breakages in *H. acuta* than in *Thiara scabra* (RMANOVA species: Wilks $\Lambda=0.379$, $F_{1,99}=162.163$, $p<0.001$): the first breakage of *H. acuta* required, on average, 8 N less than the first breakage of *Thiara scabra*, and the second breakage required, on average, 5.2 N less for *H. acuta* than for *Thiara scabra* (Figure 3). For both species, the force required for creating the second breakage was significantly smaller—on average 4 N and 1.3 N for *Thiara scabra* and *H. acuta*, respectively—than that required for the first breakage (RMANOVA break number: Wilks $\Lambda=0.735$, $F_{1,99}=35.657$, $p<0.001$), equating to a 36.2% decrease in the required force for *Thiara scabra* and a 40% decrease for *H. acuta*. The mean absolute values (±1 SD) were 11.192 ± 5.505 N and 7.135 ± 3.844 N for the first and second breakages, respectively, for *Thiara scabra*; and 3.168 ± 1.092 N, and 1.874 ± 0.941 N, respectively, for *H. acuta*. In total, the force required for breaking *Thiara scabra* for the first and second times was significantly greater than that required to break *H. acuta* for the first and second times (Figure 3). There was no significant interaction between the snail species and the breakage number (RMANOVA species × break: Wilks $\Lambda=0.986$, $F_{1,99}=1.308$, $p=0.255$).

3.3.3 | Physicochemical properties of the main shell components

The main components of the shell and their grain sizes are described in the Supporting Information (Section S4, 'Properties of the main compounds in the shells of the snails most and least preferred by *M. rosenbergii* prawn', and Figure S8).

4 | DISCUSSION

Biocontrol agents against disease-transmitting snails in aquaculture include catfish, black carp and decapods, including crayfish and prawns (Ben-Ami & Heller, 2001; Hoover et al., 2019; Ledford &

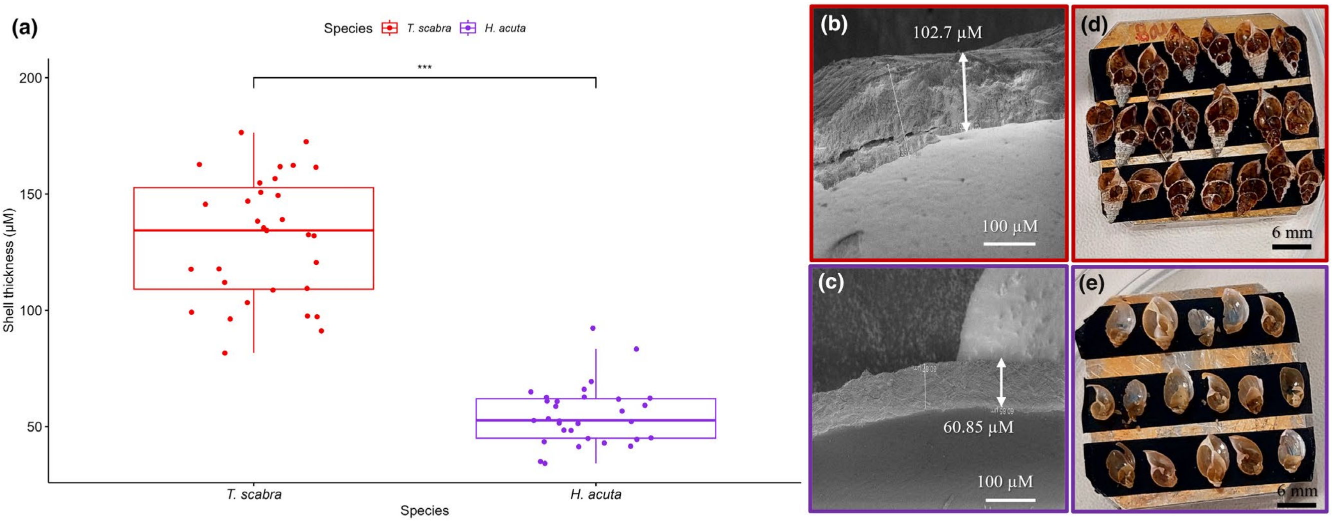

FIGURE 2 (a) Boxplot of shell thickness (μm) of the first body whorl of *Thiara scabra* (red) and *H. acuta* (purple) snails; (b, c) representative SEM micrographs showing measurements of shell thickness of *Thiara scabra* (red frame) and *H. acuta* (purple frame), respectively; and (d, e) photographs of empty and sliced shells of *Thiara scabra* (red frame) and *H. acuta* (purple frame), respectively, in preparation for shell thickness measurements.

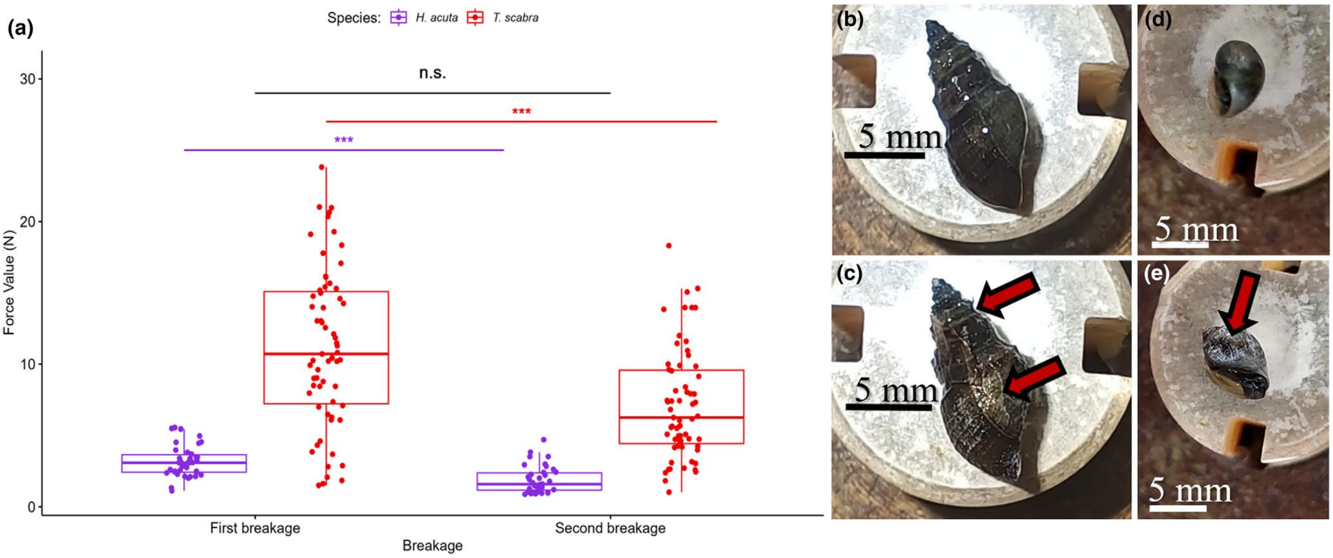

FIGURE 3 (a) Boxplot of the force (N) required to create first and second breakages in live *Thiara scabra* ($n = 63$; indicated in red) and *H. acuta* ($n = 38$; indicated in purple) snails; (b, c) a representative example of a *Thiara scabra* snail before and after compression testing, respectively; and (d, e) a representative example of an *H. acuta* snail before and after compression testing, respectively. Visible breakages are indicated with red arrows.

Kelly, 2006; Monde et al., 2016, 2017; Savaya, Glassner, et al., 2020; Sokolow et al., 2016; Swartz et al., 2015). Our findings show that *C. quadricarinatus* crayfish are more efficient predators of the four different species of disease-transmitting pest snails investigated here than *M. rosenbergii* prawn. The prawn displayed selective feeding behaviour, while the crayfish essentially displayed more opportunistic feeding behaviour. For biocontrol purposes, this difference could mean that monosex *C. quadricarinatus* could be an excellent alternative to *M. rosenbergii*, either for short-term interventions or when using *M. rosenbergii* is not possible.

The reason for the selective behaviour, or lack thereof, could lie in the physicochemical properties of the snails on a scale of easy to difficult to predate. Unsurprisingly, the snail species least preferred by prawn had a significantly thicker shell than the most preferred species, where the shell thickness corresponds to the magnitude of the force required to break the snail shells. In particular, the shell of the snail species least preferred by the prawn included a significantly greater proportion of aragonite, which is associated with increased hardness (Harbord et al., 2023; Meng et al., 2018; Parveen et al., 2020; Rumney et al., 2022). In keeping with previous work on the food choice of *Macrobrachium* prawns, in terms of snail-size selectivity or snail infection by trematodes (Savaya-Alkalay, Ovadia, et al., 2018; Swartz et al., 2015), the current study also found selective behaviour, which manifested as selective predation with preference for prey that was easier to subdue.

Behavioural observations via video recordings revealed that the two predators did not always succeed in cracking open snail shells immediately. In such cases, they would abandon the prey but return to it later, when the snail was weaker and the shell had already been partially cracked. We did not obtain any recordings of prawns fully predating on a Thiaridae snail in a single ‘sitting’, but there were a few such recordings for crayfish. It appears that the crayfish—in displaying opportunistic feeding behaviour—either does not perceive differences between snail species or ignores them, while the prawn—displaying selective feeding behaviour—does seem to perceive those species differences. It is possible that the crayfish's lack of perception can be explained by its varied diet that includes small crustaceans, snails and detritus (Liptak et al., 2019; Marufu et al., 2018), namely, a diet enabled by its chemically stronger mouth parts (vs. the prawn) (Bentov et al., 2016) that allow the crayfish to be more generalist in its prey choices (Bentov et al., 2016; Thorp & Covich, 2001). It is also possible that for handling hard shells, the greater bite force of *C. quadricarinatus* is more effective in the short term than the mastication of *M. rosenbergii* (Bentov et al., 2016). Our original premise was that differences in prey selection and predation behaviour between the two predators might also stem from the use of claws for cracking snails (Bentov et al., 2016). However, we found that crayfish rarely used their claws for snail predation, while prawns did, though mainly for holding the snails, presumably as a ‘reserve for later’ rather than for actively cracking the snails. Our findings agree with previous behavioural work on the two decapods, which found that claws are generally used for intraspecific communication rather than predation (Barki et al., 1992; Barki & Karplus, 1999; Dos Santos et al., 2018; Dos Santos & Pontes, 2016). Additional differences between the predators could be explained by general behavioural activities, including general activity levels (see Section 3.2. Predation behaviour) and roaming around the tank. The crayfish were significantly more active and tended to spend more time feeding and attacking snails than the prawns. Even though the tank dimensions and initial snail densities were identical for the two predators, the crayfish encountered more snails than the prawns, as supported by both video observations and by the calculated higher encounter rates (i.e. shorter time until a snail is encountered) compared to the prawn.

Unlike the behaviour of the crayfish, which better fits a type II functional response model for the handling time and encounter rate calculations for all four snail species (Holling, 1959), the behaviour of the prawn with regard to the two least preferred snail species, *Thiara scabra* and *Tarebia granifera*, could be better described as a type III functional response (Holling, 1959), as shown by the negative encounter rate for those species. However, since some video data showed that the prawn did encounter and attack the above two snail species, the quantified negative encounter rate could be explained by the greater force required for cracking their shells, by a learning curve for efficient handling, or by the prawn's preference for easier alternatives—behaviour supported by studies on predation preferences (Akre & Johnson, 1979; Mascaró & Seed, 2000; Rogers, 1972). The evidence of the prawns' difficulty in predating on Thiaridae snail species, especially in the short time frame of our experiments, corresponds to models developed by Van Leeuwen et al. (2013), which showed that predator efficiency is lower if the predator has not been successful in attacking that prey in the past (Lehtinen et al., 2024; Van Leeuwen et al., 2007, 2013). From a theoretical ecological perspective, a type II response would be excellent for biocontrol efforts, with crayfish predating on snails even in small abundances and potentially collapsing the snail community (Gotelli, 1959; Van Baalen et al., 2001). Theoretically, a type III response would be less desirable for a biocontrol agent, which would potentially leave a small population of snails. This could have a stabilizing effect on the snail community in the fishpond. However, for real-life biocontrol scenarios, a biocontrol agent that keeps the snail population very small, even if stable, will contribute to a reduction of trematode infections—a desirable result in trematode-infested areas, such as parts of Africa (Hoover et al., 2019; Hopkins et al., 2021; Sokolow et al., 2016; Taguemount, 2024), or in aquaculture (Savaya, Glassner, et al., 2020). We acknowledge that our experiment was relatively short; therefore, it cannot be ruled out that, over a longer time span, the observed differences between the predators would not be evident. Indeed, in practice, *M. rosenbergii* prawns were efficient at predating a mixed community of snails in a fishpond, thereby fulfilling their biocontrol purpose (Savaya, Glassner, et al., 2020). However, to determine the predators' exact response type, a proper functional response experiment is required.

An alternative explanation for the differences in feeding behaviour could be rooted in the predatory-omnivorous nature of the two predators. It is broadly agreed that prawns are considered predators (New, 2002; Taguemount, 2024), while crayfish may be considered omnivores with predatory tendencies (Dewitt et al., 1999; Haubrock et al., 2021; Marufu et al., 2018; Monde et al., 2017; Thorp & Covich, 2001). Nonetheless, we acknowledge that the fishpond is a much more complex environment compared to the experimental tanks. In real-life scenarios, fishponds constitute heterogeneous environments rich in alternative food sources for prawns and crayfish, which could distract them from their target prey, disease-transmitting snails. However, previous studies have shown that, over an entire fish grow-out season, prawns reduced the number of snails in fishponds (Savaya, Glassner, et al., 2020; Wang et al., 2023). Given the current laboratory experiment, it is expected that crayfish will behave similarly. Indeed, a field experiment is required to validate our laboratory results.

Returning to the overarching purpose of this study, which is to compare two decapods for biocontrol purposes, the ecological context of IPM must be considered. In particular, due consideration must be given to the possibilities of spillover of biocontrol agents introduced into agriculture or aquaculture (Pratt & Center, 2012; Rand et al., 2006). Spillovers or aquacultural escapees of the suggested biocontrol agents into natural areas could harm local habitats by predation on non-target species outside the fishpond, such as by predation on small fish, competition with other detritivores and impacts on freshwater flora (Haubrock et al., 2021; Silva-Oliveira et al., 2011), as described in previous literature focusing on both species' invasiveness (Haubrock et al., 2021; Silva-Oliveira et al., 2011; Van Kuijk et al., 2021). However, in the case of accidental aquacultural escapees, those monosex individuals are expected to die off after two (Nogueira et al., 2022) to five years (Van Kuijk et al., 2021), when this time span is expected to be lower for unsuitable environments (e.g. harsh winters, decapod predator presence like catfish or birds, etc.) and could limit spillover damage. Additionally, the farther aquaculture sites are from natural habitats, the lower the likelihood of escapees; barriers such as pump stations or wastewater treatment systems are expected to limit escapees even further. As with any biocontrol agent introduction, we advise responsible use and selection before release, and consider the suitability of the surrounding areas of the aquacultural sites, as discussed in the aquaculture literature, especially for *M. rosenbergii* (Savaya, Glassner, et al., 2020; Savaya-Alkalay, Ndao, et al., 2018; Shaked et al., 2024), and further emphasize the importance of monosex populations for increasing ecological safety. For example, monosex *C. quadricarinatus* could constitute an alternative when the use of monosex *M. rosenbergii* is not permitted, such as in South-East Asia, where *M. rosenbergii* is endemic, or in Brazil, where it is an introduced species (Silva-Oliveira et al., 2011). Another consideration in introducing monosex biocontrol agents is hybridization with local species, which should also be tested when close local species are present in the area (Borlase et al., 2021; Savaya-Alkalay, Ndao, et al., 2018; Szűcs et al., 2019). Indeed, monosex technology for *C. quadricarinatus* is still in its infancy (Levy et al., 2020; Shaked et al., 2024), and further local verifications of its safety are required before monosex populations of *C. quadricarinatus* could be introduced into places where other species of *Cherax* are endemic (as was done with *Macrobrachium* species; Savaya-Alkalay, Ndao, et al., 2018). It is noteworthy that accidents such as the rare emergence of the invasive parthenogenetic *Procambarus virginalis* provide a basis for valid fears regarding the introduction of all-female *C. quadricarinatus* populations (Chucholl et al., 2012; Maciaszek et al., 2022; Vogt et al., 2019; Yanai et al., 2024). It is thus crucial to emphasize the importance of using monosex technology for both decapods when introduced for biocontrol purposes. Furthermore, the future creation of sterile lines for both decapod species would be the safest solution for biocontrol purposes, as has been suggested for *M. rosenbergii* (Molcho et al., 2024). Until then, using monosex decapods for biocontrol seems to be the most appropriate solution for an IPM approach against disease-transmitting snails in aquaculture (Levy et al., 2017; Shaked et al., 2024; Wahl et al., 2023, 2025). Furthermore, monosex (or in the future, sterile) decapod biocontrol can serve a dual purpose: after predating on the snails, the crayfish or the prawns could be an excellent protein source in addition to the fish in polyculture (Brummett & Alon, 1994; Karplus et al., 2001; Rouse & Kahn, 1998). If proven successful in providing both biocontrol services and sufficient yields, monosex *C. quadricarinatus* could become an extra protein product in addition to its use for biocontrol purposes (Barki et al., 2001; Junior et al., 2012; Rouse & Kahn, 1998), thereby increasing nutritional and economic security for the farmer in a classic win-win-win situation (Hopkins et al., 2021). Furthermore, it can constitute an alternative for farmers who can use either monosex decapods as a biocontrol agent tailored against different snail pests. It could also depend on market preferences for a particular decapod as an additional value-added product in a polyculture system.

In summary, in the short term, behavioural differences were detected between the two decapod predators, *M. rosenbergii* prawns and *C. quadricarinatus* crayfish, in their food choices, or lack thereof. The physicochemical characteristics of snail prey species could explain predators' feeding preferences. Notably, both predators in our study successfully reduced the number of pest snails in the experimental tanks. In the long term, both species have the potential for win-win-win biocontrol IPM and added value as independent protein products, and constitute important additions to the IPM toolboxes of aquacultural farmers.

AUTHOR CONTRIBUTIONS

S.M.: Methodology, formal analysis, investigation, data curation, writing—original draft and visualization. S.A.S.: Investigation, data curation, and writing—review and editing. A.M.G.: Investigation and visualization. D.P.: Methodology, formal analysis, investigation, writing—review and editing, and visualization. H.K.: Methodology and resources. A.B.: Methodology, and writing—review and editing. H.G.: Investigation and resources. A.E.: Investigation and resources. E.D.A.: Methodology, resources, and writing—review and editing. A.S.: Conceptualization, methodology, resources, writing—review and editing, and supervision. O.O.: Conceptualization, methodology, formal analysis, resources, writing—review and editing, and supervision.

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CONFLICT OF INTEREST STATEMENT

No conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1002/2688-8319.70237.

DATA AVAILABILITY STATEMENT

Time to event data (Moscovitz, Shaked, Emanuel, et al., 2026), shell thickness data (Moscovitz, Green, Golan, et al., 2026), shell composition data (Moscovitz, Green, Baranov, et al., 2026) and force data (Moscovitz, Green, Shaked, et al., 2026) are available at the Mendeley data repository https://data.mendeley.com/. Video data summary is available in the supplemental data in Table S5. Full video data will be available upon request.

AI STATEMENT

In this article, we used ChatGPT AI for refining coding in R, searching for relevant academic work related to this paper, reviewing published papers, generating abstract drafts and generating the graphical abstract cartoon. We used Perplexity and Claud AI for searching for relevant academic work related to this paper and reviewing published papers. We briefly used Gemini AI for refining coding in R. After using this tool/service, the author(s) reviewed and edited the content as needed and took full responsibility for the content of the publication.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Principle of a single particle (snail) compression test in which the upper punch applies force on the particle, while the particle displacement is measured simultaneously. Image adapted from (Portnikov & Kalman, 2018). For further information, see Portnikov et al., (2013); Portnikov & Kalman, (2014, 2018).

Figure S2. Typical force–displacement experimental curve for a *Thiara scabra* snail. The apex of the plotted line, marked by a red circle and a red arrow, is identified as the breakage point. The force decreased from 14.02 N to 10.99 N, corresponding to a 21.6% reduction.

Table S1. Food-choice comparison between *M. rosenbergii* prawn and *C. quadricarinatus* crayfish: Cox proportional hazard model results. *H. acuta*, the most preferred snail, is the reference snail, and *C. quadricarinatus* is the reference predator.

Table S2. Food-choice comparison between *M. rosenbergii* prawn and *C. quadricarinatus* crayfish: Cox proportional hazard model analysis for each snail species separately (without the control tanks). *C. quadricarinatus* is taken as the reference predator. The results show the difference in the chance of death for each snail species in the presence of either predator.

Figure S3. Kaplan–Meier curves showing changes in the proportion of surviving snails over time (A) in the presence of an *M. rosenbergii* prawn, (B) in the control tanks for the *M. rosenbergii* prawn experiment, (C) in the presence of a *C. quadricarinatus* crayfish and (D) in the control tanks for the *C. quadricarinatus* experiment. The ending + sign is the censor ending for the surviving snails. *Thiara scabra* is indicated in red, *Tarebia granifera*, in blue, *M. tuberculata*, in green and *H. acuta*, in purple. The shaded areas represent the 95% confidence interval.

Table S3. *M. rosenbergii* prawn food-choice experiment: Cox proportional hazard model analysis. The categorical variable ‘snail species’ was converted into a set of binary predictor variables using the most preferred snail, *H. acuta*, as the reference group.

Table S4. *C. quadricarinatus* crayfish food-choice experiment: Cox proportional hazard model analysis. The categorical variable ‘snail species’ was converted into a set of binary predictor variables using the most preferred snail, *H. acuta*, as the reference group.

Figure S4. Representative examples of chipped and cracked snails in attempts at predation and some already predated snails, as shown by pieces of cracked empty shells. (A) *Thiara scabra* (circled in red), *Tarebia granifera* (circled in blue), *M. tuberculata* (circled in green) and *H. acuta* (circled in orange) after 45 h in a tank with an *M. rosenbergii* prawn; visible pieces of the shells of *M. tuberculata* and *H. acuta* are included in the circles. (B&C) Examples of chipped and partially cracked *Thiara scabra* snail shells, showing that the broad side closer to the operculum is cracked, as indicated by red arrows.

Video 1: Video Video1_GP029676. *M. rosenbergii* prawn predating on two *H. acuta* snails and ‘working on’ (handling without fully predating) a *Thiara scabra* snail.

Video 2: Video Video2_GH030069. *C. quadricarinatus* crayfish handling Thiaridae snails and rapidly predating on *H. acuta* snails.

Video 3: Video Video3_GH040026. *M. rosenbergii* prawn ‘working on’ (handling without fully predating) Thiaridae snails for a relatively long time and ‘collection for later’ behaviour.

Video 4: Video Video4_GP019723. *C. quadricarinatus* crayfish ‘working on’ (handling without fully predating) a Thiaridae snail and ‘giving up’ on it.

FIGURE S5: (A) Boxplots for both predator species of the proportion of snails encountered for snail species that were clearly identified, as caught on camera, where purple indicates *H. acuta*, green indicates *Melanoides tuberculata*, blue indicates *Tarebia granifera* and red indicates *Thiara scabra*. Numbers on the graphs are the mean proportions ± 1 SD. (B) Boxplots for both predator species of the proportion of snails encountered for both well-identified snail species and grouped snails that were not visually identified down to the snail species level, as caught on camera; species groups are designated as follows: purple—*H. acuta*, green—*Melanoides tuberculata*, blue—*Tarebia granifera*, red—*Thiara scabra*, turquoise—*Melanoides tuberculata* or *Tarebia granifera*, light brown—any

Thiaridae species (*Melanoides tuberculata*, *Thiara scabra* or *Tarebia granifera*), grey—an unidentified snail that could be any of the four species, and hot pink—rounder snails that could be either *Thiara scabra* or *H. acuta*.

TABLE S5: Video data comparison between predators. Total video time (min) is the sum of recording time per predator. Variance is due to the different cameras' capacities—one camera recorded 20-min-long videos, and the other camera recorded about 10-min-long videos until the battery ran out. When a predator had eliminated all the snails in its tank, the camera was moved to another tank for recording proof-of-concept predation events. 'Encounters' indicates the number (counts) of times the predator was recorded putting a snail into its mouth. The total handling time (min) represents the total handling time of a snail by the predator that was fully recorded from start to finish on camera until the snail was visibly completely predated (empty shell left behind or nothing left with pieces of shell dropping from the predator's mouth; for examples, see Videos 1 and 2).

FIGURE S6: Bar chart of the handling times from start to finish, as caught on camera, by predator species and snail species, where purple indicates *H. acuta*, turquoise indicates either *Melanoides tuberculata* or *Tarebia granifera*, light brown indicates any Thiaridae snail and red indicates *Thiara scabra*. Numbers represent mean ± 1 SD of the handling times, as recorded. See also Table S5 for detailed recording times and Table S6 for quantified handling times.

TABLE S6: Differences in encounter rates (*a*) in units of 1/h and handling time (*h*) in units of hours between *M. rosenbergii* prawns and *C. quadricarinatus* crayfish (binary variable with *C. quadricarinatus* = 0 and *M. rosenbergii* = 1) with respect to each of the four snail species and when taken together. Significant results are indicated in bold.

FIGURE S7: Boxplot of the proportion of appendages used during encounters with and ingestion of snails, according to predator species (from video data). Numbers represent the mean proportions of use of appendages ± 1 SD.

Figure S8: (A) Mean weight percent (wt%, determined by XRF) and (B) mean grain size (µm, determined by XRD) of the two main compounds, aragonite and calcite, found in the shells of *Thiara scabra* (red; $n = 3$ samples) and *H. acuta* (purple; $n = 3$ samples). Error bars represent ±1 SD.

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