RESEARCH ARTICLE AGROBIOLOGICAL RECORDS
ISSN: 2708-7182 (Print); ISSN: 2708-7190 (Online)
Open Access Journal

FEEDING ECOLOGY AND MANAGEMENT OF THE INVASIVE APPLE SNAIL *POMACEA CANALICULATA* IN DUCKWEED PRODUCTION SYSTEMS

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ABSTRACT

The invasive apple snail, *Pomacea canaliculata*, poses a serious threat to duckweed-based agricultural systems due to its heavy grazing. Despite this risk, there is limited quantitative information on the extent of damage caused by this species and on practical methods to reduce its impact. In this study, we investigated the feeding behavior of *P. canaliculata* on duckweed and evaluated potential mitigation strategies under controlled laboratory conditions. Snails collected from Haikou, Hainan Province, China, were identified using a combination of morphological characteristics and molecular analyses of mitochondrial COI and 16S rRNA genes, confirming their species identity. A series of feeding experiments was conducted to examine how starvation duration, temperature, duckweed surface density, duckweed species (*Spirodela polyrhiza* and *Lemna aequinoctialis*), and snail body weight influenced grazing intensity. The results showed that food consumption increased markedly with longer starvation periods, reached its highest level at moderate temperatures, and was greater when duckweed surface density was low. Snails consumed significantly more *L. aequinoctialis* than *S. polyrhiza,* and larger individuals exerted substantially higher grazing pressure than smaller ones. In addition, protective experiments evaluated the effectiveness of different concentrations of nutritional medium (E-Medium), niclosamide, and tea saponin in reducing snail damage. All treatments reduced grazing activity and promoted duckweed biomass in a concentration-dependent manner. However, high concentrations of niclosamide and tea saponin caused noticeable phytotoxic effects on duckweed, even in the absence of snails. Moderate concentrations provided the best balance between effective snail control and duckweed preservation. Overall, this study demonstrates the severe impact of *P. canaliculata* on duckweed cultivation and emphasizes the importance of integrated management strategies that combine ecological understanding of snail feeding behavior with carefully optimized control measures to ensure sustainable duckweed production.

Keywords: *P. canaliculata, Duckweed cultivation, L. aequinoctialis, S. polyrhiza,* Integrated pest control.

Article History (ABR-26-155) || Received: 20-Apr-2026 || Revised: 28-May-2026 || Accepted: 06-Jun-2026 || Published Online: 25-Jun-2026

1. INTRODUCTION

Duckweeds (subfamily Lemnoideae; family Araceae) are diminutive, free-floating aquatic plants noted for their remarkably rapid vegetative reproduction and high biomass yields, making them appealing for contemporary "duckweed farming" focused on protein production, feed/food utilization, and environmental functions such as nutrient recovery from wastewater. A new assessment highlights the extensive industrial potential of duckweed species and the necessity to optimize growing conditions for specific purposes (Baek et al., 2021). In practical production settings, controlled culture strategies are increasingly being examined to stabilize yields and mitigate biological risks. Coughlan et al. (2022) described indoor "duckweed bioreactors," noting that doubling times as brief as 1.24 days have been observed under such conditions. They propose stacked systems with up to 15 m² of duckweed per 1 m² of floor space, facilitated by a shallow water depth of approximately 5 cm. These advancements support the viability of large-scale duckweed cultivation while underscoring the need to understand and mitigate biotic limitations, such as herbivory. A primary factor influencing duckweed crop advancement is its nutritional significance. New research highlights that specific duckweed species can have high protein content (up to 45%) and indicates that duckweed protein can provide essential amino acids in accordance with FAO reference patterns (Xu et al., 2023). These features enhance the appeal of duckweed as a sustainable protein source, rendering the safeguarding of duckweed biomass from pests a significant practical concern. The invasive apple snail *P. canaliculata* is commonly associated with harm to wetland flora and aquatic agriculture among aquatic herbivores. The apple snail, *P. canaliculata*, is an invasive species that significantly affects wetland flora and water agriculture.

Citation: Shakoor K, Imtiaz U, Tan D and Zhang J, 2026. Feeding ecology and management of the invasive apple snail *Pomacea canaliculata* in duckweed production systems. Agrobiological Records 24: 220-233. https://doi.org/10.47278/journal.abr/2026.039

ISSN: 2708-7182 (Print); ISSN: 2708-7190 (Online)
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Although capable of utilizing various trophic supplies through distinct feeding methods, it is typically classified as a macrophytophage (Manara et al., 2024). This ambiguity highlights the necessity of controlled feeding studies in crop-relevant environments, such as duckweed farming systems, to assess grazing damage and relative vulnerability among duckweed taxa.

Precise identification of Pomacea species is crucial for linking observed crop damage to the relevant pest and determining appropriate treatment measures. A 2024 countrywide study from China indicates that P. *canaliculata* and *P. maculata* have frequently been conflated as a single species owing to physical resemblance, and the scientists employed COI (mtDNA) markers to investigate genetic diversity and structure (Wei et al., 2024). These findings support the use of combined morphological assessment and molecular confirmation in studies evaluating pest damage and management. In addition to damage characterization, duckweed farming requires practical protection options that do not compromise crop health or downstream use. Chemical molluscicides remain commonly used in some settings. For example, report metaldehyde toxicity values for adult *P. canaliculata* with median lethal concentrations of 3.792, 2.195, 1.833, and 1.706 mg/L at 24, 48, 72, and 96 h, respectively, and they document enzyme activity changes and histopathological damage under exposure (Liu et al., 2024). Such data are useful for understanding efficacy and potential biological impacts, but duckweed-specific protection protocols must also consider non-target effects on duckweed growth and recovery. Therefore, this study presents preliminary investigations into the damage and protection of duckweed farming systems threatened by *P. canaliculata*. Specifically, we confirm species identity using integrated morphological and molecular analyses, quantify feeding induced damage to two duckweed species, *Spirodela polyrhiza* and *Lemna aequinoctialis*, and assess post-feeding protection using pesticide or chemical treatments aimed at controlling *P. canaliculata* while maintaining duckweed viability. Invasive freshwater mollusks are increasingly recognized as major drivers of ecological change and economic loss, particularly in aquatic agroecosystems where biological invasions interact strongly with human land use and climate trends. The invasive apple snail *P. canaliculata* is regarded as one of the most detrimental freshwater invaders due to its rapid population growth, broad feeding range, and high tolerance to environmental fluctuations. Recent dispersion modeling and synthesis studies indicate that anthropogenic dispersal, coupled with climate change, is expected to exacerbate invasion risk and amplify repercussions in conducive areas (Huang et al., 2026). The successful invasion of *P. canaliculata* is facilitated by both its life-history characteristics and the development of molecular resources that enhance understanding of its adaptation, dissemination, and pest potential. Recent whole-genome research elucidates the genetic underpinnings of invasiveness and enhances the creation of superior monitoring and management systems (Lu et al., 2024). Moreover, physiological and microbiome-centric research indicates that thermal stress might modify internal biological mechanisms in *P. canaliculata*, underscoring the significance of environmental context in assessing feeding harm and management strategies in both laboratory and field settings (Li et al., 2022).

Duckweed (Lemnaceae) is increasingly planted for high-yield biomass production and subsequent applications, including food and value-added bioproducts, with growing interest in scalable agricultural systems. Recent evaluations highlight the swift expansion, adaptable cultivation methods, and increasing farm-to-fork potential of duckweed, thereby underscoring the growing significance of crop protection as production scales up (Ujong et al., 2025). As duckweed production expands, herbivory by generalist aquatic herbivores like *P. canaliculata* may significantly hinder productivity; yet quantitative data linking feeding ecology to effective conservation techniques in duckweed systems remain scarce. The management of *P. canaliculata* has predominantly relied on chemical molluscicides and physical extraction; however, there is a growing focus on safer, more sustainable methodologies. Recent evaluations encapsulate prevailing trends in biological and environmentally sustainable control tactics for invasive apple snails, encompassing phytochemical agents and integrated approaches aimed at diminishing dependence on highly toxic interventions (Azmi et al., 2022). Simultaneously, recent applied research are assessing alternate control methods, such as attractant-based strategies, which may facilitate environmentally sustainable suppression in contexts where chemical usage is restricted (Suzuki et al., 2025). Recent studies have evaluated "eco-friendly" agricultural chemicals and plant extracts exhibiting molluscicidal properties against *P. canaliculata*, hence reinforcing the interest in botanical control alternatives (Cho et al., 2023). Considering the growing significance of duckweed cultivation and the ongoing issue of apple snail invasion, there is a distinct necessity for research that quantifies grazing damage influenced by critical environmental and biological factors (e.g., temperature, food availability, and consumer size) while concurrently assessing protection strategies and their potential non-target effects on duckweed growth. This study investigates the feeding ecology of *P. canaliculata* on duckweed and evaluates concentration-dependent protective methods to reconcile snail management with the safety and productivity of duckweed.

2. MATERIALS AND METHODS

2.1. Study Area and Sample Collection

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Duckweed and snail specimens were collected from freshwater environments in Haikou, Hainan Province, China, where high duckweed growth and snail infestations were observed. To reduce stress, collected snails were brought to the lab in aerated containers with site water. In order to preserve freshness, duckweed samples were gathered concurrently and transferred in sterile containers. Before being used in experiments, snails were acclimated in the lab for acclimatization duration, e.g., 48–72 h under controlled circumstances (temperature28°C, photoperiod, e.g., 12 h light: 12 h dark). For further analysis, only adult snails of comparable size that were healthy and active were chosen.

2.2. Cultivation of Duckweed Strains

Before testing, duckweed cultures were cleaned of dirt and non-target organisms with clean water. *S. polyrhiza* and *L. aequinoctialis*, two kinds of duckweed, were employed in this investigation. Stock cultures E-Stock 1 (KNO_3), E-Stock 2 [$Ca(NO_3)_2 \cdot 4H_2O$], E-Stock 3 (KH_2PO_4 and $MgSO_4 \cdot 7H_2O$), E-Stock 4 (trace elements: H_3BO_3, $MnCl_2 \cdot 4H_2O$, $ZnSO_4 \cdot 7H_2O$, $CuSO_4 \cdot 5H_2O$, $Na_2MoO_4 \cdot 2H_2O$), and E-Stock 5 (iron chelate: $FeCl_3 \cdot 6H_2O$ and Na_2EDTA) were prepared separately. The working medium was prepared by diluting 10 10mL each of E-Stocks 1, 2, 3, and 5 (100X) and 1mL of E-Stock 4 (1000X) into 2000 mL of distilled water, followed by sterilization at 121°C for 15 minutes. After cooling, the medium was aseptically dispensed into sterile culture vessels. Prior to inoculation, duckweed plants were surface-sterilized by immersion in 1% sodium hypochlorite for 1–2 minutes followed by repeated rinsing with sterile distilled water. Surface sterilization was confirmed by repeated subculturing, which was kept in the nutrient medium at room temperature with light intensity (Imtiaz et al., 2026). To ensure consistent development, cultures were acclimated to laboratory conditions before feeding and control trials.

2.3. Morphological Analysis of *P. canaliculata*

Morphological identification of *P. canaliculata* was conducted following established taxonomic descriptions of apple snails. Diagnostic shell characteristics, including shell size, shape, deep suture pattern, whorl configuration, aperture morphology, and operculum structure, were examined under a stereomicroscope. Representative specimens were photographed and observed traits were compared with published morphological accounts to preliminarily confirm species identity (shell globosity, indented sutures, large oval aperture) prior to molecular validation (conventional taxonomy of Pomacea spp.). (Banerjee et al., 2022).

2.4. Molecular Analysis of *P. canaliculata*

Genomic DNA was extracted from the foot muscle tissue of *P. canaliculata* specimens using a CTAB-based protocol. DNA quality and concentration were assessed using spectrophotometry and extracted DNA was stored at −20°C until further analysis. Molecular identification of *P. canaliculata* was performed using two mitochondrial gene markers: cytochrome c oxidase subunit I (COI) and 16S ribosomal RNA (16S rRNA), which were amplified by polymerase chain reaction (PCR) as previously described (Kannan et al., 2020). Details of the PCR reaction mixture composition are provided in Table 1. PCR amplification of the COI gene was carried out using the universal invertebrate primers LCO1490 (5′-GGT CAA CAA ATC ATA AAG ATA TTG G-3′) and HCO2198 (5′-TAA ACT TCA GGG TGA CCA AAA AAT CA-3′). The 16S rRNA gene was amplified using primers 16Sar (5′-CGC CTG TTT ATC AAA AAC AT-3′) and 16Sbr (5′-CCG GTC TGA ACT CAG ATC ACG T-3′). The PCR conditions were pre-denatured at 94°C for 4min, followed by 30 cycles at 94°C, 30s; 58°C, 45s; 72°C, 1min, and a further extension at 72°C for 7min. The reaction conditions were pre-denatured at 94°C for 4min, followed by 30 cycles of 94°C, 30s; 53°C, 45s; 72°C, 1min, and a further extension at 72°C for 7min (Imtiaz et al., 2026).

Table 1: PCR Reaction mixture Compsition

Components	Volume (µL)
2x Taq PCR master mix with dye (Tiangen, KT211)	19
Forward Primers	2
Reverse Primers	2
DNA Template	2
Nuclease Free-Water	25
Total Volume	50

2.5. Sequence Processing and Phylogenetic Analysis

Sequence chromatogram files were processed using MacVector v18.2 (MacVector, Inc., USA) for trimming, editing, and quality assessment. Low-quality regions, primer sequences, and ambiguous nucleotide positions were manually removed, and forward and reverse reads were assembled to generate consensus sequences. Sequences containing more than 2% ambiguous sites or unclear chromatogram signals were re-sequenced to ensure data quality. Multiple sequence alignments were performed in MacVector using the ClustalW algorithm with a gap opening penalty of 15.0, a gap extension penalty of 6.66, and a divergent delay of 30%. Aligned sequences were subsequently imported into MEGA11 for downstream analyses (Tamura et

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al., 2021). Nucleotide substitution patterns were estimated using the Tamura–Nei model (Tamura & Nei, 1993) and phylogenetic relationships were inferred using the Neighbor-Joining method with 1,000 bootstrap replicates to assess branch support. To validate taxonomic classification, representative reference sequences of *P. canaliculata*, *P. maculata*, and related species were obtained from GenBank and incorporated into the analysis. Genetic diversity metrics, such as haplotype diversity (Hd), nucleotide diversity (π), and Watterson's theta (θw), were computed utilizing DnaSP v6.12.03 (Rozas et al., 2017). Final consensus sequences were compared to the NCBI GenBank database using BLASTn to verify species identity.

2.6. Feeding Experiments and Experimental Design

Feeding experiments were conducted to evaluate the effects of starvation duration, temperature, duckweed surface density, duckweed species, and snail body weight on feed intake of *P. canaliculata* under controlled laboratory conditions. Experimental approaches followed standard grazing assay methods used in freshwater snail feeding studies (e.g., laboratory herbivory trials on macrophytes) and have been applied in recent invasive snail research (Ismail et al., 2021). Small plastic containers filled with dechlorinated water were used for all treatments, with each experimental unit consisting of two snails and three independent replicates per treatment, and treatments randomly assigned. *S. polyrhiza* and *L. aequinoctialis* were chosen as representative floating macrophytes for the feeding assays because they are common, rapidly growing duckweed species widely used in aquatic plant research and laboratory feeding studies. Duckweeds provide a standardized food source for herbivory experiments involving freshwater snails (e.g., ecological and toxicology studies of aquatic plants), and *P. canaliculata* is a known generalist feeder on macrophyte vegetation, which supports the use of floating plants in controlled feeding trials (Manara et al., 2024). Feed intake was quantified as the difference between initial and final duckweed biomass after the trial, with control containers without snails maintained to correct for non-consumptive biomass change. The effect of starvation was assessed by depriving snails of food for 0, 24, 48, or 72 h prior to 24-h feeding trials. The impact of temperature was assessed by monitoring consumption at 20, 24, 28, and 32°C, in accordance with prior research investigating thermal influences on apple snail grazing behavior and feeding capacity (Miyata & Nakatsubo, 2024). The influence of duckweed surface density was tested by varying plant coverage across container sizes to simulate feeding availability gradients. Species-specific feeding responses were assessed by offering *S. polyrhiza* or *L. aequinoctialis* separately for seven consecutive days, with daily measurements and biomass replenishment. Finally, to examine the effect of snail body weight, individuals were grouped by size classes and allowed to feed for five days, with daily and cumulative feed intake calculated, a method comparable to size-dependent feeding experiments in gastropod ecology.

2.7. Protection Strategies against Snail Damage

Protection experiments were conducted over a seven-day period to evaluate the effectiveness of Niclosamide, tea saponin, and nutrient medium strength (E-Medium) in reducing *P. canaliculata* grazing damage on duckweed under controlled laboratory conditions. Recent investigations have proven the efficacy of Niclosamide and plant-derived saponins as molluscicidal agents against *P. canaliculata* in the context of chemical and botanical management techniques for invasive apple snails (Lu et al., 2025). All studies were conducted in polypropylene containers containing dechlorinated water, with three independent replicates per treatment and three snails of similar body weight per container, adhering to established laboratory bioassay techniques for freshwater gastropods (Miyata & Nakatsubo, 2024). Snail mortality was recorded after 72 h of exposure, a commonly used endpoint in molluscicide toxicity and efficacy assessments (Yang et al., 2023), while duckweed biomass was measured at the end of the seven-day experimental period to evaluate protection efficacy and potential phytotoxic effects. In the E-Medium assay, *Spirodela polyrhiza* and three snails were exposed to four E-Medium concentrations plus a control without E-Medium, reflecting the use of defined nutrient media to regulate duckweed growth under controlled experimental conditions (Pasos-Panqueva et al., 2024). For Niclosamide and tea saponin treatments, eight treatments were established at four concentrations, with treatments T1–T4 containing both snails and duckweed and treatments T5–T8 containing duckweed only to assess direct effects on duckweed in the absence of grazing. Snail mortality was recorded in snail-containing treatments after 72 h, and final duckweed biomass was measured in all treatments at the conclusion of the experiment.

2.8. Statistical Analysis

DNA sequence chromatograms were assembled and edited using MacVector software. Multiple sequence alignments were performed prior to downstream analyses. Phylogenetic analyses were conducted using MEGA version 11, employing appropriate nucleotide substitution models and tree-building methods. Node support was assessed using bootstrap analysis with 1,000 replicates. All physiological and biochemical experimental data were analyzed using Microsoft Excel (version 365) and STATISTIX (version 9.1). Prior to analysis, normality

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was assessed using the Shapiro-Wilk test. Differences among treatments were evaluated using one-way analysis of variance (ANOVA). Statistically significant differences were detected; mean values were compared using Tukey's HSD test. Results are presented as mean ± SD, and differences were considered statistically significant at $P<0.05$.

3. RESULTS

3.1. Morphological Analysis of *P. canaliculata*

The morphological analysis of the specimens obtained diagnostic traits aligned with *P. canaliculata*. The shell was spherical and sturdy, featuring well-defined whorls and prominent sutures (Fig. 1). The shell exhibited a color spectrum from light brown to dark olive, with a somewhat high spire. The aperture was broad and oval, featuring a thickened lip, and was sealed by a well-formed operculum (Fig. 1). The cephalic area had paired tentacles, with ocular structures situated at the base of the tentacles. A large, muscular foot was observed, extending beyond the shell aperture during locomotion (Fig. 1). Overall, the combination of shell morphology, aperture structure, operculum presence, and soft-body features observed in the specimens matched the established morphological descriptions of *P. canaliculata*, supporting species-level identification. The observed morphological characteristics of the collected specimens were consistent with registered descriptions of *P. canaliculata* (Table 2).

The Fig. 1 shows the globose shell with distinct whorls and sutures, wide aperture with a thick aperture lip, operculum, head region with paired tentacles and eyes, and the muscular foot. These diagnostic characteristics are consistent with species-level identification of *P. canaliculata*.

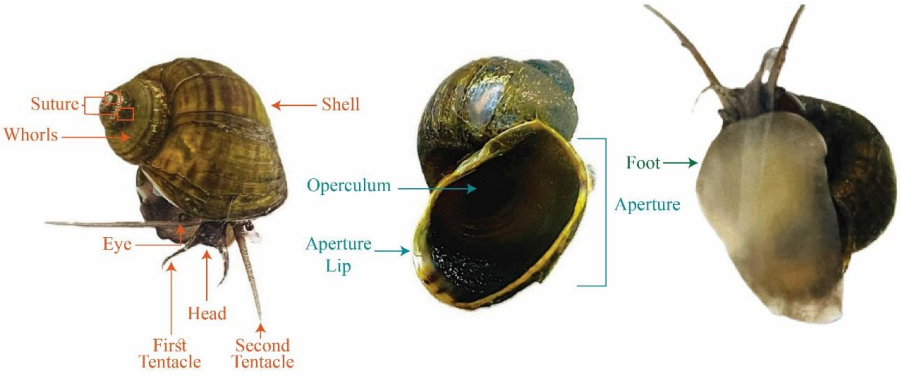

Fig. 1: Morphological features of *P. canaliculata* examined in this study.

Table 2: Comparison of observed morphological traits with registered species

Characteristics	Morphology (Registered Species) *P. canaliculate*	Morphology (used in this study) *P. canaliculate*	References
Shell Shape	Globose, rounded, large body whorl	Globose with a large body whorl	(Hayes et al., 2012)
Shell Color	Yellowish to dark brown	Dark brown, yellow	(Joshi & Sebastian, 2006)
Aperture	Wide, oval and elongated	Wide and oval	(Cowie, 2002)
Aperture Lip	Yellow, orange to brown	Yellowish and thin	(Hayes et al., 2012)
Operculum	Corneous, thin, dark brown with concentric rings	Corneous, dark brown and concentric rings visible	(Cowie, 2002)
Whorls	5–6 rounded whorls with deep sutures and rapid diameter increase	Rounded spiral whorls increasing in size	(Cowie, 2002)
Sutures	Deeply channeled suture	Lines where whorls meet and deeply indented	(Joshi et al., 2020)
Head	Well developed, tentacles and eyes at base	Well, developed, contains mouth, eyes, tentacles	(Andrews, 1965)
Eye	Simple eye for light and movement detection	Located at base of tentacle; simple structure	(Hayes et al., 2012); (Andrews, 1965)
First Tentacle	Sensory function, food and environmental detection	Tactile and chemosensory function	(Hayes et al., 2012) ; (Andrews, 1965)
Second Tentacle	Tactile and chemical sensing	Similar sensory function	(Hayes et al., 2012); (Andrews, 1965)
Foot	Muscular locomotory organ with gland cells	Large muscular foot producing mucus for movement	(Hayes et al., 2012) ; (Andrews, 1965)

3.2. Tree-Based Identification of *P. canaliculata* using COI and 16S rRNA Sequences

Phylogenetic analyses based on mitochondrial COI and 16S rRNA gene sequences supported the identification of the collected specimens as *P. canaliculata*. In the COI-based phylogenetic tree (Fig. 2A), the study sequence

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ISSN: 2708-7182 (Print); ISSN: 2708-7190 (Online)
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(HN snail COI) grouped together with reference sequences of *P. canaliculata* and *P. insularum*. This grouping is supported by high bootstrap values (100%), indicating strong statistical support for the clustering. However, the *P. canaliculata* sequences are not separated from *P. insularum,* while *P. megastoma*, *P. maculata* and *P. diffusa* form distinct neighboring clades. The phylogenetic tree further shows that other genera, including *Lanistes, Marisa, Bellamya*, and Opisthosoma, are positioned in more distant lineages with high bootstrap support, providing clear separation from the *Pomacea* clade and supporting proper tree rooting.

In contrast to the COI tree, the 16S rRNA-based phylogenetic tree (Fig. 2B) separated *P. canaliculata* and *P. insularum* into distinct clades, clearly showing that the study sequence (HN snail 16S) belongs *P. canaliculata*. This grouping is supported by a high bootstrap value (83%), indicating reliable node support. The *P. canaliculata* clade is clearly distinct from other *Pomacea* species.

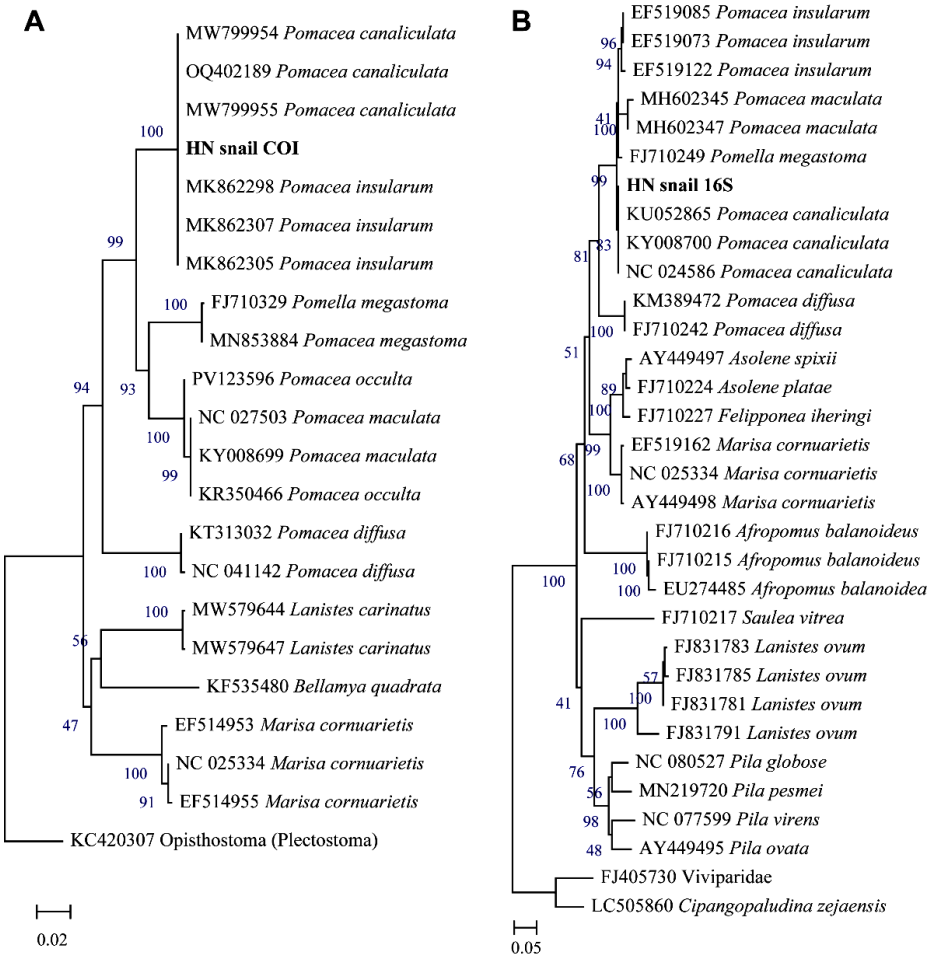

Fig. 2: Molecular identification of HN snail based on the COI (A) and the 16S rRNA gene (B) sequences. Representative sequences of *Pomacea sp.* and related species *Lanistes carinatus*, *Marisa cornuarietis, Bellamya quadrata* were retrieved from GenBank. Evolutionary history was inferred using the Neighbor-Joining method. The trees are rooted with the percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1000 replicates) shown below or beside the branches. The scale bars represent the number of base substitutions per site.

3.3. Worldwide Distribution of *P. canaliculata*

The global distribution map (Fig. 3A) shows the sampling locations and occurrence records of *P. canaliculata* included in this study. The species is widely distributed across both its native range in South America and multiple introduced regions, including East and Southeast Asia (notably China, including Hainan), North America, and Europe. The concentration of records in Asia and other non-native regions highlights the extensive spread of *P. canaliculata* beyond its native range, consistent with its well-known invasive potential. The phylogenetic relationships inferred from mitochondrial 16S rRNA gene sequences do not match the geographic distribution (Fig. 3B), indicating a lack of genetic isolation among different geographic populations and the presence of extensive gene flow.

3.4 Feeding Preferences & Consumption Rates of *P. canaliculata* on Duckweed Species

Feed intake of the freshwater snail *P. canaliculata* was significantly influenced by starvation duration, temperature, and duckweed density when fed with *S. polyrhiza* and *L. aequinoctialis* (Fig. 4). Increasing starvation duration resulted in a progressive increase in feed intake by *P. canaliculata*, with the lowest consumption observed

ISSN: 2708-7182 (Print); ISSN: 2708-7190 (Online)
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at 0 h starvation and the highest intake recorded after 72 h (Fig. 3A). When fed with *S. polyrhiza*, the snails showed a steady increase in feed intake across the starvation treatments (Fig. 4A). A similar increasing pattern was observed when *P. canaliculata* was fed with *L. aequinoctialis* (Fig. 4A), indicating that prolonged starvation enhances feeding activity and consumption rate in this species. Temperature also had a significant effect on the feeding behavior of *P. canaliculata* (Fig. 4B). Feed intake increased as temperature rose from 20°C to 28°C, reaching the highest level at 28°C, and subsequently declined at 32°C. When fed with *S. polyrhiza*, *P. canaliculata* exhibited the highest feeding rate at 28°C (Fig. 4B), suggesting that moderate temperature conditions promote optimal metabolic and feeding activity. Similarly, the snails showed maximum feed intake on *L. aequinoctialis* at 28°C (Fig. 4B), whereas both lower (20°C and 24°C) and higher (32°C) temperatures resulted in reduced consumption. These findings indicate that 28°C represents the optimal temperature for feeding activity of *P. canaliculata* under experimental conditions. Duckweed density also significantly affected feed intake by *P. canaliculata* (Fig. 5C). Feed consumption increased progressively with increasing duckweed density from 0.0165 g cm^{-2} to 0.0811 g cm^{-2}. When fed with *S. polyrhiza*, the lowest feed intake occurred at t/he lowest density, whereas the highest intake was recorded at the highest density (Fig. 4C). A similar trend was observed when *P. canaliculata* was fed with *L. aequinoctialis*, where feed intake increased consistently with increasing duckweed density (Fig. 4C). These results suggest that greater food availability enhances feeding efficiency and consumption rates of *P. canaliculata* when feeding on duckweed species.

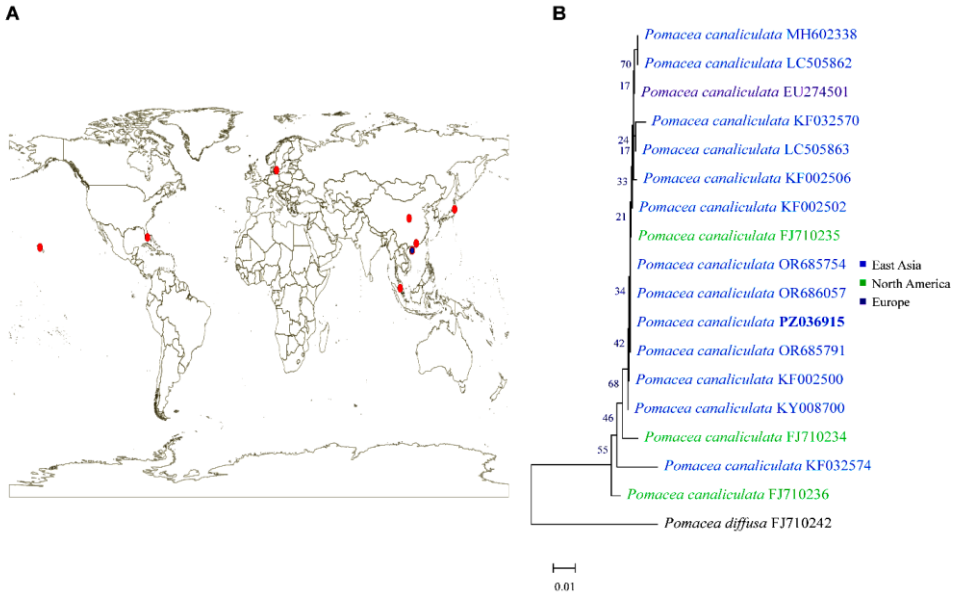

Fig. 3: (A) Worldwide distribution map showing sampling locations used in this study, including native (South America) and introduced regions such as East and Southeast Asia (e.g., China, including Hainan), North America, and Europe. (B) Phylogenetic tree inferred from mitochondrial 16S rRNA gene sequences. Bootstrap support values are shown at major nodes. *P. diffusa* was used as an outgroup.

Duckweed species and snail body weight significantly influenced the feed intake of *P. canaliculata* (Fig. 5). A significant difference in feeding preference was observed between the two duckweed species (Fig. 5A). Snails fed with *L. aequinoctialis* exhibited significantly higher feed intake compared with those fed with *S. polyrhiza*. The different letters above the bars indicate that the difference between the two treatments was statistically significant ($P<0.05$), suggesting that *L. aequinoctialis* is more readily consumed by *P. canaliculata* than *S. polyrhiza*.

Snail body weight also had a significant effect on feeding performance (Fig. 5B). Two snail weight groups, 4.5 g and 5.9 g, were used to evaluate the effect of body size on feed intake. The results showed that 5.9 g snails consumed significantly more duckweed than 4.5 g snails when feeding on both *S. polyrhiza* and *L. aequinoctialis*. In both duckweed treatments, feed intake increased with increasing snail body weight, indicating that the feeding capacity of *P. canaliculata* is positively related to body size. Statistical analysis confirmed that the differences between the two weight groups were significant ($P<0.05$), as indicated by the different letters above the bars. These findings demonstrate that larger individuals of *P. canaliculata* have a greater feeding capacity and are able to consume higher amounts of duckweed compared with smaller snails. Overall, these results demonstrate that both duckweed species and snail body weight play important roles in determining the feeding behavior and consumption rate of *P. canaliculata*.

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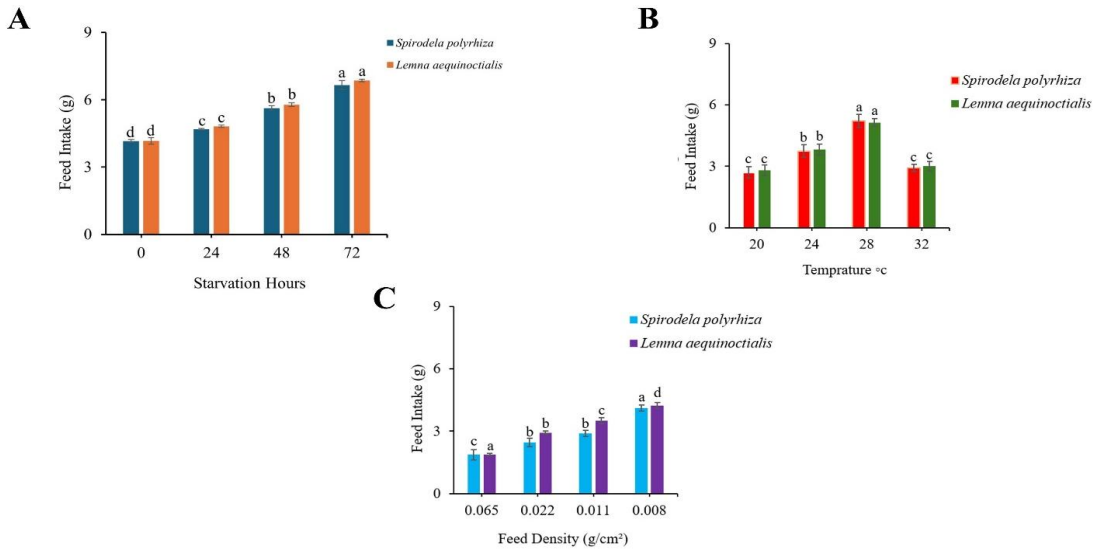

Fig. 4: Effects of starvation duration, temperature, and duckweed density on feed intake of the freshwater snail *P. canaliculata* when fed with *S. polyrhiza* and *L. aequinoctialis*. (A) show the effect of starvation duration (0, 24, 48, and 72 h) on feed intake of snails fed with *S. polyrhiza* and *L. aequinoctialis*, respectively. (B) illustrate the effect of temperature (20, 24, 28, and 32°C) on feed intake of *P. canaliculata* feeding on *S. polyrhiza* and *L. aequinoctialis*. (C) present the effect of duckweed density (0.0165, 0.0325, 0.0487, and 0.0811 g cm^{-2}) on feed intake of *P. canaliculata* fed with *S. polyrhiza* and *L. aequinoctialis*. Values represent mean ± standard error, and different letters above bars indicate significant differences among treatments (P<0.05).

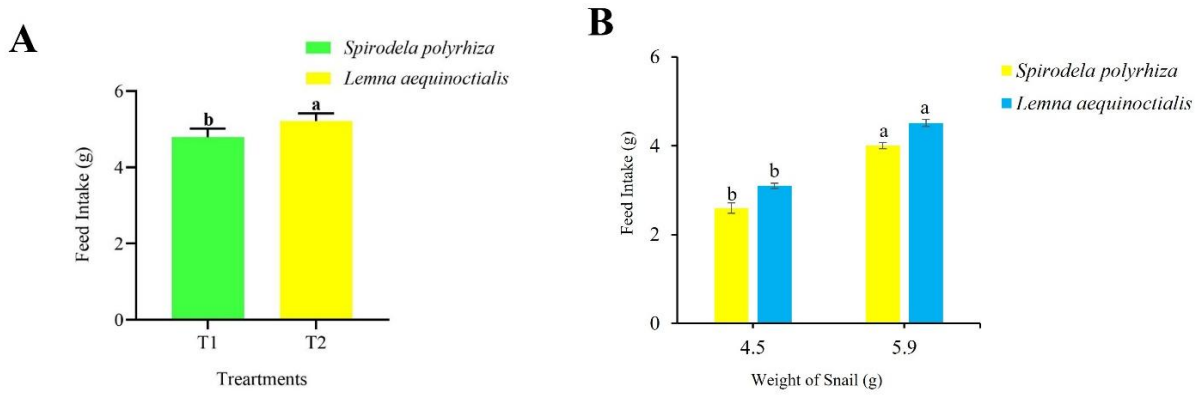

Fig. 5: Effects of duckweed species and snail body weight on the feed intake of the freshwater apple snail *P. canaliculata*. (A) Comparison of feed intake of snails fed with *S. polyrhiza* and *L. aequinoctialis*. (B) Effect of snail body weight (4.5 g and 5.9 g) on feed intake when feeding on the two duckweed species. Bars represent mean ± standard error (SE), and different letters above bars indicate statistically significant differences among treatments (P<0.05).

3.5. Protection Strategies against *P. canaliculata* Damage

3.5.1. Effect of E-Medium on Feed Intake

E-Medium concentration significantly affected both duckweed biomass and the mortality of *P. canaliculata* (Fig. 6). Duckweed biomass varied significantly across the tested E-Medium concentrations after seven days of exposure (one-way ANOVA, P<0.05; Fig. 6A). At lower to intermediate E-Medium concentrations, duckweed biomass was significantly higher compared with the control treatment, indicating reduced grazing pressure by *P. canaliculata*. However, at higher E-Medium concentrations, duckweed biomass decreased significantly, suggesting that excessive nutrient levels may negatively influence duckweed growth and physiological performance. Snail mortality also showed a significant response to increasing E-Medium concentration after 72 h of exposure (one-way ANOVA, P<0.05; Fig. 6B). Mortality of *P. canaliculata* increased progressively with increasing E-Medium concentration, indicating that higher nutrient concentrations may adversely affect snail survival. The presence of different letters above the bars indicates statistically significant differences among treatments (P<0.05). Overall, the results demonstrate that E-Medium concentration simultaneously affects duckweed performance and P. canaliculata

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survival, with intermediate concentrations striking a balance between reduced grazing pressure and optimal duckweed biomass production.

3.6. Effect of Niclosamide on Feed Intake

Niclosamide concentration significantly influenced both the mortality of *P. canaliculata* and duckweed biomass (Fig. 7). Duckweed biomass differed significantly among treatments after seven days of exposure to varying Niclosamide concentrations (one-way ANOVA, $P<0.05$; Fig. 7A). At lower Niclosamide concentrations in the snail-containing treatments, duckweed biomass increased compared with the untreated control, indicating a reduction in grazing pressure by *P. canaliculata*. However, at higher Niclosamide concentrations, duckweed biomass declined, suggesting that elevated Niclosamide levels may exert phytotoxic effects on duckweed growth. In the duckweed-only treatments, duckweed biomass also decreased significantly with increasing Niclosamide concentration, confirming a direct negative effect of Niclosamide on duckweed development in the absence of snail grazing. Snail mortality showed a significant response to Niclosamide exposure after 72 h (one-way ANOVA, $P<0.05$; Fig. 7B). Mortality of P. canaliculata increased progressively with increasing Niclosamide concentration, demonstrating the strong molluscicidal activity of the compound. The presence of different letters above the bars indicates statistically significant differences among treatments ($P<0.05$). Overall, the results indicate that Niclosamide effectively reduces snail survival and grazing pressure at moderate concentrations, but higher concentrations may negatively affect duckweed growth.

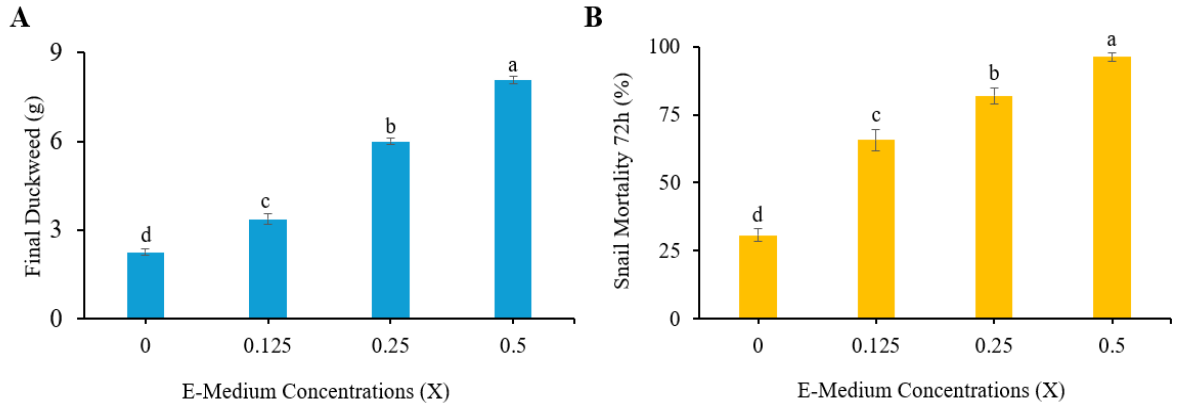

Fig. 6: Effect of E-Medium concentration on duckweed biomass and mortality of the freshwater apple snail *Pomacea canaliculata*. (A) Final duckweed biomass measured after seven days of exposure to different E-Medium concentrations. (B) Percentage mortality of *P. canaliculata* recorded after 72 h of exposure. Values represent mean ± standard deviation (n = 3). Different letters above bars indicate statistically significant differences among treatments based on one-way ANOVA followed by Tukey's multiple comparison test ($P<0.05$).

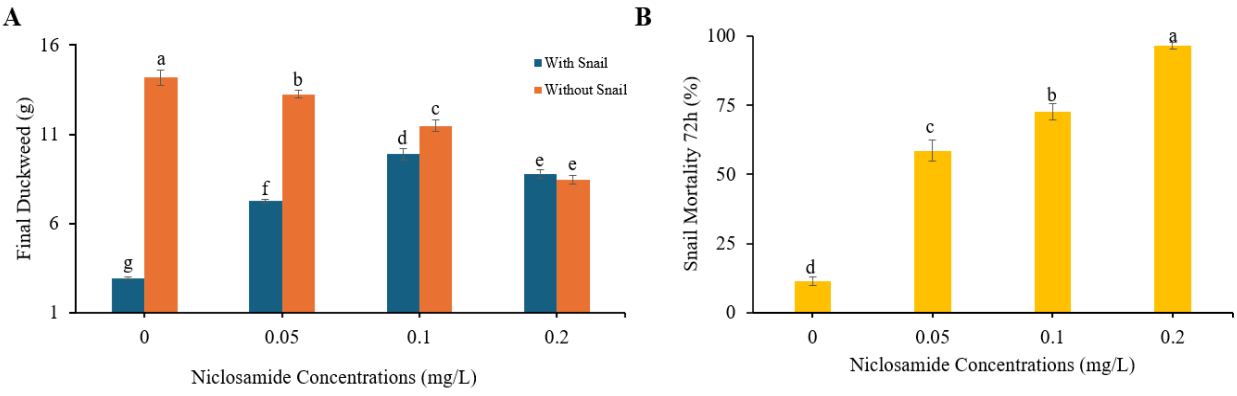

Fig. 7: Effects of Niclosamide concentration on duckweed biomass and mortality of the freshwater apple snail *P. canaliculata*. (A) Final duckweed biomass after seven days of exposure to different Niclosamide concentrations in treatments containing snails and duckweed-only treatments. (B) Snail mortality (%) recorded after 72 h of Niclosamide exposure. Values represent mean ± standard deviation (SD) (n = 3). Different letters above bars indicate statistically significant differences among treatments based on one-way ANOVA followed by Tukey's multiple comparison test ($P<0.05$).

Citation: Shakoor K, Imtiaz U, Tan D and Zhang J, 2026. Feeding ecology and management of the invasive apple snail *Pomacea canaliculata* in duckweed production systems. Agrobiological Records 24: 220-233. https://doi.org/10.47278/journal.abr/2026.039

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3.7. Effect of Tea Saponin on Feed Intake

Tea saponin concentration significantly affected both duckweed biomass and the mortality of *P. canaliculata* (Fig. 8). Duckweed biomass varied significantly among treatments after seven days of exposure to different tea saponin concentrations (one-way ANOVA, $P<0.05$; Fig. 7A). At low to intermediate concentrations in the snail-containing treatments, duckweed biomass increased compared with the untreated control, indicating a reduction in grazing pressure by *P. canaliculata*. However, at higher tea saponin concentrations, duckweed biomass declined, suggesting that excessive levels of tea saponin may exert phytotoxic effects on duckweed growth. In the duckweed-only treatments, duckweed biomass also decreased progressively with increasing tea saponin concentration, confirming that high concentrations of tea saponin can directly inhibit duckweed development in the absence of snail grazing. Snail mortality showed a significant response to tea saponin exposure after 72 h (one-way ANOVA, $P<0.05$; Fig. 8B). Mortality of *P. canaliculata* increased significantly with increasing tea saponin concentration, demonstrating the molluscicidal effect of the compound. The different letters above the bars indicate statistically significant differences among treatments ($P<0.05$). Overall, the results indicate that tea saponin can effectively reduce the survival of P. canaliculata and decrease grazing pressure on duckweed at moderate concentrations, whereas excessive concentrations may negatively affect duckweed biomass.

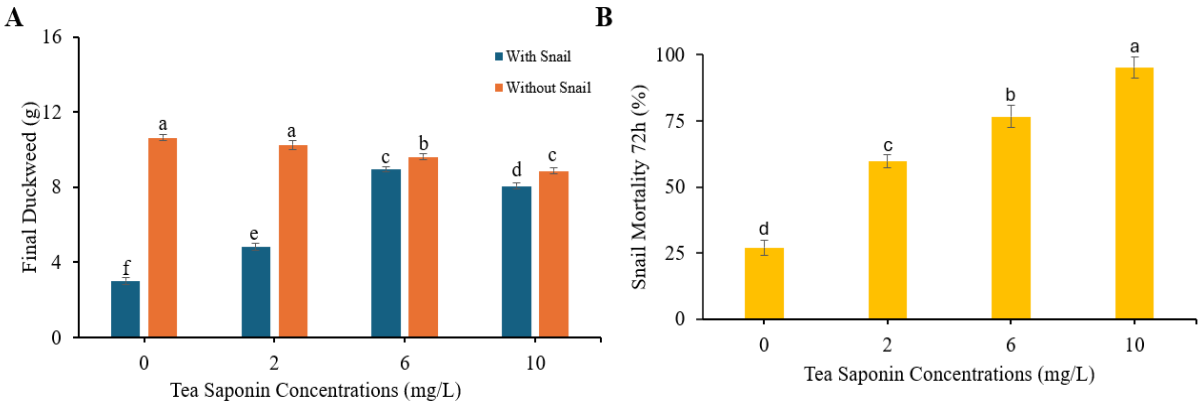

Fig. 8: Effects of tea saponin concentration on duckweed biomass and mortality of the freshwater apple snail *Pomacea canaliculata*. (A) Final duckweed biomass measured after seven days of exposure to different tea saponin concentrations in treatments containing snails (T1–T4) and duckweed-only treatments (T5–T8). (B) Snail mortality (%) recorded after 72 h of tea saponin exposure. Values represent mean ± standard deviation (SD) (n = 3). Different letters above bars indicate statistically significant differences among treatments based on one-way ANOVA followed by Tukey's multiple comparison test ($P<0.05$).

4. DISCUSSION

This study illustrates that the invasive apple snail, P. canaliculata, significantly endangers duckweed production systems, with its grazing effects strongly influenced by biological and environmental parameters. The morphological characteristics, along with mitochondrial COI and 16S rRNA analyses, validated the identification of the collected specimens as *P. canaliculata* (Figs. 1-2), underscoring the significance of integrative taxonomic methods due to the prevalent misidentification within the Pomacea species complex (Wei et al., 2024) (Hayes et al., 2012). The global distribution map (Fig. 3A) shows that *P. canaliculata* has expanded far beyond its native range in South America and is now widely distributed across Asia and other regions. This widespread occurrence reflects the species' strong invasive potential and its ability to establish populations in diverse freshwater environments. Previous studies have reported that human activities such as aquaculture, agriculture, and the aquarium trade have played important roles in facilitating the global spread of *P. canaliculata* (Seuffert & Martín, 2024). The phylogenetic analysis based on mitochondrial 16S rRNA sequences (Fig. 3B) further supports the complex invasion history of this species. The clustering of sequences into several well-supported clades suggests genetic differentiation among populations and indicates that multiple introductory events may have contributed to the current distribution of *P. canaliculata*. Similar patterns of genetic diversity and population structuring have been reported in previous studies, highlighting the role of repeated introductions and secondary dispersal in shaping the invasion dynamics of this species (Wei et al., 2024).

Feeding investigations indicated that hunger significantly influenced feeding behavior; in both *S. polyrhiza* and *L. aequinoctialis*, feed intake increased progressively with extended periods of famine (Fig. 4A). This pattern illustrates compensatory eating behavior, in which snails increase their consumption to restore their energy balance following food deprivation. Recent nutritional studies indicate that *P. canaliculata* exhibits significant dietary

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flexibility and can rapidly adjust its consumption in response to resource availability. This trait elucidates its invasive efficacy and considerable grazing influence (He et al., 2025). These compensatory feeding responses indicate that acute food scarcity may exacerbate eventual harm to duckweed crops rather than alleviate grazing pressure. Feed intake was significantly influenced by temperature, peaking at 28°C and declining at both lower (20°C) and higher (32°C) temperatures (Fig. 4B). This pattern demonstrates the dependence of ectothermic organisms' feeding and metabolic processes on temperature. Recent experimental findings indicate that the feeding activity of *P. canaliculata* increases with temperature until it reaches an optimal range, beyond which physiological stress and diminished metabolic efficiency hinder feeding performance (Miyata & Nakatsubo, 2024). The reduction in intake at 32°C noted in this study likely indicates thermal stress, implying that duckweed damage may be more pronounced during moderately warm temperatures rather than during extreme heat events. Feeding efficiency was similarly affected by feed surface density, with reduced surface densities exhibiting increased intake and elevated densities demonstrating decreased consumption (Fig. 4C). This indicates that grazing intensity is markedly affected by the accessibility of duckweed and the efficacy of its management. Narrower coverage facilitates more efficient rasping and eating, but dense duckweed mats may restrict snail mobility or diminish feeding efficiency. Apple snails consuming aquatic macrophytes demonstrate comparable density-dependent feeding responses, wherein plant arrangement influences encounter rates and feeding efficacy (Manara et al., 2024). *L. aequinoctialis* was consistently consumed in greater amounts than *S. polyrhiza*, suggesting that duckweed species significantly influenced feeding behavior (Fig. 5A). Although apple snails are generalist herbivores, they may display species-specific feeding preferences based on nutritional composition, tissue pliability, and plant structure. Recent nutritional research indicates that *P. canaliculata* exhibits flexible feeding strategies and alters its dietary composition in response to environmental conditions and plant availability (He et al., 2025). The increased consumption of *L. aequinoctialis* noted in this study indicates that the selection of duckweed species may affect susceptibility to snail grazing in agricultural systems. Feed intake exhibited a positive correlation with snail body weight, as larger snails ingested more duckweed than their lighter counterparts (Fig. 5B). Apple snails demonstrate size-dependent feeding behavior, wherein larger individuals impose significantly greater grazing pressure owing to elevated energetic requirements and feeding capacity (Carlsson & Brönmark, 2006). This finding highlights the importance of targeting larger snails in management programs to reduce overall damage intensity.

Despite their dose-dependent effects, protection studies indicated that E-Medium, Niclosamide, and tea saponin effectively reduced snail eating and increased duckweed biomass. As concentration increased, E-Medium treatments resulted in elevated snail mortality and duckweed biomass (Fig. 6A), with mortality assessed after 72 hours. Snail susceptibility is consistently demonstrated through acute toxicity assays conducted over 72 hours, commonly utilized in molluscicide assessment. When applied in appropriate proportions, E-Medium effectively safeguards duckweed by reducing grazing pressure, as evidenced by the concurrent rise in duckweed biomass and snail mortality. Niclosamide exhibited potent molluscicide activity, with snail mortality significantly increasing with concentration and nearing complete mortality at the maximum dosage (Fig. 7). In treatments devoid of snails, duckweed biomass diminished at the highest dosage, indicating phytotoxic effects. The trade-off between the efficacy of molluscicides and the toxicity to non-target plants in aquatic ecosystems has been extensively recorded, highlighting the necessity of optimizing treatment rates (Yang et al., 2023). The present results indicate that intermediate niclosamide concentrations provide the most balanced outcome, reducing snail grazing while minimizing adverse effects on duckweed growth. Strong concentration-dependent molluscicide activity was also shown by tea saponin; after 72 hours, full snail mortality was seen at the maximum concentration (Fig. 8B). Nevertheless, elevated saponin concentrations in strong tea decreased duckweed biomass in the absence of snails, suggesting phytotoxicity, similar to niclosamide (Fig. 8A). Recent investigations indicate that tea saponin is a promising plant-derived molluscicide against *P. canaliculate*, however, they also highlight the potential for non-target effects at elevated dosages (Lu et al., 2025). These findings underscore the necessity for meticulous dose optimization when utilizing botanical control agents in duckweed cultivation systems. Overall, the findings show that *P. canaliculata* is a serious threat to the production of duckweed, and that temperature, meal availability, duckweed species, snail size, and starving history all affect feeding damage. While elevated quantities of chemical and botanical control agents may impede the growth of duckweed, they can effectively reduce snail populations and grazing pressure. Recent study on invasion ecology indicates that sustainable management of *P. canaliculata* requires a compromise between environmental safety and control efficacy (Seuffert & Martín, 2024). The present study provides experimentally supported guidance for optimizing snail management strategies to protect duckweed farming systems under subtropical conditions.

5. CONCLUSION

This study offers a thorough assessment of the grazing effects of the invasive apple snail, P. canaliculata, on duckweed farming systems and investigates feasible techniques to alleviate snail-related damage in controlled

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laboratory settings. The experimental specimens were accurately identified by a combination of integrative morphological analysis and mitochondrial COI and 16S rRNA gene sequencing, confirming the species as *P. canaliculata*. Accurate species identification is crucial for understanding ecological effects and formulating appropriate management measures, especially given the taxonomic intricacies within the *Pomacea* species group. Feeding trials revealed that the grazing intensity of *P. canaliculata* is markedly variable and significantly affected by both biological and environmental factors. Feed intake markedly increased with extended famine durations, suggesting compensatory feeding behavior that may exacerbate duckweed harm after episodes of food shortage. Feeding activity peaked at moderate temperatures, with diminished intake at both lower and higher temperatures, underscoring the significance of thermal circumstances in modulating snail grazing pressure. The surface density of duckweed influenced feeding efficiency, with lower densities increasing intake rates. Distinct species-specific variations in sensitivity to grazing were noted, with *L. aequinoctialis* being consistently devoured in larger amounts than *S. polyrhiza*. Larger snails imposed significantly greater grazing pressure than smaller ones, highlighting the importance of population size structure in assessing overall damage severity. Protection tests demonstrated that E-Medium strength, Niclosamide, and tea saponin can significantly reduce snail grazing and increase duckweed biomass when administered at appropriate concentrations. Nonetheless, elevated levels of Niclosamide and tea saponin induced phytotoxicity in duckweed, even in the absence of snails, indicating that excessive pesticide use may jeopardize crop health. Intermediate concentrations achieved an optimal balance between snail management and duckweed preservation, highlighting the importance of dosage optimization. This study confirms that *P. canaliculata* significantly threatens duckweed production systems and emphasizes the necessity for integrated management strategies that merge ecological insights into snail feeding behavior with meticulously optimized control measures to ensure sustainable duckweed cultivation.

Declarations

Funding: This work was supported by the National Tropical Agriculture Science and Technology Innovation Project for the Chinese Academy of Tropical Agricultural Sciences (CATAS202617).

Conflicts of Interest: The authors declare no competing interest.

Data Availability: Data will be made available on request.

Ethics Statement: This study involved only plants and pest materials collected from natural freshwater habitats. No experiments involving human participants or animals were conducted. Therefore, ethical approval was not required. All sample collection and experimental procedures were carried out in accordance with relevant institutional guidelines and local regulations.

Author's Contributions: Khubaib Shakoor: Sample collection, Investigation, Formal analysis, original draft, revision. Umer Imtiaz: Manuscript revision. Review, Validation, Project. Deguan Tan: Formal analysis, Data curation, Revision. Jiaming Zhang: Writing review and editing, Conceptualization, Supervision, Funding acquisition.

Generative AI Statements: The authors declare that no Gen AI/DeepSeek was used in the writing/creation of this manuscript.

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