

Article

Potential Detritivorous Diet of the Invasive Apple Snail (*Pomacea canaliculata* Lamarck, 1822) in Mangroves: The Relationship between Feeding Indicators and Chemical Characteristics of Decaying Leaf Litter

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Abstract: Invasive species have had substantial impacts on global mangrove forests. Apple snails (*Pomacea canaliculata*) have invaded mangrove forests in China. To clarify the potential detritivorous diet of *P. canaliculata*, the growth and feeding indicators of invasive juvenile snails collected from mangroves in Guangzhou, China, were studied using decaying leaf litter from five mangrove species, including *Acanthus ilicifolius*, *Acrostichum aureum*, *Kandelia candel*, *Aegiceras corniculatum*, and *Sonneratia apetala*. The growth indicators of the survival ratio and specific growth rate were calculated by measuring the live weight of the snails and the number of dead snails after 30 days. The feeding indicator of the weight-specific daily feeding rate (WDR) was calculated by measuring the snail weight and the amount of leaf litter ingested after 120 h. A multiple-choice experiment was performed on the snails by providing the decaying leaf species together, while a no-choice experiment was performed using a single species of decaying leaf litter. The survival and specific growth ratio of *P. canaliculata* feeding on decaying leaf litter of *A. ilicifolius* were higher than those for *A. aureum*. The WDR values of *P. canaliculata* feeding on the decaying leaf litter of *A. ilicifolius* and *S. apetala* were both significantly higher than those for *A. corniculatum*, *A. aureum*, and *K. candel*. The lowest WDR value of *P. canaliculata* feeding on decaying leaf litter was observed for *A. aureum* in the no-choice experiment. *P. canaliculata* mainly fed on decaying leaf litter of *A. ilicifolius* and *S. apetala*. The phosphorous contents and ash of the decaying leaf litter positively affected the WDR values of *P. canaliculata* obtained in the multiple-choice and no-choice experiments. The contents of lignin, tannin, and flavonoid negatively affected the WDR values of *P. canaliculata*. The potential diet of invasive *P. canaliculata* in mangroves was closely tied to the chemical characteristics of the decaying leaf litter. *P. canaliculata* can invade *A. ilicifolius* and/or *S. apetala* mangroves by utilizing the debris on the mangrove ground. Understanding the potential detritivorous diet of *P. canaliculata* in invaded mangroves can help us to assess this species' dispersal risk and provide support for mangrove management.

Keywords: mangrove forest; food source; growth indicator; feeding behavior; multiple-choice feeding



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1. Introduction

Mangroves are coastal ecosystems with the highest level of primary productivity in (sub)tropical intertidal areas, with a global distribution of 130,000–150,000 km² [1,2]. In addition to being significantly productive ecosystems worldwide, mangrove forests exhibit multiple ecosystem services, including the maintenance of diverse habitats for coastal creatures [3], nutrient sink [4], carbon storage [5], coastline protection, and disaster mitigation [6].

As a woody plant community located in the intertidal zone, the biomass of mangroves has been significantly disturbed by both natural and anthropogenic stressors on a global scale [7]. Similar to many other ecosystems, mangrove forests are also emerging hotspots of invasion by exotic species due to the complex habitats they hold [8]. Invasive species, especially animals, have significantly or potentially influenced mangroves by means of voracious appetites [9], interspecific competition [10], predation [11], nutrient cycle interruption [12], and habitat modification [13].

Ecological and socio-economic services dependent on mangrove ecosystems have been profoundly impacted by invasive species. A fundamental step in the risk assessment and effective control of invasive species is to determine their role in the food chain in mangroves. Mangrove litter fall is an essential link in the mangrove food chain. The litter fall values of mangroves range from 1.66 to 28.81 Mg⁻¹ ha⁻¹ yr⁻¹ across the neotropics [14]. As an essential food source for benthic animals, mangrove litter largely dominates the structure of the benthic food web in mangrove forests [15]. However, mangrove litter simultaneously offers advantages for the intrusion and establishment of invasive species. For example, the detritus of mangrove *Barringtonia racemosa* leaves contributes 30% of the diet of the invasive snail *Tarebia granifera* [16].

Apple snail (*Pomacea canaliculata* Lamarck, 1822), a harmful freshwater gastropod, is listed as one of the 100 worst invasive alien species [17]. *P. canaliculata* is native to South America and has observably threatened rice productivity in Asia by directly feeding on rice seedlings [18]. *P. canaliculata* is also a crucial vector of the parasitic nematode *Angiostrongylus cantonensis*, which causes rat lungworm disease in humans in Asia [19]. *P. canaliculata* has established populations in diverse aquatic habitats in Asia, North America, South America, and Oceania and shown a tendency to genetically adapt to the climate and agricultural activities of the areas it occupies [20].

Although *P. canaliculata* is a freshwater snail, one study reported a population of this species in a Chilean lagoon with low salinity (1–2.1 ppt) [21]. A laboratory study confirmed that this species could survive in brackish water (5 ppt) [22]. Due to its ability to resist saline stress and a diverse range of microhabitats in mangrove forests [23], this species can invade mangrove forests. In 2018, a benthic investigation found that this species had invaded mangroves in the National Wetland Reserve on Hainan island, China [24]. In 2019, researchers discovered that *P. canaliculata* had invaded mangrove forests in Nansha District, Guangzhou city, China (Supplementary Figure S1) [25].

However, the characteristics of the food source of *P. canaliculata* in mangrove forests remain to be determined in detail. A previous study discovered that the leaves of a mangrove species known as *Acanthus ilicifolius* L. could effectively sustain the proliferation of adult *P. canaliculata* compared with another four species, including *Acrostichum aureum* L., *Kandelia candel* L., *Aegiceras corniculatum* L., and *Sonneratia apetala* Buch.-ham. Such a phenomenon suggests that mangrove leaf litter may facilitate the population establishment of *P. canaliculata* in mangrove forests. Most mangrove leaf litters are sturdy and hard to digest due to their high C: N ratios and concentrations of anti-nutritional secondary compounds that inhibit digestion [26]. Although such traits of leaf litter, to some extent, can protect mangrove forests from the invasion of *P. canaliculata*, the decaying process of the litter may weaken this barrier. The secondary anti-nutritional metabolites contained in leaf litter, especially tannins, saponins, alkaloids, and phytates, can slowly decrease due to the decay process of fragmentation, breakdown, leaching, and degradation of refractory components in leaf litter on the forest floor [27–29]. In addition, many researchers have reported that juvenile mangrove snails are detritivorous and shift their diets to meet their nutrient demands during development [30,31]. Considering the omnivorous appetite of *P. canaliculata* [32], we speculated that the decaying leaf litter could represent a critical step in the establishment of *P. canaliculata* in an unfavorable type of mangrove. However, little is known about the feeding behavior of *P. canaliculata* on decaying mangrove leaf litter. In light of such a scenario, we posed three questions: (1) Can the juvenile *P. canaliculata* grow on the decaying leaf litter of mangroves? (2) Have juvenile *P. canaliculata* a feeding preference

for decaying leaf litter of different mangrove species? (3) Do the chemical properties of decaying mangrove litter affect the preference of juvenile *P. canaliculata*? The resolution to these questions would help to clarify whether *P. canaliculata* can survive in mangrove forests and understand its potential detritivorous diet. This research can also help us to assess the risk of invasive snails in mangroves and support mangrove management efforts.

2. Materials and Methods

2.1. *P. canaliculata* and Decaying Leaf Litter

The tested juveniles were the progeny of apple snails, which were collected from the mangrove forests in Guangzhou, China (22°62' N, 113°66' E), in February 2019. The mean air temperature and the annual precipitation in the sampling region from 2019 to 2021 were 24.2 °C and 1677.3 mm [33]. The parental snails collected from the field location were identified as *P. canaliculata* (GenBank accession numbers: MW799954, MW799955 [25]).

Hatched *P. canaliculata* juveniles aged over two weeks old were reared in artificial seawater (3 ppt) in aquaria (80 cm × 60 cm × 60 cm) at a water temperature of 25 ± 1 °C and pH (7.3–7.5) based on the water quality of the sampling locations [25]. The artificial seawater in the aquaria comprised aerated tap water and was refreshed every day. The salinity was adjusted by supplying artificial sea salt (Yanzhibao, Guangdong, China), which was measured with a salinity meter (Shanghai Sanxin Instrument Co., Ltd., SX5051, Shanghai, China). Before the experiment, the juveniles were fed with lettuce (*Lactuca sativa* L.) every day at the same temperature (25 ± 1 °C). Healthy snails were used in the experiments. These healthy snails had the characteristic of smooth and intact shells, and they were in an active state, characterized by continuous movement in the aquaria. Juvenile snails that did not reach sexual maturity were used in the experiments [34]. After being starved for 24 h, the snails were used in experiments conducted at room temperature (25 ± 1 °C) in seawater (3 ppt).

The leaf litter of five mangrove species was used to determine the growth and feeding indicators of *P. canaliculata*. The tested mangrove species included *Acanthus ilicifolius* L. (Acanthaceae, holy mangrove shrub), *Acrostichum aureum* L. (Pteridaceae, mangrove fern), *Kandelia candel* L. (Rhizophoraceae, narrow-leaved Kandelia), *Aegiceras corniculatum* L. (Primulaceae, black mangrove), and *Sonneratia apetala* Buch.-ham (Sonneratiaceae, mangrove apple) [25].

We used plastic nets (<0.850 mm) to collect fallen leaf litter from the mangrove forest. The collected leaf litter was composed of naturally fallen leaves accumulated on the same day without human interference. Leaf litters of similar sizes were selected to ensure that they had similar physical and chemical characteristics in the experiments. We used a burying treatment to obtain the decaying mangrove leaf litter [26]. A plastic box was filled with mangrove sediments (depth 15 cm) collected from the mangrove forest. The leaf litter ($50 \text{ g} \pm 1 \text{ g}$) was placed in a net bag with a rope (30 cm × 20 cm, 5 mm mesh) before being buried at a 5 cm depth from the sediment surface. The level of artificial seawater (3 ppt) was maintained daily at 5 cm, and the seawater was replaced every 5 days before retrieving the litter bags after 30 days. The leaf litter was carefully cleaned using purified water to remove adhered salts, sediment particles, and microfauna. Part of the leaf litter was measured for its moisture content by oven drying at 105 °C (4 h) and 80 °C (48 h) to a constant weight [25]. The left leaf litter was stored at 4 °C in the refrigerator for further experiments.

The chemical characteristics of the decaying leaf litter, including the contents of carbon, nitrogen, phosphorous, calcium, protein, ash, fiber, lignin, tannin, phenol, and flavonoid, were determined according to the method of [35–41] (Table 1).

2.2. Growth of *P. canaliculata* Feeding on Decaying Leaf Litter

Five species of decaying mangrove leaf litter were separately placed in a chamber (25 cm diameter × 10 cm height) together with ten healthy snails (height: 1.42 ± 0.03 cm) [25]. The decaying leaf litter (5.0 g) and the seawater (4 L, 3 ppt) in each chamber were refreshed daily. The decaying leaf litter was cleaned with filter paper before use. The growth ex-

periment was performed in 4 replicates for each kind of decaying leaf litter and lasted for 30 days. The initial live weight (LW1, g) and the final live weight (LW2, g) of the snails were measured using an electronic balance [25]. The specific growth rate ($\% \cdot d^{-1}$) of the snails was calculated as $(\ln LW2 - \ln LW1)/30 \times 100\%$ [42]. The number of dead snails was checked and recorded daily [18]. According to the accumulated quantities of dead snails (AQ), the survival ratio was calculated as $(10 - AQ)/10 \times 100\%$ after 30 days. Dead snails were taken out of the chamber during each check. The removal of dead individuals did not affect the diet of the surviving juveniles because enough decaying leaf litter and the same water quality were provided in the chamber.

Table 1. Measurement of chemical characteristics of decaying leaf litter.

Characteristics	Measurement Method
Carbon	Potassium dichromate oxidation method [35]
Phosphorous	Ascorbic acid-antimony reduced phosphate colorimetric method [36]
Calcium	EDTA titrimetric method [37]
Protein and nitrogen content	National Standards of China (GB 5009.5-2016)
Ash	Dry ash method [38]
Crude fiber	National Standards of China (GB/T 5009.10-2003)
Lignin	Klason method [39]
Tannin and phenol	EDTA method [40]
Flavonoid	Ethanol extraction method [41]

2.3. Multiple-Choice Experiment of *P. canaliculata* on Decaying Leaf Litter

Another experiment was conducted to measure the preference of *P. canaliculata* for five kinds of mangrove decaying leaf litter under multiple-choice feeding conditions [25,43]. The mangrove decaying leaf litter was cleaned with purified water before use. Each kind of decaying leaf litter weighed from 0.9 to 1.1 g. Decaying leaf litter (5.0 g) from five mangrove species was placed in a chamber (25 cm diameter \times 10 cm height) filled with artificial seawater (4 L). *P. canaliculata*, with a height of 1.40 ± 0.03 cm, were then placed in the chamber. The artificial seawater (3 ppt) was refreshed every day. The experiment was performed in four replicates. After 120 h, the remaining mangrove decaying leaf litter was oven-dried at 105 °C (4 h) and 80 °C (48 h) to a constant weight after removing the adhered salt using purified water [25]. All the individuals were alive during the 120 h of the experiment.

2.4. No-Choice Experiment of *P. canaliculata* Feeding on Decaying Leaf Litter

Another experiment was conducted to measure the palatability of five kinds of mangrove decaying leaf litter to *P. canaliculata* under no-choice feeding conditions [25]. The mangrove decaying leaf litter was cleaned using purified water before use. Ten healthy snails with a height of 1.40 ± 0.02 cm were placed in a plastic chamber (25 cm diameter \times 10 cm height) together with a species of decaying leaf litter (5.0 g) after the recording of their live weights. Plastic chambers with artificial seawater (4 L, 3 ppt) were used in the experiment. All the individuals were alive after 120 h. The artificial seawater in each chamber was refreshed every day. The experiment was performed in four replicates. After 120 h, the remaining mangrove decaying leaf litter was oven-dried at 105 °C (4 h) and 80 °C (48 h) to a constant weight after removing the adhered salt using purified water [25].

2.5. Feeding Indicators of *P. canaliculata*

The amount of leaf litter ingested was calculated according to the initial and final dry weights. The initial dry weight of the leaf litter of five species of mangroves was obtained according to the fresh weight used in the multiple-choice and no-choice experiments and the moisture content. After 120 h of the multiple-choice and no-choice experiments, the final dry weight of the remaining mangrove decaying leaf litter was measured by drying at 105 °C (4 h) and 80 °C (48 h) to a constant weight. The remaining decaying leaf litter was

rinsed and cleaned to remove the adhered salt. The weight-specific daily feeding rate (WDR) was used to analyze the feeding behaviors of *P. canaliculata* under the multiple-choice and no-choice feeding conditions, according to Equation (1).

$$WDR(g \cdot g \cdot h^{-1}) = \frac{\text{amount of leaf litter ingested}}{\text{weight of ten snails}} \times \frac{1}{120} \quad (1)$$

2.6. Statistical Analyses

We performed all statistical analyses using R software 4.0.3 [44]. To compare the growth and feeding indicators of *P. canaliculata* on decaying leaf litter, the Kolmogorov–Smirnov test and Levene test were used to analyze the normality and homogeneity of variances of the data. We used ANOVAs (Tukey) and nonparametric tests (Kruskal–Wallis with Dunn–Bonferroni) to compare the feeding indicators of *P. canaliculata* for decaying leaf litter. We performed a collinearity test of the variables through the R package “vegan” [44–46]. To analyze the correlation between the feeding indicators and chemical characteristics of decaying leaf litter, we used Pearson’s correlation, linear fit, and redundancy analyses (RDA), implemented through the R packages “stats”, “vegan”, “ggplot2”, and “ggrepel” [44,46–48]. We used principal component analysis (PCA) implemented through the R packages “FactoMineR” and “factoextra” to further analyze the clustering of the feeding indicators of *P. canaliculata* on decaying leaf litter [44,49,50].

3. Results

3.1. The Growth of *P. canaliculata* on Decaying Leaf Litter

The specific growth ratios of *P. canaliculata* feeding on decaying leaf litter of *A. aureum*, *K. candel*, and *A. corniculatum* had negative values. The average specific growth ratio of the *P. canaliculata* that consumed the decaying leaf litter of *A. ilicifolius* was 6.6, 6.5, and 6.5 times as high as the values (absolute values) for *A. aureum* ($p < 0.01$), *K. candel* ($p < 0.01$), and *A. corniculatum* ($p < 0.01$), respectively. The survival ratio of *P. canaliculata* feeding on *A. ilicifolius* ($p = 0.027$) or *S. apetala* ($p = 0.027$) litter was significantly higher than that of snails feeding on *A. aureum*, whereas no significant differences were observed between the decaying leaf litter of *A. aureum*, *K. candel*, and *A. corniculatum* (Figure 1).

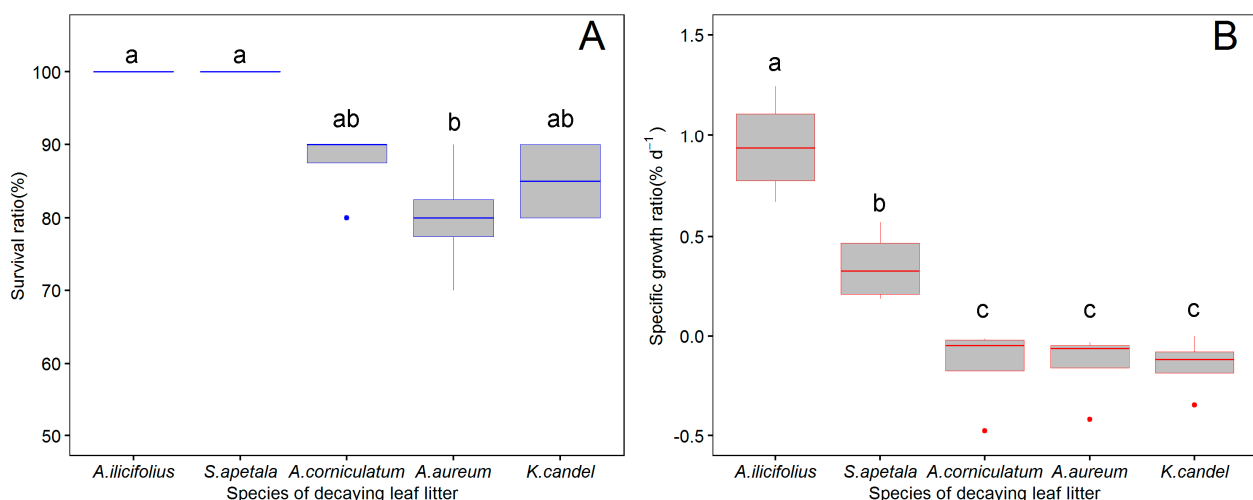


Figure 1. Boxplot of survival ratio ((A), blue) and specific growth ratio ((B), red) of *P. canaliculata* on decaying leaf litter of five species of mangroves. Species with the same letter are not significantly different (Kruskal–Wallis with Dunn–Bonferroni or Tukey tests).

3.2. The Feeding Indicators of *P. canaliculata* on Mangrove Leaves

Under the multiple-choice feeding conditions, the WDR values of *P. canaliculata* feeding on decaying leaf litter of *A. ilicifolius* and *S. apetala* were both significantly higher than those for *A. corniculatum*, *A. aureum*, and *K. candel* (Figure 2A). The lowest WDR of *P. canaliculata*

feeding on decaying leaf litter was observed for *A. aureum*. The *P. canaliculata* tended to feed on the decaying leaf litter of *A. ilicifolius* and *S. apetala* when the five mangrove species were offered simultaneously. The WDR of *P. canaliculata* feeding on the decaying leaf litter of *A. aureum* was less than 0.002.

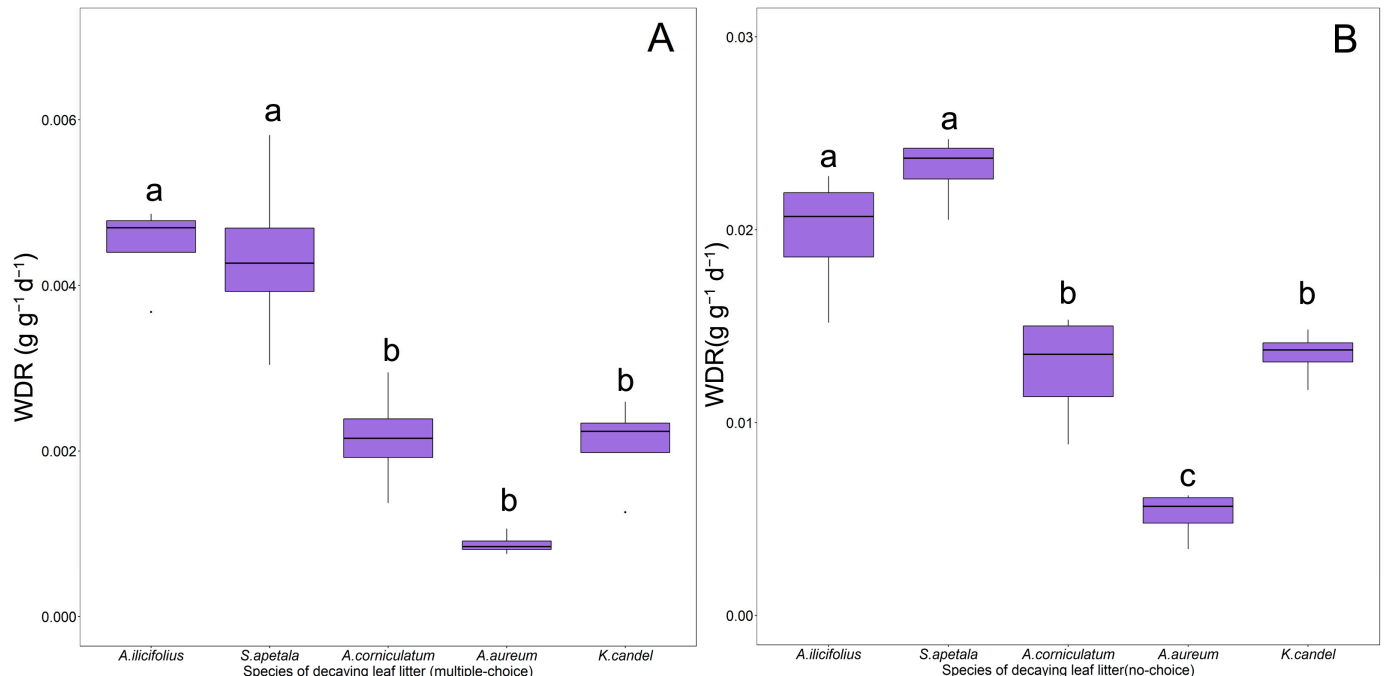


Figure 2. Boxplot of weight-specific daily feeding rate (WDR, g g⁻¹ d⁻¹) of *P. canaliculata* on decaying leaf litter of five mangroves under the multiple-choice condition (A) and the no-choice condition (B). Mangrove species includes *A. ilicifolius* (*Acanthus ilicifolius*), *S. apetala* (*Sonneratia apetala*), *A. corniculatum* (*Aegiceras corniculatum*), *A. aureum* (*Acrostichum aureum*), and *K. candel* (*Kandelia candel*). Species with the same letter are not significantly different (ANOVAs with Tukey or Kruskal–Wallis with Dunn–Bonferroni).

Under the no-choice feeding conditions, the WDR decreased as follows: *A. ilicifolius*, *S. apetala* > *A. corniculatum*, *K. candel* > *A. aureum* ($p < 0.05$) (Figure 2B). The WDR indicator showed that *P. canaliculata* mainly fed on the decaying leaf litter of *A. ilicifolius* and *S. apetala* when the five kinds of decaying leaf litter were provided independently as food. The median WDR of *P. canaliculata* feeding on the decaying leaf litter of *A. aureum* was less than 0.01. This was consistent with the result showing that *A. aureum* did not sufficiently support the snails' growth compared with *A. ilicifolius* and *S. apetala* used in the growth experiment.

3.3. Correlation Analysis between the Diet and Chemical Characteristics of Decaying Leaf Litter

The feeding indicators showed different relationships with the chemical characteristics of decaying leaf litter in the correlation analysis (Tables 2 and 3). Under the no-choice feeding conditions, the WDR indicator was significantly positively correlated with the phosphorous content and ash of the decaying leaf litter, whereas a significantly negative relationship was observed between this indicator and the contents of lignin, tannin, and flavonoid. Under the multiple-choice feeding conditions, a positive correlation of the WDR with the contents of nitrogen, phosphorous, protein, and ash was observed, whereas a significantly negative correlation was observed between the WDR and the contents of lignin, tannin, phenolic, and flavonoid.

Significantly positive linear relationships between the indicators of the WDR and WDRN and some of the chemical characteristics of the decaying leaf litter were observed under the multiple-choice and no-choice feeding conditions (Supplementary Tables S1 and S2; Supplementary Figures S3 and S4). Under the multiple-choice feeding conditions, the indi-

cator WDR had a significantly positively linear relationship with the nitrogen, phosphorous, ash, and protein contents (Supplementary Tables S1 and S2). In contrast, the same indicator WDR was significantly negatively linear related to the contents of flavonoid, lignin, phenolic, and tannin (Supplementary Table S2). Under the no-choice feeding conditions, the indicator WDRN showed a significantly positively linear relationship with the phosphorus and ash contents (Supplementary Table S1), whereas it showed a significantly negative linear relationship with the flavonoid, lignin, and tannin contents (Supplementary Table S2).

Based on the collinearity analysis, RDA was performed to distinguish the main factors influencing the feeding indicators of *P. canaliculata* (Figure 3). The results showed that the ash content in the decaying leaf litter positively influenced the indicators under the multiple-choice (WDR) and no-choice conditions (WDRN). In contrast, the lignin and flavonoid contents were significantly negatively related to the indicators. RDA confirmed that the decaying leaf litters of *A. ilicifolius* and *S. apetala* were the preferred foods for *P. canaliculata*. The chemical characteristics of *A. corniculatum*, *A. aureum*, and *K. candel* were closely related to the contents of lignin and flavonoid, indicating that they were unfavored as food sources by *P. canaliculata*.

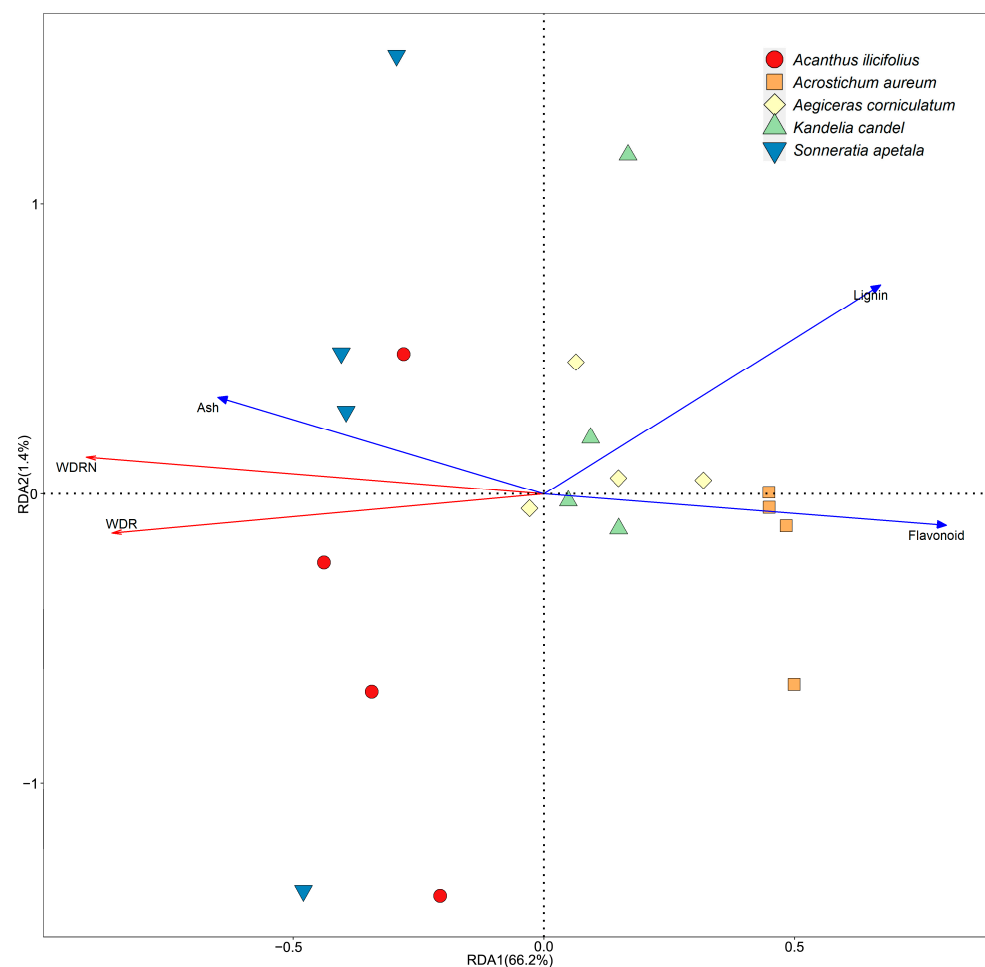


Figure 3. Redundancy analyses (RDA) of the correlations between feeding indicators and chemical characteristics of decaying leaf litter of five species of mangroves. WDR ($\text{g g}^{-1} \text{d}^{-1}$)—weight-specific daily feeding rate under the multiple-choice condition; WDRN ($\text{g g}^{-1} \text{d}^{-1}$)—weight-specific daily feeding rate under the no-choice condition.

Based on the significantly correlated chemical characteristics of the decaying leaf litter of five species of mangroves, PCA was applied for the feeding indicators of *P. canaliculata* (Supplementary Figure S2). Principal components 1 and 2 explained 65% and 19% of the

total variation (eigenvalues > 1). PCA showed that the decaying leaf litter of five mangrove species formed four clusters, and two mangrove species significantly overlapped.

Table 2. Correlation of inorganic chemical characteristics of decaying leaf litter and feeding indicators of *Pomacea canaliculata*.

Indicator (g g ⁻¹ d ⁻¹)	Carbon (g kg ⁻¹)	Nitrogen (g kg ⁻¹)	C/N Ratio	Calcium (%)	Phosphate (g kg ⁻¹)
WDR(multiple-choice)	−0.284	0.485 *	−0.396	0.109	0.685 **
WDR(no-choice)	−0.044	0.345	−0.257	0.275	0.544 *

Note: The symbols * and ** indicate significant value ($p < 0.01$ or 0.05). WDR—weight-specific daily feeding rate.

Table 3. Correlation of organic chemical characteristics of decaying leaf litter and feeding indicators of *Pomacea canaliculata*.

Indicator (g g ⁻¹ d ⁻¹)	Ash (g kg ⁻¹)	Fiber (g kg ⁻¹)	Flavonoid (g kg ⁻¹)	Lignin (g kg ⁻¹)	Protein (g kg ⁻¹)	Tannin (g kg ⁻¹)	Phenolic (g kg ⁻¹)
WDR(multiple-choice)	0.531 *	−0.169	−0.697 **	−0.695 **	0.485 *	−0.606 **	−0.552 *
WDR(no-choice)	0.644 **	−0.176	−0.755 **	−0.527 *	0.345	−0.474 *	−0.425

Note: The symbols * and ** indicate significant value ($p < 0.01$ or 0.05). WDR—weight-specific daily feeding rate.

4. Discussion

4.1. Survival and Growth on Decaying Leaf Litter

As an r-strategist species, *P. canaliculata* shows typical characteristics of high reproduction [51]. Researchers found that the number of eggs laid by a female *P. canaliculata* at one time reached 1000 individuals per mass, supporting the successful invasion of a new habitat by this population [52]. Food availability acts positively on the survival of juvenile *P. canaliculata*. The limited food sources of weed (*Lemna paucicostata*) and algae (*Zygnemataceae*) led to a decrease in the survival of *P. canaliculata* juveniles in a paddy field [53]. In this study, we replaced the decaying leaf litter every day to ensure that enough food supply was provided to the individuals. The results indicated that the decaying leaf litter of *A. ilicifolius* effectively supported the growth of *P. canaliculata* juveniles, followed by *S. apetala*. The survival of *P. canaliculata* juveniles was also influenced by the species of decaying leaf litter. Furthermore, negative values were observed for the growth of *P. canaliculata* that consumed decaying leaf litter of *A. aureum*, *K. candel*, and *A. corniculatum*, indicating that the nutrient uptake of the surviving *P. canaliculata* juveniles consuming decaying leaf litter was insufficient to compensate for their metabolic consumption. Starvation resistance is partly involved in this pattern, as previous research reported that the mortality of juvenile *P. canaliculata* reached 100% only after 16 days of starvation under moist conditions [54]. The weight of *P. canaliculata* adults feeding on leaves of *K. candel*, *S. apetala*, and *A. corniculatum* increased, although these mangrove species were not favorable to *P. canaliculata* adults [25]. Therefore, the digestive capacity or nutrient transform efficiency of *P. canaliculata* juveniles might be lower than that of adult individuals.

4.2. Feeding Preference of *P. canaliculata* on Decaying Leaf Litter

P. canaliculata can feed on the leaves of various aquatic plants in freshwater wetlands and mangrove forests [55]. Among these plants, the feeding preference of *P. canaliculata* feeding on macrophytes has been relatively well studied compared with that of *P. canaliculata* feeding on mangrove plants. In contrast, there is still much to learn about the feeding preference of *P. canaliculata* for the decaying leaf litter of mangroves. We found that *P. canaliculata* could feed on five kinds of decaying leaf litter from mangroves, and two of them (*A. ilicifolius* and *S. apetala*) were more preferentially consumed. Such a preference of *P. canaliculata* for decaying leaf litter possibly resulted in competitive conflict with several native species of leaf litter consumers, primarily crabs and gastropods, in mangrove forests. Juveniles of

the snail *Terebralia palustris* were found to be detritivorous in mangrove forests, and 19% of the juveniles' gut content was leaf debris [30]. Previous studies have found that *P. canaliculata* had a higher conversion efficiency than native snails, and it could influence native snails through food source consumption in a shared freshwater habitat [56]. Competition may exist between *P. canaliculata* and native juvenile snails.

However, the situation may be different for the mangrove crab. A previous study reported that the crab *Eriocheir japonicas* could be a natural enemy that predares on juvenile *P. canaliculata* [57]. Meanwhile, the mangrove crab *Neosarmatium smithi* can compete with the mangrove snails by pulling the decayed leaves away or pushing the snails off the leaves when they are foraging in small habitats, although the latter exhibited aggregation behavior [58]. As *P. canaliculata* also showed aggregation behaviors [59], the possible interaction of competition or predation between the native mangrove crab and invasive *P. canaliculata* juveniles requires detailed investigation. Similar to the benthic crab and snails, which frequently feed on the decaying litter of mangroves [30], the consumption behaviors of *P. canaliculata* on decaying leaf litter could accelerate nutrient release to sediments. However, stable isotopes reveal that microphytobenthos are also primary food sources for the benthic gastropod [60], and the diet of the invasive *P. canaliculata* feeding on decaying leaf litter might modify the structure of the benthic food chains from a trophic point of view.

The WDR indicator reflected the consumption rate and nutrient uptake efficiency of the decaying leaf litter in relation to the feeding duration and accumulated weight of the snails. Under the multiple-choice and no-choice feeding conditions, the WDR indicator of *P. canaliculata* showed a significant difference between group *A. ilicifolius* & *S. apetala* and group *A. corniculatum* & *K. candel*. This phenomenon suggested that the consumption rate and efficiency of nutrient uptake of the snails were different when feeding these species of decaying leaf litter.

Furthermore, we observed a decrease in the WDR of *P. canaliculata* feeding on the five species of decaying leaf litter under the multiple-choice feeding conditions compared with the no-choice feeding conditions. This phenomenon, possibly due to intraspecific competition between the individual snails, slowed the feeding rate of *P. canaliculata* under the conditions of limited preferred species of decaying leaf litter. The decaying leaf litter of *A. ilicifolius* and *S. apetala* was the preferred food of *P. canaliculata*. As these snails have specific feeding preferences in mangrove forests, we speculated that *P. canaliculata* might have a nutritional niche overlap with native benthic snails in local habitats containing *A. ilicifolius* and (or) *S. apetala* when food sources are limited.

4.3. Relationship between Feeding Patterns and Characteristics of the Decaying Litter

P. canaliculata preferred the types of decaying leaf litter rich in nitrogen, phosphorous, protein, and ash. Nitrogen demand is common among benthic animals in mangrove forests. *P. canaliculata* preferred mangrove leaves with high nitrogen contents [25]. Our results indicated that *P. canaliculata* juveniles had a similar demand for nitrogen in decaying leaf litter in mangrove forests. The decomposition rate of litter was found to be affected by the high phosphorous content of mangrove leaves [61]. As for the phosphorous content, the feeding behavior of *P. canaliculata* is possibly different from that of the native mangrove crab, as previous research reported that the predation preference of the crab *Neosarmatium malabaricum* was not related to the phosphorous content in mangrove tissues [62]. *P. canaliculata* showed a positive food selection preference for mangrove leaves [25]; thus, our finding of a similar preference for decaying leaf litter is not surprising.

We found that the fiber content in the decaying leaf litter was not correlated with the feeding indicators of *P. canaliculata*, whereas the lignin content negatively affected the feeding indicators. *P. canaliculata* can efficiently digest the fiber contained in decaying leaf litter. Previous research reported that *P. canaliculata* had a high cellulase activity and application value in enzyme engineering [63]. The cellulase activity of *P. canaliculata* (up to $1.5 \mu\text{mol} \cdot \text{min}^{-1} \cdot \text{mg}^{-1}$) [64] was much higher than the reported maximum activity (approx-

imately $0.9 \mu\text{mol}\cdot\text{min}^{-1}\cdot\text{mg}^{-1}$) measured based on eight species of benthic gastropods, crabs, and bivalves in a mangrove forest in southern China [65]. *P. canaliculata* had enough cellulase to digest the residual cellulose in the decaying leaf litter of the tested mangroves.

The ash of mangrove leaves is a complex inorganic–organic mixture and always contains abundant minerals accumulated in the mineral uptake of mangroves [38,66]. The ash content was found to be positively correlated with the feeding indicators of *P. canaliculata*. *P. canaliculata* could acquire their necessary nutrients from the ash of the decaying leaf litter of the tested mangroves. As for the lignin content, more research on the lignin-decomposing ability of *P. canaliculata* is required. We speculated that *P. canaliculata* lacks enough digestive enzymes to handle the lignin in decaying leaf litter. Likewise, calcium was not correlated with the feeding indicators of *P. canaliculata*. Seawater generally contains high concentrations of calcium. This phenomenon differs from that observed in freshwater environments, where calcium generally influences the freshwater snail populations of *pomacea* sp. [67].

Tannins, phenols, and flavonoids are chemical defense substances in fresh mangrove leaves [68]. Previous research reported that phenolic substances were detrimental to the consumption of decaying leaves of three macrophyte species [69]. Although the antioxidant and bacteriostatic activities weakened as the litter began to decay on the floor of the mangrove forest, a negative correlation between these substances and the feeding indicators of *P. canaliculata* was still observed in the study, which further proved the sensitivity of the snails to these toxic substances.

The feeding indicators of *P. canaliculata* were affected by the three representative decaying leaf characteristics, and four clusters for decaying leaf litter were observed. Compared with a single feeding indicator, the analysis of multiple indicators can help us to better understand the potential diet of *P. canaliculata*. Based on RDA and PCA, the types of decaying leaf litter can be distinguished by *P. canaliculata* in the invaded habitat. The snails can establish a population in mangroves composed of *A. ilicifolius* and *S. apetala*. Mangroves composed of *A. ilicifolius* and (or) *S. apetala* provide food for *P. canaliculata* through the accumulation of decaying leaf litter on the floor of the mangrove. In other words, even though the decaying leaf litter of the main mangrove species was not favorable for *P. canaliculata*, when coexisting with *A. ilicifolius* and (or) *S. apetala*, this species of mangrove might be vulnerable to *P. canaliculata*. A recent survey reported that the total area of *S. apetala* was 3804.86 ha in China in 2020 [70]. *S. apetala* was also an exotic mangrove species in China. It was widely planted in coastal areas and is gaining widespread attention due to its ecological impact. We discovered, for the first time, that the decaying leaf litter of *S. apetala* is suitable as a nutrient source for *P. canaliculata*, suggesting a possible hitchhike type of invasion of the mangrove ecosystem.

5. Conclusions

The feeding behavior of *P. canaliculata* was closely related to the species and characteristics of decaying leaf litter in this study. We concluded the following: (1) The decaying leaf litter of *A. ilicifolius* and *S. apetala* in mangroves could support the growth of juvenile *P. canaliculata*. (2) The juvenile *P. canaliculata* showed a different feeding preference for the tested types of decaying leaf litter. (3) The feeding preference of juvenile *P. canaliculata* was closely related to the chemical properties of decaying mangrove litter. In summary, the feeding behavior of *P. canaliculata* could accelerate nutrient release from decaying leaf litter into the sediment and alter the food chain in mangrove forests. As a global, invasive species, *P. canaliculata* potentially compromises conservation efforts for mangrove forests by acting as an invasive benthic consumer. However, the global distribution of *P. canaliculata* is restricted by climate change and local environmental factors such as water quality, interspecific competition, and nonspecific enemies. These limiting factors may partly influence the diet of *P. canaliculata* in mangroves. More studies need to be conducted on the role of *P. canaliculata* in the food chain in relation to climate change or local environmental factors in mangrove ecosystems.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/jmse11030672/s1>, Supplementary Figure S1 Newly laid egg clusters (A) and hatched eggs clusters (B) of apple snails in a mangrove forest; Supplementary Figure S2: Principal component analysis between chemical characteristics of decaying leaf litter of five mangroves and feeding indicators of *Pomacea canaliculata*. Supplementary Figure S3: Linear regression of inorganic components of chemical characteristics of decaying leaf litter and feeding indicators of *P. canaliculata*; Supplementary Figure S4: Linear regression of organic components of chemical characteristics of decaying leaf litter and feeding indicators of *P. canaliculata*; Supplementary Table S1: Linear regression parameters of inorganic chemical characteristics of decaying leaf litter and feeding indicators of *Pomacea canaliculata*; Supplementary Table S2: Linear regression parameters of organic chemical characteristics of decaying leaf litter and feeding indicators of *Pomacea canaliculata*.

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