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# Life-History Responses of Daphnia to Catfish Kairomones: Does *Ipomoea aquatica* Function as an Effective Refuge?

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**Abstract**

Zooplankton, particularly *Daphnia* sp., play a key role in aquatic food webs and exhibit strong life-history plasticity in response to predation risk mediated by chemical cues (kairomones). Aquatic macrophytes such as water spinach (*Ipomoea aquatica*) are often assumed to provide refuge that may mitigate these effects. This study examined the influence of catfish (*Clarias* sp.) kairomones and the potential moderating role of *I. aquatica* on reproduction and survival of *Daphnia* sp. using an individual-based bioassay with a randomized block design. Four treatments were applied: control, *I. aquatica*, kairomones, and kairomones + *I. aquatica*, observed in 15 days. Parameters measured included neonate number, age at first and second reproduction (AFR, ASR), Second Clutch/First Clutch ratio (C2/C1 ratio), and mortality. Kairomone exposure significantly reduced first-clutch offspring production and delayed AFR, and induced compensatory reproduction in the second clutch, reflected by the highest C2/C1 ratios (K = 2.30; H = 2.11). Mortality was also highest in kairomone treatments (>42%). The presence of *I. aquatica* did not significantly mitigate kairomone effects and was associated with increased mortality relative to the control. These results indicate that chemical predator cues dominate over physical shelter in shaping *Daphnia* sp. life-history strategies, with important implications for zooplankton dynamics in vegetated freshwater ecosystems.

## 1. Introduction

Zooplankton, including *Daphnia* sp. are a key component in aquatic ecosystems and serve as a link between primary producers (phytoplankton) and higher-level consumers (fish) (Andersen & Hessen, 2005; Ogorelec et al., 2021). The predation pressure they experience triggers the development of various defense responses, which can include changes in behavior, morphology, and life cycle (Diel et al., 2020). These responses are specific to the type of predator (Octorina et al., 2022; Baludo et al., 2024) and can be induced by chemical signals (kairomones) released by predators (Rabus et al., 2013). One important life cycle response is a change in reproduction timing and offspring number (Diel, 2020). For example, exposure to fish kairomones can cause *Daphnia* sp. to reproduce earlier with more offspring as an emergency strategy (Stibor, 1992). However, this defensive response often comes with an "ecological cost," such as reduced survival rates.

On the other hand, aquatic macrophytes such as water spinach (*Ipomoea aquatica*) play an important ecological role, one of which is as a provider of habitat and shelter for aquatic organisms, including zooplankton (El-Hady & Khalifa, 2015; Thomaz, 2017). The presence of macrophytes can influence community structure by providing refugia from predation pressure (Dos Santos et al., 2020).

Chemically, some aquatic plants such as *I. aquatica* can produce chemical compounds or allelochemicals that can affect the self-defense of *Daphnia* sp. when exposed to predator threats (kairomones) (Diller, 2023). Catfish (*Clarias sp*) like other fish carnivore release kairomone that can induce prey aquatic ecosystem (Owsley, 2017).

*Ipomoea aquatica* (water spinach) as a common floating macrophyte in tropical Asian freshwater ecosystems, where it provides structural complexity and increases habitat heterogeneity that can serve as shelter for zooplankton against visual predators (Thomaz, 2017; Dos Santos et al., 2020). Additionally, macrophytes including *I. aquatica* play important ecological roles in nutrient filtration, maintaining water quality, and supporting overall aquatic biodiversity (Wetzel, 2001; De et al., 2019). However, a key limitation that must be acknowledged is that the presence of floating macrophytes can alter microhabitat conditions through mechanisms such as reduced light penetration, decreased water circulation, and potential fluctuations in dissolved oxygen, which may create physiological stress for organisms inhabiting the water column (De et al., 2019). Furthermore, some aquatic plants are known to release allelochemical compounds that can influence the defensive responses of zooplankton such as *Daphnia* when exposed to predator kairomones, adding another layer of complexity to plant-zooplankton interactions (Diller et al., 2023). This inherent duality—offering structural protection while potentially altering water quality and releasing bioactive compounds—makes *I. aquatica* an ideal test subject for investigating whether physical refugia can moderate chemical signals from fish predators (Burks, 2002; Diel et al., 2020). Understanding this interaction is particularly important for tropical limnetic ecosystems, where research on antipredator responses of zooplankton remains limited compared to subtropical regions (Burks, 2002).

However, it is unclear whether the physical protection provided by macrophytes can eliminate or moderate the physiological responses and life cycle changes induced by kairomones. With the presence of shelter, does *Daphnia* sp. no longer need to employ the costly “live fast, die young” strategy? This study aims to examine: (1) the effect of catfish kairomones on the reproduction and life cycle of *Daphnia* sp. and (2) the role of *I. aquatica* as a shelter in moderating the impact of these kairomones.

## 2. Materials and Method

### 2.1. Time and Location of Study

This research was conducted from July to October 2025 at the Bioecology Laboratory, Faculty of Agriculture, Universitas Muhammadiyah Sukabumi, Indonesia. The laboratory is equipped with controlled environmental facilities for aquatic organism culture and experimental bioassays (USEPA, 1987). All experimental procedures, including culture maintenance, treatment preparation, and data collection, were carried out under standardized laboratory conditions to ensure consistency and reproducibility of results.

### 2.2. Experimental Design

The study employed an experimental method using a randomized block design (RBD) to evaluate the effects of catfish kairomones and the presence of water spinach (*Ipomoea aquatica*) on the life cycle parameters of *Daphnia* sp. Four treatment conditions were established (Table 1) with three replications each.

A total of 120 synchronized *Daphnia* sp. individuals (<24 hours old) were used in this experiment, with 10 individuals allocated to each replicate (30 individuals per treatment). Each experimental unit consisted of a single *Daphnia* sp. individual maintained in 250 mL of the respective treatment medium (Figure 1), following the protocol established by Octorina et al. (2022). This individual-based approach allowed for precise tracking of reproductive events and survival rates throughout the observation period in 15 days.

**Table 1.** Experimental treatment conditions used to evaluate the effects of catfish kairomones and *Ipomoea aquatica* on the life cycle of *Daphnia* sp.

| Symbol | Treatment |
|---|---|
| K | Fish conditioned water (Kairomone) |
| H | Fish conditioned water (Kairomone) + *I. aquatica* |
| A | Aerated Well water + *I. aquatica* |
| C | Aerated Well water (Control) |

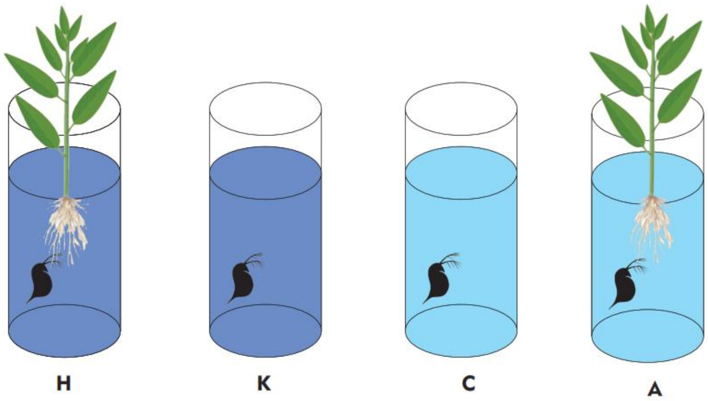

**Figure 1**. The four experimental treatments: (H) combination of I. aquatica and kairomone-conditioned water; (K) kairomone-conditioned water only; (C) control group containing neither I. aquatica nor kairomones; and (A) I. aquatica only.

### 2.3. Preparation of Kairomone Conditioned Water

Kairomone-conditioned water was prepared following the method described by Pietrzak et al. (2017). Juvenile catfish (*Clarias sp.*) measuring 3–5 cm in total length were starved for 24 hours prior to kairomone production to eliminate confounding effects from fecal material (Figure 2). The fish were then placed in 1-day-old aerated well water at a density of 5 individuals per liter for 24 hours at room temperature (25°C). After the conditioning period, the water was gently filtered through a 0.45 μm membrane filter to remove particulate matter, including bacteria and any remaining solid waste, while retaining dissolved chemical cues (kairomones). The filtered kairomone water was stored at 4°C and used within one week of preparation to ensure kairomone stability and activity (Pietrzak et al., 2017).

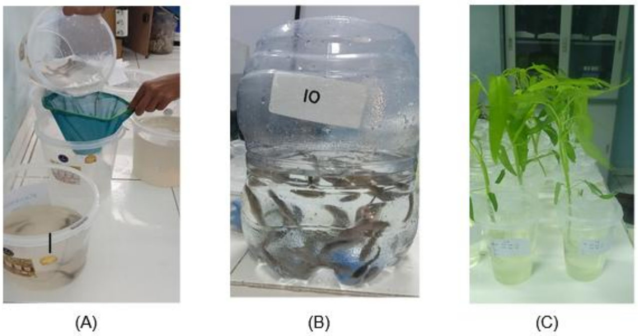

**Figure 2.** (A) Experimental preparation process, (B) including filtration of fish-conditioned water to obtain dissolved kairomones, conditioning of juvenile catfish (*Clarias* sp.), and (C) preparation of *Ipomoea aquatica* for treatment application.

### 2.4. Preparation of Water Spinach

Fresh water spinach (*Ipomoea aquatica*) plants were collected from clean, uncontaminated freshwater sources in Sukabumi, West Java. Plants were thoroughly rinsed with distilled water to remove epiphytes, sediment, and any associated organisms. Healthy specimens of uniform size (approximately 15 cm in height) were selected and acclimated in aerated well water for 48 hours prior to experimental use. For treatments requiring macrophytes (A and H), one individual plant was placed in each experimental container, with the root system fully submerged in the medium and leaves emerging above the water surface, simulating natural floating macrophyte conditions.

### 2.5. Feed Protocol

Experimental units received standardized feeding with *Chlorella sp* at a density 195,840 cells $mL^{-1}$ (Figure 3). Algal density was determined using a Sedgwick Rafter Counting Cell (SRC) under a compound microscope (400× magnification) and adjusted daily to maintain consistent food availability throughout the experiment. Feeding was performed immediately following water renewal and offspring removal to ensure stable nutritional conditions.

**Figure** 3. Cultivation and preparation of *Chlorella* sp. was used as a standardized food source for *Daphnia* sp. during the experimental period.

### 2.6. Data Collection

Data collection was performed daily for 15 consecutive days, with observations conducted at the same time each day (09:00–11:00 AM) to maintain consistency. The reproductive parameters recorded included the number of neonates in the first clutch (C1) and second clutch (C2), the age at first reproduction (AFR) and age at second reproduction (ASR) defined as the day when the first and second clutches were released, and the C2/C1 ratio calculated as an indicator of reproductive energy allocation strategy. Mortality rate was recorded daily by observing each *Daphnia* sp. with an individual considered dead when no movement or heartbeat was observed over a 30-second period, and cumulative mortality was calculated as the percentage of initial individuals that died during the experimental period.

Collected data were compiled in Microsoft Excel and analyzed using R statistical software (version 4.2.1), employing a linear mixed-effects model (LMER) with experimental replicates treated as random factors, followed by independent sample t-tests for pairwise comparisons between treatments and chi-square tests for mortality data analysis, with statistical significance set at α = 0.05 for all analyses and results presented as mean ± standard deviation (SD).

## 3. Results

### 3.1. Impact on the Number of Neonates

The kairomone treatment (K and H) showed a clear suppression of *Daphnia* sp. reproduction in the first clutch. The number of C1 neonates in K and H was significantly lower than in the control. In the second clutch, despite an increase, the K and H groups remained lower than the control. The water spinach treatment (A) actually showed a decrease in the number of neonates from C1 to C2 (Table 2 and Figure 8).

**Table 2**. Mean number of neonates produced in the first (C1) and second (C2) clutches under different treatments

| Treatment | Clutch 1 (individuals) | Clutch 2 (individuals) |
|---|---|---|
| Control | 13.59 ± 5.05 (n=41) | 19.98 ± 4.50 (n=41) |
| *I. aquatica* | 14.28 ± 2.29 (n=40) | 14.97 ± 2.94 (n=36) |
| *I. aquatica* + Kairomone | 9.92 ± 6.23 (n=25) | 17.88 ± 6.36 (n=24) |
| Kairomone | 9.85 ± 6.08 (n=26)** | 17.92 ± 3.62 (n=24) |

*Significance levels: ***p* < 0.001, *p < 0.01, p < 0.05, ns = not significant.*

### 3.2. Effect on Reproductive Age

Kairomones consistently slowed down reproductive development in the tested organisms. The values of AFR and ASR observed in treatments K and H were significantly higher than those recorded in the control and treatment A, indicating delayed reproductive maturity under kairomone exposure (Figure 6). This result suggests that the presence of predator-related chemical cues may alter energy allocation and physiological processes associated with reproduction.

In contrast, the treatment containing only water spinach did not show a statistically significant difference compared with the control treatment (Table 3). This finding indicates that water spinach alone had little influence on reproductive timing in the absence of kairomones. Overall, the results demonstrate that kairomones play a more dominant role in affecting reproductive age than the presence of aquatic vegetation.

### 3.3. C2/C1 Ratio and Mortality

The C2/C1 ratio is an indicator of reproductive energy allocation strategy calculated from the ratio of the number of neonates in the second clutch (C2) to the first clutch (C1). This parameter reflects how organisms adjust their reproductive investment under different environmental conditions and stress levels. The highest C2/C1 ratio was found in treatments K (2.3) and H (2.11) (Table 4), indicating a compensatory reproductive strategy under stressful conditions. The highest mortality rates also occurred in treatments K (45.24%) and H (42.86%), which were significantly higher than the control (2.38%) and treatment A (14.29%) (Figure 4). These findings suggest that increased reproductive allocation may occur simultaneously with elevated physiological stress and mortality risk.

The C2/C1 ratio indicates how *Daphnia* sp. allocates its reproductive energy over time under treatment stress (Table 4). Control (Ratio = 1.9): A ratio of nearly 2 indicates a normal and sustainable reproductive strategy. *Daphnia* sp. in safe conditions can increase their reproductive investment in the second generation, which is a common and healthy reproductive pattern (Stibor 1992). This pattern suggests that individuals have sufficient energy reserves and experience minimal environmental pressure during reproduction.

*I. aquatica* treatment (Ratio = 1.07): A ratio close to 1 indicates that reproduction hardly increased from C1 to C2. It can be argued that the presence of the physical structure of duckweed, although not a direct threat, may create slightly stressful microhabitat conditions or resource competition (e.g., for space or light for algal food growth), so that the energy available for increased reproduction is not significant. As a result, reproductive performance remained relatively stable between the two clutch periods.

Kairomone and Kairomone + *I. aquatica* (Ratio = 2.3 and 2.11): These are very crucial findings. Both treatments show the highest ratios, even higher than the control. This pattern indicates that *Daphnia* sp. may respond to predator-related chemical cues by increasing reproductive investment in later clutches as an adaptive survival strategy. The elevated reproductive ratio under high-stress conditions may represent an attempt to maximize offspring production before mortality occurs.

**Table 3**. Mean reproductive age of *Daphnia* sp. in the first reproductive event (AFR) and second reproductive event (ASR) under different treatments

| Treatment | AFR | ASR |
|---|---|---|
| Control (C) | 6.10 ± 0.58 (n=41) | 8.05 ± 0.44 (n=41) |
| *I. aquatica* (A) | 5.95 ± 0.22 (n=40) | 7.94 ± 0.23 (n=36) |
| *I. aquatica* + Kairomone(H) | 7.04 ± 0.84 (n=25) | 9.42 ± 1.32 (n=24) |
| Kairomone (K) | 7.35 ± 0.94 (n=26)** | 9.00 ± 0.85 (n=24) |

*Values are presented as mean ± SD. Significance levels: ***p* < 0.001, *p < 0.01, p < 0.05; ns = not significant.*

**Table 4**. C2/C1 ratio of *Daphnia* sp. under different treatments

| **Treatment** | **C2/C1 Ratio** |
|---|---|
| Control (C) | 1.9 ± 1.7 |
| *I. aquatica* (A) | 1.07 ± 0.29 |
| *I. aquatica* + Kairomone(H) | 2.11 ± 1.02 |
| Kairomone (K) | 2.3 ± 0.91 |

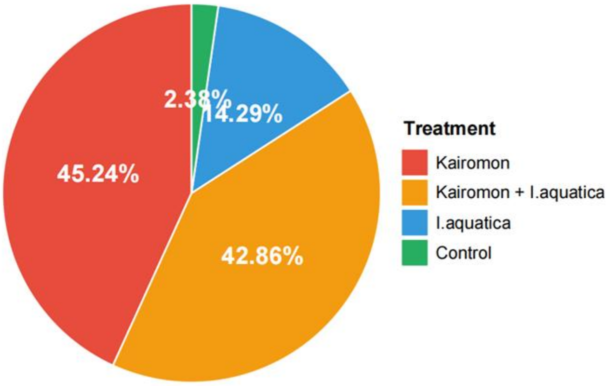

**Figure 4.** Percentage mortality of *Daphnia* sp. under different experimental treatments, including kairomone exposure, *Ipomoea aquatica*, combined treatment, and control conditions.

Mortality rate (Figure 4) provides direct evidence of the "cost" or negative consequences of kairomone exposure. Control (2.38%) indicates very low mortality, suggesting ideal maintenance conditions and the absence of significant stressors. *I. aquatica* (14.29%) shows an increase in mortality compared to the control, reinforcing the previous argument that the presence of water spinach causes some kind of pressure, possibly through competition or changes in environmental conditions (e.g., $O_2$ fluctuations), which increases stress and causes death in some individuals (Diller 2023). Kairomone and Kairomone + *I. aquatica* (45.24% and 42.86%) showed very high mortality rates, and the near-equal mortality rates in both treatments are the most compelling evidence of the negative impact of kairomone. Mortality occurred on different days from the first to the last days for each treatment.

## 4. Discussion

The results of this study indicate that catfish kairomones trigger changes in the life cycle strategy of *Daphnia* sp. The pattern of reproductive suppression in C1 followed by increased compensation in C2 (high C2/C1 ratio) (Figure 5) is consistent with the "Delayed Reproduction" as stress-induced compensatory reproductive strategy reported by Stibor (1992). In his study, *Daphnia* sp. exposed to fish kairomones also showed a decrease in the age of first reproduction and an increase in the number of offspring in the first generation, an emergency response to predation pressure.

However, this strategy does not come without a cost. The high mortality rate in the kairomone treatment reflects the substantial ecological cost of induced defense. This concept of trade-off is the basis of many inducible defense responses, in which resources allocated to one function (e.g., early reproduction) sacrifice other functions (e.g., body maintenance and long-term survival) (Diel et al., 2020).

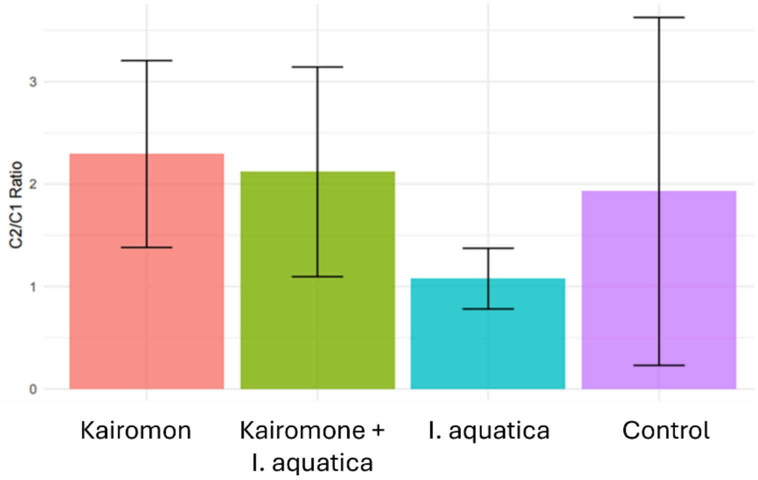

**Figure 5.** Comparison of C2/C1 neonate ratios of *Daphnia* sp. among control, *Ipomoea aquatica*, kairomone, and combined treatments.

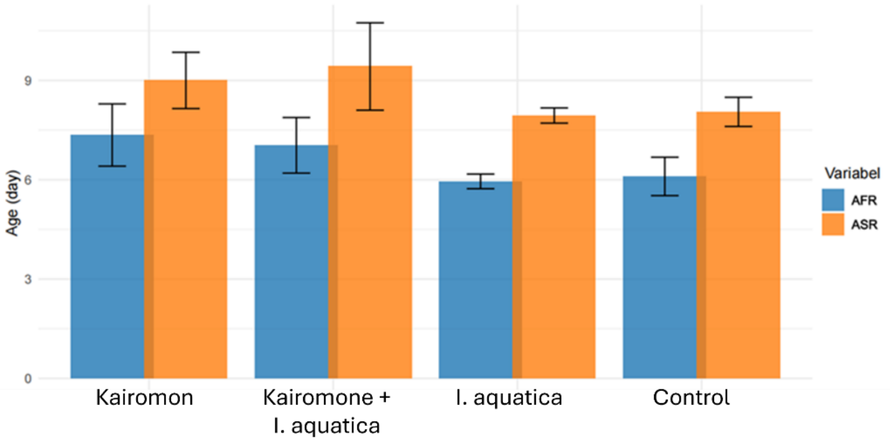

**Figure 6.** Average reproductive age in two variables, age at first reproduction (AFR) and age at second reproduction (ASR).

While our results showed that the roots of a single *I. aquatica* plant did not provide an effective physical refuge against kairomones, it remains to be seen whether submerged macrophytes with more complex morphological structures, or simply a higher density of roots, might offer the anticipated protection. The absence of consistent significant differences between the K and H treatments in all measured parameters (number of neonates, AFR, ASR, C2/C1 ratio, and mortality) suggests that chemical signals (kairomones) have a stronger and more direct influence on *Daphnia* sp. physiology than the presence of a simple physical refugia. This reinforces the findings of Van De Meutter et al. (2004) that the response of *Daphnia* sp. to kairomones is highly specific and can influence habitat selection, but in this context, physical refuge cannot "deactivate" the physiological response that has been triggered.

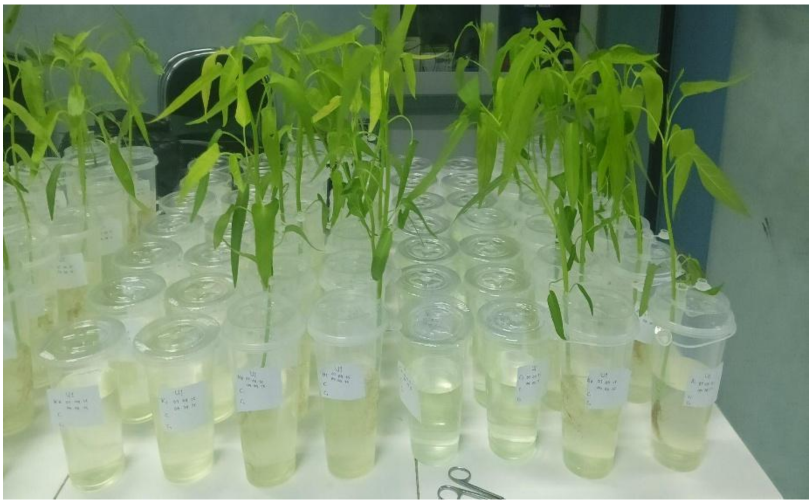

**Figure 7.** Morphological arrangement of *Ipomoea aquatica* in experimental units, illustrating the limited structural complexity of its submerged root system as potential refuge for *Daphnia* sp.

As a floating macrophyte, *I. aquatica* exhibits limited structural complexity (Figure 7). Its root system simply hangs in the water column, offering only two-dimensional protection rather than an adequate three-dimensional shelter for *Daphnia* sp. This simple architecture might be insufficient against dissolved chemical cues from predators. The effectiveness of macrophyte protection is highly dependent on the density and complexity of the architecture (Burk et.al., 2002).

However, other macrophytes, such as *Ceratophyllum* and *Myriophyllum*, possess complex leaf structures and dense branches. Whether these more structurally complex macrophytes can offer an effective refuge for daphnids warrants further investigation.

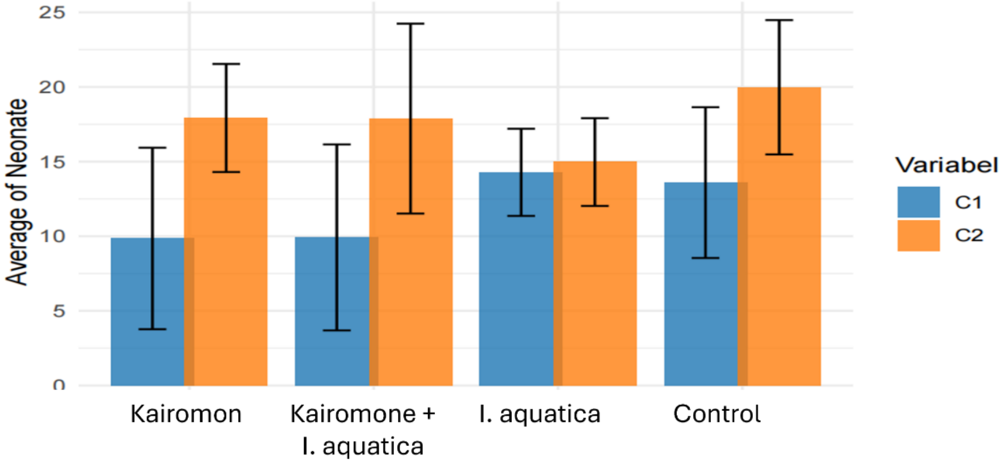

**Figure 8.** Comparison of average offspring number of *Daphnia* sp. among kairomone, kairomone *and Ipomoea aquatica*, *Ipomoea aquatica*, and control.

The function of water spinach as a habitat and shelter provider (Thomaz, 2017) appears to be limited to protection from visual predators that rely on physical contact. Against chemical stressors that spread throughout the water column (Rajchard, 2013), the presence of physical structures does not provide protection. The fact that *I. aquatica* treatment showed an increase in mortality (14.29%) compared to the control (2.38%) indicates that the presence of macrophytes can create microhabitat pressures, such as oxygen fluctuations or space competition, which are detrimental to zooplankton. The ecological implications are far-reaching: in ecosystem restoration efforts, planting aquatic vegetation without considering ecological balance can disrupt *Daphnia* sp. populations as a keystone species in the food web. This disruption has the potential to trigger chain reactions that threaten aquatic biodiversity, especially when interacting with anthropogenic stressors such as eutrophication and climate change. Therefore, ecosystem management requires a holistic approach that considers the complex interactions between habitat structure, population dynamics, and environmental pressures to maintain the balance and sustainability of aquatic biodiversity.

## 5. Conclusion

Catfish kairomones induce compensatory reproductive strategies in *Daphnia* sp. characterized by delayed early reproduction, increased later investment, and high mortality. The physical presence of *Ipomoea aquatica* does not mitigate these effects, indicating that chemical predator cues outweigh shelter availability in shaping *Daphnia* sp. life-history responses. These findings highlight the importance of chemical interactions in structuring zooplankton dynamics in freshwater ecosystems. However, the study has limitations: it used only one macrophyte and one predator species, applied a single fixed kairomone concentration, was conducted under simplified laboratory conditions, and focused only on short-term responses over two reproductive clutches, without examining transgenerational or molecular effects. Consequently, further research under more ecologically realistic conditions is needed to confirm the generalizability of these findings.

## 6. Data Availability Statement

The data supporting the findings of this study are available from the corresponding author upon reasonable request.

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## 8. Conflict of Interests

The authors declare they have no competing interests.

## 9. Acknowledgment

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## 10. Authors' Contribution

**MH:** Conceptualization (equal), Methodology (equal), Formal analysis (equal), Investigation, Data curation, Writing – original draft (equal), Writing – review and editing (equal). **MK:** Supervision, Writing – original draft (equal), Writing – review and editing (equal). **NTMP:** Supervision (Lead), Writing – original draft (equal), Writing – review and editing (equal). **PO:** Conceptualization (equal), Methodology (equal), Formal analysis (equal), Project administration (lead), Writing – original draft (equal), Writing – review and editing (equal).

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