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Research article

Freshwater shrimp (*Neocaridina denticulata*) as a nature-based restoration tool for macrophyte recovery and improved water quality in eutrophic ponds

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ABSTRACT

Globally, eutrophication poses a serious threat to freshwater ecosystems, disrupting ecological balance and biodiversity. Effective restoration requires practical, sustainable, and ecosystem-based methods to reestablish healthy aquatic systems. The presence of submerged macrophytes in controlling algal blooms is crucial; however, research on ecological treatment approaches to promote their growth remains limited. Here, we investigated the ecological restoration potential of *Neocaridina denticulata*, a native freshwater shrimp, in eutrophic freshwater ecosystems dominated by filamentous algae. We integrated feeding trials, controlled microcosm experiments, and long-term field evaluations. The feeding experiments demonstrated that shrimp consume diverse filamentous algae, periphyton, and detritus, directly contributing to biomass reduction. When introduced into microcosms, shrimps rapidly reduced filamentous algal coverage, which promoted the recovery of submerged macrophytes and enhanced water clarity. Field studies further validated these outcomes, highlighting an 11-fold increase in macrophyte abundance and significant improvement in water quality following shrimp introduction. Importantly, shrimp populations became self-sustaining under natural conditions, indicating long-term viability. Although their introduction slightly altered microbial interaction networks, overall microbial community stability was maintained, reflecting ecological resilience. These results indicate that *N. denticulata* represents an effective, nature-based restoration tool, simultaneously supporting biodiversity recovery, ecosystem service restoration, and sustainable water quality management in eutrophic freshwater ecosystems.

1. Introduction

Nutrient over-enrichment is a primary threat to the maintenance of healthy freshwater ecosystems, as it causes eutrophication and the formation of algal blooms (Smith et al., 2006). The excess nutrients in aquatic systems should ideally be consumed by primary producers, maintaining a balanced competition between submerged macrophytes and microalgae, which is essential for a healthy aquatic ecosystem (Duarte, 1995; Sand-Jensen and Borum, 1991). Therefore, promoting the resurgence of submerged macrophytes in shallow eutrophic lakes is a common strategy for mitigating eutrophication and enhancing the water quality (Hargeby et al., 1994; Hilt et al., 2006; Sayer et al., 2010). However, filamentous microalgae including *Oedogonium* sp., *Spirogyra* sp., *Pithophora* sp., *Hydrodictyon* sp., and *Zygnema* sp. can rapidly proliferate and dominate in eutrophic water bodies, reducing underwater light penetration and inhibiting the growth of submerged macrophytes (Bhateria and Jain, 2016; Duarte, 1995). These algae often form dense periphyton layers on macrophyte surfaces, further hindering their photosynthesis by blocking light absorption (Zhang et al., 2020). Additionally, excessive filamentous algal growth can clog waterways, disrupt recreational and fishing activities, and incur substantial management costs (Watson et al., 2015). In addition to nutrient enrichment,

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freshwater resources are often threatened by mining, industrial, and energy-related activities, further exacerbating ecological degradation. Although such activities may negatively affect water quality and aquatic ecosystems, rehabilitation technologies and associated costs can partially mitigate these impacts (Yıldız, 2025; Yıldız et al., 2025; Tost et al., 2020).

Recent research on harmful algal blooms has largely focused on understanding the mechanisms underlying microalgae proliferation driven by eutrophication and on developing physio-biochemical ways to control excessive microalgae growth (Gallardo-Rodríguez et al., 2019). However, addressing eutrophication remains challenging owing to nonpoint source pollution. Despite massive microalgae removal methods being employed, the problem often recurs or is eventually replaced by other microalgae species (Nwankwegu et al., 2019). Therefore, the presence of submerged macrophytes in controlling algal blooms is crucial (Asaeda and Van Bon, 1997; Wang et al., 2023; Zhang et al., 2018). However, research on ecological treatment approaches to promote their growth remains limited.

Benthic macroinvertebrates, such as snails, worms, shrimp, and aquatic insects, play a crucial role in maintaining the ecological balance in shallow aquatic ecosystems by influencing nutrient cycling, primary producer dynamics, and water quality (Poikane et al., 2016; Rosenberg and Resh, 1992). Guo et al. (2022) demonstrated that freshwater snails increased filamentous algal biomass while reducing periphyton, whereas shrimp (*Macrobrachium nipponense*) reduced filamentous algal biomass but increased periphyton in microcosms. However, larger shrimp species, such as *M. nipponense* can increase turbidity through sediment disturbances, which may inadvertently promote algal growth (Geddes and Trexler, 2003; Guo et al., 2022; Pringle et al., 1993). In addition, freshwater snails can hinder the growth of submerged macrophytes by consuming microalgae and newly grown leaves (Li et al., 2009). In contrast to larger shrimp or snail, smaller shrimp like *Neocaridina denticulata* have been shown to enhance submerged macrophyte growth (Ye et al., 2019). However, recent global assessments report significant declines in freshwater shrimp populations, highlighting that nearly one-third of shrimp species worldwide face extinction risks due to eutrophication, habitat loss, agricultural pollutants, invasive predators, and climate change (De Grave et al., 2015; Nagai and Imai, 2024; Onuki and Fuke, 2022). Such declines could severely disrupt ecosystem functioning and biodiversity, given their critical ecological roles in freshwater habitats. Moreover, the limited influx of small shrimp populations into fragmented water bodies hampers the formation of alternative secondary consumer groups capable of fulfilling similar ecological roles.

The natural populations of *N. denticulata* have markedly declined in Korea due to environmental pressures, despite its long-standing use as a traditional food source (Oh et al., 2003). Here, we aimed to evaluate the ecological role of *N. denticulata* in regulating the growth and composition of primary producers as well as its effects on water quality and microbial community composition in a filamentous microalgae-dominated eutrophic pond. To this end, feeding experiments were conducted to assess the ability of shrimp to consume three dominant microalgal complexes, each of which occurred during different periods in the target pond. Microcosm and field studies were conducted to assess the short- and long-term ecological effects of introducing shrimp on primary producer interactions, water quality, and microbial dynamics under controlled and natural conditions. We aimed to evaluate the potential of the freshwater shrimp *N. denticulata* as a practical and sustainable nature-based restoration tool for mitigating eutrophication in freshwater ecosystems. Specifically, we investigated whether shrimp introduction could effectively regulate primary producer composition, enhance submerged macrophyte recovery, improve water clarity, and positively influence microbial community dynamics in filamentous algae-dominated environments.

2. Materials and methods

2.1. Shrimp feeding on microalgae complexes

Three different types of floating microalgal complexes were collected from the field and used directly for the microalgal feeding experiments (Fig. 1). Each microalgal complex consisted of the primary microalgae *Hydrodictyon reticulatum* (hereafter designated as microalgal complex 1), *Pithophora* sp. (hereafter designated as microalgal complex 2), and *Zygnema* sp. (hereafter designated as microalgal complex 3), along with other microalgae and detritus. The collection dates for microalgal complexes 1, 2, and 3 were June 15, 2022, August 26, 2023, and June 13, 2023, respectively. These filamentous algae, which dominated the target pond during the corresponding periods, are also widely known for their ability to form blooms across diverse aquatic ecosystems worldwide (Andersen and Andersen, 2006; Flory and Hawley, 1994; O'Neal et al., 1985). The initial wet weights of microalgal complexes 1, 2, and 3 were 1.0 ± 0.06 g, 1.3 ± 0.10 g, and 2.3 ± 0.08 g, respectively. Images of the microalgal complexes were obtained using a light microscope (Olympus BX63, Japan). Each feeding experiment was performed in duplicates. For each experiment, two rectangular glass tanks (45 × 17 × 25 cm) containing approximately 15 L of water were set up. To accurately measure the consumption rate, an acrylic box (10 × 10 × 10 cm) with water permeability was placed inside each tank. Shrimp, *N. denticulata,* were reared in a reservoir located in Haman, South Korea (35.226 °N, 128.427 °E) and 15 shrimp were then introduced into the tank. The shrimp were not fed for 1 day before the feeding experiment. To ensure ongoing algal biomass measurements, the wet weights of the algal complexes were measured. Algal consumption rates were measured over a period of 3 days. To improve measurement consistency, surface water was gently removed using a sterile wiper until no further significant change in mass was observed. Given the filamentous and heterogeneous nature of the algal complexes, pigment-based metrics were not suitable due to potential extraction bias and inconsistency across samples. The rates were calculated as the quotient obtained by subtracting the natural decrease observed in the control group from the decrease in the treatment group and normalizing it to the total shrimp wet weight.

2.2. Microcosm setup

Microcosm experiments were conducted using six 15 L rectangular glass tanks described above (three control, three treatment) under controlled light and aeration conditions. Detailed setup conditions and protocols are provided in the Supplementary Materials. Briefly, after a 2-week pre-conditioning period, 60 *N. denticulata* shrimps, a *Pithophora* sp.-dominant microalgal complex (microalgal complex 2), and submerged macrophytes (*Hydrilla verticillata*) were introduced. The initial wet weights of microalgal complex 2 and submerged macrophytes were 8.5 ± 0.2 g and 10.9 ± 1.4 g, respectively. The microcosm experiments were conducted for 17 days.

2.3. Environmental factor measurements and biomass Quantification in the microcosm

During the experiment, we measured the water quality parameters, nutrients, consumption of microalgal complex 2, biomass of sedimented particles, submerged macrophytes, and periphyton. Additionally, a microbiome analysis was conducted on water samples, microalgal complex 2, and shrimp fecal matter. Details of the sample collection and analysis methods are provided in Section 2.5, as similar procedures were applied in both the microcosm and field studies. Water quality parameters (temperature, pH, and dissolved oxygen) in the microcosms were measured using a portable multiparameter instrument (HI98494, HANNA Instruments, Korea). Total dissolved nitrate, nitrite, phosphate, and ammonium nitrogen were measured using a kit (C-mac, Korea). The

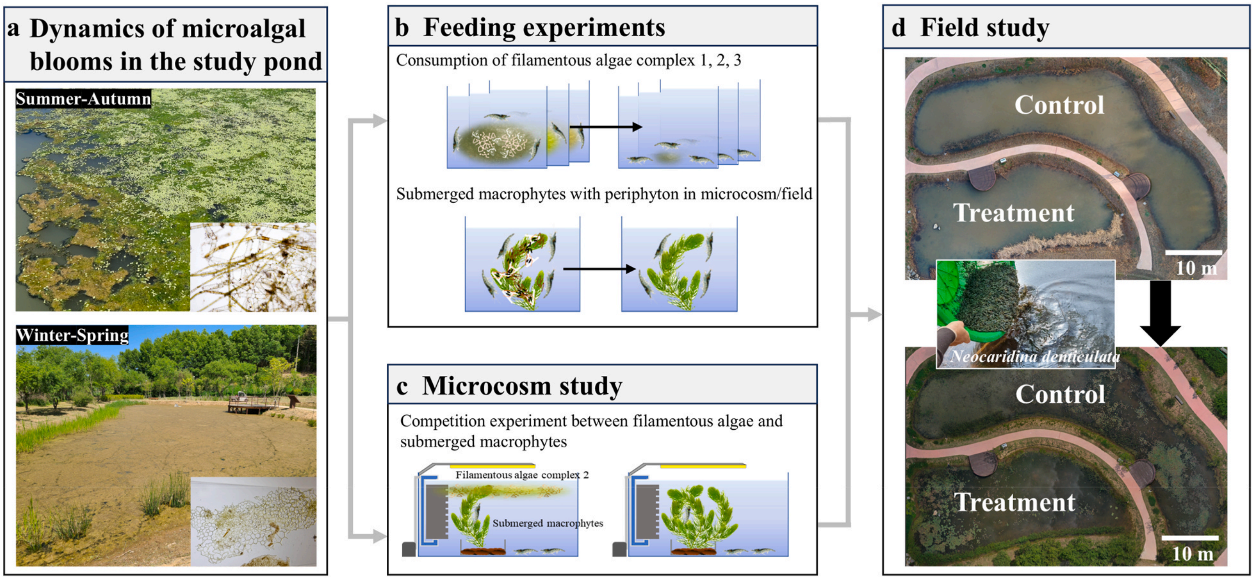

Fig. 1. Schematic diagram of the experimental framework. (a) Seasonal dynamics of microalgal blooms in the study pond. (b) Feeding experiments evaluating *Neocaridina denticulata* consumption of filamentous algae (upper) and macrophyte-periphyton complexes (bottom). (c) Microcosm study evaluating growth competition between filamentous algae and submerged macrophytes-periphyton complex induced by *N. denticulata* and the resulting impact on the aquatic ecosystem. (d) Field study investigating the ecological impact of *N. denticulata* introduction on aquatic ecosystems.

consumption of microalgal complex 2 was calculated as described above. At the end of the experiment, the wet weight of submerged macrophytes was measured to assess their growth, whereas sediment and periphyton biomasses were quantified by dry weight. Detailed procedures are provided in the Supplementary Materials.

2.4. Field study setup

The field study was conducted in ponds located within the National Institute of Ecology, South Korea (36.043 °N, 126.720 °E). Serious filamentous algal blooms nearly covered their entire surfaces (Fig. 1a–S1). The conservation of endangered species and ecological education was established in both ponds. The larger main pond (1090 m^2) was considered the control, whereas the relatively smaller pond (650 m^2) was designated as the treatment (Fig. 1). The average depth of the ponds was approximately 1 m. The plant species observed in the field included critically endangered *Euryale ferox*, *Ceratophyllum demersum*, *Typha orientalis*, *Sparganium erectum*, *Potamogeton* spp., and *Acorus calamus*. Additionally, the site hosts a variety of dragonfly species, as well as predatory insects, such as *Notonecta triguttata*, *Appasus japonicus*, *Laccotrephes japonensis*, and *Ranatra chinensis*. Before the experiment began, shrimp species, such as *N. denticulata*, *Macrobrachium nipponense*, and *Palaemon paucidens* were not observed in these ponds.

Approximately 50,000 *N. denticulata*, reared under the same conditions as in the feeding and microcosm experiments, were divided equally and introduced into the treatment pond between October 30 and November 1, 2023 (76 indiv. m^{-2}, 7.3 g m^{-2}). To minimize stress, the shrimp were transported within 3 h. The shrimp population within the treatment pond was monitored at regular intervals to check for survival and signs of mass mortality. Access to the pond interior was restricted throughout the experimental period to minimize disturbances. During the experiment, we measured environmental factors (water quality parameters and nutrients), periphyton biomass in the field, and the coverage of microalgae as described above. Furthermore, the environmental microbiomes of the water columns were analyzed. Details on the sample collection and analysis methods are provided in Section 2.5. Turbidity was measured at 750 nm using a UV spectrophotometer (UV-1800, Shimadzu, Kyoto, Japan) with 1 mm path-length cuvettes (Ballerstadt et al., 2007). To compare the biomass of periphyton in the field, we harvested the submerged macrophyte *Potamogeton cristatus* from both the control and treatment ponds on June 5, 2023, and measured the dry cell weight of periphyton on *P. cristatus* using the same method as described above. Photographs were captured using a commercial drone to monitor microalgae coverage and submerged macrophyte growth within the ponds (Mavic 2 Pro, DJI, China). The coverage of submerged macrophytes, filamentous algae, and floating plants was quantified using drone photographs. For submerged macrophytes, the calculated area may have been subjected to minor interference from overlapping filamentous algae or floating plants, which can partially obscure the underlying vegetation.

2.5. DNA-based microbial community analysis in microcosm and field experiments

Water samples were collected from each tank at 0 h (immediately after shrimp introduction), 72 h, and 168 h in the microcosm study, and monthly from each pond, between November 2022 and August 2023 (except for January 2023 and July 2023), to track the effects of introducing *N. denticulata* on aquatic microbiome dynamics in both the microcosm experiment (short-term, controlled conditions) and the field study (long-term, natural conditions). Approximately 50 mL of water was collected at each time point and immediately filtered using sterilized 0.22 μm Sterivex™ filter units (Millipore Corporation, USA). Furthermore, the microbial community compositions associated with microalgal complex 2 and shrimp fecal matter in the microcosm experiment were analyzed. Fecal matter that settled at the bottom of the microcosm tanks (treatment) was collected using a syringe fitted with a sterilized hose. To eliminate free-living microorganisms, the fecal matter were washed five times with sterilized distilled water. After filtration, all membrane filters were stored at −80 °C until DNA extraction.

Environmental DNA was extracted, and the 16S and 18S rRNA genes were amplified using universal primer sets. Amplicon libraries were constructed and sequenced on the Illumina MiSeq platform (2 × 300 bp). Amplicon sequence variant (ASV) analysis was conducted using the DADA2 pipeline (Callahan et al., 2016). Taxonomic classification was performed using the SILVA (v138.1) and PR2 databases (Guillou et al., 2012; Quast et al., 2012). Rare ASVs (singletons to tripletons) and non-target sequences were excluded for further analysis. Raw sequences are available under NCBI SRA accession number PRJNA1208684. Detailed protocols are provided in the Supplementary Materials.

2.6. Microbial network, functional, and statistical analysis

To investigate the impact of shrimp introduction on the field microbiome, microbial co-occurrence networks were constructed based on Spearman's rank correlation coefficients (ρ), using the *Hmisc* package in R (Harrell and Frank, 2019). To reduce the impact of rare ASVs in the dataset, we applied the following thresholds for each dataset: (i) at least 30 % of the observed samples, and (ii) a maximum relative proportion of >0.1 % in at least one sample. *Q*-values (adjusted *P*-values) were calculated using the Benjamini and Hochberg false discovery rate procedure (Benjamini and Hochberg, 1995). Only positive correlations with $\rho > 0.7$ and both *P*- and *Q*-values of <0.005 were selected for further analysis. The resulting networks were visualized using Cytoscape 3.8.2 (Shannon et al., 2003), and the yFiles organic layout algorithm was employed for network layout. To predict the potential bacterial functions, we performed FAPROTAX analysis using default settings (Louca et al., 2016).

All statistical analyses were performed using R software (version 3.4.0) (Ihaka and Gentleman, 1996). We used non-metric multidimensional scaling (NMDS) analysis with Bray–Curtis distances to order the samples in the prokaryotic community based on their dissimilarity, using the "metaMDS" function in *Vegan* package (Oksanen et al., 2013). The NMDS results were quantitatively evaluated using analysis of similarity (ANOSIM) and permutational multivariate analysis of variance (PERMANOVA) using the "anosim" and "adonis" functions, respectively (permutation 999). To normalize the data for diversity indices, the reads were normalized to the lowest number of reads in the "rrarefy" function. The minimum read counts were 22,786 and 9, 714 for bacteria and fungi, respectively. Chao1 index and Shannon diversity indices were calculated using "diversity" function.

3. Results

3.1. Feeding experiments

3.1.1. Shrimp feeding on three different microalgae complexes

Neocaridina denticulata consumed all three microalgal complexes, with consumption rates ranging from 0.08 to 0.24 mg/mg shrimp/day in the microcosm study (Fig. 2). The highest consumption rate (0.24 mg/mg shrimp/day) was observed for microalgal complex 2, dominated by *Pithophora* sp. (Fig. 2). In contrast, the consumption rate of *Zygnema* spp. (microalgal complex 3) was the lowest. In the early stages of the feeding experiment, shrimps preferred the softer components of the microalgal complexes and detritus, such as decayed algae, resulting in a rapid consumption rate during the first 24 h (Fig. 2a). Subsequently, the brown color of the microalgal complexes turned green, accompanied by a sharp decrease in the shrimp consumption rate. This change could be caused by the depletion of softer, more easily edible components (brown-colored detritus), which were preferentially consumed by *N. denticulata*, prompting the shrimp to shift their feeding toward tougher algal tissues (green-colored microalgal components) (Fig. 2a).

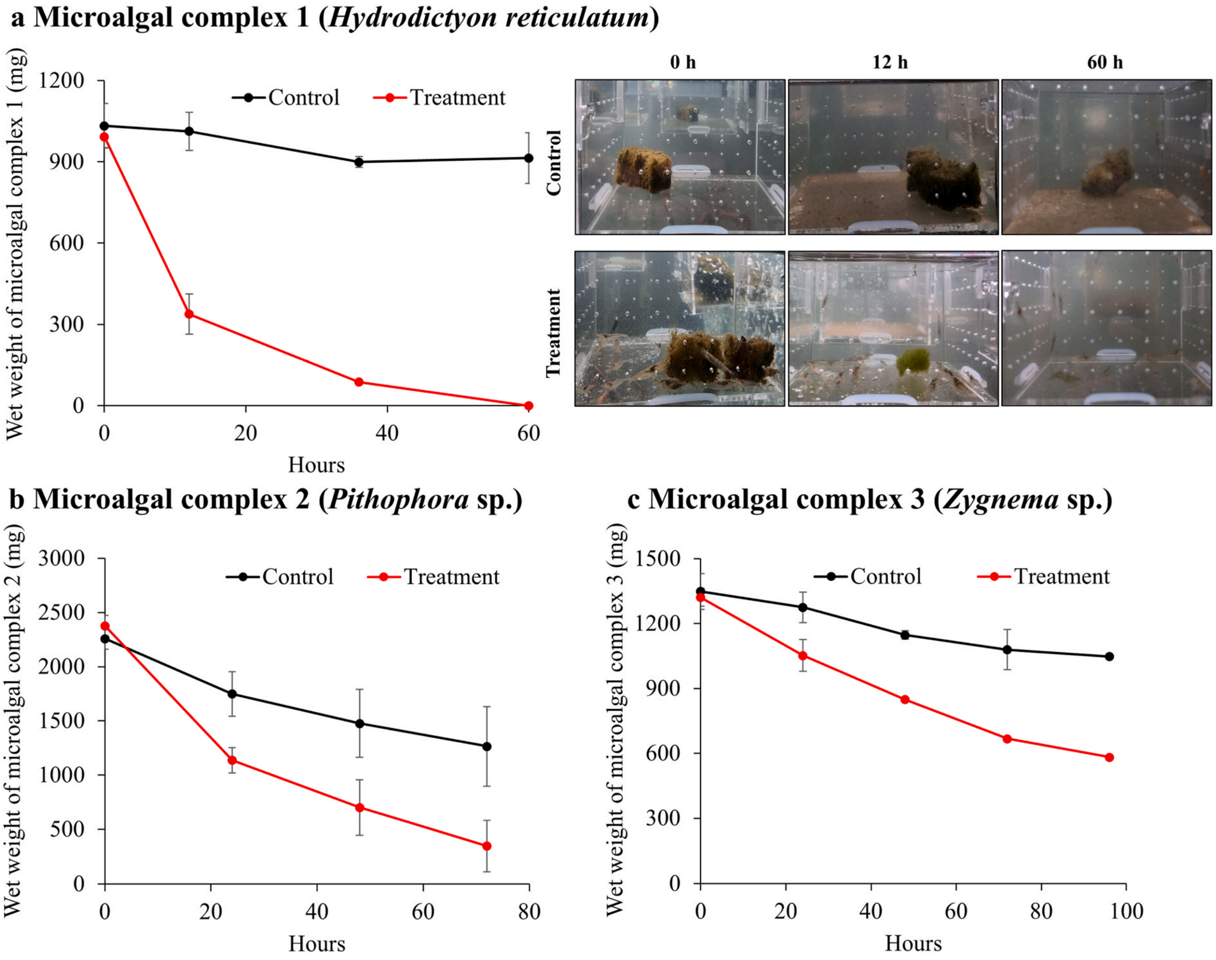

Fig. 2. Consumption of three different microalgal complexes by *Neocaridina denticulata*. Wet weight changes in the control and treatment groups are shown for (a) microalgal complex 1, (b) microalgal complex 2, and (c) microalgal complex 3. As an example, corresponding images illustrating the consumption of microalgal complex 1 by N. *denticulata* are shown on the right in (a).

In the control group, a slight decrease in the microalgal complexes was observed, accompanied by an increased water turbidity. This was likely due to the disintegration or loss of algal material during the transferring and replacing of material for measurement.

3.2. Microcosm experiments

3.2.1. Effects of N. denticulata on primary producer structure and nutrient concentrations

The introduction of shrimp significantly altered the composition and biomass dynamics of submerged macrophytes, periphyton, and filamentous microalgae in the treatment tanks during the microcosm experiment, resulting in clear differences compared with the control tanks. Approximately 85 % of the microalgal complex 2 was consumed by the shrimp within 3 days (Fig. 3a and c), and approximately 90 % of the periphyton and detritus attached to the leaves of the submerged macrophyte *Hydrilla verticillata* were removed within 4 h (Fig. 3e). The shrimp also consumed sedimented particles, including detritus, dead leaves, and detached fragments from the microalgal complex (Fig. 3b–d), resulting in a significantly lower dry weight of the sedimented material in the treatment tanks at the end of the experiment (*t*-test, $p < 0.001$). Notably, the submerged macrophyte biomass increased by 18 % in the treatment tanks compared with that in the control (*t*-test, $p < 0.05$) (Fig. 2f), suggesting that shrimp introduction had a positive effect on promoting submerged macrophyte growth, even in this short-term experiment.

The ammonia concentrations followed similar trends in both the control and treatment tanks, although the levels remained higher in the treatment tanks until 240 h. The nitrite concentrations increased sharply up to 72 h and then declined toward the end of the experiment in the treatment group, whereas they exhibited continuous reduction in the control group (Fig. S2). In contrast, nitrate and phosphorus concentrations increased steadily and remained consistently high in the treatment group throughout the experiment (Fig. S2).

3.2.2. Short-term effects of shrimp introduction on microbial composition

During the short-term microcosm experiment, the overall microbial community structure in the water column did not exhibit significant differences between the treatment and control tanks, regardless of shrimp introduction (after 408 h, bacteria: ANOSIM, $p = 0.1$; PERMANOVA, $F = 1.91$, $p = 0.1$; eukaryotes: ANOSIM, $p = 0.1$; PERMANOVA, $F = 2.01$, $p = 0.1$) (Fig. 4a and b). In both the control and treatment tanks, the bacterial communities were dominated by Bacteroidia, Gammaproteobacteria, Actinobacteria, and Alphaproteobacteria, whereas the eukaryotic communities were primarily composed of Ciliophora, Metazoa, and Cryptophyta (Fig. 4c).

Microalgal complex 2 contained a diverse range of organisms, including bacteria, Metazoa, cyanobacteria, and eukaryotic algae (Fig. 4c). Microalgal complex 2 exhibited relatively reduced microbial diversity at the initial stage compared with the water column, which

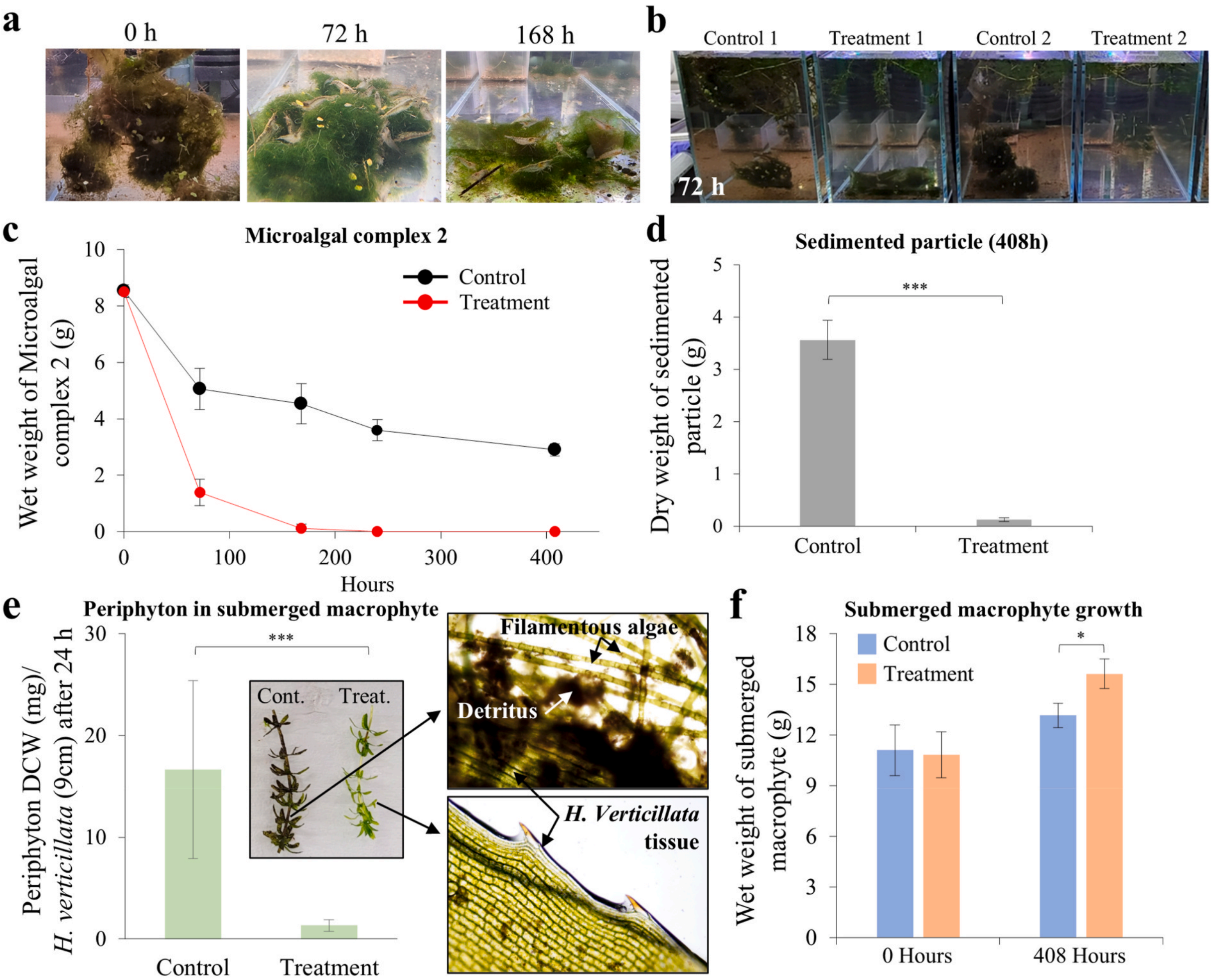

Fig. 3. Dynamics observed in the microcosm study, including filamentous algae, submerged macrophyte, and sedimented particles. (a) Representative image of microalgal complex 2 in the treatment group during the experiment. (b) Image of the microcosms used in the study. (c) Wet weight changes of microalgal complex 2. (d) Dry weight changes of sedimented particles in the microcosms. (e) Dry cell weight of periphyton relative to macrophyte *Hydrilla verticillata*. The right panel shows microscopic images of *H. verticillata* leaf surfaces in control and treatment groups after 24 h. (f) growth of submerged macrophytes in control and treatment groups.

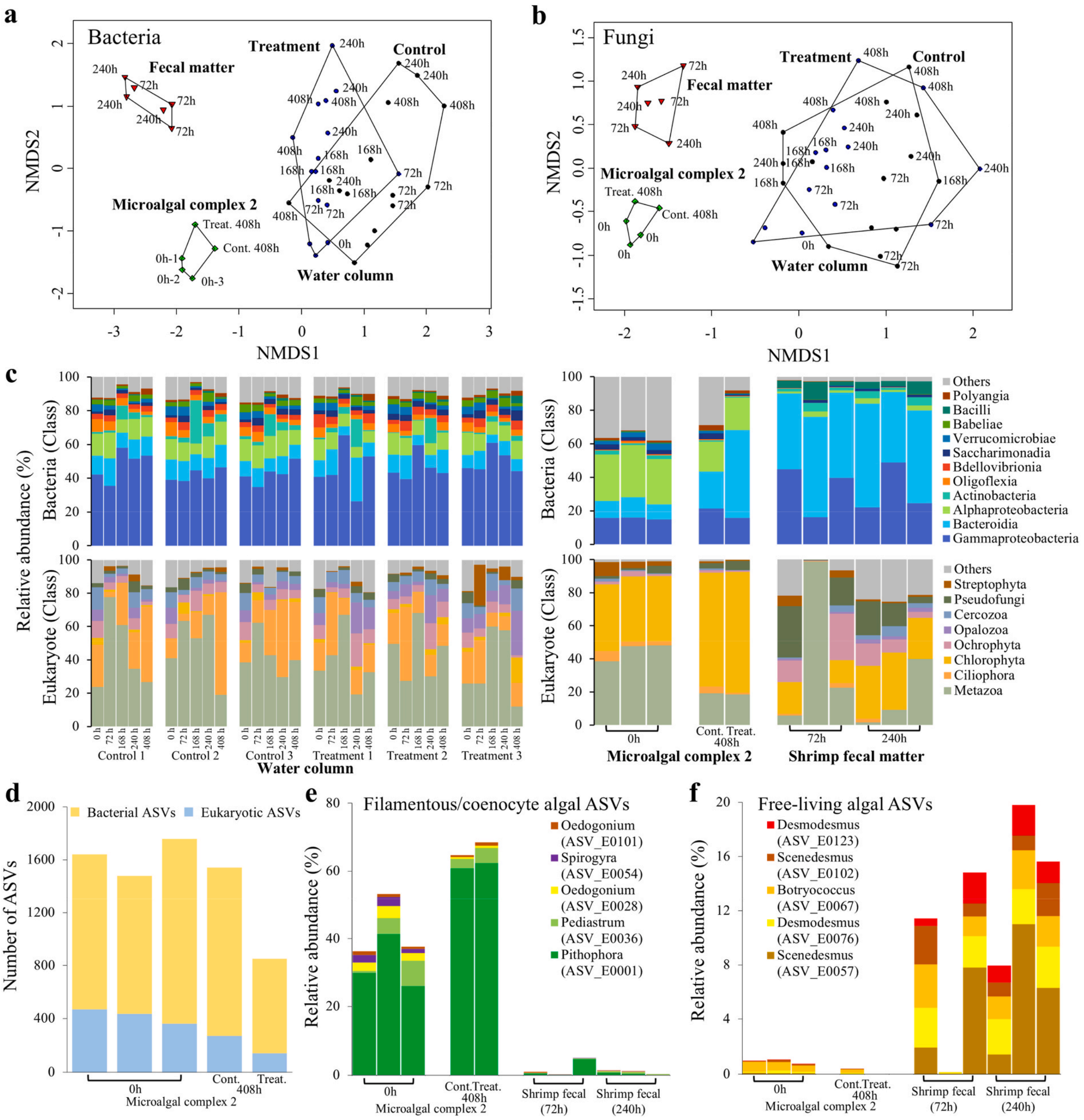

Fig. 4. Microbial dynamics observed in the microcosm study. Non-metric multidimensional scaling (NMDS) analysis of microbial community structures in the microcosm study. (a) bacterial communities. (b) eukaryotic communities. (c) Bacterial and eukaryotic community structures of the water column, microalgal complex 2, and shrimp fecal matter at the class level. (d) Number of amplicon sequence variants (ASVs) observed in microalgal complex 2. (e–f) Relative abundance of filamentous/coenocytic and free-living algal ASVs in microalgal complex 2 and shrimp fecal matter.

further declined at the end of the experiment in the treatment tanks (Fig. 4d). At the ASV level, both bacterial and eukaryotic ASV counts were reduced in the treatment tanks, reaching approximately 50 % of those observed in the control tanks (Fig. 4d). At the ASV level, *Pithophora* was the dominant algal taxon in microalgal complex 2, comprising 32.5 ± 8.0 % of algal ASVs, although other filamentous or coenocytic algae such as *Oedogonium* and *Spirogyra* were also present (Fig. 4e). After the shrimp consumed microalgal complex 2, which turned from brown to green, the microbial community composition decreased in diversity with an increased proportion of *Pithophora* (Fig. 4e). In addition, shrimp fecal matter exhibited a higher prevalence of free-living algal ASVs, such as *Desmodesmus* and *Scenedesmus* (Fig. 4f), suggesting that shrimp consume free-living algae associated with detritus from the algal complex.

3.3. Field study

3.3.1. Adaptation and population establishment of N. denticulata in natural conditions

The distribution of the introduced shrimps was not uniform, as they tended to hide among the submerged macrophytes and within the sediment immediately after release. This behavior makes it difficult to accurately monitor the population without causing significant environmental disturbances, such as sediment resuspension. Nevertheless, 1 week after introduction, shrimp survival was confirmed by capturing individuals with a dip net in the shallow areas of the treatment pond. Notably, the observation of berried shrimp in April 2023, following winter, indicated that the shrimp not only survived but also successfully adapted to the environment and began reproducing in the treatment pond, suggesting the establishment of a stable population (Fig. S3).

3.3.2. *Impact of N. denticulata introduction on primary producer dynamics and water quality*

During the study periods, water temperatures ranged from 7.3 to 30 °C and pH from 7.1 to 10.0, with no significant differences observed between the control and treatment ponds (Fig. S4). However, dissolved oxygen levels varied between 6.5 and 17.3 ppm, with the highest level recorded in the control pond on May 19, 2023 (Fig. S4). Shrimp introduction significantly improved the water quality in the treatment pond compared with that in the control pond. Although the initial concentrations of total dissolved nitrate and phosphorus were higher than those in the control pond, they declined substantially over time following shrimp introduction, eventually reaching comparable levels by June (Fig. 5d and e). Specifically, nitrate levels in the treatment pond decreased by approximately 28 %, whereas phosphorus levels decreased by 61 %. Turbidity in the treatment pond initially increased, likely because of sediment disturbance from shrimp activity, but subsequently decreased, reaching values approximately 40 % lower than those in the control pond by the end of the study period (Fig. 5f).

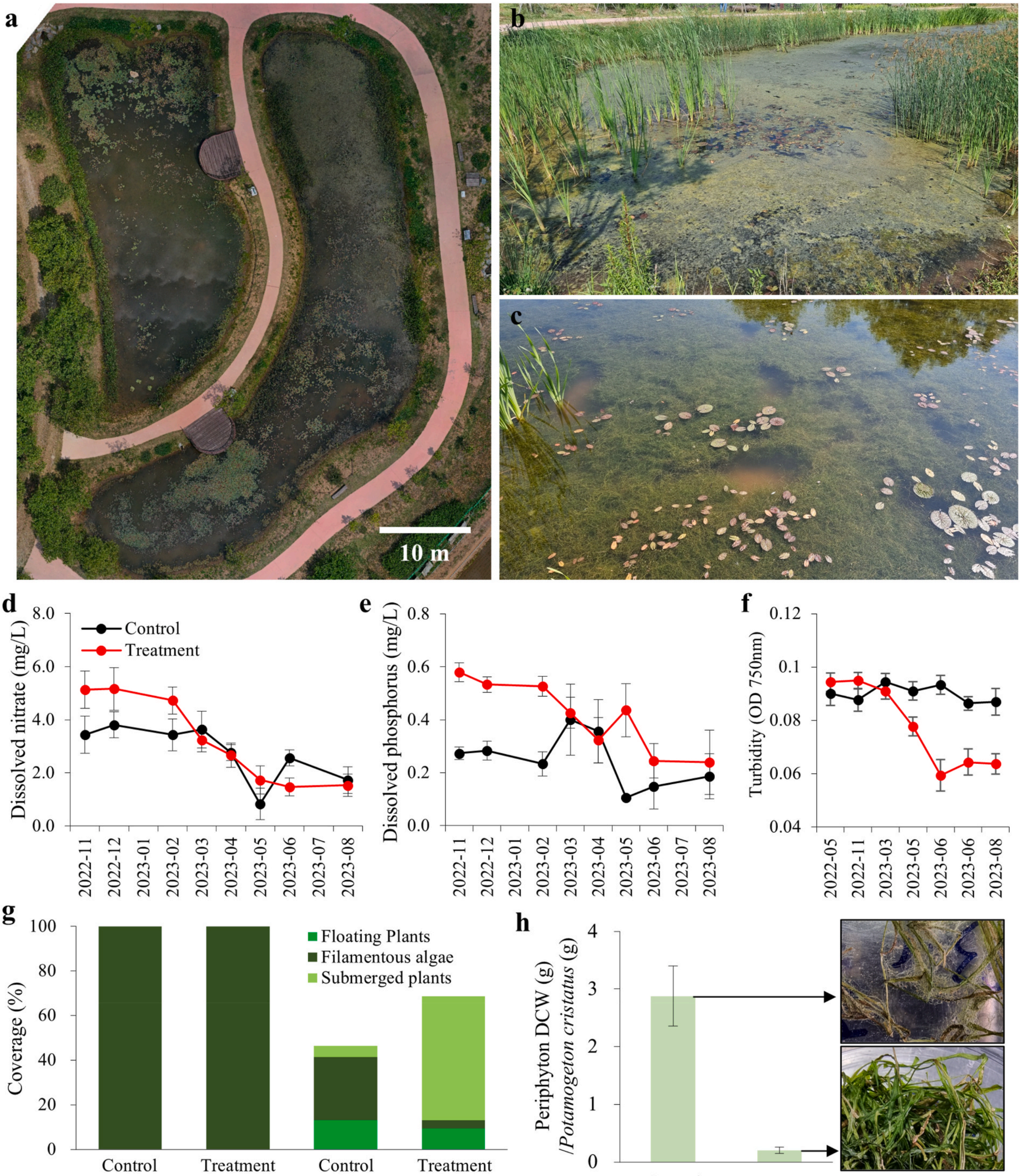

Fig. 5. Impact of shrimp introduction in the field. (a) Drone-captured image of the control and treatment ponds on June 12, 2023. (b) Image of the control pond dominated by filamentous algae. (c) Image of the treatment pond dominated by submerged macrophytes. (d–f) Changes in nutrient concentrations and turbidity in control and treatment ponds. (g) Coverage of filamentous algae, submerged macrophytes, and floating plants in control and treatment ponds. (h) Dry cell weight of periphyton relative to macrophyte *Potamogeton cristatus*. *P. cristatus* in control and treatment ponds on June 12, 2023.

Microalgal coverage was significantly lower in the treatment pond compared with the control pond. This difference is apparent from April to May 2023 (Fig. S5–6). On June 12, 2023, the microalgae covered approximately 20 % of the control pond surface, whereas in the treatment pond, the coverage was only 3.6 % (Fig. 5a–c, g and S5). In contrast, the coverage of submerged macrophytes, particularly *Potamogeton crispus*, in the treatment pond increased substantially (55 % of total area), approximately 11 times higher than that in the control pond (Fig. 5c and g). Additionally, the biomass of periphyton attached to these macrophytes was approximately 14 times greater in the treatment pond (Fig. 5h). This shift in the primary producer structure might have been partially facilitated by the reduced microalgal surface coverage in the treatment pond, which promoted submerged macrophyte growth through increased light penetration.

3.3.3. Long-term effects of N. denticulata introduction on microbial composition

Long-term field monitoring revealed that the bacterial communities did not exhibit significant differences between the treatment and control ponds, whereas the eukaryotic communities showed a distinct shift (bacteria: ANOSIM, $p > 0.05$; PERMANOVA, $F = 1.90$, $p > 0.01$; eukaryotes: ANOSIM, $p < 0.005$; PERMANOVA, $F = 2.73$, $p < 0.001$)

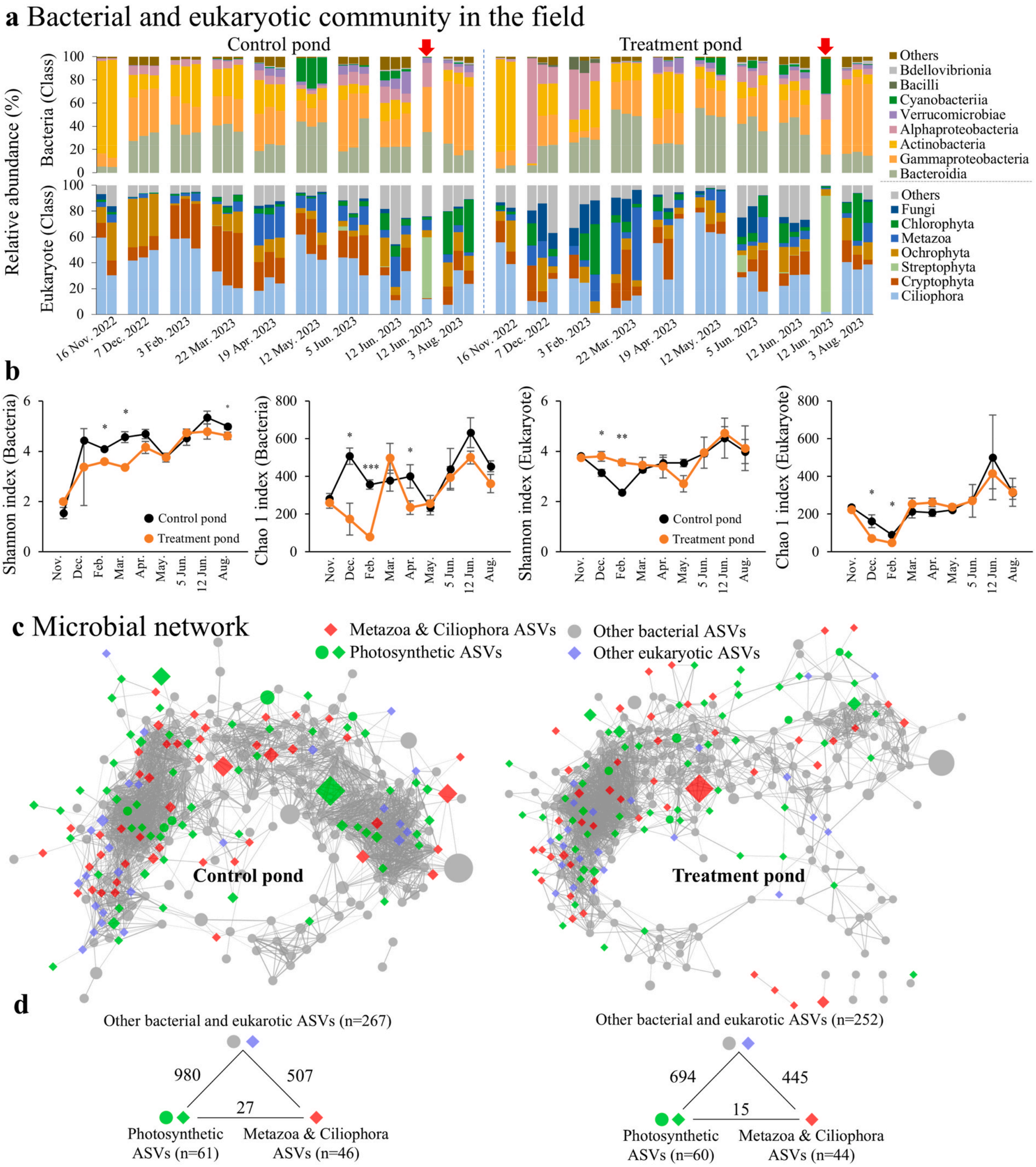

Fig. 6. Environmental microbiome analysis in the field. (a) Bacterial and eukaryotic community structures at the class level in the water column of control and treatment ponds. Red arrows indicate samples from floating microalgal complexes. (b) Diversity indices of microbial communities. (c) Microbial network structures in control and treatment ponds. (d) Numbers of nodes and edges among categorized amplicon sequence variants in the microbial networks of control and treatment ponds.

(Fig. 6a). Consistent with the microcosm findings, major bacterial and eukaryotic communities in the water column were similar to those observed in the microcosm experiments. Notably, *Pseudanabaena* sp. (ASV_B0013) bloomed in the control pond during May (occupying 19 % of the total bacteria), whereas, in the treatment pond, it only occupied 5 % and did not bloom. Alphaproteobacteria dominated the treatment pond from December to February, primarily because of an increase in ASVs belonging to the genus *Methylobacterium*. During the same period, the eukaryotic community in the treatment pond was characterized by a higher relative abundance of Fungi, Chlorophyta, and Metazoa, comprising approximately 46 % of the total community, about eight times higher compared with the control pond. In contrast, the control pond was dominated by Ciliophora, Cryptophyta, and Ochrophyta, which together comprised approximately 86 % of the total community during this period, about twice the proportion observed in the treatment pond.

During the winter–spring period at the beginning of the field study, following shrimp introduction, the bacterial diversity index and richness were significantly lower in the treatment pond compared with the control pond. However, eukaryotic diversity was higher in the treatment pond compared with the control pond during this phase, whereas eukaryotic richness showed the opposite pattern (Fig. 6b). We hypothesize that these differences could be attributed to the initial sediment disturbance caused by shrimp and the subsequent microbial adaptation to the environment.

An ecological network was constructed to assess the impact of shrimp introduction on the complexity and interconnectivity of different biological kingdoms in the field (Fig. 6c). Despite a similar number of nodes in the treatment and control ponds (323 vs. 339), the treatment pond exhibited a relatively low number of connections (2727 vs. 3567 edges), indicating reduced network complexity. Notably, the connections between the photosynthetic populations (61 ASVs in the control and 60 ASVs in the treatment) and metazoan/ciliophora populations (46 ASVs in the control and 44 ASVs in the treatment) were substantially fewer in the treatment pond (15 connections) compared with the control pond (27 connections) (Fig. 6d). In addition, the photosynthetic populations exhibited significantly fewer connections with bacterial and other eukaryotic ASVs in the treatment pond (694 connections) compared with the control pond (980 connections). Functional prediction analysis (FAPROTAX) was conducted to assess changes in microbial community functions. The predicted functions related to chemoheterotrophy and aerobic chemoheterotrophy were dominant throughout the sampling period in both control and treatment ponds (Fig. 7). However, the relative proportions were significantly higher in the control pond compared with the treatment pond. The predicted functions related to photoheterotrophy and hydrocarbon degradation were also reduced in the treatment pond, whereas photo-autotrophy showed no significant difference between the two ponds.

4. Discussion

Our study highlights the ecological functions of *N. denticulata* and demonstrates its potential as a native restoration agent for the rehabilitation of freshwater ecosystems with reduced shrimp populations. Integrating concepts from restoration ecology, our findings demonstrate that *N. denticulata* effectively suppresses the growth of filamentous microalgae, promotes the recovery of submerged macrophyte communities, and contributes to improved water quality in eutrophic aquatic ecosystems, supporting the restoration and rehabilitation of balanced freshwater environments. The multifunctional role of shrimp was illustrated in this study through a combination of controlled microcosm experiments and field-based investigations. The findings demonstrate that shrimp regulates the growth and composition of primary producers, stabilizes ecosystem structures, and enhances water quality, thus underscoring its value as a nature-based tool for ecological restoration in eutrophic freshwater systems.

4.1. *N. denticulata introduction for the suppression of filamentous algal blooms*

In natural ecosystems, algae typically form complex assemblages with other algal species, including bacteria, detritus, and organic matter

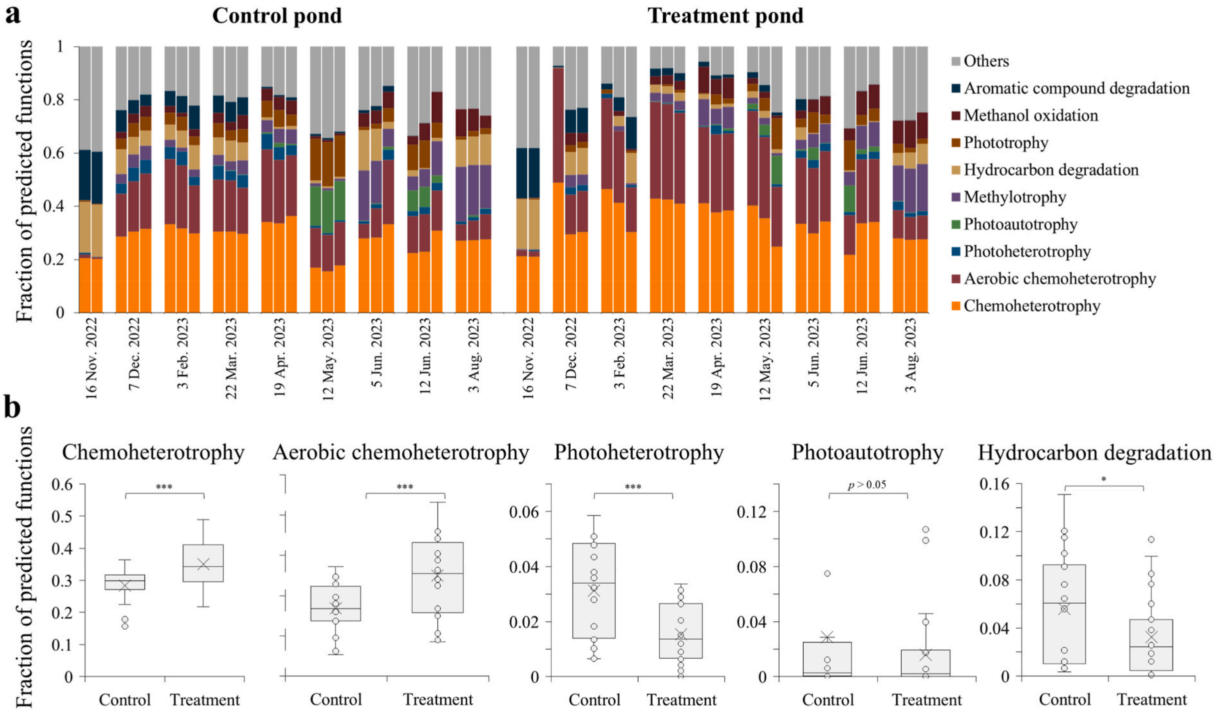

Fig. 7. Predicted microbial functions using FAPROTAX analysis. (a) Fraction of predicted functions in control and treatment ponds. (b) Box plots showing the distribution of five major predicted functions in the microbial communities.

(Cole, 1982). We found that *N. denticulata* exhibits a broad feeding capacity, consuming not only various filamentous algae, but also preferring softer, decayed algal tissues and detritus. Microscopic and sequencing-based analyses suggested that microalgal complex 2 used in the microcosm experiments was primarily composed of *Pithophora* sp., along with other algal taxa, such as *Pediastrum* sp., *Oedogonium* sp., and *Spirogyra* sp. (Fig. 4e), as well as bacterial genera, including *Rhodobacter* and *Tabrizicola*. Sequence-based evidence revealed the presence of filamentous microalgal ASVs in shrimp fecal matter (Fig. 4c), indicating direct consumption by shrimp. This effective consumption of the microalgal complex by *N. denticulata* highlights the dual role of shrimp as both a grazer and a decomposer, disrupting the intricate microbial–algal interactions that support filamentous algal persistence. Microbial taxa, such as *Rhodobacter*, known for their photosynthetic capabilities, and *Tabrizicola*, often associated with algal surfaces, play essential roles in maintaining the structure and stability of algal aggregates (Kiley and Kaplan, 1988; Park et al., 2020). By feeding on both filamentous algae and detritus, the shrimp are considered to undermine the structural and functional stability of these complexes, thereby suppressing overall algal growth and promoting ecosystem balance.

The consumption rates observed in the microcosm experiments further demonstrated the strong preference of *N. denticulata* for filamentous algae, with significant reductions in algal biomass over short timescales (Fig. 2). In the field study, a nine-fold reduction in algal surface coverage underscored the effectiveness of shrimp in controlling algal proliferation (Fig. 5). Similar regulatory effects have been documented for freshwater zooplankton, such as *Daphnia* and copepods, which suppress algal blooms through grazing (Boon et al., 1994; Chen et al., 2011; Oberhaus et al., 2007; Sommer and Sommer, 2006). In contrast to these smaller grazers, *N. denticulata* can consume larger filamentous algae, making it a potentially more effective biological control agent compared with traditional zooplankton-based strategies (Boon et al., 1994; Mitra and Flynn, 2006). These findings suggest that *N. denticulata* plays a crucial role in suppressing filamentous algal blooms, thereby contributing to the restoration of the ecological balance in eutrophic freshwater ecosystems.

4.2. *N. denticulata*-mediated promotion of submerged macrophyte growth

Submerged macrophytes are important primary producers in aquatic ecosystems and play a crucial role in maintaining water clarity by absorbing nutrients, promoting sedimentation, and preventing sediment resuspension, thereby supporting the overall ecosystem functionality (Madsen et al., 2001; Morris et al., 2003). In both microcosm and field experiments, we found that the introduction of *N. denticulata* reduced periphyton biomass and enhanced submerged macrophyte growth, consistent with previous studies on *Vallisneria denseserrulata* (Ye et al., 2019). *N. denticulata* helped to remove barriers that may limit light penetration and nutrient uptake by feeding on periphytic algae and attached detritus, subsequently enabling submerged macrophytes, such as *Potamogeton crispus* and *Hydrilla verticillata*, to recover and grow more effectively (Figs. 3e and 5h). Although floating algal mats are known to reduce light availability and oxygen levels (Morris et al., 2003; Rasmussen et al., 2012), our findings suggest that periphyton removal also plays an important role and may even have a greater impact in facilitating the recovery of submerged macrophytes. As macrophyte coverage expanded, it likely contributed to the reduced water turbidity through sediment stabilization and nutrient uptake (Fig. 5g and f). The shrimp may have created favorable conditions for macrophyte recolonization by suppressing periphyton and algal growth, thereby further limiting the nutrients available for algal proliferation. This positive feedback loop highlights how shrimp-mediated strategies can enhance ecosystem resilience and support long-term ecological balance.

Moreover, the resurgence of submerged macrophytes provides a crucial foundation for broader ecological interactions. Healthy macrophyte beds serve as important habitats and spawning grounds for various aquatic organisms, including shrimp, fish, and aquatic insects, thereby promoting biodiversity and supporting the development of more robust food webs (Christie et al., 2009; Thomaz et al., 2008). In the later phase of our field study, we observed the presence of berried shrimp, which may be linked to improved habitat conditions following the expansion of submerged macrophytes. These macrophytic communities likely provide shelter and foraging opportunities, contributing to shrimp persistence and reproduction. This suggests that macrophyte recovery may support broader ecological stability and highlights the potential role of shrimp-mediated interventions in ecosystem restoration.

4.3. Contributions of *N. denticulata* in improving water quality

Elevated turbidity and nutrient concentrations are common symptoms of eutrophication that hinder aquatic biodiversity and impair ecosystem functioning (Smith et al., 2006). Macroinvertebrates such as freshwater shrimp play a crucial role in nutrient cycling by decomposing and redistributing organic materials (Wallace and Webster, 1996). In our field study, *N. denticulata* application reduced turbidity by the end of the monitoring period by approximately 27 % (Fig. 4f), indicating a substantial improvement in water quality. Shrimp consumption of algal biomass, periphyton, and detritus likely enhanced organic matter decomposition and nutrient recycling, thereby contributing to the improved water quality in the treatment pond. In the microcosm experiment, the number of sedimented particles, primarily composed of algal detritus, was significantly lower in the treatment tanks than in the control tanks (Fig. 3d), suggesting that *N. denticulata* plays a key role in reducing particulate organic matter in both controlled and natural environments. These materials are then excreted as fecal pellets, which settle on the sediment, contributing to decreased water column turbidity and the removal of excess suspended particles. Moreover, by grazing on periphyton attached to submerged macrophyte leaves, shrimp may improve light penetration and reduce shading stress, thereby promoting macrophyte growth, stabilizing sediments, and absorbing nutrients, further improving water clarity.

4.4. Short- and long-term effects of *N. denticulata* introduction on aquatic microbiome dynamics

Existing studies on macroinvertebrates, such as shrimp, have primarily focused on their impact on macrophytes or algae (Geddes and Trexler, 2003; Guo et al., 2022; Pringle et al., 1993), but little attention has been given to their effects on the water microbiome, which is an essential component of ecosystem function. Laverock et al. (2010) demonstrated that bioturbating shrimp can influence the structure and diversity of bacterial communities in coastal marine sediments, highlighting the potential role of shrimp in shaping microbial dynamics in benthic environments.

The introduction of *N. denticulata* did not lead to significant alterations in the microbial community structure during either the short- or long-term experiments, with the exception of the eukaryotic communities in the long-term field study. These findings indicate that the overall microbial community structure remained largely stable, suggesting that shrimp introduction caused no major disruption to the aquatic microbiome. Network analysis revealed that the interspecies interactions between photosynthetic microbes and other microbial groups were substantially reduced in the treatment pond (Fig. 6d), whereas the relative abundance of photosynthetic microbes decreased in the treatment pond (Fig. 6a). Therefore, the introduction of shrimp led to compositional shifts among primary producers, marked by an increase in macrophytes, which, in turn, influenced the relative abundance of photosynthetic microbes and reduced their interspecies interactions with other microbial groups.

From a functional perspective, the predictive analysis demonstrated increased chemoheterotrophy and photoheterotrophy, suggesting that shrimp-driven organic matter decomposition converts detritus into bioavailable forms, supporting the growth of microorganisms with metabolic capabilities. An increase in such microbes could play a vital role in mitigating eutrophication during future nutrient influxes by facilitating efficient nutrient cycling and supporting a more balanced ecosystem. These findings emphasize that shrimp introduction not only aids in organic matter turnover, but also fosters microbiome functions that enhance ecosystem resilience and long-term health.

4.5. Limitations and future directions

Although this study employed only a single control and treatment pond in the field experiment, the relatively large size of each pond (650–1090 m^2) allowed for ecologically meaningful assessments that reflect realistic field conditions. Nevertheless, we acknowledge that future studies should incorporate replicated pond systems or additional sites with varied environmental conditions (e.g., nutrient regimes, hydrology, or trophic structure) to improve generalizability and assess context-dependent outcomes. In addition, shrimp were introduced in large numbers within a short period, but repeated smaller-scale introductions would represent a more precautionary and ecologically balanced strategy. Future restoration applications should therefore consider gradual stocking approaches alongside site-specific risk assessments. Although this study focused primarily on ecological functions, we also acknowledge that future research should evaluate the economic feasibility of shrimp-mediated restoration. Costs may vary depending on site-specific conditions such as shrimp rearing, transportation, nutrient input levels, and stocking scale, and assessing these factors will be essential for determining the circumstances where this approach can be the most cost-effective. Finally, while this study was carried out in experimental ponds using a native shrimp species, broader applications in natural freshwater systems should be accompanied by appropriate management and governmental oversight to ensure ecological safety and alignment with restoration goals. Despite this limitation, the strength of our findings lies in the multi-tiered experimental framework, from feeding trials and controlled microcosms to *in situ* long-term monitoring, which together provide robust evidence supporting the potential of *N. denticulata* as a nature-based restoration agent in eutrophic freshwater ecosystems.

5. Conclusion

Our study provides ecological evidence that *N. denticulata*, a small freshwater shrimp native to Korea, can serve as an effective biological tool for restoration and rehabilitation of eutrophic freshwater ecosystems. Through feeding trials, microcosm experiments, and field studies, we demonstrated that this shrimp suppresses filamentous algal blooms, reduces periphyton, promotes submerged macrophyte growth, and enhances water quality through organic matter processing and nutrient recycling. Notably, *N. denticulata* successfully survived and reproduced in natural pond environments, confirming its potential for nature-based restoration ecology. Despite these benefits, site-specific factors such as nutrient input, hydrology, and predation pressure must be considered to ensure effective rehabilitation outcomes. The small size of the shrimp makes it vulnerable to predators, highlighting the importance of providing suitable shelter such as macrophyte beds. In addition, although overall microbial community structure remained stable, network analysis indicated reduced interactions among photosynthetic and heterotrophic microbes, likely driven by shifts in primary producer composition. While challenges such as toxic cyanobacterial blooms remain, integrating shrimp into broader ecosystem management strategies offers a promising, low-cost, and sustainable approach for enhancing the rehabilitation, resilience, and ecological restoration of degraded freshwater systems.

CRediT authorship contribution statement

Seong-Jun Chun: Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Conceptualization. **Yingshun Cui:** Writing – review & editing, Formal analysis. **Jihoon Kim:** Methodology, Investigation. **Dakyum Roh:** Methodology, Investigation. **JiHyun Kim:** Methodology, Investigation. **Suji Park:** Methodology, Investigation. **Jun-Woo Lee:** Methodology, Investigation. **Kyong-Hee Nam:** Methodology, Investigation.

Ethics declarations

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Declaration of competing interest

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2025.127372.

Data availability

Raw sequences are available under NCBI SRA accession number PRJNA1208684

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