Oecologia

Direct and indirect effects of amphidromous shrimps on nutrient mineralization in streams in Japan

Hiromi Uno[1,2*], Keitaro Fukushima[1], Mariko Kawamura[3], Akira Kurasawa[1], Takuya Sato[4,1]

Affiliation

1: Center for Ecological Research, Kyoto University, 2-509-3, Hirano, Otsu, Shiga, 520-2113, Japan

2: Faculty of Environmental Earth Science, Hokkaido University, N10W5, Sapporo, Hokkaido, 060-0810, Japan

3: Seto Marine Biological Laboratory, Field Science Education and Research Center, Kyoto University, 459 Shirahama, Nishimuro, Wakayama, 649-2211, Japan

4: Department of Biology, Graduate School of Sciences, Kobe University, Kobe, Japan, 1-1, Rokkodai, Nada-ku, Kobe, 657-8501, Japan

* Corresponding author

hiromiuno1@ees.hokudai.ac.jp

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Abstract

Animals effect element cycling in ecosystems by consumption and excretion. Amphidromous shrimps frequently dominate low-mid altitude streams, where downstream connectivity to oceans is sustained. Although shrimps' direct influence on benthic communities has been studied, little is known about their influences on nutrient cycling. Here, we hypothesized that the dominance of shrimps alters nutrient mineralization by benthic macroinvertebrates in streams due to the difference in the quality and quantity of excretion between shrimps and aquatic insects. We tested this hypothesis through a field manipulative experiment, excretion measurements of animals, and field surveys. In the field manipulative experiment, the presence of shrimps slightly decreased the biomass of aquatic insects but tripled total benthic macroinvertebrate biomass directly through their own biomass. The mass-specific NH_4^+ excretion rate by shrimps was similar to aquatic insects, and the areal NH_4^+ excretion by benthic macroinvertebrates was increased by 2.5 times in the presence of shrimps. In contrast, shrimps excreted significantly less soluble reactive phosphorus (SRP) than aquatic insects, and the presence of shrimps did not affect areal SRP excretion by benthic macroinvertebrates. The field survey showed a positive correlation of NO_3^- concentration with the shrimp density, inferring the excess NH_4^+ was nitrified. Although the nutrient concentration of stream water is frequently attributed to watershed conditions, the results of this study indicate that downstream connectivity to oceans may also influence nutrient dynamics of the stream through the density of amphidromous shrimps.

Keywords

Excretion, migration, benthic, species interaction, aquatic insect

Introduction

The number of animals can vary substantially by habitats or by years for various reasons such as habitat connectivity (Hanski & Kuussaari 1995), diseases (Scheibling 1986), and natural catastrophes (Guha-Sapir et al. 2004). The density of animals can directly influence other organisms through species interactions such as direct consumption (Paine 1980; Carpenter 1985) and resource competition (Tilman 1977). Furthermore, studies on lakes have demonstrated that animals influence nutrient cycling through their excretion of waste products (i.e., nutrient mineralization by animals) (Kitchell et al. 1979; Vanni 2002). However, in streams, the effects of animal excretion have been understudied because water flow makes evaluating the effects of animal excretion on streams difficult. However, some studies have shown that the patchy distribution of fishes can create spatial heterogeneity in nutrient concentration in stream water (McIntyre et al. 2008; Sato et al. 2016), and the presence of a specific animal species can alter nutrient cycling in streams (Hall et al. 2003; Whiles et al. 2013; Atkinson et al. 2017). In reality, animals influence the ecosystem structures both through species interactions and through nutrient addition by excretion, and the combined evaluations of the biogeochemical influence of animals are required to truly understand the influence of animals on stream ecosystems (Vanni & Layne 1997).

In intact coastal streams, a large proportion of aquatic animals migrate between streams and oceans or lakes (Myers 1949). For obligate migratory animals, disruptions of migration routes limit their distribution in streams. Therefore, large variation in animal densities exists in streams, depending on the hydrological connectivity of river networks. Many studies have shown that salmon-run from the ocean can have substantial direct and indirect effects on stream ecosystems (Gende et al. 2002; Holtgrieve & Shindler 2011). Childress & McIntyre (2015) demonstrated that the migration of iteroparous fishes can also provide nutrients to stream ecosystems through nutrient inputs by excretion, decomposed unfertilized eggs, etc., improving productivity in streams. While such anadromous fishes come to streams for spawning transport nutrients from oceans or lakes to streams (Material subsidy), many other migratory animals that exhibit amphidromous or catadromous migration rather stay in streams for a prolonged period (McDowall, 1988) and should influence the local stream ecosystem as a newly added animal species (Process subsidy) (Flecker et al., 2010). However, studies evaluating the effect of process subsidies are limited compared to those evaluating material subsidies (Flecker et al., 2010).

The presence of a migratory animal as a process subsidy can not only influence resident species through species interactions but also nutrient cycling through their excretion (Taylor et al. 2006; Flecker et al., 2010). The addition of a migratory animal can reduce the biomass of other resident animals through species interactions. However, if the added species use resources more effectively than others do, the total biomass can be increased by the addition of new species (Tilman 1977). Furthermore, mass-specific excretion rates vary by animal species (McManamay et al. 2011), and the change in dominant species can influence nutrient cycling (Evans-White et al. 2005; McIntyre et al. 2007). To take those processes into account, we need to know both the direct impacts of animal species on the entire assemblage biomass and the excretion rate of resident and migratory species.

In many coastal streams in the mid-low latitude region, amphidromous shrimps frequently dominate headwater streams (Covich 1988; Mantel & Dudgeon 2004; Cross et al. 2008), but data about their ecological consequences have been collected only from a few locations in neotropics (Covich 1988; Pringle et al. 1993; Greathouse et al. 2006). Because of their migratory life cycles, where their larvae exhibit in a planktonic form in estuaries (McDowall 1988), their densities can substantially vary among streams, depending on the physical accessibility from the ocean. Physical barriers such as anthropogenic dams can frequently extirpate amphidromous shrimps from the upstream area (Greathouse et al. 2006). Several studies have demonstrated that the presence of amphidromous shrimps can suppress the aquatic insect biomass through direct consumption or resource competition (Pringle et al. 1993; Greathouse et al. 2006). Furthermore, Benstead et al. (2010) estimated the total nutrient excretion by amphidromous shrimps in tropical streams and found that total shrimp excretion was equivalent to 21% of NH_4^+ uptake and 5% of total dissolved phosphorous uptake in a tropical stream. However, the influence of shrimp on nutrient mineralization by the entire benthic macroinvertebrate assemblages remains unknown. While shrimps might excrete a large amount of nutrients, nutrient excretion by aquatic insects may decline because of their suppressed biomass. The effect of shrimps may also differ by nutrient elements because crustaceans, including shrimps, excrete little phosphorous compared to aquatic insects, whereas shrimps' excretion rate of nitrogen is equivalent to that of aquatic insects (McManamay et al. 2011).

Here, we hypothesized that the dominance of shrimps alters nutrient mineralization by benthic macroinvertebrates in streams due to the difference in the quality and quantity of excretion between shrimps and aquatic insects. To test this hypothesis, we took multiple approaches. First, we conducted a field manipulative experiment to examine how the presence of shrimps influences benthic communities. Then, we measured the per capita excretion rate by shrimp and major aquatic insect taxa and estimated the areal excretion rate from benthic macroinvertebrates in the presence/absence of shrimp based on shrimp density data collected in the field manipulative experiment. Finally, we conducted a broad field survey of streams to examine how spatial variation in shrimp densities covaries with ambient nutrient concentrations. Overall, we discern the biogeochemical influences of amphidromous shrimps on temperate stream ecosystems.

Methods

Study sites

This study was conducted in the southern part of Wakayama Prefecture, Honshu, Japan (Fig. 1). Wakayama Prefecture is located in the Kii Peninsula facing the North Pacific Ocean. In this area, the climate is largely influenced by the warm current, Kuroshio, and provides the habitats of tropical–subtropical diadromous animals (Saito et al. 2012; Nagasawa et al. 2020). In these streams, various amphidromous fishes and invertebrates, including shrimps inhabit streams, where the migration route from the ocean is sustained (Tanaka et al. 2020), and benthic macroinvertebrate assemblages consist of diverse aquatic insects and amphidromous shrimps. We found most shrimps at night, whereas < 5% of shrimps were observed in the daytime. Among diverse amphidromous shrimps, two atyid shrimps *Paratya compressa* and *Caridina multidentate* were the most abundant in the study sites, and two palaemonid shrimps *Palaemon paucidens* and *Macrobrachium formosense* were observed at a lower density. The two atyid shrimps, possessing substantially smaller chelipeds than palaemonid shrimps (Hayashi 1989a, 1989b), are collector gatherers and feed primarily on detritus and periphyton, whereas the two palaemonid shrimps are omnivore and occasional predators (Uno personal observation).

Field manipulative experiment

The field manipulative experiment was conducted in a 2nd order coastal stream, the Takase River. The drainage area of the Takase River was 7.3 km^2 and was completely covered by forest, of which 34% was natural forest and 66% was plantation conifer forest. The stream width and discharge of the Takase River were measured at the retrieval of the experiment, and they were 8.1 ± 0.5 m and 0.35 m^3 sec^{-1}, respectively.

The goal of the field manipulative experiment was to investigate the direct biological effects of shrimps on benthic communities. By excluding shrimps from certain areas of the streams, we examined how shrimps alter aquatic insect assemblages as well as their potential food resources; i.e., benthic algae and fine particulate organic matter (BFPOM). Within a 500 m segment of the river, we set four blocks in distinct pools. Each block was >50 m apart from each other, and electricity was supplied to them by distinct electric chargers. In each block, we set four experimental cages. Electricity was supplied to them from the same electric charger, and each cage was > 1 m apart from the other. Each cage consists of ~10 L of pebbles filled in a 30 × 50 × 8 cm tray with 2 cm mesh, and an electric fence on top (Fig. S1). Large animals, including shrimps, are selectively removed by electricity, but aquatic insects are not (Pringle & Blake 1994; Moerke et al. 2017). Over the experimental period, two electric fences were electrified (no shrimp treatment), and the other two were not electrified (shrimp treatment). To confirm the effect of electric fences on shrimps, we counted the number of shrimps on each cage in the first week of the experiment. At night, in shrimp treatment, we observed 14.2 ± 2.9 individuals m^{-2} (mean ± standard error, hereafter) *Paratya compressa* and 0.8 ± 0.8 individuals m^{-2} *Palaemon paucidens*, which is equivalent to their natural density in the Takase River (Fig. 2A). No shrimps were observed in the no shrimp treatment, showing we successfully excluded shrimps. The field manipulative experiment was initiated on March 17, 2020, and retrieved on April 21, 2020.

At the retrieval of the experiment, all aquatic insects > 0.5 mm in each cage were collected to estimate their densities and biomass. Aquatic insects were sorted at the family level, and then, the total dry weight of all aquatic insects in each chamber was weighed after drying in an oven set at 60°C overnight.

We evaluated the quantity of algae and BFPOM by placing tiles in each cage. At the initiation of the experiment, we placed 3 × 3-cm tiles in each cage. Then, at the end of the experiment, we collected all tiles and loose organic materials on the tiles were flushed with water onto 70-µm mesh as BFPOM. The dry weight of BFPOM was measured at the laboratory after drying in an oven set at 60°C overnight. Periphyton on each tile was brushed and washed with <100-ml stream water and collected in a bottle, then filtered onto a GF/F filter (Whatman, Maidstone, UK). Chlorophyll-a was extracted with dimethylformamide and spectro-fluorometry (RF-5300PC, Shimadzu, Japan) was used to estimate the mean chlorophyll-a mass per area on each sampling area following the methods described by Suzuki and Ishimaru (1990).

In addition, we measured the decomposition rate of leaves in each cage. Before the experiment, we collected major riparian tree leaves, *Mallotus japonicus* and *Quercus serrata,* freshly fallen on a plastic sheet, and then, we air-dried them at room temperature for seven days. Then, we weighed each bundle of five leaves of the respective species (mean ± SD: 2.1±0.2g in *M. japonicas* and 2.0±0.2g in *Q. serrata*) and tied two leaf bundles on each cage at the initiation of the experiment, exposing them to the water in the stream. Then, at the end of the experiment, the leaf bundles were gently washed in a stream to remove sediment on leaves and then were collected. We air-dried them at room temperature for seven days and weighed each bundle. Decomposition rate ($-k$) of each bundle was calculated from the equation: k = (ln [initial weight]- ln [final weight])/experimental days (35) (Benfield et al. 2017).

Nutrient mineralization by benthic macroinvertebrates

To examine the influence of shrimp on nutrient mineralization in streams, we estimated the entire stream areal nutrient excretion rate by benthic macroinvertebrates in the presence/absence of shrimp. We first measured the per capita excretion rate of major aquatic insect taxa (Ephemeroptera, Diptera, Plecoptera, and Odonata) and shrimp following the methods used by Benstead et al. (2010) and McManamay et al. (2011). The excretion measurement was performed at nighttime (20:00–25:00) on July 23, 2020, and daytime (8:00–12:00) on July 24, 2020, in the Takase River, where the field manipulative experiment was conducted. Five individuals of major shrimp and aquatic insect taxa were collected with a dip net, respectively. Each individual was held less than 15 min before the start of the excretion experiment. Incubations were performed by introducing each shrimp in 100 ml of stream water and each insect in 30 ml of stream water filtered with a GF/F filter. Because chironomid midges were small, five individuals were incubated together in 30 ml of water. Each individual was incubated for 50–70 min, and we confirmed that all individuals were behaving normally through the incubations. Then, at the end of the experiment, specimens were frozen in individual bottles, and each incubated water sample was filtered with a 0.45-μm membrane filter (25CS045AN, Toyo Roshi Kaisha, Japan) and frozen until analysis. The dry weight of each specimen was measured. All water samples were frozen in the field and transported to the laboratory facility at the Center for Ecological Research, Kyoto University. Inorganic nitrogen (NO_3^-, NO_2^-, and NH_4^+) and soluble reactive phosphorous (SRP) concentrations in the water samples were measured colorimetrically using an autoanalyzer (QuAAtro 2-HR, BLTEC, Japan). In this study, we show the sum of NO_3^- and NO_2^- concentration as NO_3^- concentration because the NO_2^- concentration was immeasurably low.

We, then, estimated the areal excretion rate of the entire benthic macroinvertebrate assemblages in the presence/absence of shrimps, based on the density data in the “shrimp” and “no shrimp” treatment in the field manipulative experiment, and the per capita excretion rate of shrimp and major aquatic insect taxa. We calculated the areal excretion rate of benthic macroinvertebrates for each experimental cage by multiplying the mean taxa specific per capita excretion rate with the density of each taxon within each experimental cage in the field manipulative experiment, summing up the excretion rate of all taxa. Furthermore, we calculated the nutrient mineralization velocity by benthic macroinvertebrate assemblage by dividing the areal excretion rate of benthic macroinvertebrates by the nutrient concentration in stream water (Baker & Webster, 2017).

Field survey

To examine if biogeochemical impacts of shrimps found in the field manipulative experiment and the measurement of animal excretion can explain the natural variation in benthic communities and water nutrient concentration among streams, we conducted a field survey of benthic communities and water nutrients at sites with a wide shrimp density range. Based on the field manipulative experiment results, we hypothesized that the density of aquatic insects, in particular Chironomidae, decreases with increasing shrimp density. Furthermore, we hypothesized that the stream water nutrient concentration, particularly nitrogen would increase with increasing shrimp density. While shrimps excrete nitrogen in the form of NH_4^+, we predicted that NO_3^- concentration in stream water could also increase because of immediate nitrification.

The field survey was conducted at 13 sites in four watersheds, the Tonda River, the Takase River, the Hiki River, and the Koza River (Fig. 1). All sites were located in distinct tributaries of the rivers, and the watershed area of the study sites ranged from 0.8 to 10.4 km^2 (Table S1). The study area is one of the most intact areas in Honshu, Japan, and most of the watershed area was covered by natural broadleaf forest or planted coniferous forest. The riverbank mostly remained natural, and the direct human impact on stream water nutrients such as sewage was minimal. The geology of the study watersheds consists of Cenozoic accretionary complexes composed of sandstone, mudstone, and shale (Tokuoka et al. 1981). No study sites had an upstream effect of dams, but five sites had large downstream effects of dams (Tonoyama-dam with a 64-m height, and Shichikawa-dam with a 59-m height). All samplings were conducted in November 2017 within 5 days, and there was no precipitation during the sampling period. At each site, samplings were repeated twice in the daytime and nighttime on the same day because shrimps were strictly nocturnal in the system. Daytime sampling was conducted between one hour after sunrise and one hour before sunset, and nighttime sampling was conducted between one hour after sunset and one hour before sunrise.

Shrimp density was estimated with a 50 × 50-cm quadrat five times at random locations in each site at night. Aquatic insect assemblages were sampled with a 30 × 30-cm Surber-net sampler three times at randomly selected locations in each site and time (daytime and nighttime) to estimate the density. Sampled aquatic insects were preserved in 99% ethanol on-site, and >0.5-mm individuals were sorted to the family level under a compound microscope at the laboratory. The total dry weight of all aquatic insects collected at each site was measured. Algae were sampled from three cobbles at each site: 36 cm^2 of the cobble surface was scrubbed with a toothbrush to collect algae, and then, chlorophyll-a density was estimated as described above. A 100-ml water sample was collected at each site, and filtered through a GF/F within 24 h. Then, the filtered water samples were frozen until analysis. Inorganic nitrogen (NO_3^-, NO_2^-, and NH_4^+) and phosphorous (SRP) concentrations in the water samples were analyzed, as described above.

Data analysis

Field manipulative experiment and nutrient excretion- The field manipulative experiment enabled us to compare the effect of shrimps on major aquatic insect taxa and their potential food sources between shrimp and no shrimp treatments. We assessed the differences of their abundance between shrimp and no shrimp treatments using a one-way analysis of variance, including a block as a random factor via linear mixed model using the lmer() function in the lme4 package (Bates et al., 2021) and the anova() function in the lmerTest package (Kuznetsova et al. 2020) in Program R (R Core Team, 2018). We log-transformed the aquatic insect density to satisfy the assumptions of normality prior to the analysis. In the same way, the calculated areal excretion rate for each experimental cage was compared between “shrimp” and “no shrimp” treatments to examine the effect of shrimps on the nutrient mineralization in a stream.

Field survey- We compared the effect of shrimps and several watershed characteristics on water chemistry and major aquatic insect density across surveyed sites. Watershed characteristics, including the elevation of the sampling site, drainage area, natural forest area (proportion of land area covered by the primary and/or secondary broadleaf forests), forest area (proportion of land area covered by the natural forests and/or the plantation conifer forests), shrimp presence, and shrimp density measured at each site (Table S1). Watershed characters were estimated using the ArcGIS system, and the forest rate and natural forest rate of each watershed were estimated on the basis of the 1:25,000 vegetation map provided by the Biodiversity Center of Japan, Ministry of the environment, Japan (http://gis.biodic.go.jp/webgis/index.html). We first checked the collinearity among all variables included in each analysis using correlation coefficients and variance inflation factors (VIFs). A VIF score > 4 and a correlation coefficient > 0.7 were used to eliminate habitat variables with a high degree of collinearity (Zuur et al. 2010). There was a high degree of collinearity and VIF scores between shrimp presence and the elevation and between the shrimp presence and density (Table S2). Therefore, we excluded the shrimp presence from the analyses. To satisfy assumptions of normality, we added a constant of one and log transformed all shrimp and aquatic insect density data prior to analyses.

We generated a list of linear mixed-effect models with the stream as a random effect and all combinations of two or fewer predictor variables as fixed effects without interactions. We standardized the independent data to a mean of 0 and standard deviation of 2 so that the effect sizes of independent variables could be compared (Grueber et al. 2011). Models with ΔAICc < 4 were retained to form candidate model sets and were averaged using the MuMIn package in R (Table S2). To evaluate the effect of shrimps and watershed character variables on water chemistry and aquatic insect density, we considered the magnitude and direction of the averaged coefficient, whether the 95% confidence intervals spanned zero, and the relative variable importance of each variable. The latter is calculated as the sum of the model weights of all models in the final confidence set in which the variable appears (Burnham & Anderson, 2002). All analyses were performed with the software R (R Core team, 2018).

Results

Field manipulative experiment

Experimental exclusion of shrimps by the field manipulative experiment showed the profound influence of shrimps on stream benthic macroinvertebrates and their food sources (Fig. 2; Table S3 for detailed statistics). Heptageniidae, Chironomidae, Baetidae, Leptophlebiidae, Athericidae, and Perlidae were the six most dominant aquatic insect taxa constituting 95% of total aquatic insect density in the study site, and the composition changed by the presence of shrimps. (Fig. 2G-L). Among the six most abundant aquatic insects, the Chironomidae density was suppressed with shrimps to 68% of that without shrimp ($p = 0.028$), and the Baetidae density was enhanced with shrimp and was 193% as high as that without shrimp ($p = 0.036$). The density of Heptageniidae ($p = 1.00$), Leptophlebiidae ($p = 0.15$), Athericidae ($p = 0.13$), and Perlidae ($p = 0.97$) were not significantly influenced by the presence/absence of shrimps. The total dry weight of aquatic insects was not significantly different in the presence/absence of shrimp ($p = 0.54$).

Chlorophyll-a with shrimp was 148% as high as that without shrimp ($p = 0.002$), and the amount of BFPOM was suppressed with shrimp to 18% of that without shrimp ($p = 0.025$). The decomposition rate of *M. japonica* and *Q. serrata* were not significantly different in the shrimp versus no shrimp treatment ($p = 0.50$; $p = 0.76$).

Nutrient mineralization by benthic macroinvertebrates

NH_4^+ and SRP were the major nutrient form excreted by shrimp and major aquatic insects, and the N/P ratio of excretion by shrimp was high compared to the majority of aquatic insects supporting our hypothesis that shrimp would exhibit different nutrient excretion patterns from aquatic insects (Table

1). Per capita excretion rate by aquatic insects ranged from 0.0035 to 0.044μmol NH_4^+ h^{-1}, 0.000 to 0.001 μmol NO_3^- h^{-1}, and 0.0008 to 0.005 μmol SRP h^{-1}, and the N/P ratio of the excretion ranged from 2.4 to 9 by taxa. In contrast, the per capita excretion rate by shrimp was higher, and the means and the ranges of the excretion rates were 0.96 (0.38-1.57)μmol NH_4^+ h^{-1}, 0.003 (0-0.05)μmol NO_3^- h^{-1}, and 0.012 (0-0.02) μmol SRP h^{-1}. The N/P ratio of excretion by shrimp was as high as 91.2.

The presence of shrimps had a large effect on the total areal nutrient excretion rate by benthic macroinvertebrate assemblages, and the effect of shrimp was different between NH_4^+ and SRP (Fig. 3). This change in nutrient excretion rate arises from the change in the total biomass of benthic macroinvertebrates by the presence of shrimp and the difference in the chemical contents of the excretion between shrimp and aquatic insects.

Insect dry weight was 912 ± 114 mg m^{-2} in the absence of shrimps but slightly suppressed to 835 ± 100 mg m^{-2} in the presence of shrimp. However, the added biomass of shrimps overcompensated for the total macroinvertebrate biomass, and the total macroinvertebrate biomass was tripled from 912 ± 114 mg m^{-2} to 2702 ± 435 mg m^{-2} by the presence of shrimps ($p = 0.001$). NH_4^+ excretion by aquatic insects was 9.9 ± 1.1μmol h^{-1} m^{-2} in the absence of shrimp and 9.7 ± 1.4 μmol h^{-1} m^{-2} in the presence of shrimp. However, with shrimps, their excretion increased the total benthic macroinvertebrate NH_4^+ excretion 2.4 times from 9.9 ± 1.1 μmol h^{-1} m^{-2} in the absence of shrimp to 24.2 ± 3.5 μmol h^{-1} m^{-2} in the presence of shrimp ($p = 0.002$). In contrast, SRP excretion was not increased by the presence of shrimps and was similar in the absence of shrimps 1.4 ± 0.1 μmol h^{-1} m^{-2} and the presence of shrimps 1.5 ± 0.2 μmol h^{-1} m^{-2} because shrimps excreted less SRP than aquatic insects.

Dividing the nutrient excretion rate estimated above by the mean ambient nutrient concentration at the time of excretion measurement, 0.32 μmol L^{-1} for NH_4^+ and 0.26 μmol L^{-1} for SRP, respective nutrient mineralization velocity by benthic macroinvertebrate assemblages was calculated. The NH_4^+ excretion velocity was 0.52 ±0.06 mm min^{-1} in the absence of shrimps and 1.26 ± 0.18 μmol mm min^{-1} in the presence of shrimps. Then, the SRP excretion velocity was 0.09 ± 0.01 mm min^{-1} in the absence of shrimps and 0.10 ± 0.01 μmol mm min^{-1} in the presence of shrimps.

Field survey

Regression models showed that not only well-known physical factors such as the drainage area of the watershed but also shrimp density can influence stream benthic communities and water chemistry, which is consistent with our findings in the field manipulative experiment, which applies to natural variations among streams (Fig. 4,5, Table S4). Generally, the densities of aquatic insects and chlorophyll-a were lower with increased shrimp density but that was not statistically significant (Fig. 4F-J, 5F-J), as the effect of shrimp is masked by the large variation, along with other factors such as the drainage area. Among nutrients analyzed in this study, NH_4^+ concentration showed no variation with shrimp density (Fig. 4A, 5A), whereas NO_3^- concentration increased with shrimp density (Fig. 4B, 5B). The SRP concentration was lower at sites with a high shrimp density and also decreased with the drainage area and elevation (Fig. 4C, 5C).

Discussion

We show that the density of amphidromous shrimps not only influences stream biota through species interactions but also influences stream nutrient mineralization through their excretion. By the combination of the field manipulative experiment and field survey, we showed processes through which shrimps influence benthic macroinvertebrates and nutrient mineralization and then potentially influence the natural variation of nutrient concentrations. This study represents one of the limited studies that evaluated both the biological and chemical effects of process subsidies (Flecker et al. 2010), and the results indicate the potential impacts of the under-appreciated amphidromous animals on the stream ecosystem.

Influence on benthic macroinvertebrates and their food sources

The presence of shrimps slightly decreased the biomass of aquatic insects but increased total benthic macroinvertebrate biomass. This result agrees with a theory that predicts an increase in the total biomass of assemblages when a more efficient species is added (Tilman et al.1997). The reduction in BFPOM indicates that atyid shrimps were more effective consumers of BFPOM (Pringle & Blake

1994) than other aquatic insects such as Chironomidae, which are also detritus feeders (Merritt et al. 2019). Alternatively, it is possible that shrimps only decreased BFPOM by bioturbation (Cross et al. 2008) and displaced aquatic insects such as Chironomidae. Generally, species with a short life span exhibit a high production/biomass ratio (Robertson 1979). Therefore, the replacement of detritivore from Chironomidae with a few months to a one-year life span (Kawai & Tanida 2018) to shrimps with > 2-year life span (Kawai & Kazuyoshi 2011) would have decreased the production/biomass ratio of benthic detritivores and contributed to an increase in the total macroinvertebrate biomass in the presence of shrimps. Furthermore, increased chlorophyll-a density in the presence of shrimps in the experiment probably occurred because of the removal of BFPOM by shrimps covering and shading periphyton in streams (Power 1990; Kupferberg 1997). The increased chlorophyll-a of periphyton by the removal of BFPOM would explain the biomass compensation for grazers such as Baetidae (Merritt et al. 2019) in the presence of shrimps.

Influence on benthic nutrient mineralization

Shrimps affected nutrient mineralization by benthic macroinvertebrate assemblages, but the effect was different between NH_4^+ and SRP. The mass-specific NH_4^+ excretion of shrimps was within the range of variation among aquatic insects, as previously documented (Vanni et al. 2017), and increased the total biomass of benthic macroinvertebrates in the presence of shrimps, simply increasing the total NH_4^+ excretion. In contrast, shrimp excreted less SRP compared to aquatic insects. As crustaceans require a large amount of phosphorous for their carapace (Vrede et al. 1999), it is a general pattern that shrimp excrete less SRP than other aquatic animals such as aquatic insects and snails (Evans-White et al. 2005; McManamay et al. 2011). Consequently, elevated benthic macroinvertebrate biomass in the presence of shrimps did not increase the SRP excretion by benthic macroinvertebrate assemblages.

A change in mineralization rate in presence of shrimp can influence nutrient dynamics in a stream. The contribution of nutrient excretion by benthic macroinvertebrates to the ecosystem-level nutrient cycling was not directly evaluated in this study because this contribution depends on nutrient uptake rates not measured in this study. However, as our best estimate, according to meta-analysis (Ensign & Doyle 2006), the interquartile range of uptake velocity in second-order streams is between 2.6 and 10.0 mm min^{-1} for NH_4^+ and between 1.2 and 6.9 mm min^{-1} for SRP. Comparing to this, we can estimate that the excretion velocities by benthic macroinvertebrates measured in this study in the absence of shrimp, 0.52 mm min^{-1} for NH_4^+ and 0.09 mm min^{-1} for SRP, are equivalent to 5%–20% of NH_4^+ uptake velocity and 1%–8% SRP uptake velocity. In presence of shrimp, the excretion velocities by benthic macroinvertebrates were elevated, and 1.26 mm min^{-1} for NH_4^+ and 0.10 mm min^{-1} for SRP, which are equivalent to 12-48% of NH_4^+ uptake velocity and 1%–9% SRP uptake velocity. Elevation of NH_4^+ excretion velocity by benthic macroinvertebrates by the presence of shrimps would have potentially large impacts on the entire stream nutrient cycling, whereas the increase in the SRP excretion velocity by shrimp was limited.

Influence on stream water nutrient concentration

The influence of migratory fishes on stream nutrients has been demonstrated in various studies (Mitchell & Lamberti 2005; Childress & McIntyre 2016; Hood et al. 2019); however, this study represents one of the limited studies that have indicated the influence of migratory shrimps (but see Benstead et al. 2010). While previous studies on fishes have demonstrated a direct increase in the NH_4^+ and SRP concentrations in stream water derived from fish excretion, this study shows that the stream water NO_3^- concentration , but not NH_4^+ nor SRP, is positively associated with shrimp density.

The NO_3^- concentration in streams with a high shrimp density was on average twice as high as those without shrimps. While spatial variation in the stream NO_3^- concentration is frequently attributed to land use (van Breemen et al. 2002) and/or geology (Holloway et al. 1998) in the watershed, the effect of such variables was not significant in our watersheds. In addition, other factors affecting the NO_3^- concentration such as climatic condition (Watmough et al. 2004), nitrogen deposition (Nishina et al. 2017; Amos et al. 2018), and forest age (Pardo et al. 1995; Tokuchi & Fukushima 2009) are almost the same within the range of our study watersheds. While the excretion of nitrogen from benthos was in the form of NH_4^+, we assume that NH_4^+ from benthic macroinvertebrate assemblages was nitrified to NO_3^- in streams by nitrifying bacteria (Newbold et al. 1983; Day & Hall 2017). The benthic zone of headwater streams, where shrimps live, is where nitrification occurs most actively in streams (Ensign & Doyle 2006; Hall et al. 2013). When the NH_4^+ concentration is increased, autotrophic nitrification should occur actively in biofilms in oxic sediments in shallow and fast-flowing mountainous streams such as where this study was conducted (Butturini et al. 2000). The reduction of BFPOM because of shrimp activity, as observed in the electroshock experiment, may have also contributed to activating nitrification by oxidizing the sediment (Stief 2013). Amphidromous shrimps studied here migrate up to headwater areas of streams, and the stream water continuously receives shrimp excretion from headwater to the sampling sites over long distances. The excreted NH_4^+ was likely nitrified over the distance.

In contrast, the SRP concentration in stream water was negatively associated with shrimp density, whereas the SRP concentration was strongly negatively correlated with the drainage area and the elevation of the sampling site. Active photosynthesis by algae downstream (Finlay et al. 2011), and/or low weathering rate of the bedrock in a higher elevation (Hartmann et. al. 2011; Lintern et al. 2018) are potential explanations for the SRP variation along the environmental gradient. The negative association of the SRP concentration with the shrimp density was unexpected, given that the results of the field manipulative experiment and the excretion measurement estimated that shrimp presence does not influence on the SRP excretion rate by benthic macroinvertebrates.It is possible that there was some unmeasured variable that covaries with shrimp density and SRP concentration.

We acknowledge that our field survey is still preliminary, given the limited sample size. Yet, the data show that stream water NO_3^- concentration covaried with shrimp density, and inferred that the elevated NH_4^+ excretion rate by benthic macroinvertebrates in presence of shrimps elevated NO_3^- concentration in stream water after nitrification. Given the potentially large impacts of the shrimps on the water chemistry, this study urge further investigations including field survey with larger sample size, and more mechanistic approach including isotopic studies to assess the control of shrimps on NO_3^- for high confidence.

Conclusion

The loss of habitat connectivity frequently results in a decline in animal diversity (Fahrig, 2003; Cardinale et al. 2012). Our results show that the loss of migratory species can change not only the community structure but also nutrient cycling. While the ecological consequences of the loss of large animals and/or animals with commercial importance such as salmonids have received considerable attention (Lichatowich et al. 2001), ecological consequences of the loss of such small and commercially unimportant animals such as shrimps are less well studied. This study represents one of the first studies that have evaluated the ecological consequences of amphidromous shrimps in Asia.

Further studies on the ecological consequences of diverse migratory organisms in wide geographic regions need to be conducted.

Biochemical characteristics of stream ecosystems are often attributed to watershed conditions, including geology (Holloway et al. 1998) and land use (Likens et al. 1970; Allan, 2004; Wakamatsu et al. 2006). Our results show that not only upstream watershed conditions but also downstream connectivity to the ocean may influence stream biota as well as nutrients in water through the presence of migratory animals. Greathouse et al. (2006) demonstrated upstream effects of dams by extirpation of amphidromous animals. Although they only found the reduction in aquatic insects through species interactions, the result of this study shows that the upstream effect of dams would be extended to nutrient cycling. Overall, this study shows that the stream ecosystems are shaped not only by the watershed/upstream conditions but also by the downstream conditions to the ocean, and emphasizes the importance of watershed-scale managemet.

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Declarations

Conflict of Interest: The authors declare that they have no conflict of interest. Ethics approval: All applicable institutional and/or national guidelines for the care and use of animals were followed. Availability of data and materials: The datasets used and/or analyzed during the current study are available from the corresponding author on request.

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(A)		NH_4^+ μmol hr^{-1}		NO_3^- μmol hr^{-1}		SRP μmol hr^{-1}		Dry weight mg	
	n	mean	SE	mean	SE	mean	SE	mean	SE
Shrimp (*Paratya compressa*)	10	0.962	0.122	0.003	0.012	0.012	0.003	124.5	28.7
Ephemeroptera (Heptageniidae)	10	0.016	0.004	0.000	0.000	0.002	0.001	1.1	0.4
Diptera (Chirnomidae)	10	0.0035	0.0011	0.0002	0.0000	0.0008	0.0002	0.045	0.035
Plecoptera (Perlidae)	10	0.019	0.006	0.002	0.001	0.005	0.002	10.8	2.1
Odonata (Gomphidae)	5	0.044	0.009	0.000	0.000	0.001	0.001	7.1	4.4

(B)		NH_4^+ μmol $hr^{-1}g^{-1}$		NO_3^- μmol $hr^{-1}g^{-1}$		SRP μmol $hr^{-1}g^{-1}$		N/P ratio
	n	mean	SE	mean	SE	mean	SE	
Shrimp (*Paratya compressa*)	10	10.24	1.66	0.00	0.02	0.11	0.04	91.2
Ephemeroptera (Heptageniidae)	10	23.96	7.19	0.94	0.58	4.55	3.19	5.5
Diptera (Chirnomidae)	10	22.48	10.15	0.77	0.38	9.82	7.28	2.4
Plecoptera (Perlidae)	10	2.11	0.68	0.20	0.16	0.67	0.21	3.4
Odonata (Gomphidae)	5	15.35	3.98	0.14	0.09	0.17	0.25	91.5

Table 1 Excretion rate of shrimp and major aquatic insect taxa per individual (A) and per biomass (B). SE means standard error

Figures

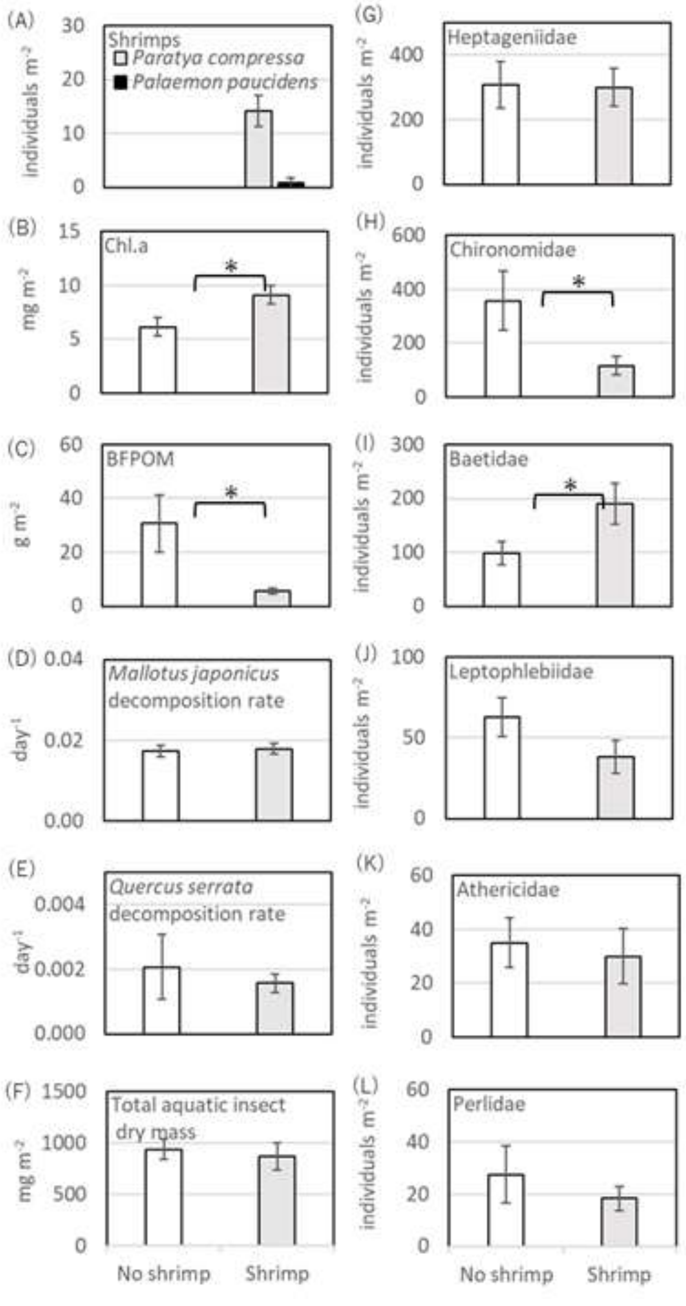

Fig. 1 Points in the map indicate surveyed sites in this study (N=13). All sites were located in distinct tributaries of the Tonda River, the Takase River, the Hiki River, and the Koza River in Wakayama, Japan. The field manipulative experiment and measurement of consumer excretion were conducted at site 1 in the Takase River

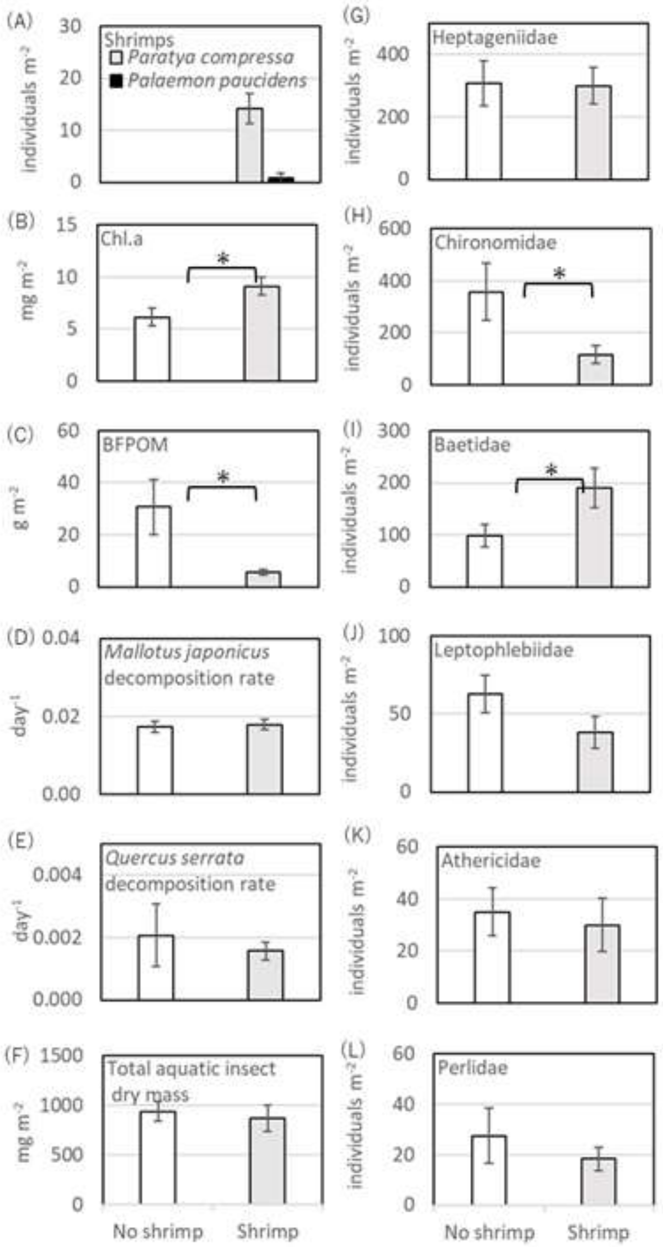

Fig. 2 Benthic aquatic community structures in the presence/absence of shrimps in the field manipulative experiment (N=8). Shrimp density (A), chlorophyll-a density (B), fine benthic particulate organic matter (BFPOM) density (C), and the decomposition rate of two dominant riparian tree leaves (D, E), total aquatic insect dry mass (F), as well as the density of the six most abundant benthic aquatic insect families in the survey (G–L)

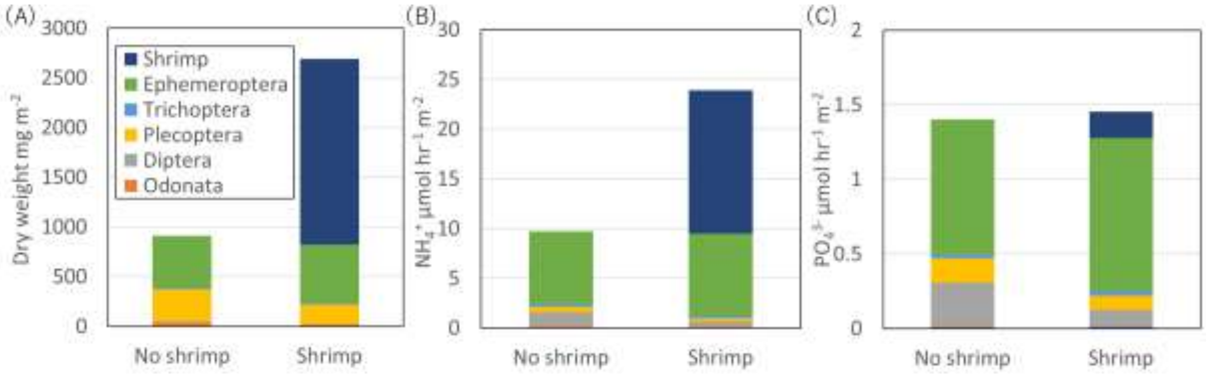

Fig. 3 Calculated mean dry weight (A), NH_4^+ excretion rate (B), and SRP excretion rate (C) of benthic macroinvertebrate assemblages from the experimental chambers with electroshock (no shrimps) and without electroshock (with shrimps)

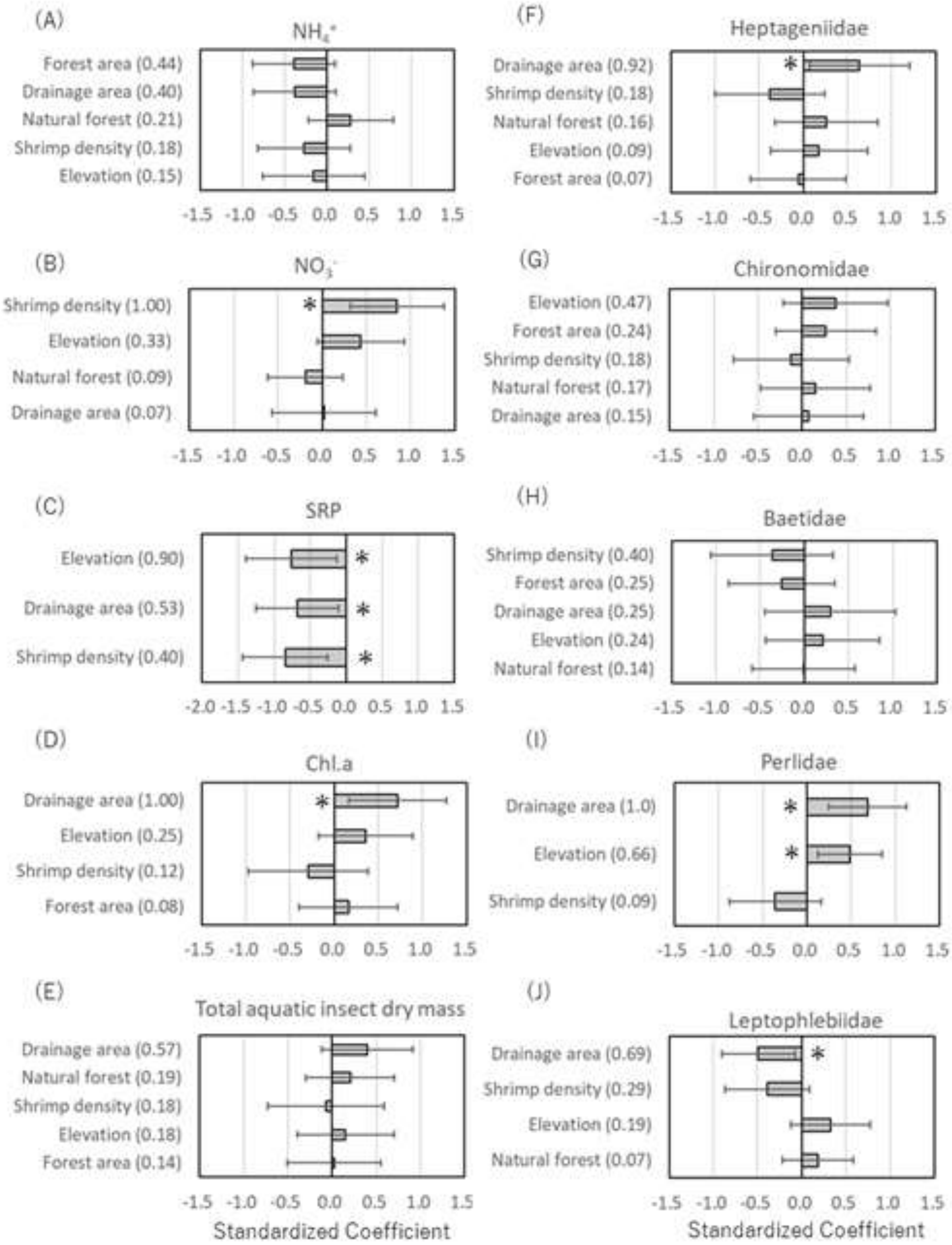

Fig. 4 Standardized coefficients for nutrient concentration (A-C), chlorophyll-a (D), total aquatic insect dry mass (E), and density of major aquatic insect taxa (F-J) (N=13). Each predictor is retained in the final confidence model set with ΔAICc＜4. The values following each predictor name are the relative variable importance (RVI), calculated as the sum of the model weights of all models in the final confidence set in which the variable appears. The asterisk indicates where 95% confidence intervals do not cross zero

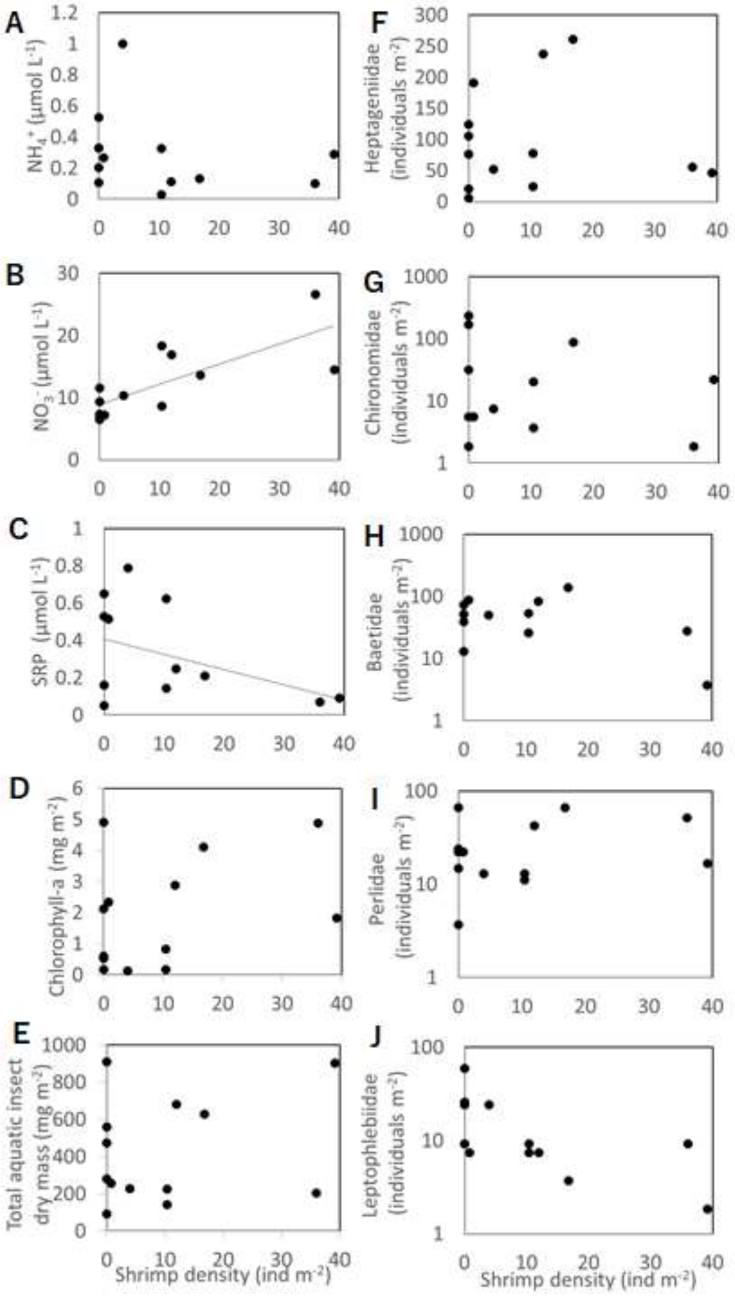

Fig. 5 Relationship between the shrimp density and nutrient concentration (A-C), chlorophyll-a (D), total aquatic insect dry mass (E), and the density of major aquatic insect taxa (F-J) (N=13). Each dot represents a surveyed site