論文の内容の要旨

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論文題目　Effects of nutrient regeneration by tadpoles in aquatic food webs
論文和訳　池沼食物網におけるオタマジャクシの栄養塩回帰効果

Consumers are usually recognized as animals reducing abundance of prey species or basal resources in the food web. The existence of a certain consumer undoubtedly causes negative effects on other members of the web through consumption, predation or competition. However, it has been revealed that consumers can positively affect the resources and enhance their biomass by releasing nutrients through their activity. This consumer-mediated nutrient recycling process is called nutrient regeneration, and has been getting focused on as important pathways in a food web.

Omnivores can regenerate nutrients from herbivory, detritivory, and carnivory, feeding basal resource such as algae and detritus as well as their prey animals. The regenerated nutrient can be incorporated into algal assemblages and microbes on detritus, and can indirectly affect herbivores and detritivores. However, when their herbivory or detritivory reduce resource that can be positively affected by their nutrient regeneration, the consumption effect may mask or override the direct/indirect effects via nutrient regeneration on the basal resources/consumers. Therefore, in order to understand the roles of an omnivore as a nutrient regenerator in structuring forest aquatic food webs, one should examine the effects of nutrient regeneration on different components of the food web, separately from the overall effect on them.

Tadpoles are omnivores comprising a large portion of the biomass in freshwater habitats including oligotrophic pools, where nutrient regeneration effects may be more important. They consume a variety of foods, such as algae, plant fragments, small animals, and detritus, and should have complicated role in aquatic food webs. Our aim was to understand the effects and relative importance of nutrient regeneration caused by omnivorous tadpoles on other components in the ecosystem.

The strength of the indirect effects of consumption of a particular food item may differ among tadpoles of different species, because the suitability of food items varies among species, and the suitability of the food can affect the consumption rate and/or assimilation efficiency. Therefore, in chapter 2, we evaluated relative suitability of different food items (leaf litter, algae, and worm) for tadpoles of four Japanese common frog species; *Rana japonica, Rana ornativentris, Rhacophorus arboreus,* and *Bufo japonicus formosus*. We compared their survival, growth and development by feeding individuals on leaf litter, algae or animal materials (sludgeworms). The suitability of algae and animal materials was different for each species of tadpoles: algae was the best food for *Ra. japonica* and *Rh. arboreus*, but worm was the best for *Ra. ornativentris*, and leaf litter was not suitable for all species. It was predicted that leaf litter might be a supplemental food for these tadpoles.

No study has examined the effect of nutrient regeneration by consumers on microbial conditioning of leaves and further indirectly on leaf-consuming detritivores. We conducted a laboratory experiment in chapter 3, feeding the three food items on the four species of tadpoles we used in chapter 2 to examine the effects of nutrient regeneration by tadpoles on leaf-eating detritivores, and to compare the difference of effects among food items. We conditioned terrestrial dead leaves with water from reared tadpoles (treatments) or food items alone (controls), and compared the C:N ratios of the conditioned leaves and the growth of the isopod *Asellus hilgendorfii* fed the conditioned leaves. Tadpole feeding activity reduced the C:N ratio of conditioned leaves, and the effect was greatest when tadpoles were fed algae. Isopod growth rates were often higher when they were fed the litter conditioned with water from reared tadpoles. Thus, nutrient regeneration by tadpoles had a positive indirect effect on detritivores by enhancing leaf quality. Tadpoles often occur in nutrient-limited habitats where leaf litter is the major energy source, and their facilitative effects on leaf-eating detritivores may be of great significance in food webs by enhancing litter decomposition.

In chapter 4, we examined the effects of nutrient regeneration and its relative importance in the consumers' overall effect. We conducted a manipulated experiment using tank mesocosms imitating natural ponds with three tadpole densities (zero, low, high). Leaf bundles of three species and tiles as substrate for algae and benthic invertebrates, exclosure and control, were added into each tank. Nutrient concentration in water, phytoplankton abundance, and emerged number of chironomid were measured every week. Tadpoles were retrieved in two weeks. After the introduction of tadpoles, phytoplankton and phosphate concentration in tank water, and epilithic algae and chironomid nest tube on exclosure tiles but not on control ones increased with higher density of tadpoles. Emerged number of adult chironomid was not affected by tadpole presence. Tadpole nutrient regeneration did not affect NP content and mass loss of leaf litter, but mineralization of leaf litter was enhanced in two out of three species of leaves. Our results showed that tadpoles had positive effects on algae, chironomid larvae, and microbial mineralization via nutrient regeneration and that their overall effects were positive on phytoplankton but canceling on epilithic algae and chironomid. Algae –

herbivory system was the important path, leading to positive overall effect on phytoplankton, and this path further had an indirect positive effect on chironomid larvae that compensated the negative effects on them.

We found positive nutrient regeneration effects by consumers both on algae and microbes on detritus. The magnitude of the effects was comparable to the negative consumption effects, sometimes exceeding it. The positive effects on basal resources further had positive indirect effects on detritivores and herbivores. We also showed the cross-resource path of nutrient regeneration effects, from epilithic algae-chironomid complex to microbes on leaf litter as well as within-resource effects. These findings showed the importance of considering direct and indirect nutrient regeneration effects on multiple components for more detailed and realistic understating of consumers' role in food web. The magnitude and direction of nutrient regeneration as in from which resource to which recipient should depend on the consumers' food habit, nutrient regeneration efficiency, and environmental conditions. We should recognize the importance of nutrient regeneration effects constituting a complicated food web, in which each consumer has its own direction and magnitude of positive and negative, direct and indirect effects on other components in the ecosystem.