Summary

Bottom-up control on mobile invertebrate community

in an eelgrass bed:

Contribution of different functional groups of epibiotic organisms

Dissertation

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Every single species has various functional traits (FTs; e.g., morphology, behavior, feeding habits, body size and development). Each functional trait of a species has an ecological and evolutionary linkage to the species identity. A study approach based on functional identity (FT based approach) beyond taxonomic identity is expected to lead to specific understanding of ecological and evolutionary issues. FT based approach has been developed with studies on terrestrial plants, and is now applied to various types of aquatic ecosystems including seagrass ecosystem.

In recent community ecology on functional traits of organisms in biological interactions in seagrass systems, findings on functional responses of macroinvertebrates have been rapidly increasing, whereas those on functional roles of producers are still poor despite diverse producer species including various epibiotic organisms (epiphytic macroalagae and sessile invertebrates) occur in seagrass beds. Although functional traits of seagrass (e.g., morphology and shoot density) have been often focused in studies on seagrass beds, the functional roles of epibiotic organisms for macroinvertebrates have been rarely considered.

In this thesis, I examined how mobile invertebrate community is structured in terms of bottom-up control focusing on functional traits of epibionts on eelgrass blades in an eelgrass (*Zostera marina*) bed of the Akkeshi-ko estuary and Akkeshi Bay. Additionally, I intended to extend conventional paradigm for understanding of biological relationships in seagrass beds in this study, because epibiotic organisms have not been focused in the previous studies in seagrass beds despite the importance has been often reported.

Eelgrass beds are known to have high ecological and economical values within coastal ecosystems of the temperate northern hemisphere although their biodiversity and functions varied greatly from sites to sites. The variation in the biomass, abundance and diversity of mobile invertebrates in eelgrass beds has been examined in relation to various abiotic and biotic factors, such as water temperature, salinity, eelgrass biomass and epiphytic microalgae presence. However, the importance of sessile epibionts, such as macroalgae and calcific spirorbid polychaetes attached to eelgrass blades, has not been the focus of previous studies. In Chapter 2, I examined the effects of three different sessile epibionts, namely, branched red algae, filamentous green algae, and calcific spirorbid polychaetes, on the biomass and diversity of mobile invertebrates in the eelgrass beds of Akkeshi in northeastern Japan. The relationships between seven abiotic and biotic variables including three types of epibionts, and biomass of 11 dominant mobile invertebrate species as well as three community-level variables (the total biomass of mobile invertebrates, species richness and the Shannon-Weiner species diversity index) were analyzed using a linear mixed model. My results show that branched red algae are correlated with *Pontogeneia rostrata*, Lacuna spp., *Nereis* sp., *Syllis* sp. and the total biomass of mobile invertebrates, filamentous green algae with *Pontogeneia rostrata*, *Ansola angustata* and the species diversity of mobile invertebrates, and spirorbid polychaetes with *Ansola angustata*, Lacuna spp., *Siphonacmea oblongata*, *Syllis* sp., the species richness and diversity of mobile invertebrates. The effect size of the epibionts was similar or even higher than that of abiotic and eelgrass factors on the total biomass of mobile invertebrates, species richness, species diversity and most of dominant invertebrate populations across the taxonomic groups. Consequently, epibiotic macroalgae and spirorbid polychaetes can be good predictors of the variation in the total biomass, species richness and species diversity of mobile invertebrates and the biomass of major dominant species, especially for species that have a relatively high dependency on eelgrass blades. These results suggest that the different functional groups of sessile epibionts have significant roles in determining the biomass and diversity of mobile invertebrates in eelgrass beds.

Biological communities in seagrass beds are composed of a diversity of organisms including plants, algae and animals. Seagrass-associated macroinvertebrates (epifauna: e.g., crustaceans, gastropods and polychate worms) especially play important roles as mediators between primary producers and higher consumers in seagrass beds. However, many aspects of the variation in epifaunal community in seagrass beds still remain to be investigated. In Chapter 3, I examined how epifaunal community structure varied seasonally and spatially with abiotic and biotic factors in an eelgrass bed of Akkeshi, northeastern Japan using multivariate analyses (non-metric multi-dimensional scaling [NMDS], permutational multivariate analysis of variance [PERMANOVA] and redundancy analysis [RDA]). I especially focused on the influence of epibiotic organisms (epiphytic macroalgae and spirorbid polychates) on eelgrass blades, that has been poorly investigated. I expected that: (1) abiotic factors are more definitive for the variation in epifaunal community than biotic factors when the eelgrass bed is less productive in early spring and late autumn; (2) biotic factors including macro-epibionts (i.e., epiphytic macroalgae and sessile animals) are more influential when the eelgrass bed is more productive from late spring and early autumn. Consequently, the epifaunal community composition was temporally and spatially varied with different sets of abiotic/biotic factors. Also, epibiotic organisms contributed to explain some parts of the variation in addition to other abiotic/biotic factors especially in summer productive seasons, despite relatively low biomass compared to that of eelgrass and epiphytic microalgae. Inconsistent with my expectation, abiotic factors were more definitive for the spatial patterns of the epifaunal communities from spring to summer when the productivity of eelgrass bed are increasing whereas biotic factors are relating more important in autumn when the productivity declines. The results implicate that the effects of epibiotic factors on environmental condition and biological/functional interaction should be more taken into account in eelgrass community studies to comprehensively understand the variation in seagrass systems.

Invertebrate consumers, such as insects and small crustaceans, are affected by multiple abiotic factors and plant traits that are essential bottom-up factors affecting their variability. The complex networks of their interactions likely vary seasonally with changes in these factors. In Chapter 4, I assessed a seasonal shift in the network structure focusing on the variation of epifaunal community abundance (ECA) along the bottom-up cascade from abiotic factors (water temperature, salinity and dissolved inorganic nitrogen) via biotic factors (eelgrass and epibionts: epiphytic micro- and macro-algae and sessile spirorbid polychaetes) in eelgrass beds in Akkeshi (eastern Hokkaido, Japan). Structural equation models (SEMs) were constructed for the seven months from May to November. My SEMs based on the bottom-up network explained over 50% of the spatial variation in ECA in most months, and showed that great variations of the direct and indirect interactions among months. The network structure was generally more complex in spring to summer than in autumn. In the former, in addition to abiotic variables like water temperature and salinity, intermediate variables like eelgrass biomass, epiphytic micro/macroalgae and sessile polychaetes contributing more frequently to the variation in ECA. In autumn, however, only the water temperature and eelgrass biomass were selected as significant factors affecting ECA variation. The relative importance of selected variables and their direction and patterns of interactions also varied from months to months, partially reflecting the seasonal changes in the degree of spatial variability and life history traits of dominant species. My results demonstrated that the network analyses using SEM are effective in elucidating temporal shifts in the interacting effects of abiotic/biotic factors affecting abundance of consumers. My monthly observation also highlighted the influential roles of epibionts such as macroalgae and sessile animals on eelgrass blade affecting abundance of mobile epifauna, which aspect had been focused only in few studies of seagrass ecology.

In Chapter 5, I comprehensively discussed the results of Chapter 2 to 4. In addition to seagrass factors (e.g., biomass, shoot density, morphology and patch structure) and epiphytic microalgae on macroinvertebrate community have been main topics in the previous studies on producer-consumer interactions in seagrass beds, I demonstrated that mobile invertebrate community structure was also influenced by epibiotic organisms (i.e., macroalgae and sessile invertebrates) through the variation in functional relationships among them in an eelgrass bed in the Akkeshi-ko estuary and Akkeshi Bay. My extension of the framework and change of perspective for biological network and relationships are expected to be effective for further understand of seagrass ecosystem.