学 位 論 文 の 要 約

博士（環境科学）　　　　　氏　名　伊藤（阿部）　美菜子

学 位 論 文 題 名

Variation in phenology, biological traits, and associated epifaunal community between native and non-native populations of the seagrass *Zostera japonica*
（海草コアマモの在来集団と移入集団の間における季節性、形質、葉上動物群集の変異）

Biological invasions, or human-mediated translocations of species to regions outside their native range, are increasing worldwide, including in seagrass ecosystems. Understanding of how seagrass and seagrass ecosystems respond to invasions are important not only for management and conservation of the ecosystem, but also provide opportunity to deepen our understandings on seagrass and invasion ecology in general.

Zostera japonica is an intertidal seagrass native in Asia, with wide distribution extending from tropical to temperate regions. In addition to its native distribution, *Z. japonica* also occurs in North America, where it was introduced in the 1950s and has established its populations since then. Because of its established non-native populations in North America, the impacts of *Z. japonica* introduction had been occasionally studied by comparing with its native populations in Asia, or by comparing with a native congener *Z. marina* in its introduced region, which is native in both Asia and North America. However, previous studies comparing native and non-native *Z. japonica* populations cannot discriminate if observed difference arose from the introduction effects or from regional differences, nor studies comparing with native congener in the introduced region alone cannot discriminate if observed difference arose from introduction effects or from species differences.

In this thesis, I proposed a use of combined methods of native and non-native regional comparison with *Z. japonica* and *Z. marina* species comparison for robust investigation of *Z. japonica*

introduction effects. The proposed combination method is promising to separate the introduction effects from those caused by regional or species differences (Fig. 1). The main objective of this thesis is to investigate introduction effects **ON** and **OF** *Z. japonica*, with special focuses on three aspects of seagrass ecosystems, (1) seagrass phenology, (2) seagrass biological traits and (3) seagrass-associated animal communities, which were examined in three independent chapters (Chapters 2 to 4).

In Chapter 2, I investigated the influence of abiotic factors on seagrass biomass and reproductive phenology of *Z. japonica*. Large-scale analysis along latitude or temperature gradients can be an effective method for exploring the potential roles of light and temperature in controlling seagrass phenology. I collated available data on phenological traits (timings of peak biomass or reproduction, durations of biomass growth and reproductive season, and maximum biomass or reproductive ratio) from publications and my own observations. Traits were compared among geographic groups: Asia-tropical, Asia-temperate, and North America-temperate. I further examined relationships between traits and latitude and temperature for 3 population groups: Asian (native), North American (non-native), and all populations. Through geographic and population comparisons, I found that phenological traits varied greatly among regions affected by abiotic factors, such as latitude and temperatures, and that traits varied among populations, but results also varied among analyzed traits. While maximum biomass and peak reproductive timings were significantly affected by temperature for *Z. japonica* populations in general, growth durations and reproductive ratios were affected by latitude and only for non-native populations. Maximum biomass was highest at mid-latitudes or intermediate temperatures and decreased toward distribution range limits, and peak reproductive timing occurred later in the year at higher latitudes or cooler sites. Non-native populations showed shorter growth durations and greater reproductive ratios at higher latitude. These observed difference in responses between native and non-native populations indicate the presence of the introduction effects on seagrass phenology.

Study of non-native species traits is important not only for management purposes but also provides beneficial opportunities to examine potential trait shifts during biological invasions. In Chapter 3, I conducted multi-site comparisons of seagrass biological traits of *Z. japonica* between native (Japan) and non-native (Canada) regions, along with those of *Z. marina* that is native in both regions. By using a combination of intraspecific and interspecific comparisons, I was able to distinguish introduction effects from regional environmental differences. Results suggested that non-native *Z. japonica* showed constant shoot size, lower shoot density, leaf area index (LAI) and biomass, and higher reproductive ratio compared to native populations, whereas *Z. marina* showed no regional difference in any of analyzed traits. Likewise, multivariate analyses revealed that traits differed greatly between regions only for *Z. japonica*. Regional trait differences observed only for *Z. japonica* support that these differences are in fact induced by introduction and not by regional environmental difference which would affect both *Zostera* species. Due to constant shoot size, reduced LAI and biomass were considered as resulting from reduced shoot density. While enhanced reproduction observed for non-native *Z. japonica* may be a cause of successful introduction or a result of adaptation to environmental stresses, concurrent reduced shoot density suggests a trade-off between vegetative and sexual production. These results indicated that significant trait change occurred during the introduction of *Z. japonica* to North America, potentially through rapid evolution.

Foundation species is a dominant and disproportionately important species that defines the ecosystem, determines local and regional diversity, and community dynamics. Seagrasses are amongst the most dominant foundation species in shallow coastal areas and provide habitat for various types of organisms, making them known as one of the richest coastal ecosystems for marine biodiversity. Seagrass-associated epifaunal invertebrate communities are a major component of seagrass ecosystems and play a key role in food web dynamics. The addition of non-native foundation species through biological invasion can alter the epifaunal communities in seagrass beds. In Chapter 4, I compared seagrass-associated epifaunal invertebrate communities between *Z. japonica* and *Z. marina* from multiple sites in Japan where both seagrass species are native, and multiple sites in Canada where *Z. japonica* is non-native. I analyzed and compared variation in epifaunal abundance, epifaunal diversity, and composition of epifaunal species specifically associated with each seagrass species, and then compared seagrass species effect between the regions. I found that epifaunal abundance were similar between native and non-native *Z. japonica*, whereas epifaunal diversity was lower for *Z.*

japonica compared to *Z. marina*, only in Canada, and was equally diverse for both species in Japan. Additionally, while epifaunal community on native *Z. japonica* were distinct from that of *Z. marina* in Japan, species associated with non-native *Z. japonica* were mainly a subset of that of *Z. marina* in Canada, suggesting that non-native *Z. japonica* has not established a species-specific community in its introduced region. These findings revealed that non-native *Z. japonica* can provide additional habitat for epifaunal communities that extend to shallower intertidal areas. However, non-native *Z. japonica* has not yet established a species-specific community as in its native region, and epifaunal species associated with non-native *Z. japonica* is still limited, even after decades of introduction. These results demonstrated that observed diversity reduction for non-native *Z. japonica* is caused by its non-native status and not by seagrass species identity.

From three independent studies shown above, I constantly found that non-native *Z. japonica* populations differ from native populations highlighting the significant introduction effects **ON** and **OF** *Z. japonica*. My study indicated that the non-native seagrass differs in their phenological and biological traits from native populations and hosts less diverse epifaunal community compared to the native congeneric species in the introduced region. Significant introduction effects suggested from this study pointed out the importance of accounting non-native seagrass differently from native seagrass for seagrass ecosystem management, which had been overlooked in seagrass ecology. Findings of this thesis contribute to deepen our understanding on invasion ecology and seagrass ecology in general, in addition to giving valuable implications on marine biodiversity conservation and ecosystem management (Fig. 2).

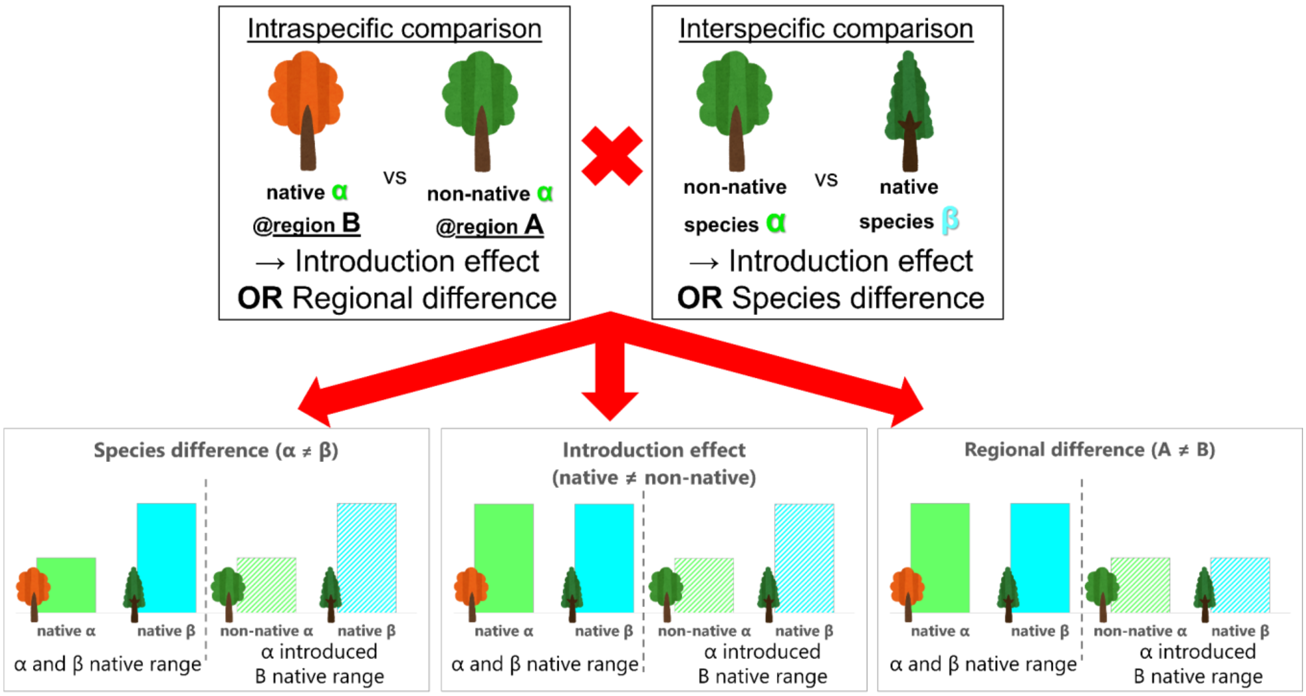

Figure 1. Schematic graphics showing limitations of comparison methods used alone and how proposed combined methods approach can improve them.

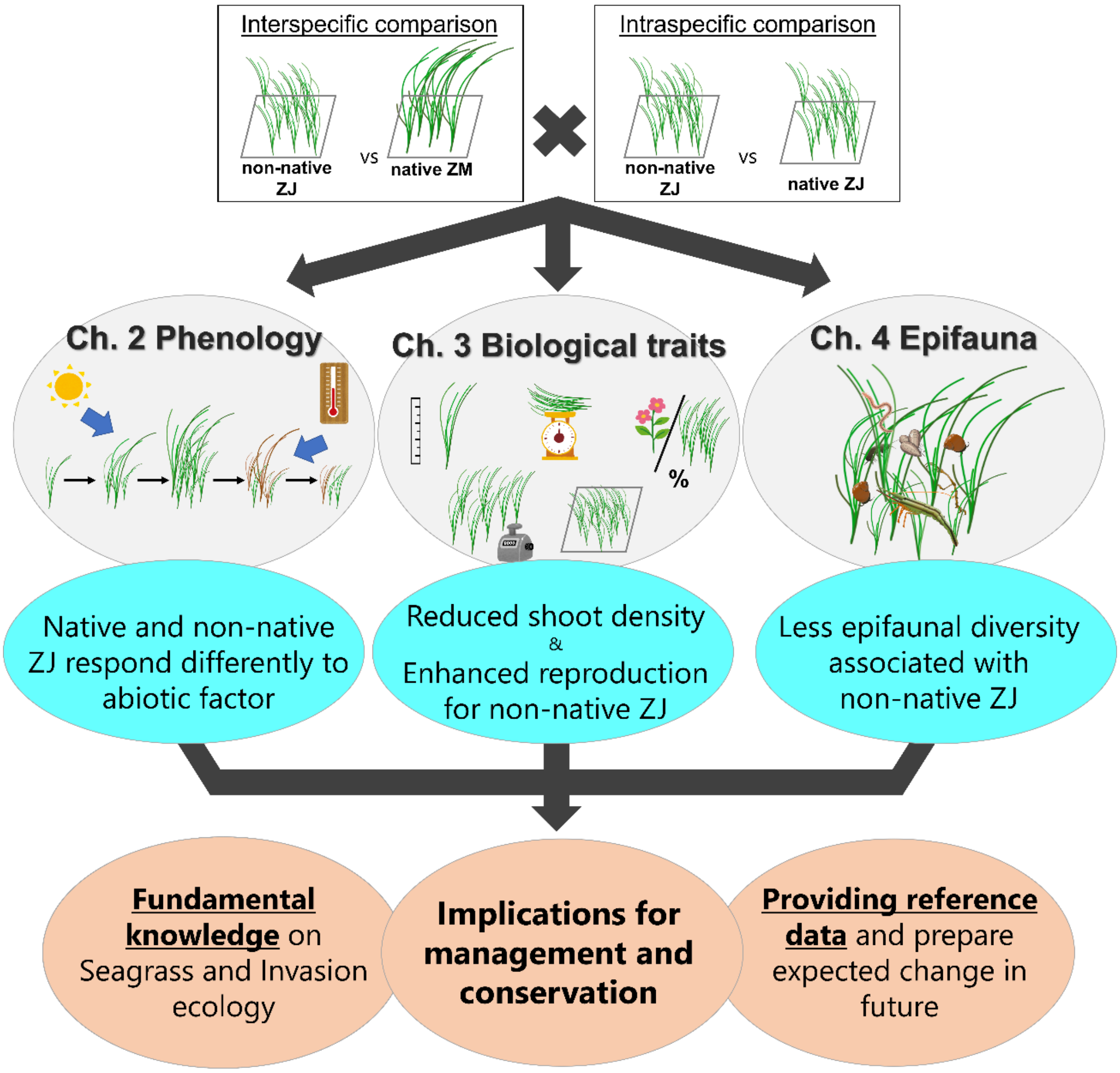

Figure 2. Schematic graphics summarizing the proposed approach, focused seagrass aspects and their major findings, and implications provided from this thesis.