# 1 General introduction

One of the essential issues in ecology is to reveal the causes and consequences of temporal variability in assemblages sharing the same resource. This chapter addresses the background of community dynamics and this thesis. First, I briefly introduce rocky intertidal sessile assemblages, which are the study system of this thesis. Then, I review community dynamics in the aspects of seasonal and long-term dynamics of this system. Lastly, I outline the objectives of this thesis.

## 1.1 Intertidal sessile assemblages and its contributions to community ecology

Rocky intertidal sessile assemblages have contributed to offering general hypotheses which are applicable for various ecosystems, and to developing ecological theories as a model system for research in community ecology. In this section, I introduce their ecological features and review previous studies.

### 1.1.1 Sessile assemblages in intertidal rocky shore

Intertidal sessile assemblages are an ideal system to investigate community dynamics and its processes. Intertidal sessile assemblages consist of two contrasting functional groups: sessile invertebrates and algae. These organisms compete with each other for space which is a common resource for them. Their population size can be easily quantified as the proportion of occupied area (Roughgarden et al. 1985), i.e. coverage, which is increased by recruitment of larvae or propagules, and by individual body growth, and is decreased by intra- and interspecific competition, by consumption, and by physical disturbance.

Rocky intertidal habitats are characterized by two dominant gradients in physical conditions. First, there is a notable vertical gradient of the physical environment due to the effects of tides and waves. Toward the upper intertidal zone, where the immersion period is shorter than in the lower intertidal zone, the physical harshness is greater due to the longer period of exposure to high temperature and desiccation. Second, there is also a horizontal gradient of the physical environment due to the effects of wave exposure. Toward the tips of rocky headlands, the forces of waves and swells are greater.

### 1.1.2 Previous studies of rocky intertidal sessile assemblages

Research on intertidal sessile assemblages has a long history. From 1800s to mid 1900s, the subject of these studies was to understand the distribution patterns of sessile organisms. These studies which were conducted using a qualitative approach, revealed that vertical patterns of sessile organisms along environmental gradient (i.e. zonation) were universal around the world. These patterns were thought to be determined by the physiological tolerance of each species directly.

After the mid 1900s, field manipulative experiments involving the transplantation or removal of focal organisms, had increased. Up to the 1980s, not only the physical environment but also biotic processes, such as predation and competition, were focused on as the factors affecting community structure. These studies suggested that the upper limitation of species distribution was mainly determined by the physical environment, whereas the lower limitation of species distribution was determined by species interactions, such as predation and competition.

In the 1990s, environmental factors relating primary productivity, such as nutrient concentration and amount of phytoplankton, and biotic processes, such as recruitment of larvae and propagules, and facilitation, were focused on as the factors affecting community structure. These studies revealed that the effects of abiotic and biotic factors on community structure were very complex and varied spatiotemporally, representing strong context dependency.

In the 2000s, much more attention was paid to how community structure and its determining factors, such as abiotic environment and biotic processes, varied with spatial scale. These studies found that in abiotic environments, recruitment processes and community structure varied at a scale of 10s of km, suggesting that abiotic and biotic processes varying at mesoscales can play an important role to determine community structure in rocky intertidal sessile assemblages.

## 1.2 Temporal variability of community structure in intertidal sessile assemblages

Elucidation of temporal variability of community structure (e.g. species richness, species composition, and total biomass) and its underlying mechanisms contribute to deepening our understanding of the essential issues in community ecology, such as species coexistence mechanisms, community stability, and ecosystem function. The studies on temporal variability of community structure were mainly conducted in two aspects: seasonal and long-term fluctuations.

### 1.2.1 Seasonal community dynamics

Understanding of the patterns and processes of seasonal changes in community structure contributes to increasing our knowledge of species coexistence through temporal niche differentiation among species in environments that fluctuate cyclically. It also improves predictability of the response ecosystems have to changes in seasonal patterns of the environment caused by climate change. Although studies focusing on seasonal dynamics in rocky intertidal sessile assemblages have been reported since the 1950s, the seasonal changes in community structure have not been received attention prior to 1980s; alternatively, the major objective was to reveal the seasonal changes in effects of herbivores on sessile assemblages. These studies using observation or manipulative experiments reported that algal coverage was effected by herbivores but decreasing algal coverage during the harshest season was directly caused by mortality from physical stress.

After the 1980s, most studies aimed at how both species interaction other than grazing and the abiotic environment, contributed to seasonal dynamics in sessile assemblages. The major objective of early studies was to reveal the effects of herbivores on seasonal changes in sessile assemblages. These studies using manipulative experiments suggested that seasonal fluctuations in algal coverage was caused by seasonal variation in rates of algal growth and rates of algal loss by physical stress and herbivory. It was found that the effects of removing herbivores from algal assemblages were different from those caused by the physical environment, such as wave exposure and tidal height.

After the 1990s, the major objectives were to reveal not only the effects of consumption and the abiotic environment, but also the effects of biotic processes such as recruitment and interspecific competition. Various physical factors driving seasonal changes in sessile assemblages, such as light intensity, water and air temperature, ice foot and ice scour, nutrient concentrations, and phytoplankton, were given attention. These studies using field experimental approaches pointed out that variation in recruitment intensity during the recruitment season affected community structure, but its effect did not remain for a longer period because post-settlement mortality differed among species and sites. In addition, an experimental study demonstrated that seasonal changes in community structure was caused by recruitment of early-appearing species during seasons with more bare rock, and subsequently transition for late-appearing species.

After the mid 2000s, many studies focused on spatial variation in seasonal changes of sessile assemblages, especially the differences in those patterns among sites where the physical environment was distinct. The studies using an observational approach reported that seasonal changes in various community properties such as abundance of each species, total biomass and the number of species were different, or similar among sites where the physical environment such as wave exposure and tidal height was distinct.

In summary, the above findings suggest that seasonal changes and these spatial variations in sessile assemblages of intertidal rocky shores, were caused by seasonal fluctuations in the abiotic environment directly and indirectly through abiotic processes, and the spatial variations in these direct and indirect processes, respectively. Several questions, however, remain to be unanswered. First, quantitatively patterns of seasonal changes at the community level are not known because previous studies were conducted on seasonal changes in abundance of each species without time replicates. Second, driving processes of the quantitatively patterns of seasonal changes and spatial variations are not known at the community level.

### 1.2.2 Long-term community dynamics

The knowledge of community dynamics in long-term temporal scales, generally, contributes to understanding slow, rare, or complex changes in natural systems. Further, these processes (e.g. climate change, anthropogenic disturbance, and stochastic events) aid to our understanding of community dynamics which are not detectable on short-term scales. Up to the 1990s, the subject of studies was to reveal the inter-annual fluctuations in sessile organisms and these driving processes. These studies were conducted by observation of the coverage of each species in transects and quadrats. Major studies were inter-annual variations in four species of barnacles and driving factors. These studies suggested that the population fluctuations of these barnacles was derived from the variation in recruitment intensity through the fluctuation in water temperature.

After the mid 1990s, major attention was paid to prediction and understanding of ecological consequence of anthropogenic alternation of the environment, such as climate change, anthropogenic disturbance, such as eutrophication and water pollution, and the invasion of alien species. Thus, there was an increase in studies which aimed to examine how rocky intertidal sessile assemblages changed between the present and decades ago. In most cases, these studies conducted by resurvey occurrence of species and the abundance of each species using the same methods in the same site, compared with the previous and resurvey data. For the aspect of impact of climate change on species distribution, species ’ ranges shifted northward and abundance of each species increased among southern species, whereas species’ ranges and abundance was reduced in northern species, which related to the geographic ranges of each species. Many studies were concerned that these results were caused by increasing water temperatures with climate change. On the aspect of impact of water pollution on species diversity, the number of species increased with eutrophication through bottom-up effects, whereas the number of species decreased and went extinct as a result of water pollution, and recovered by building a submarine sewage terminal. On the aspect of impact of biological invasion on endemic assemblages, alien mussel ameliorated the physical stress and modified habitat complexity, consequently abundance and the number of species in native species increased, this differed with tidal height and wave exposure.

In summary, the above findings suggest that long-term community dynamics in rocky intertidal sessile organisms were caused by fluctuation of the abiotic environment such as water temperature. Several questions, however, remain to be answered yet. First, the temporal pattern of community properties such as turnover and variation had not been quantitatively examined in previous studies. Second, the role of biotic processes on long-term community dynamics are almost un-understood, except for Dye (1998) which suggested that temporal variation in recruitment intensity affected long-term community dynamics.

## 1.3 Objectives of this thesis

In this study, I examined the spatial variation in community dynamics and its processes by analyzing decadal time series data of rocky intertidal sessile assemblages along the Pacific coast of eastern Hokkaido, Japan.

# 2 Seasonal changes in community structure along a vertical gradient: patterns and processes in rocky intertidal sessile assemblages

I examine how seasonal changes in community structure vary along a vertical gradient. Specific questions are: (i) How does the magnitude of seasonal changes in community structure change vertically? (ii) How does the processes driving seasonal changes in community structure change vertically? I found that the magnitude of seasonal changes in community structure was the largest at mid shore. I also found that the major processes driving seasonal changes in community structure changed vertically, reflecting the indirect influence of vertical distributions of species.

# 3 Spatial variation in compositional dynamics and its mechanism in intertidal sessile assemblages

I examine the underlying mechanisms of compositional dynamics and its spatial variation by parameterizing a discrete Lotka-Volterra model. First, to evaluate how the species compositions were regulated, I examine the strength of correlation between the compositional turnover and the temporal compositional variance, and the relative strengths of intra- versus interspecific density dependence. Then, I test the hypothesis that the compositional turnover of communities should strongly depend on the magnitude of community-wide endogenous population fluctuations. Lastly, to reveal the cause of spatial variation in underlying mechanisms of compositional dynamics of communities, I examine the relative contribution of demographic and environmental stochasticities in determining the magnitude of endogenous population fluctuations, then how those two stochasticities varied among species and sites. I found that compositional dynamics was under strong density-dependent processes. I also found that the spatial variation in the compositional dynamics largely depended on the community-wide magnitude of endogenous population fluctuations, where most part is environmental stochasticity.

# 4 General discussion

One of the essential issues in ecology is revealing the mechanisms that determine spatial variation in community dynamics. Temporal variability in community structure (e.g. the number of species, species composition, and total biomass) and its spatial variation are mainly determined by three factors: abiotic environment, biotic processes, such as biological interaction (e.g. predation and competition) and dispersal, and spatial distribution of species. These factors affect community dynamics in an interactive way. The effects of biotic processes and spatial distribution of species on community dynamics are affected by the abiotic environment. In addition, biotic processes are affected by the spatial distribution of species; for example, mortality and recruitment rate often depend on both conspecific and heterospecific densities. In this study, I examined the spatial variation in temporal variability of community structure and its mechanism by analyzing decadal time series data of rocky intertidal sessile assemblages along the Pacific coast of eastern Hokkaido, Japan.

## 4.1 Temporal scale dependency in pattern of community dynamics and its underlying processes

Examining the major patterns of community dynamics at multiple temporal scales is of great importance because it helps us to mechanistically understand how community composition changes at larger temporal scales. Although many studies have been tried how temporal variability of community structure in sessile assemblages are driven at various scales, such as season and year-to-year scales in intertidal habitats, none of these studies simultaneously quantified both seasonal and year-to-year dynamics changes with spatially varying environments within a community. In this thesis, I quantified the effects of spatially varying environments on both seasonal and year-to-year dynamics, although vertical patterns of seasonal community dynamics seemed to be mainly caused by the vertical distribution of species which reflected the tidal excursion gradient, not by the vertical difference in magnitude of seasonal fluctuation of the physical environment, horizontal variation in year-to-year community dynamics seemed to be mainly caused by environmental stochasticity. Although community dynamics was under the control of strong intraspecific density dependence. These findings suggest that the paths of the causal relationship from abiotic environment to community dynamics were different among time scales in rocky intertidal sessile assemblages. This temporal scale dependence of the effect of abiotic environments on community dynamics may relate to the relationship between generation time and time scales of fluctuations in the abiotic environment. In general, the range of physical tolerance such as desiccation and freezing were much wider than seasonal fluctuations of the physical environment in natural systems because they cannot spatially refuge from harsh environments through mobility and therefore relatively easily evolve physiological tolerance to harsh environments occurring within their generation time. Such physiological adaptation, however, will be difficult for extreme climate events which occur every few years. Thus, community dynamics of sessile organisms should be significantly affected by harsh environmental changes occurring every few years but within generation time. Indeed, difference in the effect of the abiotic environment on community dynamics among time scales was reported in a previous study. A recent meta-analysis focusing on aquatic organisms such as macro benthos, zoo plankton, seaweed, and fish, found that seasonal-compositional turnover increased toward high latitude and interannual compositional turnover decrease toward high latitude, although the physical environment largely fluctuate seasonally and inter-annually at high latitudes.

## 4.2 The importance of the population response to physical environment

For rocky intertidal sessile assemblages, population dynamics represented spatial variation at two temporal scales: the magnitude of seasonal dynamics for each ecological state tended to be different among tidal levels (chapter 2), and the magnitude of environmental stochasticity of each species tended to be difference among sites (chapter 3). These results suggest that our knowledge about spatial variation in community dynamics will be greatly improved by elucidation of the population response to the physical environment and it can be analyzed by a discrete Lotka-Volterra model as follows:

$$\ln N_{i,t+1,k} - \ln N_{i,t,k} = \alpha_{i,k} - \beta_{i,k} N_{i,t,k} - \gamma_{i,k} M_{i,t,k} + \epsilon_{i,t,k}.$$

$N_{i,t,k}$ and $M_{t,k}$ are coverage of species $i$ and of other species in plot $k$ at year $t$, respectively. $\alpha_{i,k}$, $\beta_{i,k}$ and $\gamma_{i,k}$ are intrinsic growth rate, strengths of intra- and interspecific density dependence of species $i$ at plot $k$, respectively. $\epsilon_{i,t,k}$ is a random variable characterized by normal distribution with zero mean and variance $\sigma^2_{i,k}$. $\epsilon_{i,t,k}$ represents the variation which was affected by effects other than intra- and interspecific density dependence of species $i$ at plot $k$. Therefore, we can elucidate the features of the population response to the physical environment and its spatial variation by analyzing the difference in the properties of temporal variabilities of $\epsilon_{i,t,k}$ (e.g. the magnitude and variability) among species and sites.