Early phase of the invasion of the barnacle *Balanus glandula* along the coast of eastern Hokkaido, Japan: changes in abundance and distribution, and their underlying processes

Thesis

In partial fulfillment of the requirements

for the degree of Doctor of Environmental Science

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September 2013, Sapporo

Summary

Chapter I

To understand dynamics of invasions, knowledge about the patterns and processes during the early phase (when the population is not close to its equilibrium level) of invasion are crucial. However, knowledge about the early phase of marine invasion is still limited. This may be due to (i) difficulties in the detection of invasion front at a broad area, (ii) irregular dispersal probabilities instead of systematical dispersal, and (iii) logistical difficulties in tracking of marine organisms with complex life cycles. Two important questions about the early phase of an invasion are: how propagule pressure, that is, propagule numbers and spatiotemporal patterns in the arrival of propagules, limits the success of the invasion, and which factors influence the invasion success of introduced species.

Marine sessile animals are a major component of marine ecosystems and are found in a variety of habitats. Because of their immobility at the benthic stage, dispersal of sessile animals relies almost completely on larval dispersal. Recruitment should thus play an important role in invasion dynamics of marine sessile animals. In addition, species interactions, including predation, competition, facilitation, and their interactive effect (i.e., indirect effect) may play an important role on the invasion success of marine sessile animals.

The barnacle *Balanus glandula* has recently invaded along the Pacific coast of Hokkaido. In 2000, its distribution had reached along the Pacific coast up to Hiroo of Hokkaido. However, there is lacking of knowledge about the early phase of invasion dynamics of *B. glandula* and underlying processes affecting its abundance and distribution along the coast of Japan.

This study was performed to elucidate the patterns and understand the processes of population dynamics of *B. glandula* during the early phase (when the population is not close to its equilibrium level) of invasion at 144 km east of eastern invasion front of this species in 2000, and to evaluate the influences of direct and indirect effects by endemic barnacles, seaweeds and invertebrate predators on the invasion success of this barnacle.

Chapter II

To elucidate the patterns and understand the processes of population dynamics of *B. glandula* during the early phase of invasion along the Pacific coast of eastern Hokkaido, I analyzed data obtained by population censuses from 2002 to 2011 at five shores, each consisting of five sites, along 49 km of coastline located 144 km east of the eastern invasion front of this species in 2000. The specific questions I asked were as follows: (1) how do the abundance, distribution, and recruitment density increase with time after an invasion? (2) does the rate of local extinction decrease with time, and what are the effects of recruitment density and coverage on local extinction? (3) does the length of the lag time between population establishment and initial arrival of recruits decrease with time and what is the effect of recruitment density on the lag time of local population establishment? and (4) does the relative contribution of recruitment to adult population size increase with time? The results show that larval recruitment was first detected in 2004, but the establishment of a population was not observed until two years later at the westernmost shore of the study area. Occurrence drastically increased, from 4 % in 2006 to 100 % in 2011, but mean coverage remained low (< 5 %) in 2011. Most local population coverage fluctuated without indicating clear temporal trends, but coverage of one population showed a consistent pattern of rapid increase. Local

extinctions occurred, but rates of local extinction decreased with time as larval recruitment increased. Lag times between initial arrivals of recruits and the establishment of populations in most cases (~ 64 %) ranged from 1 to 4 years. Lag times decreased after five years, when larval recruitment increased. The relative contribution of recruitment to the adult population size increased with time as recruitment density increased throughout the study area. In conclusion, propagule pressure, i.e., larval supply, was crucial for successful invasion of the rocky intertidal barnacle, *B. glandula*.

Chapter III

To evaluate both direct and indirect effects by endemic barnacles, seaweeds, and invertebrate predators on the invasion success of *B. glandula* at the rocky intertidal coast of eastern Hokkaido, a field experiment, in which the presence or absence of whelk, endemic barnacles, and seaweeds were manipulated, was conducted from June 2011 to October 2012. The specific question I asked was as follow: do the endemic barnacles, seaweeds, and invertebrate predators affect the invasion success of *B. glandula*? The results show that seaweeds did not significantly affect the abundance of *B. glandula*. The endemic barnacle, *Chthamalus dalli* and whelk, *Nucella lima* negatively affected the invasion of *B. glandula*. However, the simultaneous effect of *C. dalli* and *N. lima* was compensative rather than additive due to keystone predation. In conclusion, competition by endemic barnacle, *C. dalli* and predation by invertebrate predator, *N. lima* decreased invasion success of *B. glandula*, and the negative influence of the *C. dalli* on *B. glandula* was weakened by predation of *N. lima* on *C. dalli* in intertidal rocky shore along the coast of eastern Hokkaido.

Chapter IV

The implications of this study are threefold. First, monitoring of recruitment is essential for the early detection of invasions by sessile marine organisms and prediction of their range expansion. Indeed, in this study recruitment census detected a significant finding. The initial arrival of recruits occurred at least two years before the establishment of a population in this study area. Majority of local populations were established after a time lag that followed the initial arrival of recruits.

Second, conservation of endemic invertebrate predators may be crucial to impede abundance and distribution of introduced barnacles in rocky intertidal habitats. Previous studies and this study demonstrate that abundances of rocky intertidal barnacles are often limited by invertebrate predation.

Third, a field experiment, in which densities of endemic predator and competitor are factorially manipulated, seems to offer a unique opportunity to evaluate influence of net effect of predation on a target species, in addition to evaluation of direct effects by endemic predator and competitor. This is because, it is quite difficult to predict net effect of predation on the introduced species, since the net effect can vary depend on various factors, such as densities of predator and prey, as well as prey preference by predator.