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

The barnacle *Balanus glandula* has recently invaded along the Pacific coast of Hokkaido. This study was performed to elucidate the patterns and understand the processes of population dynamics of *Balanus glandula* during the early phase (when the population is not close to its equilibrium level) of invasion along the Pacific coast of eastern Hokkaido, and to evaluate the influences of direct and indirect effects by endemic barnacles, seaweeds and invertebrate predators on the invasion success of this barnacle.

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 conducting 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? 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.

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/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 showed that 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 presumably 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*.

The implications of this study are fourfold. First, the intensity of larval recruitment determined invasion dynamics during this early phase of *B. glandula* invasion. Second, the monitoring of recruitment is essential for early detection of invasions by sessile marine organisms and prediction of their range expansion. Third, the endemic competitor and predator may have played important roles in decreasing invasion success of *B. glandula* in natural habitats. Fourth, conservation of endemic predators may be crucial to impede invasion of introduced barnacles in rocky intertidal habitats.