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# Early phase of the invasion of *Balanus glandula* along the coast of Eastern Hokkaido: changes in abundance, distribution, and recruitment

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**Abstract** To understand the patterns and processes associated with the population dynamics of *Balanus glandula* during the early phase of invasion along the Pacific coast of eastern Hokkaido, population surveys were conducted from 2002 to 2011 at five shores, each consisting of five paired plots (scraped recruitment plot and unscraped establishment plot), along 49 km of coastline located 144 km east of the eastern front of the invasion of this species in 2000. Larval recruitment was first detected in 2004, but the establishment of a population was not observed until 2 years later at the westernmost shore of the study area. Occurrence increased from non-native barnacle present in 4 % of plots 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 in one plot 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 recruitment and establishment occurred for 64 % of the paired plots and ranged from 1 to 4 years. Lag times decreased after 5 years, when larval recruitment increased. These findings suggest that the intensity of larval recruitment determined invasion dynamics during this early phase of the invasion, and the monitoring of recruitment is therefore essential for early detection of invasions by sessile marine organisms and prediction of their range expansion.

**Keywords** Barnacle · Invasion dynamics · Marine sessile · Pacific coast · Range expansion · Rocky intertidal

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## Introduction

A biological invasion starts with the arrival of small numbers of propagules beyond the native range of the species. The propagules then become established and reproduce, the result being spatiotemporal changes in the distribution and abundance of invading species (Williamson 1996; Sakai et al. 2001). The early phase, when the population is not close to its equilibrium level, is crucial to understanding the dynamics of invasions (Rouget et al. 2004; Azzurro et al. 2006; Liebhold and Tobin 2008) and to designing management responses (Kolar and Lodge 2001; Hulme 2006). An important question during the early phase of an invasion is how propagule pressure, that is, propagule numbers and spatiotemporal patterns in the arrival of propagules, limits the success of the invasion. Propagule pressure often plays an important role in determining whether the introduced species is able to successfully establish itself and extend its distribution (Lockwood et al. 2005; Drake and Lodge 2006; Roman and Darling 2007; Johnston et al. 2009; Simberloff 2009). Although many previous studies have focused on the early phase of invasion dynamics (Strayer et al. 1996; Carey 1996; Crooks 2005, 2011; Gaubert et al. 2009), most of these studies have not included an estimate of propagule supply (Cohen and Carlton 1998; Costello and Solow 2003; Marchetti et al. 2004; Jeschke and Strayer 2005; Brown et al. 2008; Miller and Ruiz 2009; Marsico et al. 2010), especially in marine habitats (but see Ruiz et al. 2000; Verling et al. 2005; Clark and Johnston 2009; Vaz-Pinto et al. 2012).

Sessile marine animals are a major component of marine ecosystems and are found in a variety of habitats. Most of them exhibit complex life cycles that include pelagic larval and benthic phases linked by recruitment (Todd 1998). Because of their immobility at the benthic stage, dispersal of sessile organisms relies almost completely on larval dispersal. Recruitment should thus play an important role in invasion dynamics. A simultaneous evaluation of abundance, distribution, and larval recruitment should therefore greatly benefit our understanding of the early phase of invasion by sessile marine organisms.

There are at least three fundamental questions that concern the dynamics of the early phase of invasion by sessile marine animals. First, how do abundance, distribution and recruitment change with time after invasion (Brown and Kodric-Brown 1977; Hanski 1991, 1998, 1999; Stachowicz et al. 2002; Clark and Johnston 2009)? Previous studies have focused on the establishment phase of invasions, whereas there have been few studies concerning abundance, distribution, and recruitment during the early phase of invasions in marine habitats (Burlakova et al. 2006; Lucy 2006; Kraemer et al. 2007). Second, does the rate of local extinction decrease with time as the result of a temporal increase of recruitment or population size? The probability of local extinction may decrease with increasing recruitment density that results from the rescue effect of a metapopulation (Brown and Kodric-Brown 1977; Hanski 1991). Third, does the length of the lag time between population establishment and initial arrival of recruits decrease with time when recruitment density increases? If recruitment is low, there may be a high risk of death of all individuals before maturation because of demographic stochasticity (Lande et al. 2003; Clark and Johnston 2009). To our knowledge, the above questions have not yet been simultaneously answered for a single invasion event. This fact presumably reflects logistic difficulties: for this purpose a survey should be performed over a long timeframe along a long coastline located adjacent to the leading edge of an invasion front.

The native range of the barnacle *Balanus glandula* is the east Pacific coast from the Aleutian Islands to Baja California (Newman and Ross 1976; Newman and Abbott 1980). This species becomes sexually mature at 1 year of age (Barnes and Barnes 1956) and releases about 30,000 larvae per brood (Newman and Abbott 1980). These planktonic larvae exist in the water column for 2–4 weeks (Brown and Roughgarden 1985; Strathmann 1987).

*Balanus glandula* has invaded in the southwest Atlantic coast of Argentina (Vallarino and Elias 1997), the southeast Atlantic coast of South Africa (Simon-Blecher et al. 2008), and the northwest Pacific coast of Japan (Kado 2003). In Japan, this barnacle was first found in 2000 at Sasazaki (39°3′N, 141°43′E) (Kado 2003). However, Kado (2003) speculated that in Japan, the first arrival of *B. glandula* was in 1992 (in Geller et al. 2008). In 2000, its distribution expanded along the Pacific coast of northern Japan up to Hiroo (42°17′N, 143°19′E) of Hokkaido (Fig. 1a) (Kado 2003).

To elucidate the patterns and understand the processes that control the population dynamics of *B. glandula* during the early phase of invasion along the

**Fig. 1 a** Map showing study area located on the Pacific coast of eastern Hokkaido and presence (*filled circle*) or absence (*open circle*) of *B. glandula* at ports along the coast of Hokkaido in 2000 (Kado 2003), **b** map indicating the five shores studied
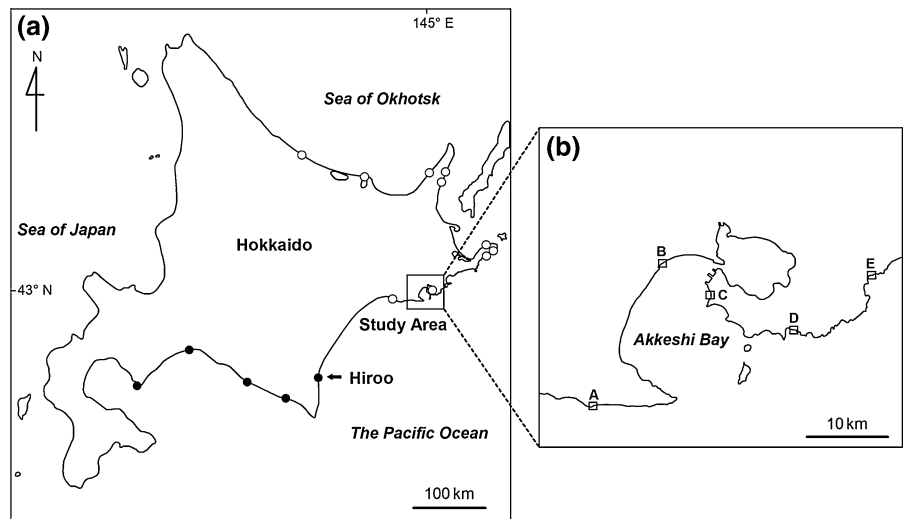


Pacific coast of eastern Hokkaido, we conducted population surveys from 2002 to 2011 at five shores, each consisting of five paired plots, along 49 km of coastline located 144 km east of the eastern invasion front of this species in 2000. The specific questions we asked were as follows: (1) how do the 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 on local extinction; and (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?

## Methods

### Study area

The study area was located along the 49 km of coastline between Nikomanai (shore A) and Mochirippu (shore E), 144 km east of Hiroo, which was reported to be the eastern invasion front of *B. glandula* in 2000 (Kado 2003) (Fig. 1a). The study area is within a sub-arctic zone (Briggs 1995; Asakura 2003) impacted by the cold Oyashio (Kurile) current, and is a region where ice scour occurs once every few years. Low spring tide occurs during the day from late March to early September and during the night from late September to early March. The mid tidal zone examined in this study is dominated by a native barnacle, *Chthamalus dalli* (Fukaya et al.

2013). Other typical space occupants include *Semibalanus cariosus* (barnacle; Nakaoka et al. 2006), and the seaweeds *Analipus japonicus*, *Chondrus yendoi*, *Corallina pilulifera*, *Gloiopeltis furcata*, and *Hildenbrandia* sp. (Okuda et al. 2004). Invertebrate predators include the whelk *Nucella lima* and sea star *Leptasterias ochotensis*, with the latter species uncommon and restricted to a lower tidal zone (Nakaoka et al. 2006; Munroe and Noda 2010). *N. lima* preys on barnacles at the mid tidal zone on these shores (AKM Rashidul Alam, personal observation).

### Survey design

A hierarchical design (Noda 2004) was used for the arrangement of the study, with five paired plots nested within each of five shores for a total of 25 paired plots (Fig. 1b). Shores were separated by 10–24 km; plots were separated by 10–15 m. Each paired plot consisted of an adjacent recruitment and control plot separated by several tens of cm and marked with permanent anchors drilled into roughly vertical rock. The vertical midpoints of both plots corresponded to the mean tidal levels, and their vertical heights were 30 cm. This vertical dimension was chosen to approximately correspond to the vertical range of *B. glandula* recruitment determined from a pilot survey (AKM Rashidul Alam, unpublished data). The horizontal widths of the control and recruitment plots were 50 and 30 cm, respectively.

Recruitment plots were cleared of all surface organisms each year during low tide events in May by burning and then scraping the rock surface with a wire brush.

This clearing was also conducted immediately after each survey. Sampling of recruitment plots was performed thrice every year, in May, August, and October. This sampling began in 2004 and continued until 2011. Sampling of recruitment plots involved using an Olympus Digital Camera (Model no. µ1030 SW) to photograph square, 25-cm$^2$ quadrates. Photographs of 12 replicate quadrates were taken from each recruitment plot. A pilot survey indicated that recruitment density in photographs taken in May was quite low compared with August and October (AKM Rashidul Alam, unpublished data). Thus, at each location, we added recruits in August and October to estimate the annual recruitment density of *B. glandula* based on its major recruitment period.

Control plots were surveyed in each August, beginning in 2002 and continuing through 2011. Occurrence of *B. glandula* was based on presence or absence in a plot. Estimates of barnacle coverage as a surrogate of the population size were performed by using a grid placed over the sample plot, with observation points at evenly spaced intervals (5 cm vertically and 5 cm horizontally; 60 grid points total). Presence or absence of *B. glandula* at each point on the grid was used to estimate coverage of *B. glandula* for each control plot at each survey.

Data analyses

*Evaluation of temporal changes in occurrence and distribution*

If a control plot occupied by *B. glandula* became unoccupied in the next year, the local population was considered to have gone extinct. The rate of local extinction for each year was obtained by dividing the total number of extinctions that occurred in a given year by the total number of control plots occupied in the previous year. To evaluate the effect of recruitment density on extinction, the annual recruitment densities from the previous year were compared between extinct and surviving populations for each year by a Mann–Whitney U test.

*Elucidation of timing of the local population establishment*

When *B. glandula* was present on a control plot in at least two consecutive years, including the final year of
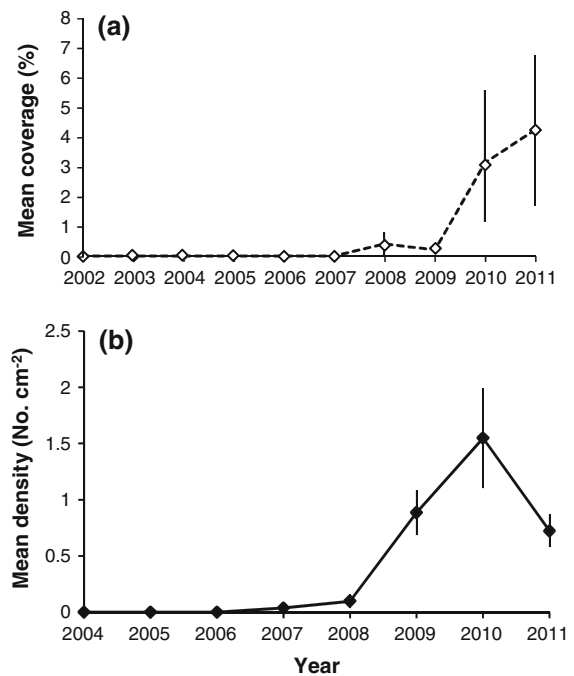


Fig. 2 Temporal changes in coverage and annual recruitment density of *B. glandula* on the study area; **a** mean coverage during 2002–2011 at control plots, and **b** mean annual density of recruits at recruitment plots during 2004–2011. *Vertical bar* indicates standard errors

the survey, the local population was considered to be established. To elucidate the time lag associated with local population establishment, we calculated the number of years between the initial arrival of recruits at the recruitment plot and population establishment at the control plot. To assess the effect of recruitment density on the lag time associated with local population establishment, log transformed annual recruitment densities of populations that became established at the initial arrival of recruits without a time lag and with a time lag were compared by a Mann–Whitney U test.

Results

Temporal changes in coverage and recruitment density

Until 2009, the mean coverage of *B. glandula* was low (<0.5 %) (Fig. 2a). Coverage then increased rapidly and approached 5 % in 2011. The coverage of *B. glandula* population in all plots except for one

**Fig. 3** Presence of *B. glandula* at **a** control plots during 2002–2011, and **b** recruitment plots during 2004–2011. Five paired plots were established on each of five shores (*A*, *B*, *C*, *D*, *E*) from west to east on the study area; *Rectangle* indicates presence; *asterisk* plot was covered by sediment; *triangle* a photo survey could not be performed
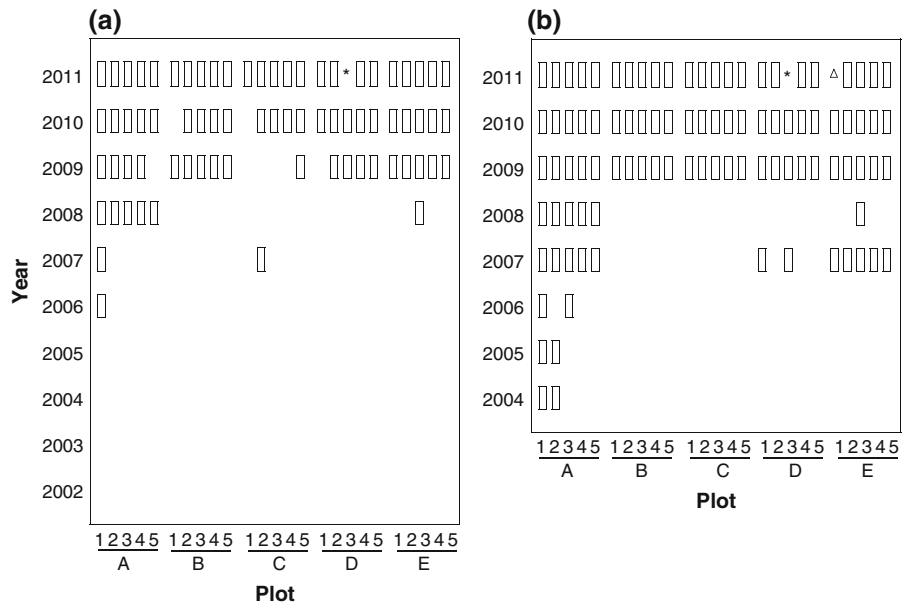


(in A1) varied substantially from year to year. In A1, there was a steady increase to 60 % coverage from 2008 to 2011.

On recruitment plots, *B. glandula* was first detected in 2004 (Fig. 2b). The mean annual recruitment density remained low ($<0.5$ cm$^{-2}$) until 2008, increased in 2010, and declined in 2011.

Occurrence dynamics

*Control plots*

*Balanus glandula* was first detected in this study area in 2006, on one plot of the westernmost shore, A (Fig. 3a). In 2007, *B. glandula* was found at one plot of A and another plot of C. In 2008, its occurrence was recorded at six plots located on two shores: A and the easternmost shore, E. After 2009, this species was detected at all shores, the number of occupied plots increasing from year to year. Extinction and recolonization were detected in the cases of three local populations (C2, A5, and B1). Populations that colonized plots C2 in 2007, A5 in 2008, and B1 in 2009 were locally extinct in 2008, 2009, and 2010, respectively.

*Recruitment plots*

The number of recruitment plots where *B. glandula* occurred increased during 2004–2011. On recruitment plots, *B. glandula* was first detected at the westernmost shore (A) of the study area in 2004 (Fig. 3b). During 2005–2006, the occurrence was observed at two A plots. *B. glandula* was found on 12 plots from three shores (A, D, and E) in 2007 and on six plots from two shores (A and E) in 2008. At shores B and C, recruitment occurred first in 2009. From 2009 to 2011, *B. glandula* was detected on all plots of all five shores.

*Comparison of control and recruitment plots*

We found similarities and differences in the occurrence of *B. glandula* between the control and recruitment plots. On both control and recruitment plots, *B. glandula* was first found at the westernmost shore (A) of this study area. The occurrence was first detected simultaneously on control and recruitment plots of shore B in 2009. After 2009, *B. glandula* was found on both types of plots at all shores. During 2004–2010, except 2008, the presence of this barnacle was higher on recruitment plots than on control plots. In 2007, *B. glandula* was present on recruitment plots of the easternmost two shores, D and E, whereas *B. glandula* was not detected on D and E control plots in 2007.

Local extinction

Three extinction events occurred. The rate of local extinction gradually decreased from 50 % during

**Table 1** Temporal changes in local extinction rate of *B. glandula* during 2006–2011 at 25 control plots

| Duration | No. of extinctions | No. of plots occupied during previous year | Extinction rate (%) |
|----------|--------|---------------------|-----------|
| 2006–2007 | 0 | 1 | 0.0 |
| 2007–2008 | 1 | 2 | 50.0 |
| 2008–2009 | 1 | 6 | 16.7 |
| 2009–2010 | 1 | 16 | 5.3 |
| 2010–2011 | 0 | 23 | 0.0 |

2007–2008 to 0 % during 2010–2011 (Table 1). The log-transformed annual recruitment densities (mean ± SE cm$^{-2}$) of surviving and extinct populations were $-0.20 \pm 0.08$ and $-0.75 \pm 0.38$, respectively. The former was significantly higher than the latter (Mann–Whitney U test, $t_s = 2.68$, $P < 0.01$).

Timing of the local population establishment

Out of 22 cases, eight populations became established in the year when the arrival of recruits was first detected (Fig. 4). Among the remaining 14 populations, there were time lags between the years of initial arrival of recruits and population establishment. The duration of the time lags ranged from 1 to 4 years. The slope of the linear regression between the years of initial arrival of recruits and population establishment significantly differed from one ($P < 0.001$), suggesting that the lag time between the years of initial arrival of recruits and population establishment decreased over the course of invasion. The log-transformed annual recruitment densities (mean ± SE cm$^{-2}$) of populations established in the year of initial arrival of recruits (no time lags) and populations that became established only after time lags were $-0.32 \pm 0.12$ and $-1.56 \pm 0.19$ cm$^{-2}$, respectively. The former was significantly higher than the latter (Mann–Whitney U test, $t_s = 3.42$, $P < 0.01$).

**Discussion**

Spreading pattern and underlying processes

The front of *B. glandula*'s invasion was located beyond the western boundary of this study area in 2000 (Kado 2003). The subsequent spreading pattern and underlying processes were estimated on the basis
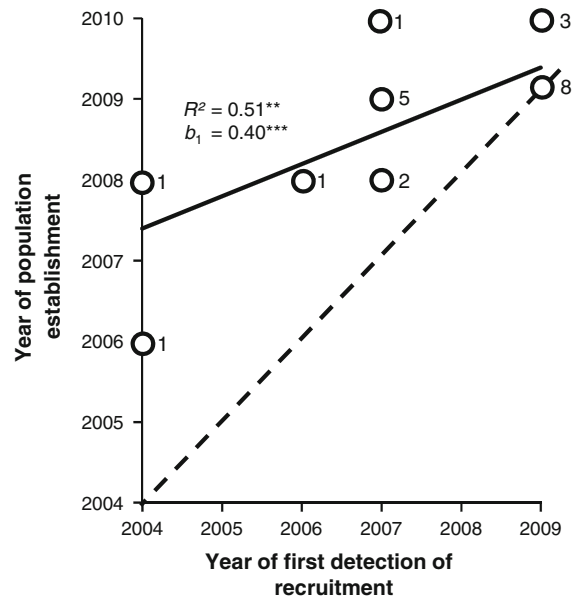


**Fig. 4** Temporal relationship between the year of first detection of recruitment and establishment of *B. glandula* populations along the coast of eastern Hokkaido during 2002–2011. Numeric character adjacent to *each circle* indicates number of plots where barnacles were established. The *solid line* is the linear regression between year of first detection of recruitment and year of population establishment. The value of $R^2$ and slope ($b_1$) are shown. *Each asterisk* on the value of $R^2$ and $b_1$ indicates whether the slope of regression is different from 0 and 1.0, respectively, at a significance level of **$P < 0.01$, and ***$P < 0.001$. *Dash line* corresponds to no lag in population establishment

of information that was obtained from recruitment and population surveys. At least in 2004, larvae reached the westernmost shore, A; larvae may have been released from a source located beyond the western boundary of this study area. The supply of larvae to A did not result in population establishment until 2005. In 2007, larvae did not arrive at shores B and C, but instead arrived at shores D and E; these larvae may have been released from unknown external sources located to the east of E or from the western shore around A. The larval supply to D and E did not result in population establishment until 2008 and 2009 at E and D, respectively. In 2009, larvae reached B and C and established local populations immediately; these larvae may have been released from multiple sources located on the east and west of both B and C.

For the majority of the locations there were time lags between the initial arrival of recruits and population establishment. These time lags may be partially

explained by the negative impact of endemic assemblages. At control plots, preemption by endemic sessile organisms may have limited recruitment density. Indeed, the mean coverage of all sessile organisms was ~60 % (AKM Rashidul Alam, unpublished data), the indication being that free space available for larvae of *B. glandula* was limited. In addition, predation by the whelk, *N. lima*, may have affected survival of this barnacle. At control plots, *N. lima* has been commonly found, but it was rarely found at recruitment plots (Takashi Noda, personal observation). Actually, the absence of the introduced barnacles often reflects inhibition associated with interactions with endemic species, such as competition (Zabin 2009) and predation (Laird and Griffiths 2008; Sanford and Swezey 2008).

The arrival of larvae at both B and C was delayed compared with shores D and E. There are two hypotheses that may explain the causes of the delay. First, less exposure to waves caused a lower larval flux (Noda et al. 1998; Archambault and Bourget 1999; Gaylord and Gaines 2000; Jenkins and Hawkins 2003) within Akkeshi Bay. On the basis of this hypothesis, the dependency of larval flux on wave exposure should be independent of barnacle species (Macho et al. 2010; Pfaff et al. 2011). However, the larval recruitment density of *B. glandula* was lower at B and C than at D and E, whereas larval recruitment density of *C. dalli* was higher at B and C than at D and E (AKM Rashidul Alam, unpublished data). This hypothesis is therefore not supported. Second, the main coastal current that transports barnacle larvae does not sweep the coast of a bay (Gaines and Bertness 1992; Todd 1998; Jonsson et al. 2004). However, there is no available information on coastal currents in this area.

Local population dynamics

Most of the local populations fluctuated randomly, whereas the population at A1 consistently increased during 2009–2011. Even a few such successful and growing populations may contribute greatly to range expansion. The supply of larvae from a hotspot, a small portion of the locations with remarkably high abundance, plays an important role in range expansion (Semmens et al. 2004; Leslie et al. 2005; Ruiz et al. 2011). Indeed, the temporal pattern in the coverage at A1 was similar to that of the mean population coverage. If plot A1 is removed from calculations,

the average cover exhibits more unclear temporal trend, reaching only 2 % at the end of the study period (i.e., 2011).

Extinction and local population establishment

During the early phase of the *B. glandula* invasion, population dynamics were characterized by a higher rate of local extinction and a longer lag time (4 years after the initial invasion at this study area) for population establishment. One of the major underlying mechanisms may be demographic stochasticity, especially for the survival of recruits, caused by low recruitment intensity. We assumed annual mortality to be 0.97, the mortality of *B. glandula* recruits in their native range (Menge 2000). From 2004 to 2008, recruitment plots where *B. glandula* was present had an average density of 0.144 cm$^{-2}$. Accounting for the fraction of free space on control plots (0.4), the probability of complete die-off of recruits before maturation (1 year of age) was estimated to be 0.5 (SE = 0.077, n = 24). In contrast, from 2009 to 2011, recruitment on to plots where *B. glandula* was present occurred at 1.06 cm$^{-2}$, and the corresponding estimate of die-off within 1 year was much lower at 0.05 (SE = 0.018, n = 73).

The implications of this study are twofold. First, propagule pressure (i.e., larval supply) was crucial for successful invasion of the rocky intertidal barnacle, *B. glandula*, within a few years after the arrival of the first larvae at a given location. When recruitment density was low, there was a time lag between the initial appearance of recruits and the establishment of a population at a location, and local extinction sometimes occurred. Indeed, both the rate of local extinction and the probability of failure to establish a population depended on recruitment density. Second, monitoring of recruitment is essential for the early detection of invasions by sessile marine organisms and prediction of their range expansion. The first arrival of recruits was detected 2 years before the establishment of a population in this study area. The majority of local populations were established after a time lag that followed the initial arrival of recruits. It can be said that a recruitment survey is cost-effective for monitoring of a marine invasion. A recruitment survey can be performed by setting larval collectors such as shells of bivalves and artificial substrata, which can be useful for the rapid detection and identification of similar

multiple species at the same time, are cheap and easily available for monitoring of a marine invasion.

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