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An experimental evaluation of the direct and indirect effects of endemic seaweeds, barnacles, and invertebrate predators on the abundance of the introduced rocky intertidal barnacle *Balanus glandula*

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Abstract

The barnacle, *Balanus glandula* has recently invaded along the Pacific coast of eastern Hokkaido, Japan. To evaluate the direct and indirect effects of endemic seaweeds, barnacles, and invertebrate predators on the abundance of *B. glandula* on the rocky intertidal coast of eastern Hokkaido, we conducted a field experiment from June 2011 to October 2012 in which we manipulated the presence or absence of these factors. Seaweeds showed no significant effect on the abundance of *B. glandula*. The endemic barnacle *Chthamalus dalli* and the invertebrate predator *Nucella lima* reduced the abundance of *B. glandula*. However, the simultaneous influence of *N. lima* and *C. dalli* was compensative rather than additive, probably due to keystone predation. These findings suggest that competition by the endemic barnacle *C. dalli* and predation by the invertebrate predator *N. lima* decreased the abundance of *B. glandula*, but that *N. lima* predation on *C. dalli* weakened the negative influence of *C. dalli* on *B. glandula*. The implications of these findings are twofold: the endemic competitor and invertebrate predator may have played important roles in decreasing the abundance of *B. glandula* in natural habitats, and conservation of endemic invertebrate predators may be crucial to impede the establishment and survival of introduced barnacles in rocky intertidal habitats.

Keywords Competition · Indirect effect · Invasion success · Macrobenthos · Predation · Rocky intertidal

Introduction

The fate of introduced species is influenced by various factors, including species interactions with the endemic species assemblages (Stachowicz and Byrnes 2006). For examples, predation, competition, and facilitation may affect the abundance of invasive species. Predation often decreases colonization (Schoener and Spiller 1995; Dumont et al. 2011; Simkanin et al. 2013) and increases mortality of introduced species (Reusch 1998). Competition for resources such as space (Stachowicz et al. 2002) and food (Petren and Case 1996) can also reduce the chance of colonization by introduced species. Facilitation can sometimes act as a driver for successful invasion when it alleviates an environmental stress (Altieri et al. 2010). In addition, such species interactions may play an important role on abundance via indirect effect (White et al. 2006). However, few empirical studies have simultaneously investigated both direct and indirect effects of endemic species assemblages on introduced species especially in marine habitats (White et al. 2006).

Many exotic barnacle species have invaded on the coasts of various regions of the world (Southward et al. 1998; Allen et al. 2006; Schwindt 2007; Carlton et al. 2011). Recently, the barnacle *Balanus glandula* has invaded intertidal rocky shores along the Pacific coast of eastern Hokkaido, Japan (Alam et al. 2014). The distribution and abundance of barnacles, including *B. glandula*, are often influenced by predation of invertebrate predators, such as whelks (Connell1970) and seastars (Menge 1972), and by competition with other barnacles (Farrell 1991; Navarrete 1996), and facilitation (Bertness et al. 1999) and competition (Jernakoff 1985) by seaweeds. In addition, indirect effects have considerable impacts on the structure of rocky intertidal communities. An analysis of the importance of indirect effects in field manipulative experiments suggests that 40–50 % of the change results from indirect effects (Menge 1995).

To evaluate both the direct and the indirect effects of endemic barnacles, seaweeds, and invertebrate predators on the abundance of *B. glandula* on the rocky intertidal coast of eastern Hokkaido, we conducted a fully factorial field experiment in which we manipulated the presence or absence of the invertebrate predators and the coverages by endemic barnacles and seaweeds.

Materials and Methods

Study site and organisms

We selected a rocky intertidal area of Monshizu, in Akkeshi Bay, eastern Hokkaido, Japan (43°2′59″N, 144°46′41.5″E), to study the effects of predation, competition, and facilitation on the abundance of *B. glandula* (Fig. 1). The study area was located on a semi-exposed, roughly vertical (slopes varied from 58° to 87°) metamorphic rocky shore at the northern end of the bay, on an outcropping that faced roughly to north. The maximum tidal amplitude at this location is roughly 160 cm. At the mid-tidal zone of the study area, the most dominant sessile organism is an endemic barnacle, *Chthamalus dalli* (Fukaya et al. 2013). In addition, the perennial seaweeds *Analipus japonicus*, *Chondrus yendoi*, *Corallina pilulifera*, *Gloipeltis furcata* and *Hildenbrandia* sp. are commonly found on this shore (Okuda et al. 2004). As invertebrate predators, the whelk *Nucella lima* and the seastar *Leptasterias ochotensis* are present (Nakaoka et al. 2006; Munroe and Noda 2010), but the later species is rare, and its vertical distribution is restricted to the low tidal zone (A.K.M.R. Alam, personal observation). At the Monshizu shore, *B. glandula* was first detected in 2009, but was present at low densities (Alam et al. 2014).

Field experiment

To quantify the effects of competition, predation, and facilitation on the abundance of *B. glandula*, we conducted a field experiment between June 2011 and October 2012 in which we

manipulated the presence or absence of invertebrate predators, endemic barnacles, and seaweeds in a fully factorial design. In May 2011, we selected seven blocks, each covering 5 to 25 m of shoreline, separated from adjacent blocks by 1 to 18 m. In the mid tidal zone of each block, we haphazardly established eight experimental plots, which corresponded to a 2 × 2 × 2 combination of the presence or absence of invertebrate predators, endemic barnacles, and seaweeds. Each plot was 20 × 20 cm, with a distance of 15 to 50 cm between neighboring plots within each block.

At the initial of experiment, *B. glandula* is removed from all plots, then endemic barnacles and seaweeds were manually removed using forceps, needles, and a router in all manipulations. Invertebrate predators were excluded from the plots using stainless-steel cages, each 20 × 20 × 5 cm (mesh size: 10 mm), with an outer margin of 5 cm for the plastic mat that was used to inhibit the immigration of predators. The cages were attached to the rock using anchors and screws; when we detected gaps between the rock surface and the cages, we filled the space with marine epoxy. Plots without predator manipulation were covered by the same cage, but the sides were opened.

Manipulations were repeatedly performed, as necessary, to control the abundance of the focal organism. The removals of seaweeds, barnacles, and invertebrate predators that accidentally intruded into the cages were conducted at four weeks interval from June to October 2011. From November 2011 to March 2012, manipulation was not performed because the rates of recruitment and growth of sessile organisms, and the feeding activity of invertebrate predators, are low due to low temperatures at this time of year in the region (Hori and Noda 2001; Noda et al. 2003; Fukaya et al. 2013). In April 2012, the manipulation was resumed until October 2012 at two weeks intervals; during this period, we increased the frequency to increase the effects of manipulation.

To confirm the validity of the manipulation (i.e., that it produced a statistically significant change in the population of the manipulated organism), the abundance of invertebrate predators and the coverages by endemic barnacles and seaweeds were obtained from the central 15 × 15 cm of each 20 × 20 cm plot in August and October 2011, and in April, August, and October 2012. The coverages of endemic barnacles and seaweeds were measured by a point sampling method in which the occurrence of focal organism was recorded using 3 × 3 cm grid placed over the plot after opening the cover of each cage, with 25 grid points in total. To examine the results of our long-term manipulations and species interactions, we measured the abundance of *B. glandula*, the coverages of endemic barnacles and seaweeds, and the abundance of invertebrate predators in the central 15 × 15 cm of each plot at the end of the experiment in October 2012.

Data analyses

We confirmed that the manipulation produced the desired effect (i.e., significantly reduced the population of the focal organism eliminated from the cages) using three-way ANOVA, in which the manipulation was treated as the fixed factor and the cumulative abundance of invertebrate predators and the cumulative coverages of endemic barnacles and seaweeds from five observations (in August and October 2011, and April, August, and October 2012) at each plot were treated as response variables. Before performing the ANOVA, we confirmed homogeneity of variances across the treatments using Cochran's C test (Winer 1971) for the cumulative abundance of invertebrate predator ($C = 0.28$, $P > 0.05$) and the cumulative coverages of seaweeds ($C = 0.18$, $P > 0.05$) and endemic barnacle ($C = 0.33$, $P > 0.05$).

We used version 2.13.1 of the R statistical software (R Development Core Team 2011) to develop generalized linear models (GLMs) with a negative binomial error structure and a log-link function to examine the effects of predators, barnacles, and seaweeds on the abundance of *B. glandula* in October 2012. We used a log-likelihood ratio test of the explanatory variables

while controlling for the remaining variables with the command 'Anova' in a package 'car' of the R software to test the statistical significance of each coefficient in the models. We performed GLM with a negative binomial error structure instead of using ANOVA because data on the final abundance of *B. glandula* revealed strong heteroscedasticity.

Results

Community composition

We observed the endemic barnacle *C. dalli*, the invertebrate predator *N. lima*, and several seaweeds in the experimental plots. Among the seaweeds, the dominant species was *G. furcata*, followed by *A. japonicus*, *C. pilulifera*, and *C. yendoi*. At the end of the experiment, the basal diameter of *B. glandula* in the experimental plots ranged between 2 and 6 mm.

All manipulations successfully reduced the abundance of each focal species. The cumulative abundance of *N. lima* (Fig. 2a) was significantly decreased by invertebrate predator manipulation (ANOVA, $F_{1, 52} = 16.17$, $P < 0.001$). The coverages of seaweeds (Fig. 2b) and *C. dalli* (Fig. 2c) were significantly decreased by the manipulation of seaweeds (ANOVA, $F_{1, 52} = 106.83$, $P < 0.001$) and *C. dalli* (ANOVA, $F_{1, 52} = 251.89$, $P < 0.001$), respectively.

Effects of the endemic seaweeds, the barnacle *C. dalli* and the predator *N. lima* on the abundance of *B. glandula*

Seaweeds did not significantly affect the abundance of *B. glandula* (Table 1, Fig. 3). In contrast, *C. dalli and N. lima* significantly reduced the abundance of *B. glandula* (Table 1, Fig. 3). The magnitudes of the effects of *N. lima* and *C. dalli* on the abundance of *B. glandula* were similar (for *C. dalli*: $\beta \pm SE = -2.8792 \pm 0.8278$; for *N. lima*: $\beta \pm SE = -2.2914 \pm 0.8005$). There was a significant positive interaction between *C. dalli* and *N. lima* ($\beta \pm SE = 2.3867 \pm 1.1879$, $P = 0.014$). Thus the interaction positively influenced the density of *B. glandula*, but it was not as strong as the main effects, because *B. glandula* decreased when both the predator and the competitor were present (Fig. 3). The presence of *C. dalli* did not significantly increase the abundance of *N. lima* (paired *t* test, $t = 2.12$, $P > 0.05$) (Fig. 4a) whereas the presence of *N. lima* significantly decreased the coverage of *C. dalli* (paired *t* test, $t = 10.74$, $P < 0.001$) (Fig. 4b).

Discussion

Nucella lima had a significant negative direct effect on the abundance of *B. glandula*. In both the native and introduced ranges of *B. glandula*, its abundance is often controlled by whelk predation. In San Juan Islands on the east Pacific coast of North America, the abundance of *B. glandula* is limited by predation by the whelks, *Nucella lamellosa* and *Nucella emarginata* (Connell 1970) and by *Nucella canaliculata* (Palmer 1984). In Oregon, on the Pacific coast of North America, the abundance of *B. glandula* is also limited by *N. emarginata and N. canaliculata* (Berlow 1999). In northern California, on the east Pacific coast of North America, the abundance of *B. glandula* is decreased by *Nucella ostrina* (Harley and O'Riley 2011). In sites ranging from Eland Bay to Misty Cliffs along the coast of South Africa, the abundance of *B. glandula* is limited by predation by the whelks *Burnupena cincta* and *Burnupena lagenaria* (Laird and Griffiths 2008).

The endemic barnacle *C. dalli* had a significant direct negative effect on *B. glandula*. One possible mechanism is pre-emption of larval settlement by adult *C. dalli* rather than post-settlement interference as a result of overgrowth, undercutting, and crushing. Previous studies reported that *B. glandula* is a superior competitor than *C. dalli* (Dayton 1971; Stanley and Newman 1980), suggesting that post-settlement interference by *C. dalli* on *B. glandula* would not be effective. In contrast, pre-emption by adult *C. dalli* can undoubtedly reduce the free space available for the larvae of *B. glandula*. Indeed, in April, before the recruitment season for *B.*

glandula, we examined plots where the invertebrate predators were manually removed but the endemic barnacles were not manipulated, and found that the mean coverage by *C. dalli* and the amount of bare space were ca. 55% and ca. 35% of the plot, respectively, suggesting that pre-emption by *C. dalli* significantly decreased the free space available for the larvae of *B. glandula*.

In our study, competition by *C. dalli* decreased the abundance of *B. glandula*. In its native range, along the Pacific coast of North America, *B. glandula* competitively decreases *C. dalli* (Dayton 1971), whereas there is no effect of *C. dalli* on *B. glandula* (Farrell 1991). The competitive strength of *B. glandula* therefore differs between its native and introduced ranges. Two mechanisms may explain this contradiction. First, the competitive advantage of the introduced *B. glandula*, such as its faster growth rate than that of the Chthamaloids (Stanley and Newman 1980), might have been lost as a result of a genetic bottleneck. However, the fact that Geller et al. (2008) found no evidence of a genetic bottleneck in *B. glandula* on the Japanese coast suggests that this hypothesis is unlikely to explain the changes in the relative competitive strength of this barnacle. Alternatively, regional differences in the abiotic environment, such as the climate and tidal regime, may alter competitive hierarchies of these barnacles. Indeed, Poloczanska et al. (2008) found that climatic differences can shift the competitive balance between *Chthamalus* and *Semibalanus* on the coast of southwestern England. Presumably, the introduced *B. glandula* is still not well adapted to the environment of the invaded region, and its performance may therefore be lower than that in its native habitat.

Our experiment detected a significant indirect interaction between *N. lima* and *C. dalli* in terms of their effect on *B. glandula*. This indirect effect could result from keystone predation of *N. lima* on both barnacle species. This is because both the predator (*N. lima*) and the competitor (*C. dalli*) directly decreased *B. glandula*, and the predator also decreased *C. dalli*; thus, it both reduced the strength of the competitive effect and may have caused predator satiation, thereby decreasing the strength of the predation pressure on *B. glandula*. In addition, the negative influence of *C. dalli* on *B. glandula* became weaker when *N. lima* was present. While it is unknown why the whelk *N. lima* consumed exclusively the native barnacle, congeneric whelks are known to as selectively foragers, depending on prey profitability (Palmer 1984) and prior feeding experience (West 1986). In rocky intertidal habitats, the most common indirect effect is keystone predation (Menge 1995). Keystone predation occurs as the changes in the abundance of predators or competitors due to high growth rates, high recruitment rates, and a rapid numerical response to prey availability, and these results produce a rapid indirect species response (Menge 1997).

Seaweeds did not show any significant effect on the abundance of *B. glandula*. Previous studies have demonstrated that the effects of seaweeds on barnacles are variable. Seaweeds often decrease barnacle by inhibiting larval settlement by physically wiping larvae from the rock surface as a result of their movement in response to waves (Menge 1976; Leonard et al. 1999) whereas seaweeds sometimes increase barnacle by enhancing the growth and survival of barnacles via alleviation of desiccation stress (Bertness et al. 1999). Another study found no effect of seaweeds on the abundance and distribution of barnacles (Denley and Underwood 1979). Such variable effects may depend on the size and morphology of the seaweeds and on differences in desiccation stress due to variation in the tidal height and climate (Leonard 2000).

When both the endemic predator and the competitor are expected to have a negative influence on the invasibility of an introduced species, it is quite difficult to predict the net effect of predation on the introduced species, because the net effect depends on factors such as the relative densities of predators and prey, as well as prey preferences by the predators (Menge et al. 1994; Abrams et al. 1996; Berlow 1999). In such cases, a field experiment such as the present study in which the densities of both the endemic predator and the competitor are factorially manipulated offers a unique opportunity to evaluate the net influence of predation and competition on a target species. Such a study can also permit an evaluation of direct effects

that result from interactions between the endemic predator and the competitor. Indeed, our experiment clearly showed that the direct effect of predation on *B. glandula* by *N. lima* was stronger than keystone predation by *N. lima* on *B. glandula* that was mediated through *C. dalli*; consequently, the net effect of predation on *B. glandula* exhibited negative impact. In rocky intertidal habitats, both competition for space and predation are important factors that determine the distribution and abundance of sessile organisms (Menge et al. 1994). Thus, field experiments with a design similar to that in the present study will provide strong insights into how biological interactions affect the abundance of an introduced sessile species.

In conclusion, competition by the endemic barnacle *C. dalli* and predation by the endemic whelk *N. lima* both decreased the abundance of *B. glandula*, whereas their interaction decreased the impact on *B. glandula*, in the intertidal zone of a rocky shore along the coast of eastern Hokkaido, Japan. The implications of these findings are twofold. First, the endemic competitor and predator may have played important roles in decreasing the abundance of *B. glandula* in their natural habitats. Indeed, *B. glandula* is relatively abundant in man-made habitats such as wave breaks and concrete embankments (Kado 2003), but remains rare on natural rocky shores with a high density of whelks and endemic barnacles. Second, the conservation of endemic invertebrate predators may be crucial to impede the establishment and survival of introduced barnacles in rocky intertidal habitats. Previous studies demonstrated that the abundance of rocky intertidal barnacles is often limited by invertebrate predation. In the north Atlantic coast of New England, the abundance of introduced *Semibalanus balanoides* (Menge 1978) and *Elminius modestus* (Barnett 1979) are decreased by predation by *Nucella lapillus*. In the southwest Pacific coast of New South Wales, the abundance of *Tesseropora rosea* is decreased by *Morula marginalba* (Underwood et al. 1983). In the southeast Pacific coast of Chile, the abundance of *Chthamalus scabrosus* is decreased by *Concholepas concholepas* (Jara and Moreno 1984). In the northeast Pacific coast of US, *Pisaster ochraceus* decreases the abundance of *C. dalli* (Dayton 1971) and *Balanus cariosus* (Menge 1972), and *Leptasterias hexactis* decreases the abundance of *B. glandula* (Menge 1972).

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Table 1 Results for the generalized linear models to test the effects of the invertebrate predator (*N. lima*), the endemic barnacle (*C. dalli*), and seaweeds on the abundance of *B. glandula*. The predator *N. lima* and the barnacle *C. dalli* were found in the experimental plots. The coefficient (β) represents the effect of the presence of a focal species (the main effect) or the presence of a set of focal species (the interaction effect); negative and positive values indicate a decrease and increase, respectively, in abundance of *B. glandula*

Explanatory variable	β ± SE	χ^2 (*df* = 1)	*P*
N. lima	–2.2914 ± 0.8005	12.54	< 0.001
C. dalli	–2.8792 ± 0.8278	15.00	< 0.001
Seaweeds	0.7398 ± 0.7667	0.87	0.351
N. lima × *C. dalli*	2.3867 ± 1.1879	6.05	0.014
N. lima × Seaweeds	–0.6344 ± 1.1283	1.19	0.276
C. dalli × Seaweeds	0.1765 ± 1.1434	0.16	0.899
N. lima × *C. dalli* × Seaweeds	–0.6003 ± 1.6697	0.13	0.719

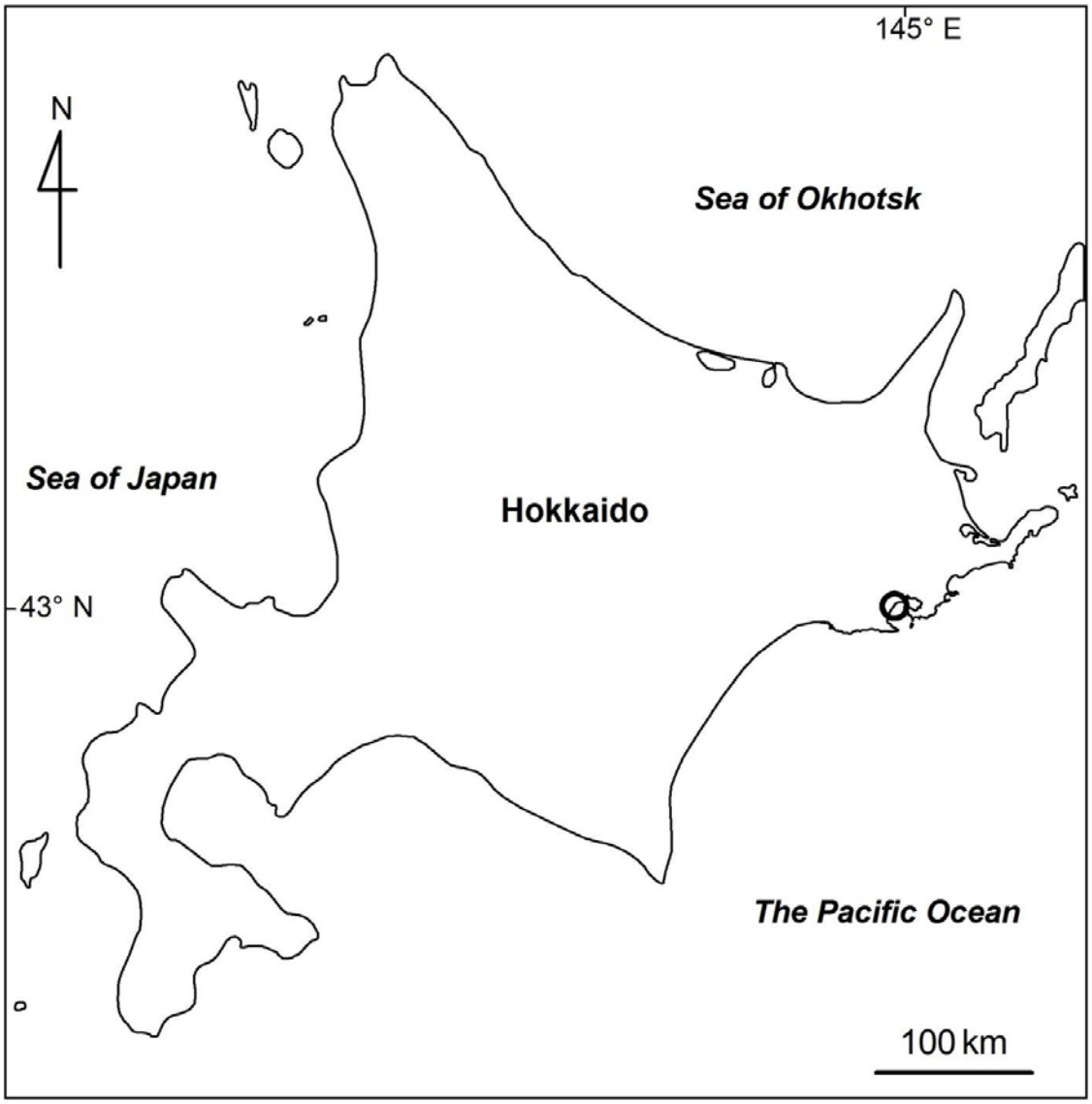


Fig. 1 Map showing the study site located on the rocky intertidal shoreline at Monshizu, Akkeshi, eastern Hokkaido, Japan

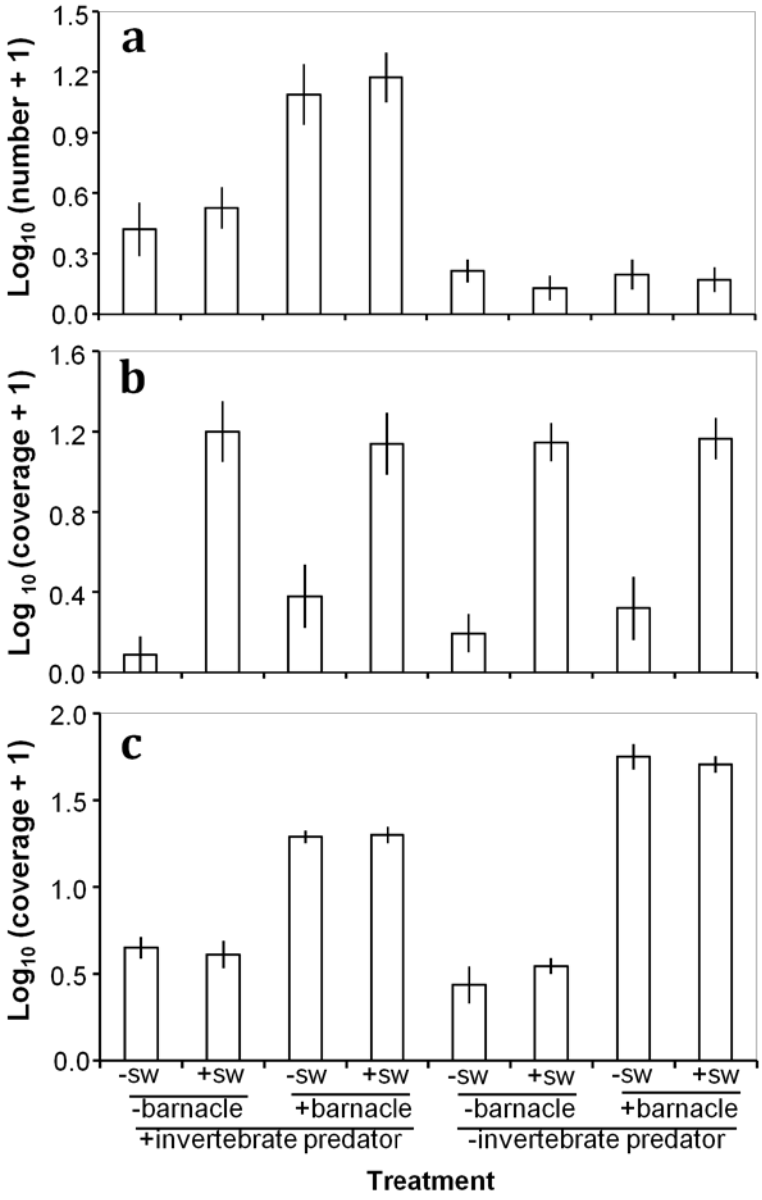


Fig. 2 Cumulative (A) abundance of *N. lima*, (B) percentage coverage of seaweeds, and (C) percentage coverage of *C. dalli* in the eight treatments from August 2011 to October 2012. Treatments: + and – indicate the presence and absence, respectively, of the focal species (seaweeds (sw), endemic barnacle, and invertebrate predator). Cumulative abundance and percentage coverage are means ± SE (n = 7)

Fig. 3

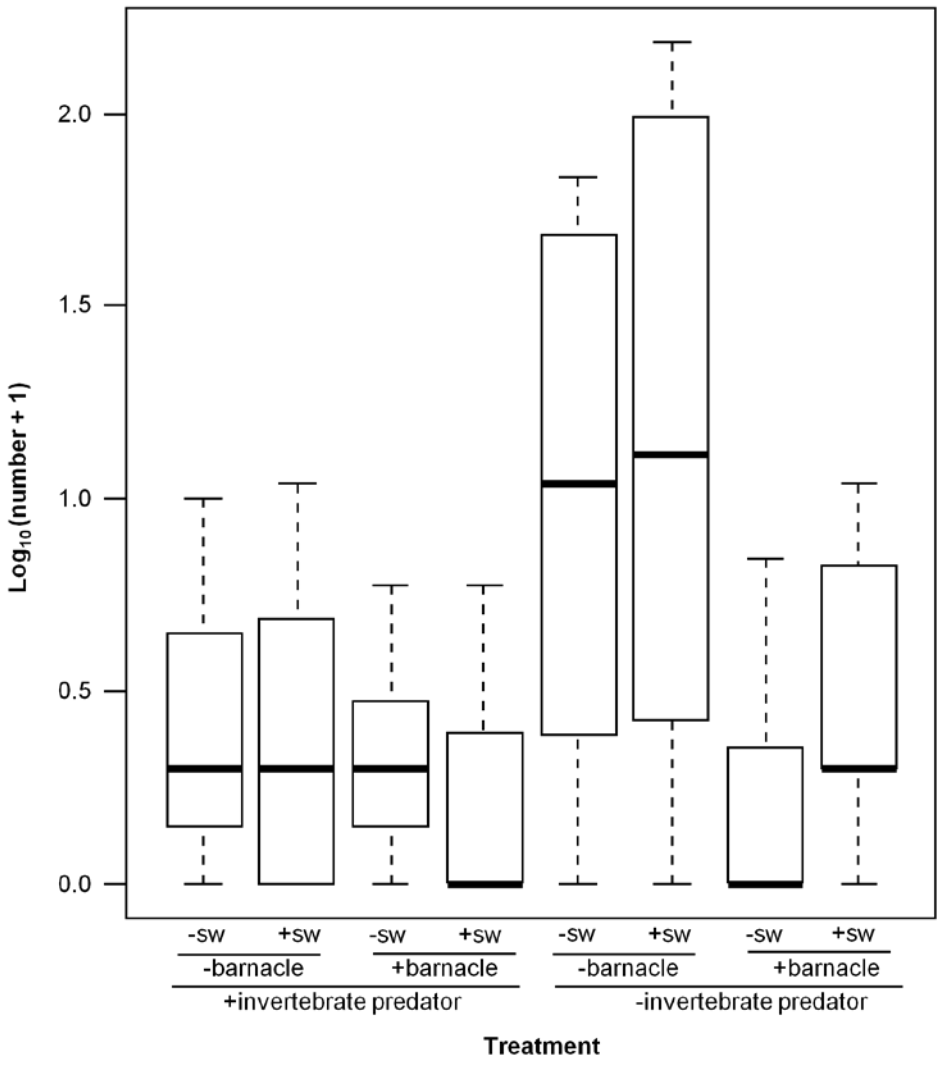


Fig. 3 Boxplots describing the abundance of *B. glandula* in the eight treatments in October 2012. Treatments: + and – indicate the presence and absence, respectively, of the focal species (seaweeds (sw), endemic barnacle, and invertebrate predator). The horizontal line within the box represents the median. The bottom and top of the box show the 1st and 3rd quartiles, respectively. Dotted line represents standard deviations from the mean value (n = 7)

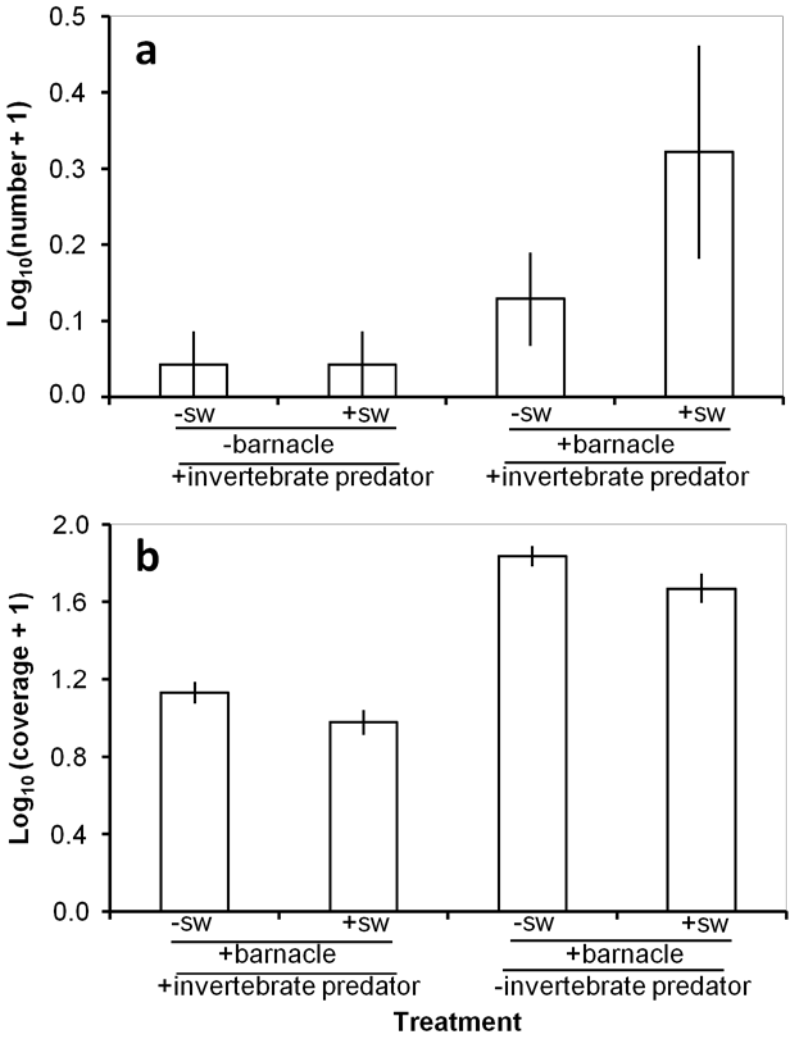


Fig. 4 (A) Abundance of *N. lima* in four treatments in which the invertebrate predator was not manipulated, and (B) percentage coverage of *C. dalli* in four treatments in which the endemic barnacle was not manipulated. Treatments: + and – indicate the presence and absence, respectively, of the focal species (seaweeds (sw), the endemic barnacle, and the invertebrate predator). Abundance and percentage coverage are means ± SE (n = 7)