

Short- and long-term effects of disturbance and propagule pressure on a biological invasion

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Summary

1. Invading species typically need to overcome multiple limiting factors simultaneously in order to become established, and understanding how such factors interact to regulate the invasion process remains a major challenge in ecology.
2. We used the invasion of marine algal communities by the seaweed *Sargassum muticum* as a study system to experimentally investigate the independent and interactive effects of disturbance and propagule pressure in the short term. Based on our experimental results, we parameterized an integrodifference equation model, which we used to examine how disturbances created by different benthic herbivores influence the longer term invasion success of *S. muticum*.
3. Our experimental results demonstrate that in this system neither disturbance nor propagule input alone was sufficient to maximize invasion success. Rather, the interaction between these processes was critical for understanding how the *S. muticum* invasion is regulated in the short term.
4. The model showed that both the size and spatial arrangement of herbivore disturbances had a major impact on how disturbance facilitated the invasion, by jointly determining how much space-limitation was alleviated and how readily disturbed areas could be reached by dispersing propagules.
5. *Synthesis.* Both the short-term experiment and the long-term model show that *S. muticum* invasion success is co-regulated by disturbance and propagule pressure. Our results underscore the importance of considering interactive effects when making predictions about invasion success.

Key-words: biological invasion, biotic resistance, disturbance, establishment probability, propagule pressure, *Sargassum muticum*

Introduction

Biological invasions are a global problem with substantial economic (Pimentel *et al.* 2005) and ecological (Mack *et al.* 2000) costs. Research on invasions has provided important insights into the establishment, spread and impact of non-native species. One key goal of invasion biology has been to identify the factors that determine whether an invasion will be successful (Williamson 1996). Accordingly, ecologists have identified several individual factors (e.g. disturbance and propagule pressure) that appear to exert strong controlling influences on the invasion process. However, understanding how these processes interact to regulate invasions remains a

major challenge in ecology (D'Antonio *et al.* 2001; Lockwood *et al.* 2005; Von Holle & Simberloff 2005).

Propagule pressure is widely recognized as an important factor that influences invasion success (MacDonald *et al.* 1989; Simberloff 1989; Williamson 1996; Lonsdale 1999; Cassey *et al.* 2005). Previous studies suggest that the probability of a successful invasion increases with the number of propagules released (Panetta & Randall 1994; Williamson 1989; Grevstad 1999), with the number of introduction attempts (Veltman *et al.* 1996), with introduction rate (Drake *et al.* 2005), and with proximity to existing populations of invaders (Bossenbroek *et al.* 2001). Moreover, propagule pressure may influence invasion dynamics after establishment by affecting the capacity of non-native species to adapt to their new environment (Ahlroth *et al.* 2003; Travis *et al.* 2005). Despite its acknowledged importance, propagule pressure has rarely been manipulated experimentally and the interaction of propagule pressure with other processes that regulate invasion success is not well understood (D'Antonio *et al.* 2001; Lockwood *et al.* 2005).

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Resource availability is a second key factor known to influence invasion success and processes that increase or decrease resource availability therefore have strong effects on invasions (Davis *et al.* 2000). Resource pre-emption by native species generates biotic resistance to invasion (Stachowicz *et al.* 1999; Naeem *et al.* 2000; Levine *et al.* 2004). Consequently, physical disturbance can facilitate invasions by reducing competition for limiting resources (Richardson & Bond 1991; Hobbs & Huenneke 1992; Kotanen 1997; Prieur-Richard & Lavorel 2000). In most communities disturbances occur via multiple mechanisms and the disturbances created by different agents vary in their intensity and frequency (D'Antonio *et al.* 1999). Recent empirical (Larson 2003; Hill *et al.* 2005) and theoretical (Higgins & Richardson 1998) studies suggest that not all types of disturbance have equivalent effects on the invasion process. Moreover, most of what we know about the effects of disturbance on invasions comes from short-term experimental studies. It is presently unclear how different disturbance agents influence long-term patterns of invasion.

In order for any invasion to be successful, propagule arrival must coincide with the availability of resources needed by the invading species (Davis *et al.* 2000). Therefore, the interaction between propagule pressure and processes that influence resource availability will ultimately determine invasion success (Brown & Peet 2003; Lockwood *et al.* 2005; Buckley *et al.* 2007). In this study we used the invasion of shallow, subtidal kelp communities in Washington State by the Japanese seaweed *Sargassum muticum* as a study system to better understand the effects of propagule pressure and disturbance on invasion. In a factorial field experiment we manipulated both propagule pressure and disturbance in order to examine how these factors independently and interactively influence *S. muticum* establishment in the short term. We supplement the experimental results with a parameterized integrodifference equation model, which we use to examine how different natural disturbance agents influence the spread of *S. muticum* through the habitat in the longer term. Although a successful invasion clearly requires both establishment and spread of the invader, most studies have looked at just one of these processes (Melbourne *et al.* 2007). We take an integrative approach by employing both a short-term experiment and a longer-term model, allowing us to examine the effects of disturbance and propagule limitation on the entire invasion process.

Methods

STUDY SYSTEM

Our field research was based out of Friday Harbor Laboratories on San Juan Island, Washington State, USA. The field experiment was carried out at a site within the San Juan Islands Marine Preserve network adjacent to Shaw Island, known locally as Point George (48.5549 N, 122.9810 W). Field work was accomplished using SCUBA in shallow subtidal communities.

The native algal community characteristic of sheltered, rocky subtidal habitats in this region is species-rich and structurally complex (see Britton-Simmons 2006 for a more detailed description). In this ecosystem, space is an important limiting resource and in the

absence of disturbance there is little or no bare rock available for newly arriving organisms to colonize. This habitat has a diverse fauna of benthic herbivores, including molluscs and sea urchins, that create disturbances by clearing algae from the rocky substrata. The green sea urchin *Strongylocentrotus droebachiensis* is a generalist herbivore that reduces the abundance of native algae and creates relatively large disturbed patches (Vadas 1968; Duggins 1980). In the shallow zone where *S. muticum* is found, the green urchin is highly mobile and often occurs in aggregations (Paine & Vadas 1969; Foreman 1977; Duggins 1983; personal observation). Green urchins avoid areas where *S. muticum* is present because it is not a preferred food resource (Britton-Simmons 2004), but they can be found feeding in uninvaded areas adjacent to existing *S. muticum* populations (personal observation). Green urchins therefore create intermittent but relatively intense disturbances in areas where *S. muticum* is absent and some proportion of these disturbances can potentially be exploited by dispersing *S. muticum* propagules. In contrast, herbivorous benthic molluscs (chitons, limpets and snails) are ubiquitous in the shallow subtidal and unlike sea urchins they are unaffected by the presence of *S. muticum* (Britton-Simmons 2004). Herbivory by individual molluscs creates relatively small-scale disturbances, thereby providing a consistent supply of micro-sites that can be colonized by newly arriving species, including *Sargassum muticum* (see Appendix S1 in Supplementary Material for more information about mollusc diets).

THE INVADER

Sargassum muticum is a brown alga in the order Fucales that was introduced to Washington State in the early 20th century, probably with shipments of Japanese oysters that were imported for aquaculture beginning in 1902 (Scagel 1956). It is now common in shallow subtidal habitats throughout Puget Sound and the San Juan Islands (Nearshore Habitat Program 2001, personal observation). In the San Juan Islands, *S. muticum* has a pseudoperennial life history. Each holdfast produces as many as 18 laterals in the early spring, each of which can grow as tall as three metres. In late summer to early autumn the laterals senesce and are lost, leaving only the basal holdfast portion of the thallus to overwinter.

Sargassum muticum has a diplontic (uniphase) life cycle, is monoecious, and is capable of selfing. Reproduction typically occurs between late June and late August in our region. During reproduction the eggs of *S. muticum* are released from and subsequently adhere to the outside of small reproductive structures called receptacles. Once fertilized, the resulting embryos remain attached while they develop into tiny germlings (<200 µm in length) with adhesive rhizoids (Deysher & Norton 1982). Germlings then detach from the receptacle and sink relatively quickly, recruiting in close proximity to the parent plant (Deysher & Norton 1982). Although most recruitment occurs within 5 m of adult plants, recruits have been found as far as 30 m from the nearest adult (Deysher & Norton 1982). Longer distance dispersal probably occurs when plants get detached from the substratum and subsequently become fertile after drifting for some period of time (Deysher & Norton 1982). One distinctive feature of the *S. muticum* invasion is that it is extremely limited in vertical extent. In the San Juan Islands, *S. muticum* is found from the low intertidal to the shallow subtidal zone (Norton 1977; personal observation), from approximately -0.5 m Mean Lower Low Water (MLLW) to -7 m MLLW. However, it is most abundant in the shallow subtidal, from approximately -2 m MLLW to -4 m MLLW. Thus, in areas where *S. muticum* has invaded it forms a narrow band along the shore.

FIELD EXPERIMENT

We used a two-way factorial design manipulating propagule pressure (six levels) and disturbance (two levels) with three replicates per treatment combination. Subtidal plots (30 cm × 30 cm) at a depth of 3–4 m below MLLW were selected so that differences in the identity and abundance of taxa, aspect, and relief were minimized and the plots were randomly assigned to treatments. None of the experimental plots contained *S. muticum* prior to the experiment. However, some *S. muticum* was present at Point George and it was removed prior to the reproductive season in order to prevent contamination of the experimental plots from external sources of *S. muticum* propagules.

The disturbance treatment had two levels: control and disturbed. Control plots were not altered in any way, but they did vary somewhat in how much natural disturbance had occurred in them prior to the experiment (mean = 7.7% of plot area). Plots in the disturbance treatment were scraped down to bare rock so that no visible organisms remained. These two treatments represent extremes in the levels of disturbance that are likely to occur in nature. The unaltered control plots contained a rich assemblage of native species. The disturbed plots were similar in spatial scale to a patch that a small group of urchins might create, but represent an unusually intense disturbance because all native species, including crustose coralline algae (which cover an average of 27.7% of the substratum at this depth), were removed. These treatments maximized our ability to detect an effect of disturbance in our experiment.

Immediately following the imposition of the disturbance treatment (July 2002) the plots were experimentally invaded by suspending 'brooding' *S. muticum* over them. This was accomplished by collecting *S. muticum* from the field and transporting them to the lab where the appropriate ratio of sterile to reproductive tissue (see below) was placed in 30 cm × 30 cm vexas bags. The bags were returned to the field the same day and suspended over the experimental plots for 1 week. Propagule pressure was manipulated by varying the ratio of sterile to reproductive tissue in the bags while holding the total biomass of *S. muticum* tissue constant. The propagule pressure treatment had six levels, corresponding to the following amounts of reproductive tissue (in grams): 0, 50, 100, 175, 250 and 350 (average mass of mature *S. muticum* in this region is 174 g). Based on propagule production–mass relationships derived by Norton & Deysher (1988) for *S. muticum*, we estimate that approximately 5 million propagules were released in each replicate of our highest propagule pressure treatment. We assumed a linear relationship between the mass of adult reproductive tissue and propagule output because we know of no *Sargassum* study that suggests otherwise. Sterile tissue was added to bags as necessary in order to bring the total biomass to 350 g. Reproductive and sterile tissue was mixed in the bags so that the reproductive tissue was well distributed throughout. This experimental manipulation mimics the level of propagule input that would occur in an incipient invasion or if a drifting plant became tangled with attached algae and subsequently released its propagules.

Recruitment of *S. muticum* was quantified by counting the number of *S. muticum* juveniles that were present in the plots 5 months after the experimental invasion, which is the earliest they can reliably be seen in the field. We resurveyed the plots to count the number of *S. muticum* adults present 11 months after the invasion (just prior to reproductive season) and then removed all *S. muticum* from the experimental plots in order to prevent it from spreading.

STATISTICAL ANALYSIS

We analysed the *S. muticum* recruitment data using a two-way ANOVA followed by separate regression analyses on each disturbance treatment. For the control treatment, we performed a multiple regression to determine what proportion of recruitment variation was explained by propagule input and space availability. For the disturbed plots, which did not vary in the amount of available space, we carried out a simple linear regression to determine the impact of propagule input on recruitment. We used the results of these analyses to inform the construction of mechanistic candidate functions for the relationship between propagule input, space availability and recruitment. These candidate functions were compared using differences in the Akaike's information criteria (AIC differences; Burnham & Anderson 2002). We then used model averaging, a form of multimodel inference in which parameter estimates from more than one candidate function are used jointly to describe the data, in order to select a parameterized recruitment function for the *S. muticum* spread model.

The *S. muticum* survivorship data did not conform to the assumptions of ANOVA (even after a number of different transformations) so we used a non-parametric Kruskal–Wallis test to ask whether *S. muticum* survivorship differed in the disturbed and control treatments. We then fitted five different survivorship functions, assuming binomial error, to the data to test whether *S. muticum* survivorship (number of adults per recruit) was density-dependent. Because the Kruskal–Wallis test suggested that survivorship differed significantly between the two disturbance treatments (see Results) we chose to fit the models to those two treatments separately to test for density dependence. In addition to type 1 (linear), type 2 (saturating), and type 3 (sigmoidal) functions, we also fitted a constant survivorship model. These candidate functions were compared using the Akaike's information criterion (AIC differences; Burnham & Anderson 2002).

The numbers of adult *S. muticum* (after 11 months) also violated the assumptions of ANOVA (despite transformations), so we used non-parametric statistics to test two hypotheses: (i) adult density is independent of disturbance treatment (Wilcoxon Signed Ranks Test), and (ii) adult density is independent of propagule pressure treatment (Kruskal–Wallis Test).

MODEL

We used an integrodifference equation (IDE) model to describe the spatial spread of an *S. muticum* population. IDE models assume that the habitat is continuous in space, and that reproduction and dispersal occur in discrete bouts. The depths inhabited by *S. muticum* comprise a relatively narrow vertical band, so the spread of the population was assumed to occur in a one-dimensional habitat. The model follows two state variables through time. $N_t(x)$ is the density of *S. muticum* at a location x along this habitat at time t , and $Z_t(x)$ is the amount of bare rock at x during t . The values for these state variables are determined by functions representing the important ecological processes in this system. *Sargassum muticum* density is determined by the production and recruitment of propagules and by adult survival. Bare rock is created by benthic herbivore disturbances, since herbivores consume native algae and thus alleviate space limitation. The form of our model is then

$$N_{t+1}(x) = sP(x)f(P_t(x), Z_t(x)) + rN_t(x), \quad \text{eqn 1}$$

$$Z_{t+1}(x) = (1 - \eta_t(x))gZ_t(x) + \eta_t(x)A. \quad \text{eqn 2}$$

$P_i(x)$ is the number of propagules at location x at the start of year t , and equals the number of propagules produced at x and remaining near their parent plant plus the sum of propagules from all other locations within the habitat (with endpoints a and b) which disperse to x . $P_i(x)$ is governed by the equation $P_i(x) = \int_a^b \omega N_i(y)k(x-y)dy$.

Each adult produces ω propagules and their dispersal is described by the function k . The function $f(P_i(x), Z_i(x))$ in equation 1 gives the fraction of propagules which successfully recruit, given that the amount of bare rock at location x equals $Z_i(x)$ and there is an initial input of $P_i(x)$ propagules. Based on data from the experiment, we assume that recruitment function has the form $f(P_i(x), Z_i(x)) = \rho_1(Z_i(x) + \rho_2)^{\rho_5} P_i(x) / [1 + \rho_3(Z_i(x) + \rho_2)^{\rho_5} + \rho_4 P_i(x)^2]$, with values for the ρ_i and methods for fitting this function given in Appendix S2. s and r are fractions of germlings and adults, respectively, that survive to the following year. Parameters for *Sargassum* fecundity and dispersal were attained from the literature (Deysner & Norton 1982; Norton & Deysner 1988) and all other parameter values used in our simulations were estimated from our own field data. The methods and results for fitting parameters are given in Appendix S2.

In equation 2, $\eta_i(x)$ is the proportion of the habitat scraped clear by grazers. If left ungrazed, we assumed that bare rock at a given location experiences geometric decay, with rate g , as it becomes utilized by native algae. The parameter A in equation 2 is a scaling constant representing the size of the habitable area at each point x . We modelled benthic herbivore disturbance in two different ways. First, we constructed a stochastic model for $\eta_i(x)$ based on our understanding of the natural history of the system. Second, we built a more generalized stochastic model for $\eta_i(x)$. In the *S. muticum* system, bare rock is generated in small patches when an area is grazed by molluscs (chitons and limpets), or in larger patches by sea urchin grazing. Both types of disturbance create bare rock for *S. muticum* to potentially exploit, and the disturbance types differ only in their size and spatial distribution. We assumed that the mollusc disturbances are ubiquitous, whereas large urchin-grazed areas are patchily distributed across the habitat. Due to uncertainty in the exact size and frequency of these disturbances, we ran simulations over a very wide range of possible parameter values. In the generalized model for $\eta_i(x)$, we allowed disturbances of any size to occur with any degree of spatial aggregation, rather than requiring large disturbances to be patchy and small ones to be spread throughout the habitat. Our methods for drawing values for $\eta_i(x)$ in these simulations are described in Appendix S3 and summarized in Table C.1 therein.

In our system, native benthic grazers do not eat *S. muticum* adults (Britton-Simmons 2004; personal observation), but it is unknown whether they will consume new *S. muticum* recruits when they are very small (e.g. Sjøtun *et al.* 2007) and hence difficult to avoid ingesting incidentally. Whether or not disturbance events can directly cause mortality of the invader can be very important in determining invasion success (Buckley *et al.* 2007). In our simulations, we therefore considered both the case where *S. muticum* is never eaten by grazers, and the case where *S. muticum* is eaten at the rate $\eta_i(x)$ until it reaches the age of 1 year.

Results

The field experiment showed that recruitment of *S. muticum* was higher in plots that were disturbed compared to control plots (Fig. 1a) suggesting that resource availability limited recruitment. Increasing propagule pressure led to significant increases in average *S. muticum* recruitment in both distur-

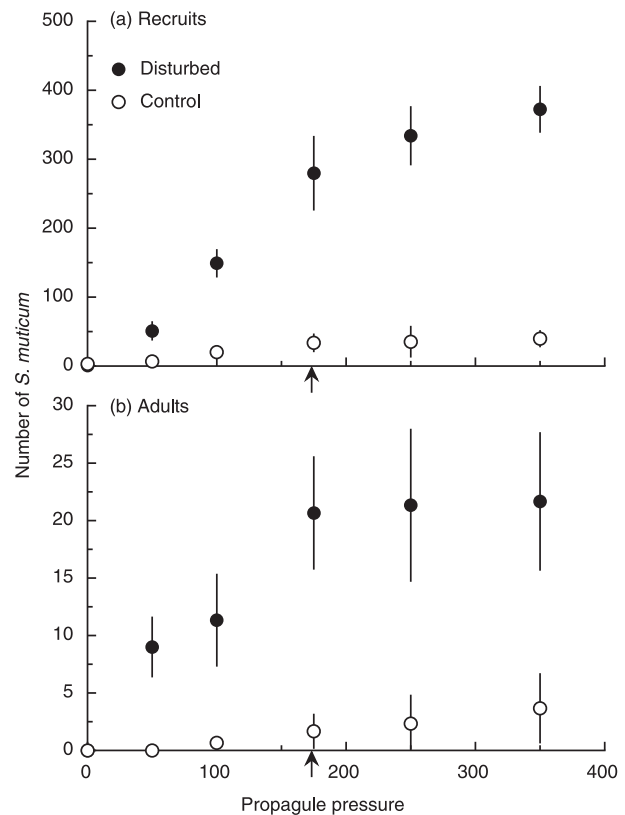


Fig. 1. Number of *Sargassum muticum* (a) recruits and (b) adults in field experiment plots (900 cm²). Propagule pressure is grams of reproductive tissue suspended over experimental plots at beginning of experiment. The average mass of an adult *S. muticum* (174 g) is indicated by an arrow. Data are means \pm 1 SE ($n = 3$).

bance treatments (Fig. 1a). Finally, a significant interaction between disturbance and propagule pressure ($F_{5,24} = 3.77$, $P = 0.01$) indicates that the plots in the two disturbance treatments differed in the extent to which they were limited by propagule availability. Multiple regression analysis of the *S. muticum* recruitment data from the control treatment, with space and propagule input as continuous explanatory variables, explained most of the recruitment variability ($R^2 = 0.87$, Fig. 1a). This analysis showed that both space (Fig. 1a, $b = 0.703$, $P < 10^{-4}$) and propagule treatment (Fig. 1a, $b = 0.657$, $P < 10^{-3}$) had strong influences on recruitment in the control treatment. Because there was no variation in space availability in the disturbed treatment, we used simple linear regression analysis to examine the relationship between propagule input and *S. muticum* recruitment in the disturbed treatment (Fig. 1a, $R^2 = 0.84$, $P < 10^{-6}$). The results suggest that in the absence of space limitation propagule input explains most of the variability in *S. muticum* recruitment.

We used these results to create a set of mechanistic candidate functions for the relationship between *S. muticum* recruitment, propagule pressure and space availability (see Appendix S2). The only candidate models supported by the data (AIC differences < 4 ; Burnham & Anderson 2002) show a type 3 (sigmoidal) relationship between propagule pressure and

recruitment, and either a type 2 (saturating) or type 3 relationship between available space and recruitment (Appendix S2, Table B.1). Due to practical constraints on the number of treatments that could be replicated in the field, we have data only on very low available space (control plots) and very high available space (disturbed plots), and insufficient data at intermediate values to resolve the functional relationship between space-limitation and recruitment. We therefore used model averaging (Burnham & Anderson 2002) to combine our parameter estimates for the two supported models and used the resulting function to describe space- and propagule-limitation in recruitment in the simulation model. We also ran simulations using each of the supported recruitment models separately. The results from the two supported models and the averaged model were very similar, so we present results only from the averaged model.

Survivorship (from 5 months to 11 months of age) of *S. muticum* was significantly higher in disturbed plots ($U = 76.5$, $P < 0.05$). Mean survivorship (± 1 SD) in control plots was 3.4% ($\pm 3.8\%$), compared to 6.1% ($\pm 2.2\%$) in disturbed plots. Our analysis of survivorship as a function of recruitment density suggests density-independence (Appendix S2, Table B.2), so we used the mean survivorship across all experimental plots as the germling survival rate (s) in our model.

Simulations of the parameterized model under various disturbance regimes reveal several interesting patterns. Using the disturbance scenario with ubiquitous mollusc disturbances and large, patchily distributed urchin disturbances, we found that a single adult *S. muticum* was almost always sufficient to start a successful invasion. This is in agreement with our empirical observation that propagule input always resulted in positive recruitment, even in space-poor control plots. We quantified population growth in our model by reporting the density of *S. muticum* after 100 years, averaged across the invaded area, and we use the length of habitat occupied by *S. muticum* after 100 years as a measure of invasion rate. When we assumed that *S. muticum* was never consumed by benthic herbivores, both the mean *S. muticum* population density and the length of the invaded area increased with both the mean intensity of mollusc grazing and with the size and number of urchin disturbances (Fig. 2, solid lines). Changing the variance in the intensity of mollusc grazing had essentially no effect (not shown). Unless urchin disturbances were extremely large and numerous (top 3 lines, Fig. 2g–j), the mollusc grazing had a much stronger effect on *S. muticum* density than did urchin grazing.

When we assumed that native grazers eat *S. muticum* germlings, *S. muticum* density and the length of habitat invaded still increased with the intensity of mollusc disturbance, as long as molluscs grazed less than 50% of the habitat bare (Fig. 2, dashed lines). Actual mollusc disturbances are typically much smaller than 50% (personal observation). Indeed, we note that if all of the bare rock in the experiment's control plots was attributed to mollusc grazing, the average grazing intensity would be only 7.7%. Within the realistic range of parameter values, then, molluscs facilitate the invasion in the model even when they consume young *S. muticum*.

Urchin disturbances that were few and/or small had little effect on the invasion, but large and numerous urchin disturbances decreased the final *S. muticum* density and the size of the invaded area when grazers consumed new recruits (Fig. 2e–j). *Sargassum muticum* failed to establish when urchin disturbances were both very large (20–50 m of linear habitat scraped bare per disturbance) and extremely abundant (100–200 such disturbances per year). These results are corroborated by the generalized model of disturbance, which showed that when the total proportion of the habitat disturbed per year is held constant smaller disturbances affecting a greater number of locations resulted in the highest final *S. muticum* densities and invaded areas (Appendix S2, Fig. C.1). When these disturbed locations were more clumped in space, this resulted in a slight decrease in the final size of the invaded area.

The treatment effects were still apparent when adults were counted at the end of the experiment (Fig. 1b). Adult *S. muticum* density was higher in the disturbed treatment than in the control treatment ($Z = -3.41$, $P < 0.001$). In addition, adult *S. muticum* density appeared to be positively related to propagule pressure (Fig. 1b, $H_5 = 16.10$, $P = 0.006$), with high propagule pressure resulting in a maximum of between 20 and 25 adults per plot (900 cm²).

How was the probability of successful invasion influenced by propagule pressure? We defined successful invasion of an experimental plot as the presence of one or more adult *S. muticum* at the end of the experiment (11 months after invasion). We consider this a reasonable way to define invasion success given that reproduction of these adults was imminent (< 1 month away), survivorship is very high at this life-history stage (Appendix S2, Table B.3), and both our model and experimental results indicate that a single individual is capable of establishing a population. We plotted the proportion of plots in each treatment combination that were successfully invaded as a function of propagule pressure (Fig. 3). Because we had only three replicates per treatment combination the probability values were constrained to four possible values (0, 0.33, 0.66, or 1.0). In addition, we tested only six levels of propagule input and therefore have limited capacity to resolve the details of this relationship. Therefore, we did not attempt to fit statistical models to these data. In disturbed plots, invasion was certain even at the lowest level of propagule pressure in our experiment (Fig. 3). However, in control plots the probability of invasion was less than 1 until propagule pressure reached a level of 250 g of reproductive tissue, an amount of tissue greater than the average mass of an adult *S. muticum* (Fig. 3).

Discussion

Our experimental results demonstrate that space- and propagule-limitation both regulate *S. muticum* recruitment. Our finding that *S. muticum* recruitment was positively related to propagule input is similar to those of two previous studies (Parker 2001; Thomsen *et al.* 2006), in which the propagule input of invasive plants was manipulated. In our control

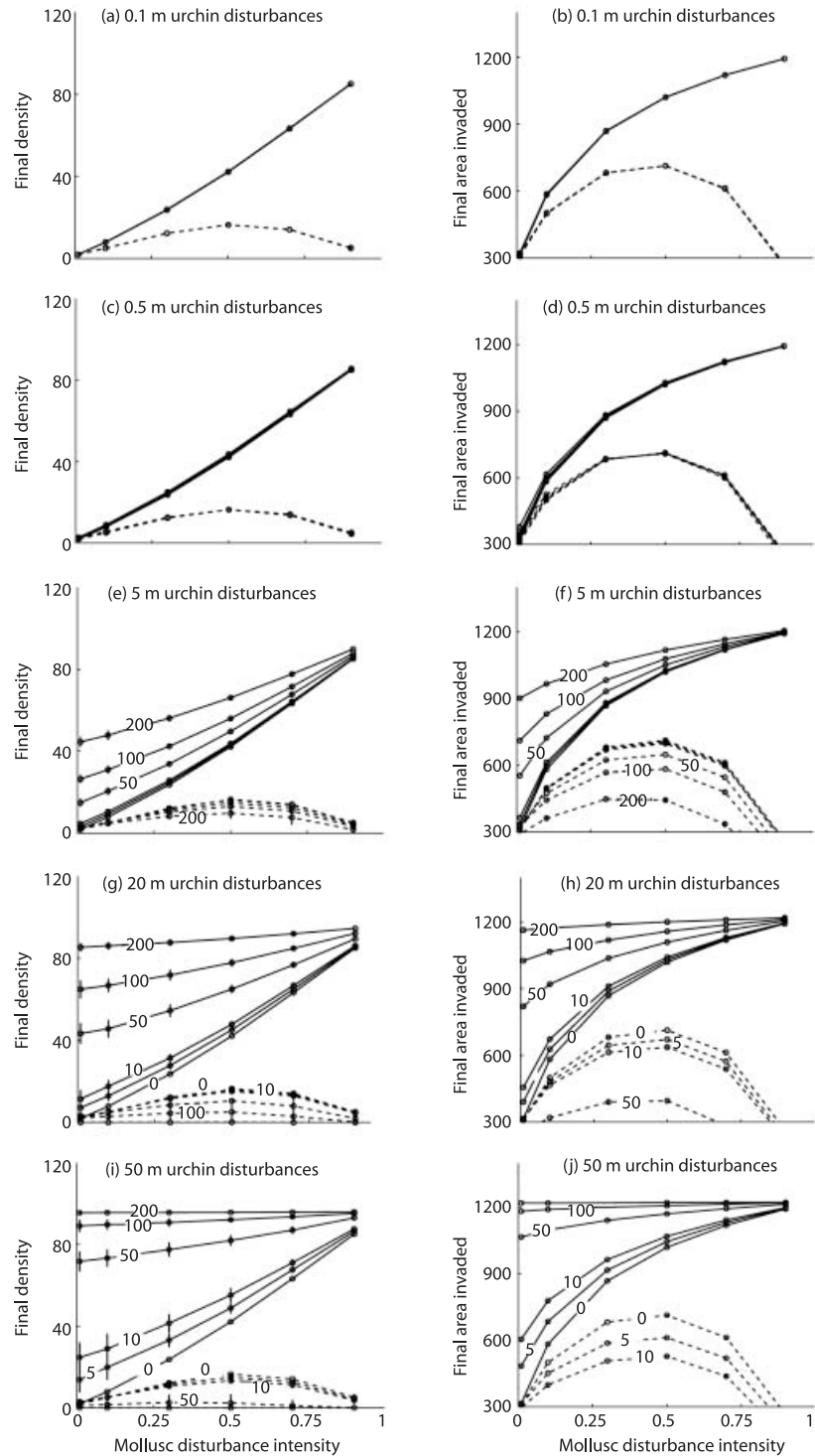


Fig. 2. Simulation results using the mollusc/urchin model for disturbance. The first column (a, c, e, g and i) shows the mean *Sargassum muticum* density (individuals per 900 cm²) and the second column (b, d, f, h and j) show the length of habitat occupied (metres) after 100 years. Solid lines are the results when native grazers never eat *S. muticum* and dashed lines are results when *S. muticum* recruits (less than 1 year old) are eaten by grazers. The x-axis in all plots shows the average proportion of rock scraped bare by molluscs. The number superimposed on each line is the number of urchin disturbances per year (numbers are omitted when the lines overlap completely or are very close together). The mean size of these urchin disturbances increases from the top row (a–b) to the bottom row (i–j) and is printed at the top of each graph. Error bars, when large enough to be visible, are ± 1 SE ($n = 100$, as averages were taken across two values for the variance in mollusc intensity with 50 replicates each).

treatment space was limiting, a result that has also been found in previous studies of *S. muticum* recruitment (Deysler & Norton 1982; De Wreede 1983; Sanchez & Fernandez 2006). Consequently, increasing propagule pressure had a relatively weak effect on recruitment in undisturbed plots (Fig. 1a). However, when space limitation was alleviated by disturbing the plots, increasing propagule pressure caused a dramatic increase in recruitment (Fig. 1a). This suggests that in the presence of adequate substratum for settlement, propagule

limitation becomes the primary factor controlling *S. muticum* recruitment. These results indicate that *S. muticum* recruitment under natural field conditions will be determined by the interaction between disturbance and propagule input.

Only a few previous studies have investigated the effect of resource supply on the relationship between propagule pressure and recruitment of an introduced species. Although disturbance generally increases invasion success by increasing resource availability (Richardson & Bond 1991; Bergelson

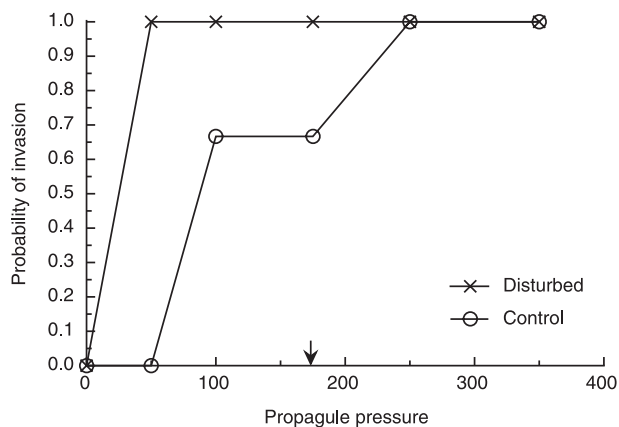


Fig. 3. Probability of invasion as a function of propagule pressure. Probability of invasion is the proportion of plots in each treatment combination ($n = 3$) that contained at least one adult *Sargassum muticum* at the end of the experiment. The average mass of an adult *S. muticum* (174 g) is indicated by an arrow.

et al. 1993; Levin *et al.* 2002; Valentine & Johnson 2003; Clark & Johnston 2005), Parker (2001) found evidence that disturbance reduced Scotch broom (*Cystisus scoparius*) recruitment from seed at all levels of propagule input. This effect occurred because the native flora actually facilitated Scotch broom germination, probably by increasing soil moisture and/or nutrients (Parker 2001). Similarly, Thomsen *et al.* (2006) showed that in the absence of a water addition treatment establishment of an exotic perennial grass was greatly reduced, even at high levels of propagule input. Finally, Valentine & Johnson (2003) found that disturbance facilitated invasion by the introduced kelp *Undaria pinnatifida* even when propagule pressure was high. These studies and our own work provide empirical evidence that the interaction between propagule input and the biotic and abiotic processes that mediate resource availability will be key to understanding patterns of invasion.

The effects of the disturbance and propagule pressure treatments that were manifest in the *S. muticum* recruitment data persisted until the end of the experiment (Fig. 1b). That adult *S. muticum* density was higher in the disturbed treatment than in the control treatment suggests that disturbance may increase the population growth rate of *S. muticum* during the initial stages of the invasion. Natural disturbances that are less intense than our experimental scrapings might have a more modest effect on *S. muticum* density, but our simulation results suggest that even small disturbances can play a major role in facilitating the invasion. Our simulations further suggest that this effect should persist over long time-scales (Fig. 2).

In subtidal habitats both biotic and abiotic disturbances occur, but it is doubtful that they are both relevant to the *S. muticum* invasion in this system. Consumption of algae by the diverse fauna of benthic herbivores in this system (see Methods) is a common and consistent source of disturbance that is

likely to be relevant to the *S. muticum* invasion and was therefore the focus of our model. Abiotic disturbances are unlikely to play an important role in this regard because tidal currents are not a substantial cause of algal mortality in this region (Duggins *et al.* 2003) and the inland waters of Puget Sound, the San Juan Islands and the Strait of Georgia are protected from the ocean swells that play a key role on the outer coast of Washington State. Although locally generated storm waves are an important source of disturbance during the winter (Duggins *et al.* 2003), storms during the summer months when *S. muticum* is reproductive are rare.

SIMULATED URCHIN/MOLLUSC DISTURBANCES

In addition to enhancing *S. muticum* recruitment, disturbance increased the survivorship of juvenile *S. muticum*. In our system, the green urchin (*Strongylocentrotus droebachiensis*) creates relatively large disturbed patches and *S. muticum* that recruit to these patches probably benefit from reduced competition with native algae. Unlike other systems where sea urchins feed on both native and non-native algae alike (Valentine & Johnson 2005), green urchins do not consume adult *S. muticum* (Britton-Simmons 2004) although it is possible that they incidentally consume new recruits. Studies in other systems have also reported positive effects of disturbance on the survivorship of non-native species (Gentle & Duggin 1997; Williamson & Harrison 2002). In general, disturbance probably enhances survivorship because it reduces the size or abundance of native species that compete for resources with invaders (Gentle & Duggin 1997; Britton-Simmons 2006). Indeed, our modelling results suggest that even when juvenile survivorship is reduced by herbivory, the net effect of grazers is still usually positive (Fig. 2).

The simulation model suggested that not all disturbance agents have equivalent effects on space-limitation. Small bare patches throughout the habitat facilitated *S. muticum* spread (Fig. 2 and Appendix S3, Fig. C.1) by increasing the amount of bare rock near any given reproductive adult. Molluscs are ubiquitous in these subtidal habitats and although they typically create very small disturbances, the model suggests that this is sufficient for *S. muticum* to successfully invade, even in the absence of other disturbance agents (e.g. urchins and humans).

Urchins create much larger open spaces, but urchin disturbances could not be used by settling propagules unless a reproductive adult happened to be nearby or a long-distance dispersal event occurred. When there are many urchin disturbances in a year, the chance that such a disturbance occurs near an *S. muticum* adult increases and, because long-distance propagule dispersal is rare, this greatly enhances the likelihood that a propagule will reach the disturbed area. Accordingly, small numbers of urchin disturbances in our model did not affect the spread of *S. muticum* (Fig. 2a–d), but numerous and sufficiently large disturbances did (Fig. 2e–j). Washington State is at the southern end of the green urchin's range in the eastern Pacific and at the majority of sites in the San Juan Islands this species is absent or at relatively low

abundance. Consequently, molluscs are probably the most important source of disturbance for *S. muticum* in this region; green urchins may be a more important disturbance agent in more northerly portions of its range (where it reaches higher densities). That urchin disturbance was not necessary for successful invasion by *S. muticum* in the model is an important result because *S. muticum* has invaded many areas in this region where urchins are absent. Indeed, urchins avoid areas where *S. muticum* is present (Britton-Simmons 2004) and since this effect was not included in the model, urchin disturbances probably contribute even less to *S. muticum* spread than our simulations suggest.

PROPAGULE PRESSURE AND INVASION SUCCESS

How much invasion risk does a given level of propagule pressure pose? Previous studies have demonstrated a positive relationship between propagule pressure and the establishment success of non-native species (Grevstad 1999; Parker 2001; Ahlroth *et al.* 2003; Cassey *et al.* 2005). However, we know very little about the relationship between establishment probability and propagule pressure or the factors that affect it (Lockwood *et al.* 2005). Possibilities include a linear relationship (Lockwood *et al.* 2005) as well as more complex relationships containing thresholds or other non-linearities (Griffith *et al.* 1989; Ruiz & Carlton 2003; Lockwood *et al.* 2005; Buckley *et al.* 2007). Our experimental results suggest that the relationship is non-linear (Fig. 3). Indeed, all communities in which abiotic factors do not preclude invasion are probably vulnerable to invasion such that above some threshold level of propagule input successful invasion is a virtual certainty. Consequently, this relationship must be nonlinear because by definition it saturates at a probability of one. In our system disturbance appeared to reduce the level of propagule pressure necessary to ensure invasion success. However, even control plots had a high probability of invasion once the level of propagule pressure exceeded that produced by an average adult *S. muticum*. Unfortunately, the limited number of treatment levels in our experiment constrains our ability to resolve the details of this relationship. Nevertheless, in the control treatment there was some evidence of a threshold level of propagule pressure below which invasion was very unlikely to occur (Fig. 3).

Our model reflects what we believe to be the most important factors limiting invasion success (propagule-limitation and competition for space) but other factors we did not include in the model, such as stochastic mortality, density-dependent mortality of adults, competition with native species for resources besides space (e.g. light, Britton-Simmons 2006) and abiotic conditions, could constrain *S. muticum*'s distribution and abundance in the field. Empirical studies have demonstrated the importance of biotic resistance in regulating invasions (see reviews by Levine & D'Antonio 1999; Levine *et al.* 2004) and the community that *S. muticum* is invading is no exception (Britton-Simmons 2006). However, some authors have suggested that propagule pressure has the potential to overcome biotic resistance (D'Antonio *et al.* 2001; Lockwood *et al.* 2005). Levine (2000) found that seed

supply overpowered biotic resistance that was generated by plant communities at small spatial scales (18 cm × 18 cm). A more recent terrestrial experiment also reported that propagule pressure was the primary determinant of invasion success, overwhelming the effects of other factors, such as disturbance and resident diversity, which were concurrently manipulated (Von Holle & Simberloff 2005). However, 'propagules' in that study were seedlings transplanted into experimental plots and seedlings may not be regulated by the same factors as seeds, which are the life stage responsible for invasion spread in natural systems. Nevertheless, if propagule pressure can indeed overcome those factors that were not included in our model then one might ask why *S. muticum* has not completely taken over the shallow subtidal zone in this system, as our model predicts under most disturbance regimes. Interestingly, whether *S. muticum* is indeed in the process of doing so is not entirely clear. There are very few areas in the San Juan region where *S. muticum* is completely absent at the appropriate depths (personal observation), yet at many sites *S. muticum* is currently at low abundance and it is unclear whether these sites represent incipient invasions or whether something is inhibiting local population growth.

Conclusions

In our system, neither disturbance nor propagule input alone was sufficient to maximize invasion success (i.e. establishment probability and invader population density). Increasing propagule pressure had relatively little effect on total recruitment in control plots (Fig. 1a), though at high levels it ultimately overcame space limitation and ensured successful invasion (Fig. 3). However, even at high levels of propagule input, final *S. muticum* density was low in the absence of disturbance (Fig. 1b). Based on our experimental results alone, we might have predicted strong effects of both molluscs and urchins on the *S. muticum* invasion in the long term. However, the simulation model suggested that these two natural disturbance agents should have different effects on long-term invasion due to differences in the spatial structure of these disturbances. The model results demonstrate that caution should be exercised when extrapolating the results of short-term disturbance experiments over longer time intervals. In this marine community invasion success was co-regulated by propagule pressure and biotic resistance. Our results underscore the importance of considering interactive effects when making predictions about invasion success.

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Supplementary material

The following supplementary material is available for this article:

Appendix S1. Detailed diet information for benthic, subtidal mollusc species.

Appendix S2. Model parameter values and functions.

Appendix S3. Models for disturbance.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2745.2007.01319.x>

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