

The roles of competition and disturbance in a marine invasion

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Abstract

Two hypotheses for the decline of native species are the superior exploitation of disturbance by exotic species and the competitive displacement of native species by their exotic counterparts. Theory predicts that functional similarity will increase the intensity of competition between native and invasive species. Ecologically important “foundation” species, *Zostera marina* and other seagrasses have globally declined during the past century. This study used transplant and vegetation removal experiments to test the hypotheses that disturbance and competitive interactions with an invasive congener (*Z. japonica*) are contributing to the decline of native *Z. marina* in the northeastern Pacific. Interspecific competition reduced *Z. marina* and *Z. japonica* above-ground biomass by 44 and 96%, respectively, relative to intraspecific competition. Disturbance substantially enhanced *Z. japonica* productivity and fitness, and concomitantly decreased *Z. marina* performance, effects that persisted two years following substratum disturbance. These results demonstrate that disturbance and competitive interactions with *Z. japonica* reduce *Z. marina* performance, and suggest that *Z. japonica*'s success as an invasive species stems dually from its ability to persist in competition with *Z. marina* and its positive response to disturbance. These results highlight the importance of understanding the interconnected roles of species interactions and disturbance in the decline of seagrass habitats, and provide a rationale for amending conservation policy in Washington State. In the interest of conserving native eelgrass populations, the current policy of protecting both native and invasive *Zostera* spp. should be refined to differentiate between native and invader, and to rescind the protection of invasive eelgrass.

Introduction

Understanding factors that control the establishment and spread of invasive species is a major goal of ecology and invasion biology. Competitive interactions with native species influence the establishment and spread of invasive populations (e.g., Corbin and D'Antonio 2004) and are important mechanisms of invader impacts to native taxa (e.g., Morrison 2000; Brown et al. 2002; Branch and Steffani 2004). The consequences of competition with resident species for

invasion success are the basis of the hypothesized link between native species richness and invasion resistance. According to the diversity–invasion resistance hypothesis, speciose communities are less invasible than depauperate communities because fewer unexploited resources are available to invaders (Elton 1958; Case 1990; Stachowicz et al. 2002). Recent niche theory has corroborated the link between species richness and invasion resistance by linking resource competition between native and invasive species to reductions in invader “niche opportunities”, or conditions

favoring establishment (Shea and Chesson 2002). Unless resources are spatially or temporally partitioned, species with similar resource and habitat requirements are predicted to compete intensely (Dudgeon et al. 1999). Thus, strong competition is expected to arise between functionally similar native and invasive species.

Many invasive species are, however, weak competitors whose establishment and spread is facilitated by disturbance. Often a key determinant of the invasibility of natural communities (Elton 1958; Moyle 1986; Mack 1989; Minchinton and Bertness 2003), disturbance can facilitate invasion success by removing competitively superior native species, by mediating interactions between native and invasive species, or by physically or chemically altering the environment in ways that favor invaders (Lake and Leishman 2004). Perennial, native eelgrass (*Zostera marina*) is the dominant macrophyte of low intertidal and shallow subtidal flats in the northeastern Pacific (i.e., the Pacific Northwest coast of North America). On low intertidal flats, it co-occurs with annual, invasive dwarf eelgrass (*Z. japonica*). *Z. japonica* is rapidly invading both unvegetated mudflats and vegetated flats historically dominated by intertidal *Z. marina* populations. Like many kelps, mangroves and corals, *Zostera* spp. and other seagrasses are “ecosystem engineers” (sensu Jones et al. 1994, 1997) that physically modify substrate and water column characteristics and provide the structural foundation for their associated communities (Orth 1977; Heck and Orth 1980; Fonseca et al. 1982). Assessing their relative competitive abilities and responses to disturbance are important to understanding their interaction, which has direct implications for the management and conservation of intertidal seagrass habitats in the Pacific Northwest.

The occurrence of *Z. japonica* in the Pacific Northwest was first recorded in 1957, in the southern Washington estuary of Willapa Bay (Harrison and Bigley 1982). It was probably introduced with Pacific oyster (*Crassostrea gigas*) aquaculture stock shipments, which have been imported from Japan to Willapa Bay since the 1920s (Phillips 1984). Willapa Bay is one of the leading oyster-growing regions in the U.S., producing approximately 15% of the national harvest (Dumbauld et al. 2000, B. Dumbauld, pers.

comm.). *Z. japonica* currently occupies the majority of intertidal mudflats in Willapa Bay and has also spread to several estuaries between the Coquille River Estuary, Washington, and the southern Strait of Georgia, British Columbia (Larned 2003). In invaded estuaries, native *Z. marina* and introduced *Z. japonica* can overlap in tidal elevational ranges and occupy vast mixed-species meadows.

In the species' native ranges, *Z. marina* is widely distributed in the Pacific and Atlantic basins, and *Z. japonica* occurs between northeastern Russia and tropical Vietnam (den Hartog 1970). Little is known of the interaction of *Z. marina* and *Z. japonica* in either their native or introduced habitats (but see Nomme and Harrison 1991a, b). Although native Asian populations of the species co-occur, the Pacific Northwest population of *Z. marina* has evolved in the absence of *Z. japonica* and could experience fitness reductions as the result of novel interactions with its congener.

Understanding the interaction between *Z. marina* and *Z. japonica* is germane to the management and conservation of seagrass habitats, which have globally declined over the past century. These declines have generated considerable ecological and economic concern, as seagrasses perform vital ecosystem services, including primary production, habitat generation for ecologically and economically important finfish and shellfish species, and shoreline buffering from erosion and eutrophication (Phillips and Menez 1988; Alberte et al. 1994; Williams and Davis 1996). *Z. marina* is the most abundant seagrass in the Northern Hemisphere (Baden et al. 2003) and the dominant native macrophyte of Pacific Northwest mudflats. It has experienced an unquantified decrease from its historical distribution in Washington State (Levings and Thom 1994). Seagrass declines have been attributed to a number of factors, including coastal development, sediment and nutrient loading, and disease (Short and Wyllie-Echeverria 1996; Williams and Davis 1996; Green and Short 2003). This study is the first to experimentally assess the roles of disturbance and competition with an invasive seagrass in the decline of a native seagrass.

In response to regional native seagrass declines, the state of Washington has adopted a

“no-net-loss” policy for the management of eelgrass habitats (Pawlik and Olson 1995). This policy is based on the documented habitat values of native eelgrass beds to fish and wildlife, including the importance of intertidal beds as foraging habitats for shorebirds and waterfowl (Fresh 1994; Hershman and Lind 1994; Wyllie-Echeverria et al. 1995). At present, the policy does not distinguish between invasive *Z. japonica* and native *Z. marina*. Hence, the species are conferred equal protection, despite the paucity of information on their interaction and on the ecological value of *Z. japonica* habitats (but see Posey 1988). However, if interactions with *Z. japonica* are contributing to *Z. marina* declines, the protection of invasive eelgrass may conflict with the conservation of native eelgrass habitats. Data on the impacts of *Z. japonica* invasions to *Z. marina* are needed to formulate appropriate management and policy responses to the spread of *Z. japonica*.

This study used manipulative competition and disturbance experiments to evaluate the relative competitive abilities of *Z. marina* and *Z. japonica* and to compare the species' responses to disturbance. The specific objectives were to (1) compare the relative effects of intra- and interspecific competition on growth and productivity, and (2) determine the effects of disturbance on above-ground biomass and reproductive output (a proxy for fitness). Nomme and Harrison (1991 a, b) implicitly evaluated the interaction between *Z. marina* and *Z. japonica* by (1) comparing *Zostera* spp. morphology in monospecific patches (sods) transplanted into three different tidal zones, and by (2) conducting multivariate analyses of individuals in naturally established mixed and monospecific beds. In their study, monospecific *Zostera* spp. beds were located in different tidal zones than mixed beds, potentially confounding the effects of species interactions with that of tidal elevation. In contrast, this study employed experimental manipulations that controlled for tidal elevation and explicitly tested for interaction between the two congeners. The results of this study provide a basis for re-evaluating current management policies for seagrass species, and demonstrate how understanding species' interactions and autecology can contribute to species conservation and invasive species management.

Methods

Study system

Field experiments were conducted from July 2002 to June 2004 at Stackpole Slough in the Willapa National Wildlife Refuge in northwestern Willapa Bay, Washington (124°06' W, 46°24' N). Willapa Bay is a shallow, 260-km² estuary that contains approximately 18,800 ha of intertidal mudflats and extensive *Zostera* spp. beds. Annual *Z. japonica* typically occupies tidal elevations of +1 to +3 m relative to mean lowest low water (MLLW), and perennial *Z. marina* typically occupies elevations of -1 to +2 m MLLW (Dumbauld and Wyllie-Echeverria 2003). This study evaluated the interaction between the two species in their range of tidal elevational overlap (+1 to +2 MLLW). In this zone of overlap, *Z. marina* forms a taller canopy and grows in lower shoot densities than *Z. japonica*. Background data on percent cover, shoot lengths, and shoot densities were collected in the mixed eelgrass zone of Stackpole Slough in 2001 along 21 random transects perpendicular to the shoreline. The average shoot lengths of *Z. marina* and *Z. japonica* were 76.77 ± 28.29 cm and 31.84 ± 12.99 cm, respectively (all values herein are mean ± one standard deviation). Background shoot densities per 0.25 m² were 14.30 ± 14.60 for *Z. marina* and 82.70 ± 70.25 for *Z. japonica*. Average percent cover in 0.25 m² quadrats was 48.4 ± 34.88% for *Z. marina* and 54.80 ± 34.62% for *Z. japonica*. Previous studies have demonstrated that variation in seagrass habitat structure can influence infaunal community structure (Webster et al. 1998), habitat use by fishes (Jenkins and Sutherland 1997), and algal recruitment and mortality (Inglis 1994). Thus, morphological and structural differences between *Z. marina* and *Z. japonica* may translate to differences in the structure and ecological functions of their associated communities (but see Posey 1988).

Competition experiment

Experimental design

In July 2002, 27 0.25-m² study plots were established in an intertidal mixed-eelgrass meadow on

a transect parallel to the shoreline. Nine blocks of three 0.5×0.5 -m plots were cleared by hand of all existing above- and below-ground vegetation. In addition, 0.5-m wide buffer zones were cleared around plot margins to prevent the encroachment of surrounding vegetation. Plots within blocks were spaced by 2 m and blocks were separated by 5–10 m. A shallow layer of water (1–3 cm) covered all plots during low tides. Three treatments were randomly assigned to plots within each block: monospecific *Z. japonica*, mixed-species, and monospecific *Z. marina*.

Transplants were collected from a mixed-eelgrass meadow adjacent to the study site. Eight individuals were transplanted into each plot in an even array, with four individuals of each species planted for the mixed-species treatment. Each transplanted individual consisted of a terminal ramet, its adjacent ramet (short shoot), and their shared root–rhizome complex. The ramet density of transplants in the experimental plots ($16/0.25 \text{ m}^2$) was within the natural range of *Zostera* spp. ramet densities in Willapa Bay. Mean leaf lengths, recorded at the time of transplanting, were 70.9 ± 25.5 cm for *Z. marina* transplants and 27.1 ± 14.6 cm for *Z. japonica* transplants ($n=108$). Transplants were rinsed of sediments and anchored in the substratum with 20-cm long ground staples.

The 27 plots were monitored for transplant survival and maintained at 2-week intervals by clearing any vegetation that had encroached from the vegetated outer mudflat into the 0.5-m buffer zones surrounding study plots. No transplants encroached from the study plots into the buffer zones. Transplants were allowed to recover from transplant shock for 1 month prior to marking leaves for leaf growth rate estimates. Leaves were marked on 21 and 22 August 2002 and all above-ground biomass was harvested on 7 September for leaf growth rate and dry-weight (DW) biomass measurements.

Although this experiment was conducted using a randomized complete block design (RCBD), block effects were non-significant for biomass and leaf growth rate responses and treatment effects were subsequently analyzed in a completely randomized design (CRD) framework. Variations in biomass and leaf growth rates between treatments were analyzed for both species

with one-way analysis of variance (ANOVA) in JMP 5.0 (SAS 2002).

Leaf growth rates and above-ground biomass

Leaf growth rates were measured with a variation of Zieman's (1974) leaf-marking technique, in which each non-growing leaf sheath and its enclosed growing leaves were punctured with sewing pins. Transplant leaves were marked with two adjacent pinholes to aid in the differentiation of leaf-marking scars from other leaf damage. Approximately 2 weeks after leaf marking, transplants were revisited and all above-ground biomass was clipped, bagged, and transported to a laboratory for measurement. Leaves were wiped clean of epiphytes and leaf growth rates were measured as the distances between pinhole scars on the leaf sheaths and leaves, divided by the number of days between marking and measurement. One leaf was randomly selected from each shoot for measurement. After leaf growth measurements were conducted, the contents of each plot were separated by treatment and species. Samples were dried in paper bags in a drying oven for 14 days at 60°C for DW biomass measures.

Interaction intensities

Relative interaction intensities were calculated for each species to evaluate the symmetry of inter- and intraspecific competition. Relative competition intensity (RCI) and log response ratio ($\ln \text{RR}$) were calculated as metrics of competitive intensity based on experimental biomass measurements. RCI is the most commonly used interaction strength metric in experimental plant ecology (Goldberg et al. 1999) and is most commonly applied with biomass as a response variable. RCI was calculated as $\text{RCI} = (X_{\text{monospecific}} - X_{\text{mixed}}) / X_{\text{monospecific}}$ where X = final individual biomass. To address the morphometric differences between the two study species, standardized interaction intensities were also calculated as $\ln \text{RR} = \ln(X_{\text{monospecific}} / X_{\text{mixed}})$. A RCI of 0 indicates no effect of interspecific interaction; a positive RCI indicates competition (i.e., reduced performance); and a negative RCI indicates facilitation (enhanced performance).

Disturbance experiment

Experimental design

The destructive vegetation sampling in September 2002 of the 27 plots utilized in the transplant experiment constituted the vegetation removal treatment for the disturbance experiment. The disturbance associated with vegetation removal was roughly analogous to several forms of disturbance common to mudflat habitats (e.g., shellfish dredging, crushing by watercraft, and trampling), though perhaps more severe because all above- and below-ground vegetation were removed. The plots were allowed to naturally revegetate for 2 years. In June 2004, all above-ground biomass was collected from the original 27 0.25-m² plots to assess the recovery of *Z. marina* and *Z. japonica* following disturbance. In addition, 27 0.25-m² control plots were randomly sampled from a transect parallel to and spaced 2 m from the experimental plots. In the shallow bathymetry of Willapa Bay mudflats, a 2-m distance on a tidal plain is insufficient to produce a detectable difference in tidal elevation, provided that channels are avoided. Disturbance and control plots were thus located at equivalent tidal elevations. The following variables were measured for each species in each plot: (1) number of shoots, (2) number of flowering shoots, (3) average number of inflorescences per shoot, (4) maximum number of inflorescences per flowering shoot, and (5) average shoot length of five randomly selected shoots (or all shoots if fewer than five were present). After these measurements were completed, samples were dried for 14 days at 60 °C for DW biomass measures.

Results

Competition experiment

Above-ground biomass

The final mean above-ground biomass of *Z. marina* individuals was 55% higher in the monospecific treatment plots than in the mixed-species treatment plots (ANOVA; $F_{1,17}=9.01$; $P<0.01$; Figure 1). Mean above-ground biomass of *Z. japonica* was 165% higher in the monospecific plots than in the mixed-species plots (ANOVA; $F_{1,14}=7.80$; $P=0.015$; Figure 1).

Leaf growth rates

Mean daily leaf growth rates of *Z. marina* in the mixed-species treatment did not differ from that in the monospecific treatment plots (ANOVA; $F_{1,17}=1.43$; $P=0.25$; Figure 1). Similarly, the mean leaf growth rate of *Z. japonica* did not differ between mixed (0.46 ± 0.22 cm, $n=7$) and monospecific treatment plots (0.78 ± 0.53 cm, $n=9$) (ANOVA; $F_{1,17}=1.43$; $P=0.25$; Figure 1).

Interaction intensities

In both species, RCI and ln RR demonstrated that interspecific competition had much stronger negative effects on above-ground biomass than intraspecific competition. RCI values indicated that interspecific competition reduced *Z. marina* biomass by 35% (RCI=0.35) and *Z. japonica* biomass by 62% relative to intraspecific competition. Similarly, ln RR values indicated that interspecific competition reduced *Z. marina* and *Z. japonica* biomass by 44 and 96%, respectively.

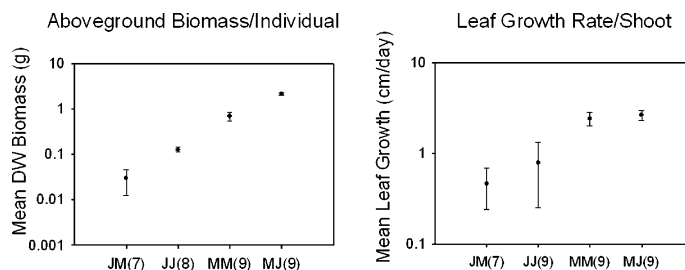


Figure 1. Competition experiment. Mean values \pm 1 SD for *Z. marina* and *Z. japonica* response variables in the presence and absence of congeners. Sample sizes (number of plots) are in parentheses. JM = *Z. japonica* in mixed plots, JJ = *Z. japonica* in monospecific plots, MM = *Z. marina* in monospecific plots, and MJ = *Z. marina* in mixed plots.

Disturbance experiment

Productivity

Disturbance resulted in a 14-fold reduction in *Z. marina* biomass ($F_{1,53}=163.4$; $P<0.0001$), a 4-fold reduction in shoot density ($F_{1,51}=79.2$; $P<0.0001$), and a 50% reduction in average shoot length ($F_{1,48}=78.4$; $P<0.001$; Table 1). In contrast, disturbance was associated with an 11-fold increase in *Z. japonica* biomass ($F_{1,52}=21.6$; $P<0.0001$), a 12-fold increase in shoot density ($F_{1,51}=33.1$; $P<0.0001$), and no effect on shoot length. Thus, while the biomass of the native decreased 14-fold, that of the invader increased 11-fold, giving the invader a massive [(14 × 11)-fold] advantage in disturbed plots ($F_{1,48}=0.05$; $P=0.83$; Table 1).

Reproductive output

Disturbance had no effect on the number of *Z. marina* flowering shoots produced per plot ($F_{1,52}=1.52$; $P=0.22$) or the average number of inflorescences per flowering shoot ($F_{1,9}=3.56$; $P=0.81$). However, disturbance was associated with a 6-fold decrease in the maximum number of inflorescences per *Z. marina* flowering shoot ($F_{1,9}=14.0$; $P<0.01$). In contrast, disturbance resulted in a 19-fold increase in *Z. japonica* flowering shoot production ($F_{1,53}=6.25$; $P=0.016$), but had no effect on average number of inflorescences per shoot ($F_{1,21}=0.062$; $P=0.81$) or the maximum number of inflorescences per flowering shoot ($F_{1,21}=0.0058$; $P=0.94$; Table 1).

Discussion

Although *Z. japonica* is common and abundant in Willapa Bay and other invaded estuaries, its impacts on native communities and ecosystems remain poorly understood. The consequences of *Z. japonica* invasion on native eelgrass, and the functional differences between native and invasive eelgrass, are questions of immediate relevance to management. Previous studies have demonstrated that *Z. japonica* invasions alter estuarine nutrient dynamics (Hahn 2003; Larned 2003), cause sediment and infaunal community changes (Posey 1988), and modify waterfowl foraging habitats (Baldwin and Lovvorn 1994). *Z. japonica*'s impacts on fish and shellfish have yet to be evaluated, but structural differences between *Z. japonica* and *Z. marina* beds may translate to differences in planktonic larval retention and the quality of epibenthic nursery and feeding habitats (e.g., Jenkins and Sutherland 1997; Webster et al. 1998). This study is the first to empirically demonstrate the strength and asymmetry of interspecific competition between *Z. marina* and *Z. japonica*, and the differential effects of disturbance on the performance of each species.

The competition experiment revealed that both species experienced substantial reductions in above-ground biomass in response to interspecific competition, relative to intra-specific competition. The relative reduction in biomass was greater for *Z. japonica*, indicating that *Z. marina* is a better competitor in the absence of disturbance. However, when the species were

Table 1. Disturbance experiment.

Response Variable	<i>Zostera marina</i>		<i>Zostera japonica</i>	
	Disturbed	Control	Disturbed	Control
Biomass (g)	1.46 (1.90)**	20.2 (7.39)**	3.36 (3.39)**	0.29 (0.52)**
# Shoots	5.19 (5.05)**	22.3 (8.48)**	123 (1.1)**	10.2 (12.0)**
# Flowering shoots	0.11 (0.33)	0.37 (1.00)	5.56 (10.9)*	0.30 (1.03)*
Ave # Inflorescences/Shoot	2.00 (1.00)	6.94 (4.35)	2.33 (1.06)	2.17 (0.76)
Max # Inflorescences/Shoot	1.50 (1.29)*	8.83 (3.71)*	3.42 (1.89)	3.33 (1.53)
Average shoot length	43.1 (13.4)**	92.3 (23.0)**	27.2 (11.0)	27.9 (9.78)

Mean values (standard deviations in parentheses) for *Z. marina* and *Z. japonica* response variables in disturbed and control plots.

*0.001 < P < 0.05; ** P < 0.001.

subjected to disturbance, *Z. japonica* productivity and fitness improved dramatically, while *Z. marina* performance correspondingly declined. Thus, disturbance and some competitive ability (i.e., the ability to persist in competition with *Z. marina*) appear to underlie the invasiveness of *Z. japonica*. *Z. japonica*'s positive response to disturbance is particularly relevant to its invasion success, as tidal flats are dynamic systems that experience high levels of natural and anthropogenic disturbance, including bioturbation, coastal development, boating, shellfish culture, and in some regions, invasive smooth cordgrass (*Spartina alterniflora*) control. The additive and/or synergistic effects of disturbance and competition with *Z. japonica* could have profoundly negative effects on intertidal *Z. marina* and its associated community.

Previous studies that have assessed the effects of competition and disturbance on plant invader success have frequently demonstrated that exotic dominance is determined by the interaction of competitive traits with disturbance. Gerlach and Rice (2003) demonstrated that star thistle (*Centaurea solstitialis*) invasiveness stemmed from the species' ability to persist in competition with annual grasses, combined with its plastic growth and reproductive responses to disturbance. In contrast, the competitive dominance of Scotch broom (*Cytisus scoparius*) (Paynter et al. 2003) and some invasive perennial grasses (MacDougall and Turkington 2004) appear to depend on the absence of disturbance. Ultimately, an invader's success may depend on the interaction of competitive abilities, disturbance regime, and the availability of limiting resources (MacDougall and Turkington 2004).

Possible mechanisms for the performance reductions observed in association with competition and disturbance include light and nutrient limitation. Impaired water clarity, epiphyte loading, and overgrowth by macroalgae are all plausible outcomes of disturbance that would result in eelgrass decline driven by light limitation (Hauxwell et al. 2003). Competition for nutrients may be a common phenomenon among seagrasses, which are often nutrient-limited (Short 1983; Dennison et al. 1987), and simultaneously exploit nutrients in sediments and the water column (Iizumi and Hattori 1982; Thursby and Harlin

1982; Short and McRoy 1984; Williams and Ruckelshaus 1993). *Z. japonica* has a higher surface area–volume ratio and a higher NO₃ influx rate per above-ground biomass unit than *Z. marina* (Larned 2003), which suggests that it is a superior competitor for water-column nutrients.

Considering the responses of foundation species to varying disturbance intensities is necessary to formulate effective management plans for habitats that experience dynamic disturbance regimes. The disturbance experiment demonstrated the dramatic and persistent enhancement of *Z. japonica* fitness, and reduction of *Z. marina* fitness, following disturbance. The competition experiment demonstrated that interspecific competition between *Z. marina* and *Z. japonica* was stronger than intraspecific competition. Stronger inter- than intraspecific competition is destabilizing, and may accelerate the displacement of *Z. marina* by *Z. japonica*. Previous studies have suggested that *Z. marina* and *Z. japonica* perform similar ecological functions (e.g., Posey 1988). The disparities in *Zostera* species' responses to disturbance highlight the importance of studying the autecology and interactions of native and invasive species that appear to be functionally similar.

These experimental results, combined with the simultaneous irruption of *Z. japonica* and decline of *Z. marina* in the Pacific Northwest, strongly suggest that disturbance and interactions with *Z. japonica* are factors in *Z. marina* declines. Estuarine mudflats are subject to high levels of natural and anthropogenic disturbance. Since *Z. japonica* is able to persist in competition with *Z. marina*, and since disturbance confers a substantial and persistent fitness advantage to *Z. japonica*, the invader is likely to dominate disturbed areas, to the detriment of its native congener. Although this study did not mechanistically link the results of the competition and disturbance experiments to naturally occurring *Z. marina* declines, they are consistent with observed patterns of decline. The results of this study suggest that the current Washington State policy of conferring blanket protection to any *Zostera* spp. is inconsistent with the goal of protecting native eelgrass. The effective conservation of intertidal *Z. marina* habitats may require refining this policy to differentiate between native and invasive eelgrass species. Although additional information is needed to determine the

relative costs and benefits of controlling *Z. japonica*, the information at hand suggests that at the very least, the protection of invasive eelgrass should be rescinded in the interest of conserving native intertidal eelgrass habitats.

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