

Buried alive: an invasive seagrass (*Zostera japonica*) changes its reproductive allocation in response to sediment disturbance

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ABSTRACT: Disturbance has both direct and indirect effects that may allow non-native species to proliferate outside of their native range. Disturbance facilitates invasions indirectly by mediating negative interactions with native species, but less is known about the role of direct effects, which are typically considered to be negative. However, the direct effects of disturbance may increase spread of the invader if the damage causes reallocation of resources to reproduction. To examine this possibility, we considered the direct effects of disturbance on reproductive allocation of the dwarf eelgrass *Zostera japonica* Aschers. & Graebn. across different sediment disturbance regimes in Yaquina Bay, Newport, Oregon, USA. We pair data from 2 yr of monitoring at 6 sites with a field experiment at 3 sites. Both the observational and experimental studies showed that there was a negative linear relationship between vegetative biomass of *Z. japonica* and sediment deposition among the sites; the experiments showed a 50% decline at sediment deposition of $\sim 1 \text{ cm mo}^{-1}$ and nearly 100% decline at rates above $\sim 3.5 \text{ cm mo}^{-1}$. The experiments also showed that flowering responded unimodally to increasing sediment deposition; it was greatest at sediment deposition rates of $\sim 0.75 \text{ cm mo}^{-1}$ and declined at $\sim 1.5 \text{ cm mo}^{-1}$, and for rates up to 1.0 cm mo^{-1} , flowering biomass was negatively correlated with vegetative biomass, suggesting a tradeoff was occurring. The results show that there are tradeoffs in resource allocation in response to disturbance, favoring sexual reproduction as a potential escape response to increasing severity.

KEY WORDS: Disturbance experiments · Direct effects · Resource allocation · Reproductive strategy · Biological invasion · Sedimentation · Seagrass · Tradeoff · *Zostera japonica*

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INTRODUCTION

Disturbance is both a natural and human-induced process that causes the loss of biomass or mortality of individuals, which ultimately can have direct and indirect consequences for populations and communities (Rykiel 1985, Sousa 2001). A direct effect of disturbance results when individuals are damaged or killed and may lead to an indirect effect by freeing up resources for other individuals or species. The balance of direct and indirect effects can influence species abundance, distribution, and ultimately the diversity of communities (Connell 1978).

Since Elton (1958), disturbance has been considered an important factor affecting species invasions (see D'Antonio et al. 1999 for review). Often, studies focus on the indirect facilitation of non-native species when disturbance creates gaps and decreases competition with native species. However, much less is known about the direct effects of disturbance on non-native species establishment and whether disturbance might be an important mechanism hindering invasion or thwarting it all together (except see Buckley et al. 2007). In particular, it is of interest to understand the disturbance regimes non-native species experience, what effect the disturbance regimes

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may have on the spread of potential invaders, and whether changes in these regimes could make communities more susceptible to invasion and thus of management concern (D'Antonio et al. 1999).

We might expect that because disturbance causes the loss of biomass or mortality, the direct effects on invaders will generally be negative and increase with the severity of the disturbance. However, the potential exists for positive direct effects of disturbance on invaders if disturbance causes an increase in reproductive effort. For this to occur, we would predict that disturbance could force tradeoffs between the allocation of resources to growth and reproduction, with those tradeoffs favoring reproduction as disturbance severity increases. This then could result in the potential colonization of new sites and the spread of the invasion.

One type of non-native functional group where we might see tradeoffs increase invasion success are clonal plants, particularly grasses (e.g. Lambrinos 2001, Hacker & Dethier 2009). In grasses, reproduction occurs via vegetative growth (i.e. branching of a rhizome or underground stem) and sexual reproduction (i.e. flowering and the production of seeds). Overall, plants must partition a finite number of resources between growth, defense, and reproduction, with ideal allocation maximizing fitness given the current environmental conditions (e.g. Bazzaz et al. 1987, Loehle 1987). For example, if a particular genotype is well suited to the local environment, then a clonal strategy may be favored rather than risking the alteration of key traits by sexual reproduction, whereas a genotype that is not well suited to the local environment may favor sexual reproduction to increase adaptive ability (Lambrinos 2001).

A simple model can be devised that considers the effects of disturbance on life history tradeoffs of vegetative production versus sexual reproduction in plants (Fig. 1). We hypothesize that as disturbance severity increases, vegetative biomass will decline until there is complete mortality of the population. Moreover, we suggest that flowering biomass will increase with disturbance to some intermediate level but then decline as disturbance severity increases. This increase in flowering biomass is the result of a tradeoff in which individuals reallocate resources from vegetative biomass to flowering biomass as disturbance increases the mortality risk and reduces the fitness of clonal progeny. This tradeoff results in a negative relationship between vegetative and flowering biomass as disturbance increases in severity to intermediate levels. Ultimately, that tradeoff is not possible at high levels of disturbance, where mor-

tality decreases both vegetative and reproductive biomass.

Here, we use empirical data to explore this model as it applies to a non-native species. In particular, we considered the effects of disturbance on the reproductive allocation of a clonal plant, the dwarf eelgrass *Zostera japonica* Aschers. & Graebn., across different sediment disturbance regimes in Yaquina Bay, a North American Pacific coast estuary in central Oregon. *Z. japonica* is an intertidal eelgrass species originally native to the estuaries along the Western Pacific Ocean, from subtropical Vietnam to the Kamchatka Peninsula (Den Hartog 1970). It was accidentally introduced to estuaries along the Eastern Pacific Ocean within the past century (Harrison 1982a), possibly as packaging material in shipments of Japanese oyster *Crassostrea gigas* aquaculture (Wonham & Carlton 2005). It is not known how many times *Z. japonica* was introduced, but it currently occupies most estuaries from Northern California to Southern British Columbia and, given its broad temperature and salinity tolerances, is likely dispersal-limited in the south (Larned 2003, Shafer et al. 2008, Kaldy & Shafer 2011).

In its non-native range, *Z. japonica* invades the high elevation zone of un-vegetated intertidal mudflats, with ranges reported between +1 and +3 m above mean lower low water (MLLW) (Dumbauld & Wyllie-Echeverria 2003, Kaldy 2006), and often co-occurs with the native burrowing shrimp, *Neotrypaea californiensis* (Dumbauld & Wyllie-Echeverria 2003), as well as in beds of shellfish species used for aquaculture (Tsai et al. 2010). In some cases, *Z.*

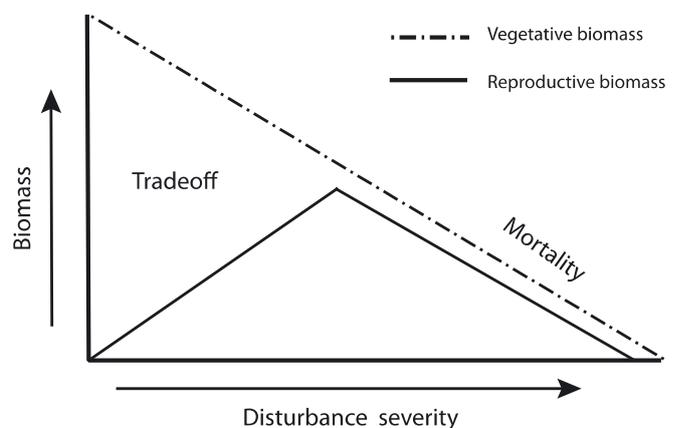


Fig. 1. Conceptual model diagramming the relationship between disturbance severity and the vegetative (asexual) and reproductive (sexual) biomass in a clonal plant. As disturbance severity increases, tradeoffs in the allocation of resources results in increased sexual and decreased asexual biomass. At high levels of disturbance, there is increased mortality, reducing the overall biomass of the plant

japonica patches may abut or intermingle with the native congener, *Zostera marina*, though generally the 2 species are spatially separated (see Shafer et al. 2014 for a description of zonation in *Z. japonica*). In its invaded range, reproductive shoots have been found to compose 2 to 70% of the total population (Harrison 1982b, Kaldy 2006), and recruitment from seeds has been reported as high as 30% of the individuals within a population (Ruesink et al. 2010).

The influence of biotic and abiotic environmental factors on flowering in *Z. japonica* is not well understood. Observational studies show differences in flowering among years at a site (Harrison 1982a, Kaldy 2006), among sites in an estuary (Larned 2003, Ruesink et al. 2010), and with latitude across the Pacific Northwest (Shafer et al. 2014). One experiment, in which disturbance was induced by a pulse removal of above- and below-ground biomass of *Z. japonica*, showed a 19-fold increase in flowering shoots compared to control plots after 2 yr of recovery from the disturbance manipulations (Bando 2006). In addition, research on *Z. marina* and sediment disturbance shows an increase in sexual reproduction in disturbed versus undisturbed environments (Keddy & Patriquin 1978, Meling-López & Ibarra-Obando 1999). Thus, there is convincing evidence that sediment disturbance could contribute to *Z. japonica* spread, potentially through tradeoffs in asexual and sexual reproduction.

The soft-bottomed intertidal mudflat habitat *Z. japonica* invades is prone to sediment disturbance driven by a number of abiotic and biotic processes. Peterson et al. (1984) considered the hydrology, and the resultant effects on sediment transport, in 6 estuaries that were classified as sharing similar hydrographic characteristics (area, volume, depth, freshwater discharge, and tidal prism) to Yaquina Bay, Oregon. They found that sediment transport occurs both landward and seaward, with fine sediments (silts and clays) being carried seaward during high freshwater-discharge events, and sand being carried into the estuary during high tides. Once deposited in the estuary, sediments become entrained in smaller-scale abiotic processes such as wind-driven waves, which primarily affect sites with open embayments (Norkko et al. 2002), and the seasonal migration of sediment to different elevations depending on the turbidity maxima (Bale et al. 1985). Finally, another major factor influencing sediment movement is bioturbation by the burrowing shrimp *N. californiensis*, whose burrowing activity can negatively impact the expansion of *Z. japonica* (Harrison 1987, Dumbauld & Wyllie-Echeverria 2003).

To examine the possibility that sediment disturbance can exert changes in resource allocation in the invasive eelgrass *Z. japonica*, we performed observational and experimental studies within Yaquina Bay, Oregon USA. We asked the following questions: (1) Does a correlation exist between sediment deposition and the allocation to vegetative growth and sexual reproduction in *Z. japonica*? (2) If so, at what sediment deposition rates do tradeoffs in vegetative growth and sexual reproduction occur for *Z. japonica*, and how might this affect its spread? To answer these questions, we monitored *Z. japonica* vegetative and sexual reproduction dynamics in a 2 yr survey at 6 sites representing a natural gradient of sediment disturbance, in addition to a field experiment at a subset of sites where sediment disturbance was explicitly manipulated to search for mechanisms.

MATERIALS AND METHODS

Observational study

The research was conducted within Yaquina Bay, a drowned river-mouth estuary located on the Central Oregon Coast, USA (see the National Estuarine Eutrophic Assessment at <http://ian.umces.edu/nea/> for more details). Field surveys were conducted at 6 sites for 2 yr (starting in January 2011 and ending in November 2012; sampling months in the wet season were November, January, and April, and sampling months in the dry season were June, July, August, and September) to establish the seasonality of sediment deposition and the demographics of *Zostera japonica*. The wet season was defined as months in which seasonal rains resulted in frequent large discharge events from watersheds in Oregon's Coast Range, while the dry season was defined as months in which large discharge events were infrequent or nominal (see <http://wdr.water.usgs.gov/> for discharge summaries for Oregon basins). Sites were spread throughout the marine-influenced portions of the estuary and included Driveshaft Beach (DB), Alligator Creek (AC), Little Nye Beach (LNB), Mad Dog Patch (MDP), Barnaby's Barge (BB), and Honkers Flatt (HF) (Fig. 2; descriptions of sites are given in Table 1). At each site, the *Z. japonica* bed extended between +1 and +3 m above MLLW and was sampled within an area that stretched 50 m along the shore. Salinity (PSU) was measured in standing water on the mudflat at low tide at each site with a refractometer (n = 3). Temperature of the water was monitored at each site using Onset HOBO dataloggers (n = 3) logging at 30 min intervals.

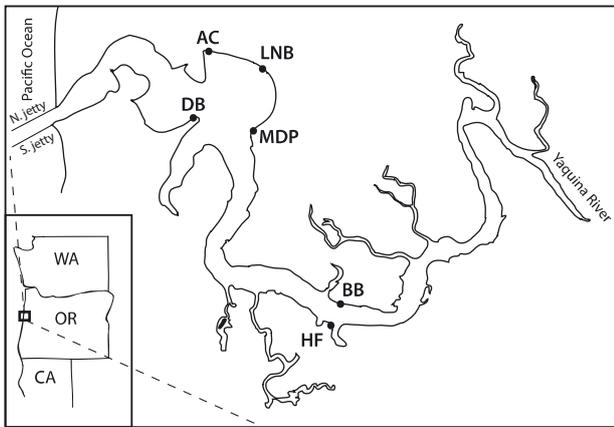


Fig. 2. Location of study sites in Yaquina Bay, Oregon, USA. Fresh water enters the bay from a 634 km² catchment area and enters the Pacific Ocean through 2 jetties at the mouth of the bay. Sites, as ordered from the Pacific Ocean toward Yaquina River: Driveshaft Beach (DB), Alligator Creek (AC), Little Nye Beach (LNB), Mad Dog Patch (MDP), Barnaby's Barge (BB), Honkers Flatt (HF). See Table 1 for descriptions of sites

We characterized sediment deposition at each of the 6 sites by measuring the amount of sediment that accumulated on ceramic tiles. Ceramic tiles (15 × 15 cm) were placed on top of the sediment surface (n = 10 at each site) during the beginning of each sampling month, and sediment deposition was measured for depth (cm) in the center of the tile and collected for dry weight at the end of each sampling month. Because there was a strong relationship between sediment depth and sediment dry weight for the tiles (Sediment depth [cm] = 0.0892 + 0.004 × sed-

iment dry wt [g] tile⁻¹; linear regression adj. R² = 0.94, F_{2,28} = 439.8, p < 0.0001), we used sediment depth as our response variable throughout the study.

Eelgrass biometrics and the occurrence of other species were measured each sampling month at each site. The percentage cover of *Z. japonica* and macroalgae as well as the number of burrowing infauna holes were surveyed within 0.5 × 0.5 m haphazardly tossed quadrats (n = 20) at each site. Near the quadrats, we collected 15 cores (10.3 cm diameter × 10 cm deep) of above- and below-ground biomass of *Z. japonica*. Cores were rinsed through a 2 mm sieve, which separated the plants from the mud, and then a 710 μm sieve, to isolate seeds and seedlings. In each sample, we counted the number of spathes (flowering and seed bearing structures on reproductive shoots), the number of seeds in the sediment, and the number of seedlings (identified by the presence of a seed coat attached to rootlets). We then separated above- (shoots) and below-ground (roots and rhizomes) biomass and dried (60°C) and weighed each.

Experimental study

To examine the effects of disturbance on *Z. japonica*, we experimentally manipulated sediment deposition events in plots at 3 sites starting in July 2012. Sites were chosen to represent the gradient of ambient sediment deposition events to which populations were exposed during the dry season and included a low sediment deposition site (BB), an intermediate sediment deposition site (HF), and a high sediment

Table 1. Characteristics of the 6 study sites within Yaquina Bay, Oregon, USA

Site	Code	Latitude	Longitude	Description
Driveshaft Beach	DB	44° 36' 51.59" N	124° 01' 41.94" W	Strongly sloping; sand dominated; located 200 m downstream of the mouth of King Slough
Alligator Creek	AC	44° 37' 42.82" N	124° 01' 26.97" W	Flat gravel and silt dominated; located in the NW corner of Sally's Bend within an aggregation of the burrowing shrimp
Little Nye Beach	LNB	44° 37' 33.33" N	124° 00' 33.33" W	Flat sand and silt dominated; located on the north shoreline of Sally's Bend within an aggregation of burrowing shrimp <i>Neotrypaea californiensis</i>
Mad Dog Patch	MDP	44° 36' 41.10" N	124° 00' 38.76" W	Moderately sloping; gravel, clay, and sandstone dominated; located on the NE corner of Sally's Bend
Barnaby's Barge	BB	44° 34' 32.19" N	123° 59' 06.00" W	Strongly sloping; silt and clay dominated; located upstream of the Oregon Oyster Farm dock
Honkers Flatt	HF	44° 34' 14.59" N	123° 59' 07.52" W	Flat silt and clay dominated; located across the channel from the Oregon Oyster Farm docks and downstream from the mouth of a small un-named slough

deposition site (LNB). Sediment deposition events were determined by examining the sediment tile data from 2011 (see Fig. 3). Experimental plots (0.5 × 0.5 m) were subjected to 1 of 3 treatment levels: no sediment deposition or control (+0 cm sediment added), low sediment deposition (+0.2 cm sediment added), or high sediment deposition (+3.2 cm sediment added). Sediment for the additions came from the top 5 cm of sediment on unvegetated mudflat adjacent to vegetated patches and appeared to have a similar consistency and grain size as the sediment within the plots. We established 3 blocks per site with 3 replicates per treatment for a total of 9 replicates per treatment per site.

Sediment treatments were applied twice (July 2012 and August 2012) during the flowering season. Ambient sediment deposition was measured by placing 5 ceramic tiles (15 × 15 cm) within each block but outside of the plots so they did not receive sediment from the treatment. Sediment deposition (cm) on each tile was measured monthly, and total deposition per plot was calculated by adding the ambient sediment depth within the block to the treatment sediment depth added to the plot.

After 3 mo (September 2012), the experiment was terminated, and all above- and below-ground biomass of eelgrass was collected from 0.25 × 0.25 m quadrats placed in the center of each treatment plot. The samples were sorted according to the protocol of the core surveys above, with 2 exceptions: (1) above-ground biomass was separated into flowering (including spathes and flowering shoot material) and vegetative portions before being dried (60°C) and weighed, and (2) spathes were examined under a dissecting scope, and each developed seed was counted (fertilized, as indicated by a dehisced stigma, swelling, hardening, and browning).

Statistical analyses

All statistical analyses were conducted using the R platform (R Development Core Team 2011).

Observational study

Eelgrass biometrics (percent cover, total biomass [above and below ground], spathe density, seed density in the sediment, and seedling density), sediment deposition, and other physical and biological factors (salinity, temperature, burrow hole density, and percent cover of macroalgae) from the 2 years of obser-

vational surveys were analyzed by fitting mixed effects models in the Linear and Nonlinear Mixed Effects Models package in R (nlme package; Pinheiro et al. 2001 as described by Zuur et al. 2009) to the response variable, with site, season, and year, and their possible interactions, specified as fixed effects. A nesting structure was incorporated into the model to account for the repeated measures of month within season and year. Tukey HSD post hoc tests were conducted on significant factors, unless interactions were found, in which case 1-factor ANOVAs and Tukey HSD post hoc comparisons were conducted between levels of each factor (Underwood 1997).

Yearly means (\pm SE) of percent cover, total biomass (above and below ground), spathe density, seed density in the sediment, seedling density, and sediment deposition (cm) were calculated by averaging all monthly samples at a site for 1 yr for each metric (6 sites × 2 yr). Yearly means were used because we assumed the overall effects of disturbance would be the result of the cumulative effects of disturbance events that occurred throughout the year. These data were then used in regression models to establish the relationship between various *Z. japonica* biometrics and sediment deposition.

Experimental study

Response variables (total vegetative biomass, spathe density, flowering biomass, and total seed density on the spathes) from the experiment were analyzed by fitting a mixed effects model using the nlme package. Treatment was specified as a fixed effect, while site and block were specified as random effects. A nested structure was included in the model to account for the replicate plots within blocks. Tukey HSD post hoc tests were conducted on significant factors, unless interactions were found, in which case 1-factor ANOVAs and Tukey HSD post hoc comparisons were conducted between levels of each factor (Underwood 1997).

Given that sedimentation for the control and treatment plots likely depends on the ambient sedimentation at the site (i.e. ambient or control sediment deposition rate plus the treatment sediment deposition rate), we also examined the response variables of vegetative biomass, flowering biomass, and spathes across the continuous variable of sediment deposition per plot. Regression analyses were conducted on total vegetative biomass, spathe density, and flowering shoot biomass in response to sediment deposition, using generalized additive models (GAM) from

the Mixed GAM Computational Vehicle with GCV/AIC/REML Smoothness Estimation package in R (mgcv package; Wood 2006 as described by Zuur et al. 2009). All GAMs were checked against a null model with no 'knots' (i.e. a straight line) for goodness of fit by visual inspection, comparison of adjusted R^2 , and AIC values. Adjusted R^2 values are reported rather than p-values as an estimate of model fit due to the potential for over-fitting the model, which can lead to significant, but misleading, p-value estimates.

Direct evidence for a tradeoff was examined using a linear regression model of flowering biomass in response to vegetative biomass across the range of sediment deposition rates (0.0 to 1.0 cm sediment

deposited mo^{-1}) where we expected to observe a tradeoff based on the results from the GAM.

RESULTS

Patterns of physical and biological factors across sites

Salinity did not vary by site, but did by season, and was higher in the dry season than in the wet season (Table 2). Temperature was higher at site LNB than at site MDP, but no other differences between sites were found in pairwise comparisons (Table 2). Sediment deposition varied among sites, but not seasons,

or years, though there was an interaction among these factors (Fig. 3, Table 2). Sediment deposition was strongly site-dependent, with high sedimentation at sites DB, AC, and LNB, moderate at site HF, and low at sites MDP and BB (Fig. 3, Table 2). Sediment deposition was greater in the dry season than the wet season for all sites (Fig. 3, Table 2). Finally, the density of burrow holes was highest at sites AC and LNB (Table 2), and the percent cover of macroalgae was very low at all sites, even during the dry season (Table 2).

Dwarf eelgrass abundance over time and with sediment deposition

The growing season generally began around April each year and extended into the dry season (Fig. 4). Percent cover of eelgrass varied by site, season, and year, and there was site \times season \times year interaction (Fig. 4, Table 3). Total biomass of eelgrass varied by site and season, but not by year, and there was a site \times season \times year interaction (Fig. 4, Table 3). Post hoc tests for percent cover and total biomass of eelgrass abundance showed that sites BB and MDP had the greatest abundance, sites HF, DB, and LNB had intermediate abundance, and site AC had the lowest abundance (Table 3). Not surprisingly, percent cover and total biomass were greatest in the dry season (Fig. 4, Table 3). Finally, there were negative

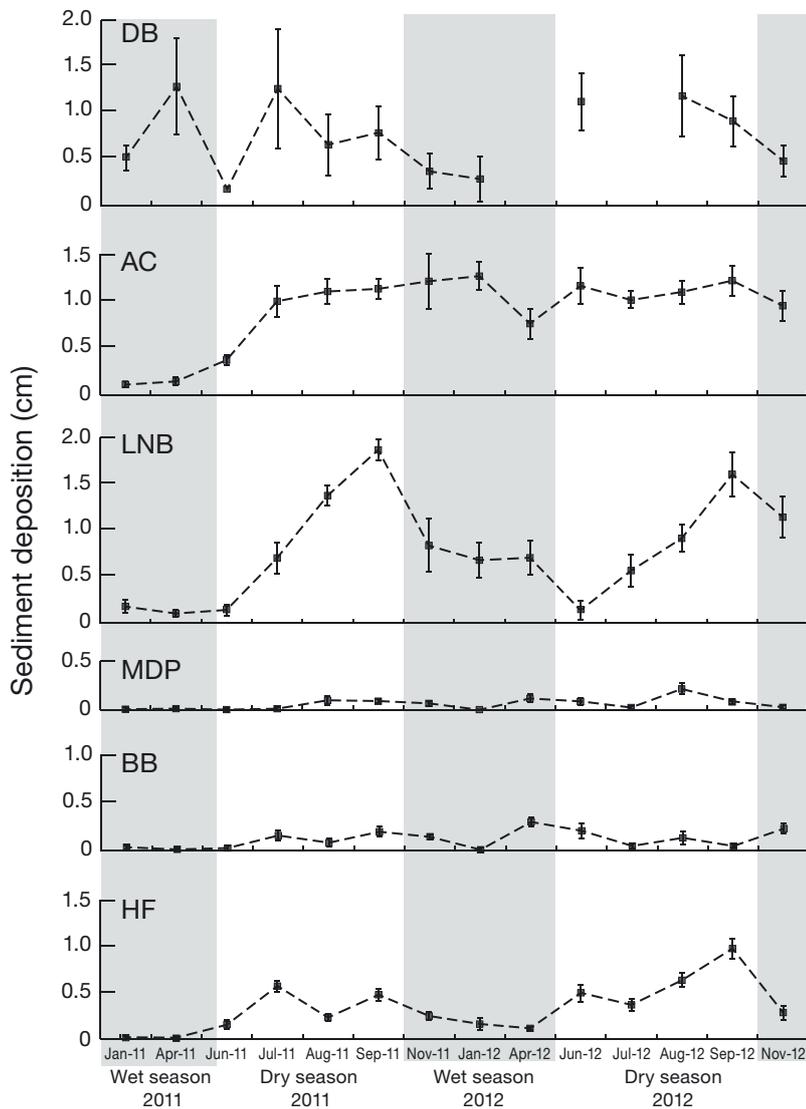


Fig. 3. Mean (\pm SE) monthly sediment deposition (cm) on top of ceramic tiles at 6 sites (DB, AC, LNB, MDP, BB, and HF; Fig. 2) located within Yaquina Bay, Oregon, from January 2011 to November 2012

Table 2. Physical and biological parameters at 6 sites (DB, AC, LNB, MDP, BB, and HF; Fig. 2) in Yaquina Bay, Oregon, from January 2011 to November 2012. (A) Means \pm SE, determined from pooled samples of all dry season (June to September) and wet season (November, January, and April) months sampled. (B) ANOVA test statistics. Salinity, temperature, sediment deposition, burrow hole density, and percentage cover of macroalgae were used as response variables with site, season, and year as fixed effects. A nested structure was specified in the model as month | season | year. Tukey HSD post-hoc tests (**bold**: significant at $p < 0.05$) were conducted to examine differences between sites and season

(A) Pooled means \pm SE											
Site	Salinity (PSU)		Temperature ($^{\circ}$ C)		Monthly sediment deposition (cm depth)		Burrow holes (no. per 0.5 \times 0.5 m)		Macroalgae (% cover)		
	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	
DB	31 \pm 0.6	17 \pm 2	16 \pm 0.5	10 \pm 0.8	0.6 \pm 0.1	0.5 \pm 0.1	6.5 \pm 0.7	3.9 \pm 0.5	4.8 \pm 0.8	0.5 \pm 0.3	
AC	30 \pm 0.3	17 \pm 2	16 \pm 0.4	10 \pm 0.8	0.8 \pm 0.1	0.6 \pm 0.1	28 \pm 1.0	3.8 \pm 0.6	2.4 \pm 0.5	0.1 \pm 0.1	
LNB	31 \pm 0.2	17 \pm 2	18 \pm 0.6	10 \pm 0.9	0.7 \pm 0.1	0.5 \pm 0.1	23 \pm 1.2	4.5 \pm 0.8	0.3 \pm 0.2	0.0 \pm 0.0	
MDP	31 \pm 0.5	17 \pm 2	15 \pm 0.5	10 \pm 0.7	0.1 \pm 0.1	0.1 \pm 0.1	2.6 \pm 0.3	0.1 \pm 0.0	4.7 \pm 0.9	0.3 \pm 0.1	
BB	30 \pm 0.8	18 \pm 2	17 \pm 0.5	10 \pm 0.8	0.2 \pm 0.1	0.2 \pm 0.1	1.0 \pm 0.2	0.0 \pm 0.0	1.5 \pm 0.4	1.5 \pm 0.4	
HF	32 \pm 0.8	16 \pm 2	17 \pm 0.5	10 \pm 0.8	0.4 \pm 0.1	0.2 \pm 0.1	1.3 \pm 0.2	0.2 \pm 0.1	0.8 \pm 0.3	0.0 \pm 0.0	
(B) ANOVA and post-hoc Tukey HSD test results											
	df	F	p	Tukey HSD ($p < 0.05$)							
Salinity											
Site	5, 137	0.45	0.81	–							
Season	1, 5	8.00	0.04	Dry > Wet							
Year	1, 1	4.03	0.29	–							
Site \times Season \times Year	5, 137	0.67	0.65	–							
Temperature											
Site	5, 50	34.74	<0.001	LNB > DB, AC, BB, HF > MDP							
Season	1, 5	24.97	0.004	Dry > Wet							
Year	1, 5	0.01	0.93	–							
Site \times Season \times Year	5, 50	0.32	0.90	–							
Sediment deposition											
Site	5, 721	77.00	<0.001	DB, AC, LNB > HF > MDP, BB							
Season	1, 5	2.24	0.20	–							
Year	1, 5	4.21	0.10	–							
Site \times Season \times Year	5, 721	6.50	<0.001	–							
Burrow hole											
Site	5, 1626	297.89	<0.001	AC, LNB > BB, HF, MDP, DB							
Season	1, 5	27.46	0.003	Dry > Wet							
Year	1, 5	0.49	0.51	–							
Site \times Season \times Year	5, 1626	4.50	<0.001	–							
Macroalgae											
Site	5, 1626	12.26	<0.001	DB, MDP, AC > LNB, HF, BB							
Season	1, 5	2.65	0.16	–							
Year	1, 5	2.46	0.18	–							
Site \times Season \times Year	5, 1626	2.20	0.06	–							

linear relationships between the mean percent cover and the mean total biomass of *Zostera japonica*, and sediment deposition among the sites (Fig. 5).

Dwarf eelgrass sexual reproduction over time and with sediment deposition

The flowering season began around June each year and generally lasted until November (Fig. 6).

The number of seeds in the sediment began to rise in the late dry season (July or August) to the late wet season (April), but seeds were absent by June at all the sites (Fig. 6). Seedlings were observed from September to April, with peaks observed from November to January (Fig. 6).

Spathe density differed among sites, seasons, but not year, and there was a site \times season \times year interaction (Fig. 6, Table 3). Spathes were most abundant at sites LNB, HF, DB, MDP, and BB and were

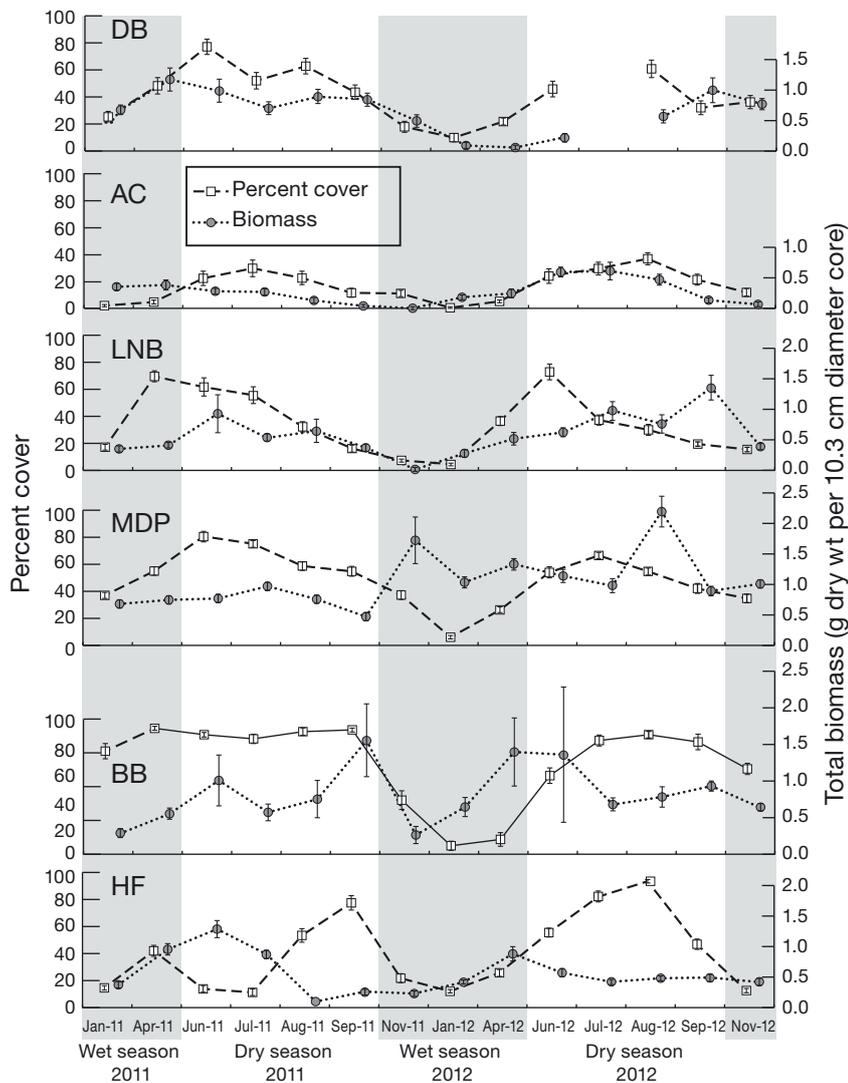


Fig. 4. Mean (\pm SE) percent cover (measured on 0.5×0.5 m quadrats) and total biomass (above and below ground; 10.3 cm diameter \times 10 cm deep cores) of *Z. japonica* measured at 6 sites (DB, AC, LNB, MDP, BB, and HF; Fig. 2) in Yaquina Bay, Oregon, from January 2011 to November 2012

least abundant at AC. Seed density in the sediment differed among sites but not seasons or years, and there was a site \times season \times year interaction (Fig. 6, Table 3). Seed densities were highest at sites LNB, HF, and DB, intermediate at site BB, and lowest at sites MDP and AC. Seedling densities differed among sites but not seasons or years, and there was a site \times season \times year interaction (Fig. 6, Table 3). Seedlings were most abundant at sites DB, LNB, HF, BB and least abundant at sites MDP and AC. As opposed to vegetative parts of the plants, regression analyses showed that the mean number of spathes, seeds in the sediment, and seedlings were not correlated with mean sediment deposition

(spathes = $-0.025 - 24.10x^2 + 20.19x$; adj. $R^2 = 0.16$, $p = 0.186$; seeds = $0.38 - 20.54x^2 + 16.06x$; adj. $R^2 = 0.03$, $p = 0.352$; seedlings = $0.08 - 4.19x^2 + 3.53x$; adj. $R^2 = -0.07$, $p = 0.549$). The mean number of spathes, seeds in the sediment, and seedlings were not correlated with mean vegetative biomass (spathes = $2.084 + 1.209x$; adj. $R^2 = 0.06$, $p = 0.447$; seeds = $1.669 + 1.075x$; adj. $R^2 = 0.04$, $p = 0.5432$; seedlings = $0.2149 + 0.3253x$; adj. $R^2 = 0.06$, $p = 0.4571$).

Experimental manipulations of sediment deposition on dwarf eelgrass

Sediment deposition affected eelgrass vegetative biomass, spathe density, and flowering biomass by treatment and site, with treatment \times site interactions (Fig. 7A–C, Table 4). Eelgrass vegetative biomass decreased in the high sediment deposition treatments but did not differ in the control and low sediment treatments (Fig. 7, Table 4). There was a decrease in eelgrass vegetative biomass within the high sediment treatments at sites BB (low) and HF (intermediate) but not at site LNB (high) (Fig. 7A, Table 4). Spathe density was highest in the control sediment treatment, intermediate in the low sediment treatment, and lowest in the high sediment treatment (Fig. 7B, Table 4). There were fewer spathes at sites BB (low) and HF (intermediate) but not at site LNB (high) (Fig. 7B, Table 4).

Eelgrass flowering biomass was reduced in the high sediment treatments but not in the low sediment treatments (Fig. 7C, Table 4). A treatment effect was observed for each level for site HF (intermediate) but not at sites BB (low) and LNB (high) (Fig. 7C, Table 4). Seed density on spathes differed by treatment and site, and there was a treatment \times site interaction (Fig. 7D, Table 4). Seed density was lowest in the high sediment treatments, and sites BB (low) and HF (intermediate) produced fewer seeds than LNB (high) (Fig. 7D, Table 4).

The experiments showed a decrease in total vegetative biomass with increasing sediment deposition

Table 3. Demographic parameters of *Zostera japonica* at 6 sites (DB, AC, LNB, MDP, BB, and HF; Fig. 2) in Yaquina Bay, Oregon, from January 2011 through November 2012. (A) Means \pm SE, determined from pooled samples of all dry season (June to September) and wet season (November, January, and April) months sampled. (B) ANOVA test statistics. Percent cover, total biomass, spathe density, seed density, and seedling density were used as response variables with site, season, and year as fixed effects. A nested structure was specified in the model as month | season | year. Tukey HSD post-hoc tests (**bold**: significant at $p < 0.05$) were conducted to examine differences between sites and season

(A) Pooled means \pm SE										
Site	Percent cover		Total biomass (g dry wt core ⁻¹)		Spathe density (no. core ⁻¹)		Seed density (no. in sediment core ⁻¹)		Seedling density (no. core ⁻¹)	
	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
DB	53.4 \pm 2.4	26.6 \pm 2.0	0.76 \pm 0.06	0.56 \pm 0.06	6.0 \pm 1.1	0.7 \pm 0.2	1.0 \pm 0.2	2.7 \pm 0.6	0.2 \pm 0.1	1.9 \pm 0.6
AC	24.6 \pm 1.8	5.8 \pm 0.7	0.37 \pm 0.03	0.13 \pm 0.02	2.6 \pm 0.6	0.1 \pm 0.1	0.1 \pm 0.1	0.3 \pm 0.1	0.1 \pm 0.1	0.1 \pm 0.1
LNB	40.7 \pm 2.2	25.1 \pm 2.3	0.67 \pm 0.06	0.46 \pm 0.06	6.7 \pm 1.0	0.2 \pm 0.1	4.6 \pm 0.7	2.2 \pm 0.5	0.1 \pm 0.1	1.2 \pm 0.3
MDP	60.8 \pm 1.5	32.7 \pm 1.7	1.12 \pm 0.06	0.97 \pm 0.08	3.2 \pm 0.4	0.5 \pm 0.2	0.5 \pm 0.1	2.3 \pm 0.7	0.1 \pm 0.1	0.3 \pm 0.1
BB	87.0 \pm 1.2	58.4 \pm 2.8	1.27 \pm 0.09	1.22 \pm 0.10	4.2 \pm 0.6	2.0 \pm 0.3	2.9 \pm 0.5	4.1 \pm 0.5	0.1 \pm 0.1	1.2 \pm 0.3
HF	54.2 \pm 2.6	21.5 \pm 1.4	0.70 \pm 0.04	0.37 \pm 0.02	6.1 \pm 1.1	0.1 \pm 0.1	5.0 \pm 0.9	3.6 \pm 0.6	0.1 \pm 0.1	0.9 \pm 0.2
(B) ANOVA and post-hoc Tukey HSD test results										
	df	F	p	Tukey HSD ($p < 0.05$)						
Percent cover										
Site	5, 1626	246.54	<0.0001	BB, MDP > HF, DB, LNB > AC						
Season	1, 5	20.62	0.006	Dry > Wet						
Year	1, 5	1.34	0.298	–						
Site \times Season \times Year	5, 1626	9.6	<0.001	–						
Total biomass										
Site	5, 1195	77.6	<0.0001	BB, MDP > HF, DB, LNB > AC						
Season	1, 5	7.7	0.04	Dry > Wet						
Year	1, 5	6.91	0.06	–						
Site \times Season \times Year	5, 1195	5.4	<0.001	–						
Spathe density										
Site	5, 1195	4.8	<0.001	LNB, HF, DB, MDB, BB > AC						
Season	1, 5	14.1	0.013	Dry > Wet						
Year	1, 5	0.4	0.56	–						
Site \times Season \times Year	5, 1195	11.1	<0.001	–						
Seeds										
Site	5, 1195	25.8	<0.001	LNB, HF, DB > BB > MDP, AC						
Season	1, 5	0	0.92	–						
Year	1, 5	1.9	0.23	–						
Site \times Season \times Year	5, 1195	5	<0.001	–						
Seedling density										
Site	5, 1195	4.3	<0.001	DB, LNB, HF, BB > MDP, AC						
Season	1, 5	3.6	0.12	–						
Year	1, 5	4.9	0.08	–						
Site \times Season \times Year	5, 1195	6.2	<0.001	–						

(Fig. 8A). The GAM indicated that total vegetative biomass decreased by approximately 50% at sediment deposition rates of 1 cm mo⁻¹, and there was nearly 100% mortality at sediment deposition rates above 3.5 cm mo⁻¹. Spathe density and flowering biomass both showed a unimodal response with increasing sediment deposition (Fig. 8B,C). The generalized additive model showed that spathe density and flowering biomass were greatest at sediment deposition

rates of approximately 0.75 cm mo⁻¹ and were effectively inhibited at sediment deposition rates above 1.5 cm mo⁻¹. There was no relationship between seed density on spathes and sediment deposition.

Flowering biomass was negatively correlated with vegetative biomass (flowering biomass = 0.3792 – 0.1122 (vegetative biomass); adjusted R² = 0.12, p = 0.0232) for plots that experienced sediment deposition rates of 0.0 to 1.0 cm mo⁻¹.

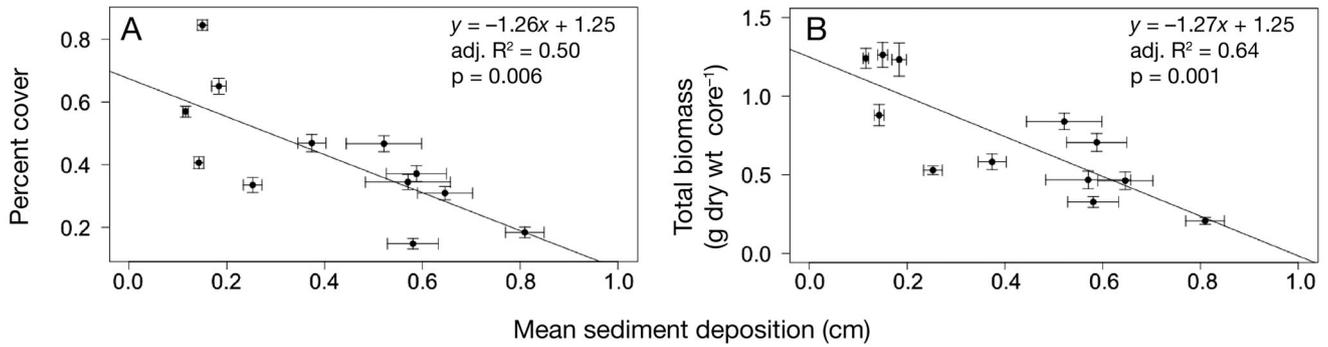


Fig. 5. Linear regressions of (A) mean (\pm SE) percent cover (measured on 0.5×0.5 m quadrats) and (B) mean (\pm SE) total biomass ($\text{g dry wt core}^{-1}$) of *Zostera japonica* versus mean (\pm SE) sediment deposition per month. Samples were pooled by year and site

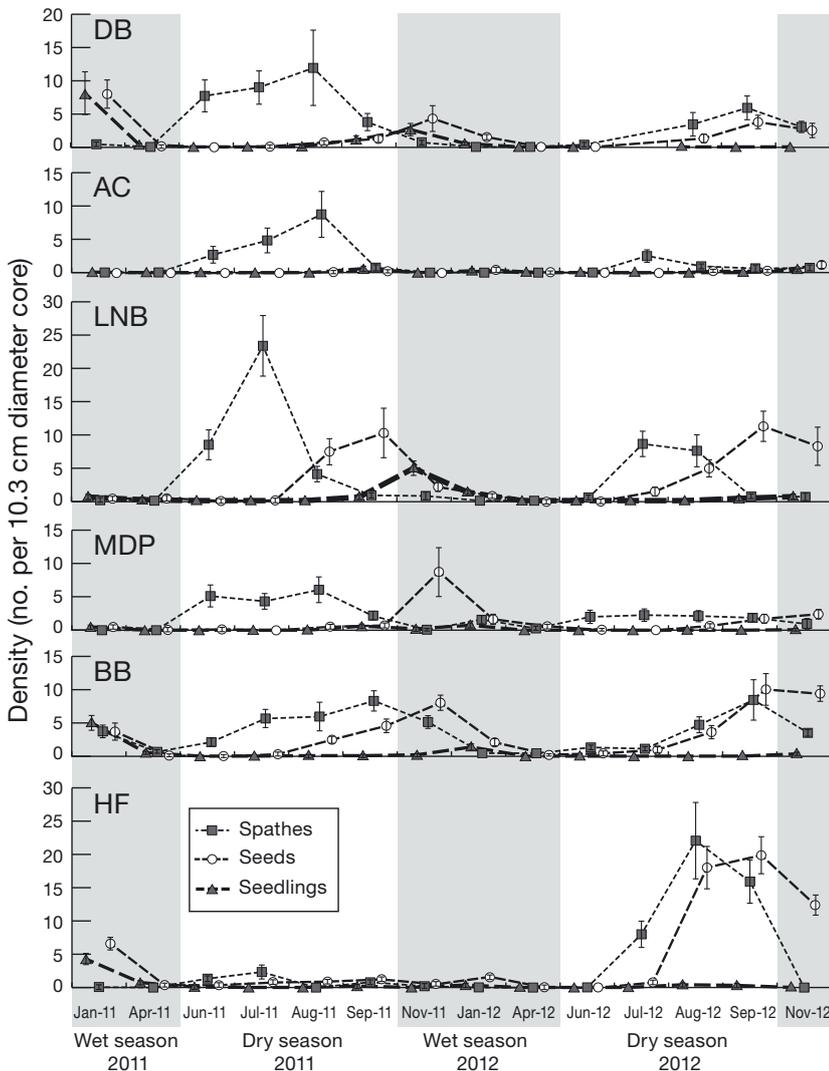


Fig. 6. Mean (\pm SE) density of spathes, seeds in the sediment, and seedlings (no. per $10.3 \text{ cm diameter} \times 10 \text{ cm deep core}$) of *Z. japonica* at 6 sites (DB, AC, LNB, MDP, BB, and HF; Fig. 2) in Yaquina Bay, Oregon, from January 2011 to November 2012

DISCUSSION

Tradeoffs in vegetative and sexual reproduction with sediment deposition

Our study suggests that within the estuaries of the NE Pacific Coast, the invasion of previously un-vegetated mudflats by the non-native dwarf eelgrass *Zostera japonica* has likely been impacted by variation in sediment deposition rates across these dynamic soft-bottomed intertidal habitats. We observed that increasing disturbance from sediment deposition resulted in negative direct effects on *Z. japonica* (Fig. 5). As sediment deposition increased, there was a linear decline in vegetative cover and biomass of this species, with the most disturbed sites having cover as low as 25% compared to the least disturbed sites with nearly 85% cover. In addition, our experiments confirmed that artificially increasing the rate of sediment deposition led to a decline in total vegetative biomass at all the sites (Fig. 7A), and this effect showed a negative linear relationship over a range of sediment conditions as indicated by the results of the GAM (Fig. 8A). A different pattern was evident for sexual reproduction. Here, a unimodal relationship was evident over the range of sediment conditions, with an increase in

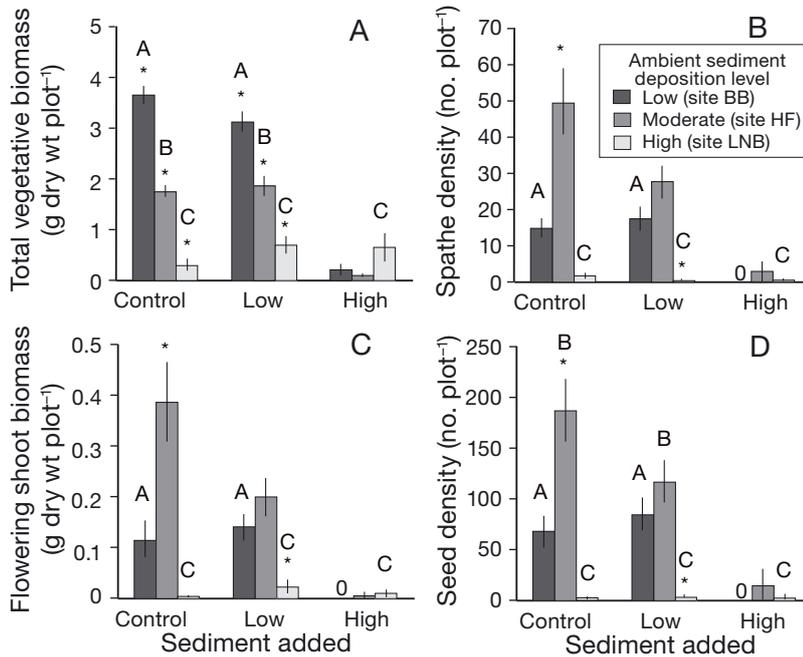


Fig. 7. Mean (\pm SE) total vegetative biomass (above and below ground), spathe density, flowering shoot biomass, and seed density (the number of seeds on spathes in a plot) from the experimental manipulation of sediment deposition (treatments: control [+0 cm sediment], low [+2 cm sediment], high [+3.2 cm sediment]) on dwarf eelgrass growth and reproduction at 3 sites that vary in ambient sediment disturbance (low = BB, moderate = HF, high = LNB; Fig. 2) in Yaquina Bay, Oregon, in summer 2012 ($n = 9$). Significant post-hoc tests (Tukey HSD, $p < 0.05$) are denoted by asterisks for within-treatment comparisons and by capital letters for within-site comparisons (A = BB, B = HF, C = LNB)

Table 4. Linear mixed effects model results from the experimental manipulation of sediment deposition [treatments: control (+0 cm sediment), low (+2 cm sediment), and high (+3.2 cm sediment)] on dwarf eelgrass growth and reproduction at 3 sites that vary in ambient sediment disturbance (low = BB, moderate = HF, high = LNB; Fig. 2) in Yaquina Bay, Oregon, in summer 2012. Total vegetative biomass, spathe density, flowering shoot biomass, and seed density on spathes were used as response variables with treatment and site as fixed effects. A nested structure was specified in the model as plot | block | site. Tukey HSD post hoc tests (significant at $p < 0.05$) were conducted to examine differences between sites for a given treatment, and to examine differences between treatments for a given site

Response	N	Fixed effect	df (fixed effect, error)	F (p)	p
Total vegetative biomass	81	Treatment	2, 45	82.5	<0.0001
		Site (block)	2, 45	79	<0.0001
		Treatment \times Site (block)	4, 45	33.2	<0.0001
Spathe density	81	Treatment	2, 45	23.5	<0.0001
		Site (block)	2, 45	34.3	<0.0001
		Treatment \times Site (block)	4, 45	9.6	<0.0001
Flowering shoot biomass	81	Treatment	2, 45	17.9	<0.0001
		Site (block)	2, 45	14.9	0.0001
		Treatment \times Site (block)	4, 45	6.5	0.0004
Seed density on spathes	81	Treatment	2, 45	22	<0.0001
		Site (block)	2, 45	33.9	<0.0001
		Treatment \times Site (block)	4, 45	8.6	<0.0001

flowering and seed production as sedimentation increased to intermediate levels, and then a decline at high levels of sediment deposition (Fig. 8B,C).

Our data fit the model we developed to predict the impact of disturbance on biomass and reproduction in populations of clonal plants exposed to gradients in disturbance severity (Fig. 1). We hypothesize that the unimodal response of sexual reproduction is the result of a tradeoff between vegetative growth and sexual reproduction with increasing disturbance. We found a significant negative correlation between vegetative and flowering biomass as disturbance increased up to an intermediate level but then a decline in overall biomass at high levels of disturbance. Why might we expect to see tradeoffs between vegetative growth and sexual reproduction? Theory suggests that vegetative growth is the safest reproductive strategy in a stable environment, while sexual reproduction is thought to be a mechanism for escaping disturbance (Silvertown 2008). In a sense, sexual reproduction produces a package (the seed) that allows for a spatial or temporal escape from disturbance. This idea is similar to the escape hypothesis (i.e. dispersal is a mechanism to prevent progeny from being eliminated by events that cause mortality to their parents; Grime 1979, Howe & Smallwood 1982), except that the processes limiting seedling recruitment (disturbance) are independent of density. As with the escape hypothesis, selection favors individuals that escape an inhospitable environment by producing seeds. These individuals presumably shift resources to reproduction as they experience damage inflicted by the disturbance event. Natural selection has been shown to drive the timing of flowering in plants exposed to herbivory and disturbance by fire (Schemske 1984, Keeley & Bond 1999), and increased reproductive effort has been observed across a plant community

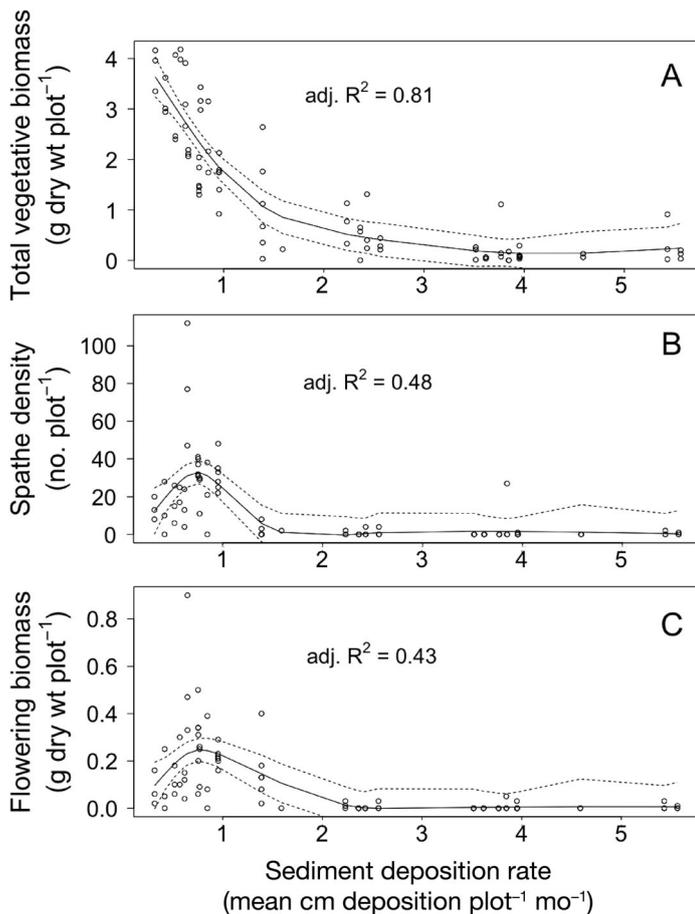


Fig. 8. The relationship of (A) total vegetative biomass (above and below ground), (B) spathe density, and (C) flowering shoot biomass with the amount of sediment deposition (cm), using generalized additive models. Sediment deposition is the ambient + treatment sediment deposition measured each month over a 3 mo period

immediately following a severe disturbance event (Hopkins & Graham 1987). It would thus seem plausible that physiological mechanisms exist that would allow for selection to favor individuals that flower in response to increasing disturbance. This response could be particularly important for introduced, non-native species that are entering a novel environment.

Effects of sediment deposition on dwarf seagrass

Our experimental data showed that vegetative biomass declined linearly with sedimentation, whereas flowering and seed production were greatest within a narrow range of sediment deposition but declined precipitously above that level (Fig. 8B,C). These results suggest that increasing sediment deposition results in a tradeoff between vegetative biomass and

flowering up to the point that mortality begins to drive biomass downward, which occurs at sediment deposition rates of approximately 0.75 cm mo^{-1} . At levels of sediment deposition beyond 1.5 cm mo^{-1} , disturbance is too great for plants to persist.

The methods employed in this study focused on disturbance processes that occurred at a scale small enough to be specific to particular sites in Yaquina Bay. Our drivers of disturbance at this scale were likely both abiotic and biotic. The sites with the highest sedimentation rates were AC, LNB, and DB respectively (Fig. 3, Table 2), which were also the sites with the highest number of infauna burrows (Table 2). We suspect that burrowing shrimp play a substantial role in sediment deposition, as burrow holes and sediment accretion were greatest in the dry season months (Fig. 3, Table 2). The disturbance caused by burrowing infauna is generally assumed to create a layer of silt that smothers benthic organisms (Dumbauld & Wyllie-Echeverria 2003). In addition to biotic disturbance, sediments can also be mobilized and re-deposited by wind-driven waves (Marba & Duarte 1995), which could be important in the wet season as large storms move through. In this study, though, we did not directly measure the abiotic drivers of disturbance, so we cannot reliably separate the individual contributions of various processes that constituted sediment disturbance.

In the literature on seagrasses, disturbance from sediment deposition has generally shown direct negative effects on shoot density and biomass. The amount of sedimentation that seagrasses can tolerate varies by species and is a function of blade width and shoot length, with smaller, thinner species susceptible to negative effects at lower levels of sedimentation than larger, wider species (Cabaço et al. 2008). The effects on seagrass sexual reproduction have not been well documented, but one study found, contrary to our results, that there was no effect of increasing sedimentation on sexual reproduction (Cabaço & Santos 2007).

Implications of sediment deposition for dwarf eelgrass invasion

The potential tradeoff in vegetative and sexual reproduction with sediment disturbance has implications for the ongoing invasion of *Z. japonica* in NE Pacific estuarine systems. We hypothesize that the dynamic nature of sediment movement in these systems has been facilitating the invasion by creating both spatial and temporal mosaics of sediment distur-

bance (Fig. 3). Populations of *Z. japonica* inhabiting this mosaic display increased flowering and seed density when a site is exposed to intermediate levels of sediment disturbance (Fig. 7), and it may be that this results in a differential contribution to dispersal from particular sites. Other authors have found that disturbance increases flowering in *Z. japonica* (Bando 2006) and have suggested that traits associated with its 'weedy nature,' such as short generation times, high reproductive output, and high growth rates, have contributed to the proliferation of this invasive species (Ruesink et al. 2010). This study corroborates those findings and provides insight into a potential mechanism that could result in greater spread of this invasive species under certain sediment conditions. If disturbance increases sexual reproduction, it may facilitate the invasion by increasing propagule pressure and genetic diversity. This could create an increased likelihood that *Z. japonica* reaches new sites, and, as has been shown in other invasive grasses, could allow this species to successfully proliferate across a wider range of environmental conditions (Lambrinos 2001).

We suspect that both land-use practices and climate could have the potential to impact the sediment disturbance regimes in NE Pacific estuaries. Changes in land use that increase runoff and changes in climate that increase the severity or frequency of storms have been shown to increase the amount of sediment deposited in estuarine systems, with negative impacts on benthic communities (Ellis et al. 2000). In addition, wet season precipitation is known to increase under certain phases of natural climate cycles such as the ENSO and PDO (Kiladis & Diaz 1989, Brown & Comrie 2004). These factors could impact local disturbance regimes by increasing runoff, which would push the turbidity maximum and the sedimentation associated with it seaward and also increase the amount of fine sediments cycling through the system.

Overall, this work highlights the importance of considering the direct effects of disturbance on the invasion success of non-native species. These effects could be particularly important for invasive species that occupy open niche habitats, such as we see with dwarf eelgrass. Additionally, habitats that have disturbance regimes that are dynamic could create mosaics of sink or source populations that could sustain or hinder a particular invasion over time. As disturbance regimes change due to natural and anthropogenic causes, it is important to document potential life-history tradeoffs and whether they could contribute to making communities more susceptible to invasion, and thus of greater management concern.

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