# Distribution and Performance of the Nonnative Seagrass *Zostera japonica* across a Tidal Height Gradient on Shaw Island, Washington[1]

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**Abstract:** In the Northeast Pacific the nonnative seagrass *Zostera japonica* frequently exists at the same sites as the native seagrass *Zostera marina*. Although at some sites their vertical distributions overlap, at most sites in the Pacific Northwest there is a distinctive unvegetated zone between them. The objective of this study was to better understand why a gap between the lower limit of *Z. japonica* and the upper limit of *Z. marina* exists. To address this issue we carried out transplant experiments, conducted *in situ* monitoring of existing *Z. japonica* patches, and collected sediment samples at South Beach on Shaw Island, Washington, during the spring and summer of 2006. Transplant and *in situ* monitoring data indicate that survival and performance of *Z. japonica* are reduced lower in the intertidal zone. In addition, *Z. japonica* patches tended to be smaller and more spaced out at lower tidal heights. Although we found no *Z. japonica* seeds within or outside extant *Z. japonica* patches, high transplant mortality indicates that *Z. japonica* dispersal limitation is an unlikely cause of the unvegetated gap zone. Our field observations further suggest that herbivory, bioturbation, and epiphytes are unlikely causes of the gap pattern at our study site. Instead, we hypothesize that light limitation prevents *Z. japonica* from occurring lower in the intertidal. A review of published vertical distribution data for both *Zostera* species indicates that the lower limit of *Z. japonica* is relatively invariant among sites. In contrast, the upper limit of *Z. marina* is highly variable, ranging by more than 4 m within some subregions in Washington State. Consequently we hypothesize that intersite variability in the vertical distribution of *Z. marina* is the primary driver of spatial variability in the presence of the unvegetated gap.

THE SPREAD OF nonnative species is a global problem with substantial economic and ecological consequences (Mack et al. 2000, Pimentel et al. 2005). Marine and estuarine habitats in the Puget Sound region of the United States have been invaded by numer-
ous nonnative species (Cohen et al. 2000), some of which have caused ecological and economic damage (e.g., *Spartina anglica* [see Hacker et al. 2001]). *Zostera japonica* Ascherson & Graebner is a common species in the northern Puget Sound region, including the

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San Juan Islands. *Zostera japonica* was introduced sometime before 1957 (Harrison and Bigley 1982) and is now widespread in coastal areas of British Columbia, Washington, and Oregon (Nomme and Harrison 1991*a,b*). It is thought that *Z. japonica* arrived accidentally as a hitchhiker on the Pacific oyster (*Crassostrea gigas*), which was imported to this region for aquaculture beginning in the early twentieth century (Harrison and Bigley 1982).

Much of the concern surrounding introduced species stems from the potential for negative interactions with native species (Grosholz et al. 2000, Byers 2002, Levin et al. 2002). Indeed, throughout much of its distribution in this region *Z. japonica* co-occurs at the same sites as the native seagrass *Zostera marina* L. However, because of their respective vertical distributions there is little overlap in the habitats used by these two species. Whereas *Z. marina* extends from the subtidal into the lower intertidal, *Z. japonica* occurs primarily in the high intertidal zone, with some populations extending into the lower intertidal, where the distributions of these two seagrasses sometimes overlap (Nomme and Harrison 1991*b*, Baldwin and Lovvorn 1994). When *Z. japonica* and *Z. marina* encounter one another there is the potential for competitive interactions to occur. *Zostera marina* has much longer and wider leaves and experiments in the laboratory and field suggest that it is the superior competitor (Nomme and Harrison 1991*a,b*). Consequently, it has been suggested that the lower limit for *Z. japonica* may be set by competitive interactions with *Z. marina* (Nomme and Harrison 1991*a,b*).

At many sites in the Northeast Pacific there is no overlap in the vertical distribution of *Z. japonica* and *Z. marina* (69% of sites [Shafer 2007]). At those sites there is a distinct unvegetated zone in the mid- to low intertidal zone (hereafter referred to as a "gap zone") that separates the upper edge of *Z. marina* and the lower edge of *Z. japonica*. Considering that *Z. japonica* is generally capable of surviving in the low intertidal and shallow subtidal zones (Nomme and Harrison 1991*b*) and that it grows better when continuously submerged (Harrison 1982), it should

be able to grow at the tidal heights where these unvegetated strata occur. In this study we focused on three research questions: (1) Can *Z. japonica* survive above and below its natural vertical range if transplanted into the extreme high intertidal and into the unvegetated gap zone? (2) Is there a difference in the performance of *Z. japonica* at the upper and lower edges of its natural vertical range? (3) What is the role of seeds in maintaining distribution patterns? To address these questions we carried out transplant experiments, conducted in situ monitoring of existing *Z. japonica* patches, and collected core samples at South Beach on Shaw Island, Washington, during the spring and summer of 2006.

## MATERIALS AND METHODS

### Site Description

Our study site was South Beach (also known as Indian Cove), located on the southeastern side of Shaw Island in the San Juan Islands, Washington State, USA (48° 33.845′ N, 122° 56.131′ W). South Beach is a sandy intertidal site that is exposed to the southwest, the direction from which the dominant winds blow in that area. *Zostera japonica* populates a gently sloping beach in a relatively large intertidal zone and consists of approximately 100 patches that vary in size (see schematic representation in Figure 1). In contrast, the *Zostera marina* bed, the upper edge of which began in the lower intertidal, was relatively uniform, lacking the patchiness that was characteristic of *Z. japonica*. Sampling occurred on 17 April, 15 May, and 13 July 2006. Bioturbating organisms such as burrowing shrimp have not been observed at this site since at least 1996 (S.W.-E., pers. obs.).

### Vertical Distribution of Zostera spp.

We measured the vertical distribution of *Z. japonica* and *Z. marina* along eight randomly placed vertical transects in the intertidal zone at South Beach (Figure 1). Along each transect we measured the tidal heights at the lower and upper limits of *Z. japonica* and the
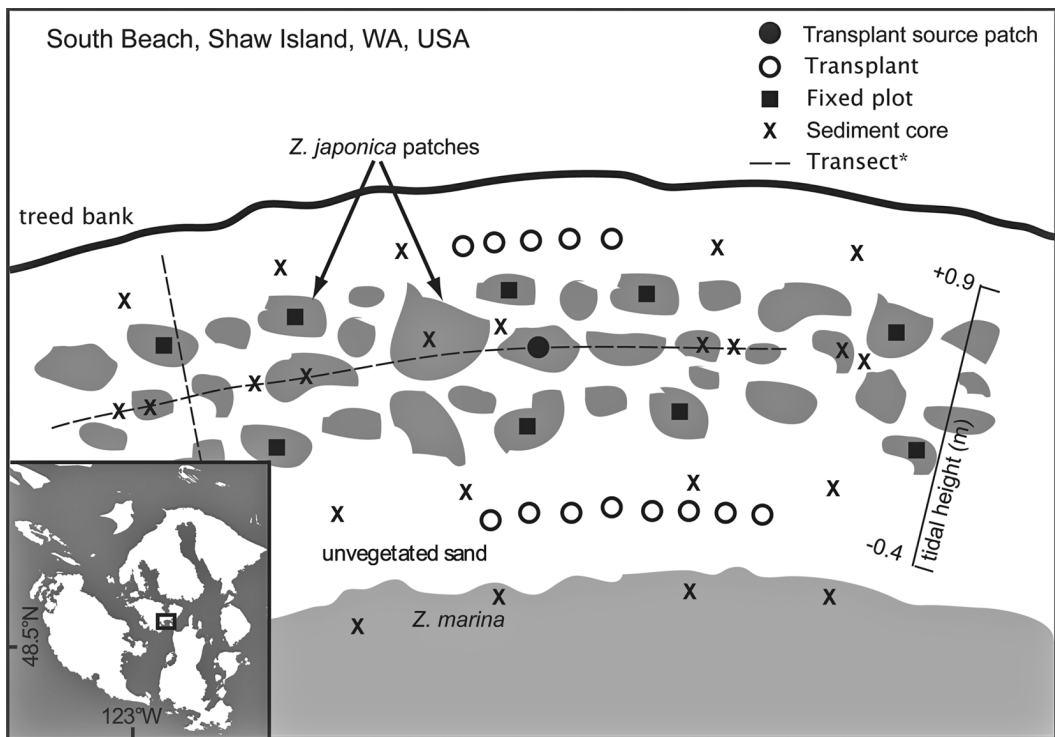
FIGURE 1. Schematic diagram of South Beach study site and sampling methodology. Inset shows San Juan Archipelago, Washington, USA. For clarity only one horizontal (three total) and one vertical (eight total) transects are shown. Three of the low transplants were used for biomass production sampling. Diagram is not to scale.

upper limit of *Z. marina*. All tidal height measurements were taken using standard transit survey equipment and tide tables. In addition, we measured the distance along the substrate between the bottom of the *Z. japonica* bed and the top of the *Z. marina* bed (i.e., the size of the gap zone between the two species).

### Patch Width and Spacing

We measured the spatial distribution of *Z. japonica* patches at three tidal heights: 5 m below the upper limit of the bed, the vertical center of the bed, and 5 m above the bottom edge of the bed. At each of these tidal heights we laid a 200 m transect across the beach and measured the width of all patches bisected by the transect as well as the distance between patches along the transect (Figure 1).

### Fixed Plots

Fixed plots were established at two tidal heights near the upper and lower limits of *Z. japonica*, at approximately +0.4 m mean lower low water (MLLW) and 0 m MLLW, respectively. At each of the two tidal heights five *Z. japonica* patches at approximately the same tidal height and separated by between 10 and 30 m were haphazardly selected. A fixed plot measuring 30 cm by 30 cm was established at the center of each patch (Figure 1).

Using a 30 cm by 30 cm quadrat subdivided into nine uniform sections, we estimated the percentage cover of leaves and counted the number of shoots in three randomly selected subsections within each quadrat. We then randomly selected three *Z. japonica* shoots from within the plot, counted

the number of leaves per shoot, and measured the length and width (1 mm above the sheath) of the longest leaf of each shoot selected. Data from these samples were averaged for each plot to increase the precision of numbers used in statistical analyses. The presence or absence of an intact leaf tip was also noted.

Plots were established and data were initially collected on 17 April 2006. They were subsequently resampled on 15 May and 13 July 2006.

### Transplants

Phillips (1976) discussed the value of transplanting as a technique to assess the tolerance of seagrass species to a range of environmental conditions. We transplanted *Z. japonica* to two tidal heights: +0.9 m MLLW and −0.2 m MLLW on 17 April 2006. The higher-elevation transplant location was above the *Z. japonica* distribution and the lower elevation transplant was located in the unvegetated zone, between *Z. japonica* and *Z. marina* (Figure 1). Our transplant technique involved removing a 10 cm diameter intact rhizocore (whole plant shoots and associated sediment) with a polyvinyl chloride corer to create a transplant unit. Each transplant unit was planted into an excavated hole created using the same coring device. All transplant units were taken from a single *Z. japonica* patch located near the vertical center of the population.

Five cores were transplanted to the higher elevation and eight cores were transplanted to the lower elevation. The shoots from three of the low transplant units were excised 1 cm above the sediment immediately after transplanting. Shoots from these treatments were excised on each subsequent sample date using the same technique to quantify aboveground biomass production. Tissue was bagged separately and transported to the laboratory, where it was dried to a constant weight at 60°C and weighed to the nearest milligram. Shoots in the remaining five cores in the lower elevation zone and all of the transplant cores at the upper tidal height were kept intact for shoot density counts and to measure the longest leaf of five haphazardly selected shoots in each unit on each sample date. No transplant control treatment was used to evaluate the effect of transplanting.

### Seed Bank Evaluation

On 17 April we collected sediment cores along five vertical transects. Each transect was laid so that it bisected a *Z. japonica* patch at approximately the midpoint of the vertical distribution of the *Z. japonica* population. The location of the first transect was haphazardly chosen. However, the subsequent four transect locations were determined by measuring a horizontal distance along the beach 23 m from the previous transect and selecting the patch that was closest to that point and approximately at the midpoint of *Z. japonica*'s vertical distribution. The transect was then laid so that it bisected this patch. Sediment cores (5 cm diameter, 10 cm depth) were then collected at four tidal heights along each transect: above the *Z. japonica* zone (+0.9 m MLLW), within the *Z. japonica* zone (+0.2 m MLLW), the unvegetated zone between the two *Zostera* species (−0.1 m MLLW), and just inside the *Z. marina* bed (−0.6 m MLLW) (Figure 1).

At the sampling station within the *Z. japonica* bed we collected two cores: one in the patch bisected by the transect and one in unvegetated sand at the same tidal height. At all other sampling stations we collected a single core per tidal height. Thus we collected five cores per transect along five transects for a total of 25 cores. Cores were transported to the laboratory, where they were sieved in a nest of five mesh sizes (10 mm, 1.4 mm, 1 mm, 0.8 mm, 0.2 mm) to capture the range of *Z. japonica* seed sizes that occur (2.38 mm ± 0.119 mm, mean ± 1SD [Phillips and Menez 1988, Wyllie-Echeverria et al. 2006]). The contents of each sieve were examined using a dissecting microscope to look for the presence of seeds or seed coats.

### Statistics

The patch width and distance between patch data were each analyzed independently using one-way analyses of variance (ANOVAs).

Both data sets were natural log transformed before analysis to conform to the assumptions of ANOVA. Fixed plot data were analyzed using repeated measures ANOVA with tide height and time as main effects. The fixed plot percentage cover data were arcsine square-root transformed before repeated measures ANOVA analysis. We combined the broken leaf tip data for each tidal height across all sample dates and used a contingency test to ask whether the proportion of leaves that were broken differed between the two tidal heights (Sokal and Rohlf 1995). All data presented in figures are untransformed.

### RESULTS

#### Vertical Distribution of Zostera spp.

The two species of *Zostera* present at South Beach have distinct, nonoverlapping vertical distributions (Figure 2). The average vertical range of *Z. japonica* was from 0.05 m to 0.34 m MLLW. The upper limit of the *Z. marina* averaged −0.39 m MLLW. Thus, there was a vertical distance of 44 cm between the two species on the tide flat (Figure 2). Because the beach at this site was gently sloping this vertical gap translated into a large horizontal discontinuity. The average horizontal distance along the substratum between the two species was 22.2 m ± 6.1 m (mean ± 1 SD).

#### Patch Width and Spacing

Both the patch width and patch spacing data were natural log transformed before analysis to conform to the assumptions of ANOVA. There was no difference in the width of *Z. japonica* patches among tidal heights (one-way ANOVA, $F = 0.14$, df = 2, $P = .86$) (Figure 3). Similarly, the distance between *Z. japonica* patches did not vary significantly across the vertical distribution occupied by this species (one-way ANOVA, $F = 0.08$, df = 2, $P = .92$) (Figure 3).

#### Fixed Plots

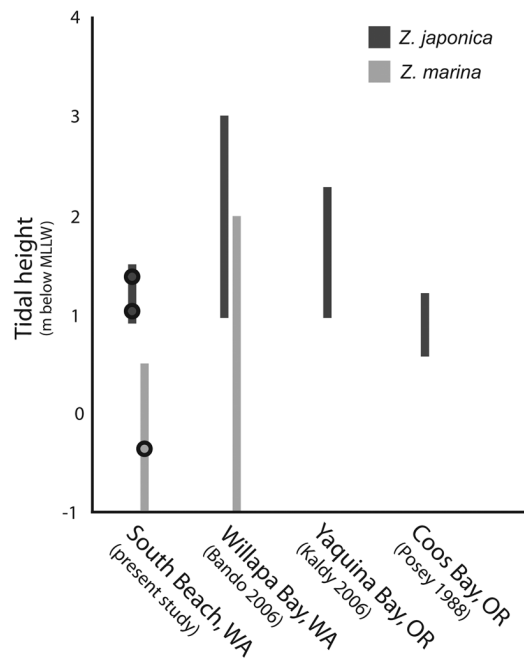The percentage cover and shoot abundance data from fixed plots indicated that *Z. japonica*



FIGURE 2. Vertical distribution of *Z. japonica* and *Z. marina* at South Beach ($n = 8$ transects) and three additional sites from the literature. Only one of the other studies reported tidal range data for *Z. marina*. Dark circles denote mean upper and lower tidal heights for the two species at our study site. At South Beach the average horizontal distance along the substratum between the top edge of the *Z. marina* bed and the bottom edge of the *Z. japonica* bed was 22.2 m.

performed better in patches near the upper edge of its vertical distribution. Although the percentage cover of *Z. japonica* was very similar at the two tidal heights in April, it subsequently increased at the upper limit of the bed and decreased at the lower limit of the bed in May and July (Figure 4a). Tidal height explained a significant amount of variation ($P = .002$) (Table 1), indicating that percentage cover was (on average) significantly higher in patches at the upper limit of the population. The time effect was not significant ($P = .55$) (Table 1). However, a significant time by tidal height interaction occurred ($P = .028$) (Table 1) because the difference in percentage cover between the two treatments increased over time (Figure 4a).
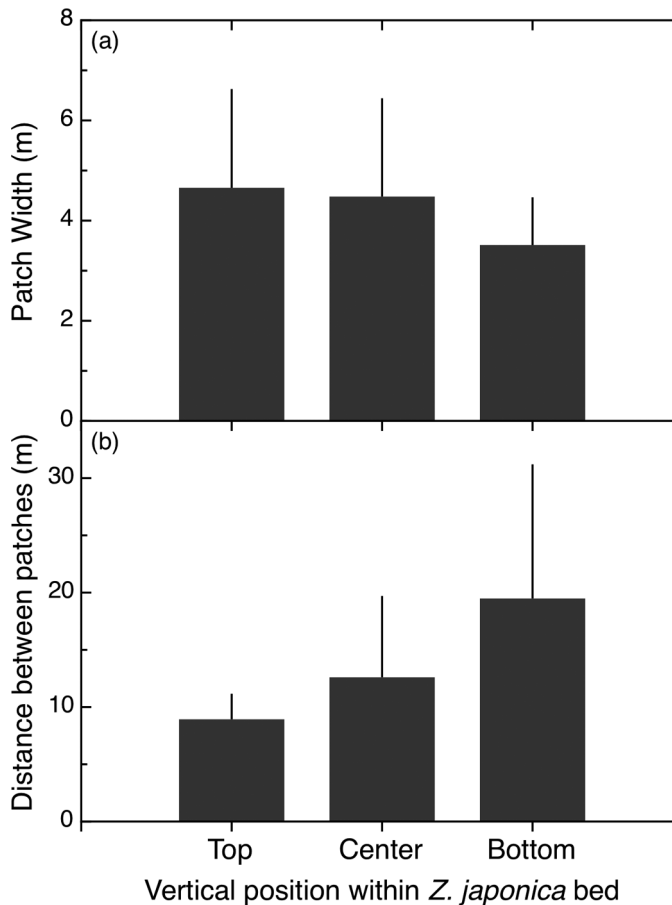
FIGURE 3. Width of (*a*) and horizontal spacing between (*b*) patches of *Z. japonica* at three tidal heights at South Beach (*n* = 3 transects). The top and bottom measurements were taken 5 m inside the upper and lower edges of the bed, respectively. Data are means ± 1 SE.

The number of *Z. japonica* shoots in fixed plots was consistently higher in patches at the upper limit compared with those at the lower limit (*P* = .009) (Table 1, Figure 4*b*). In addition, there was a significant effect of time in the ANOVA model as shoot density at both tidal heights initially increased between April and May and then decreased between May and July (*P* = .003) (Table 1). Because the temporal dynamics in shoot density were synchronous in both upper and lower patches, the time by tidal height interaction was not significant (*P* = .44) (Table 1, Figure 4*b*).

The leaf length data indicate that *Z. japon-ica* leaves were longer at the upper limit compared with the lower limit (Figure 4*c*). The main effect of tidal height was not significant (*P* = .06) (Table 1) because the leaves in high patches were initially slightly longer than those in low patches (Figure 4*c*). However, leaf length increased between April and July in the high patches but not in the low patches, as indicated by the significant time by tidal height interaction (*P* = .007) (Table 1). During this 3-month period leaves in the high patches increased in length by an average of 91%, and those in low patches decreased in length by an average of 8% (Figure 4*c*).
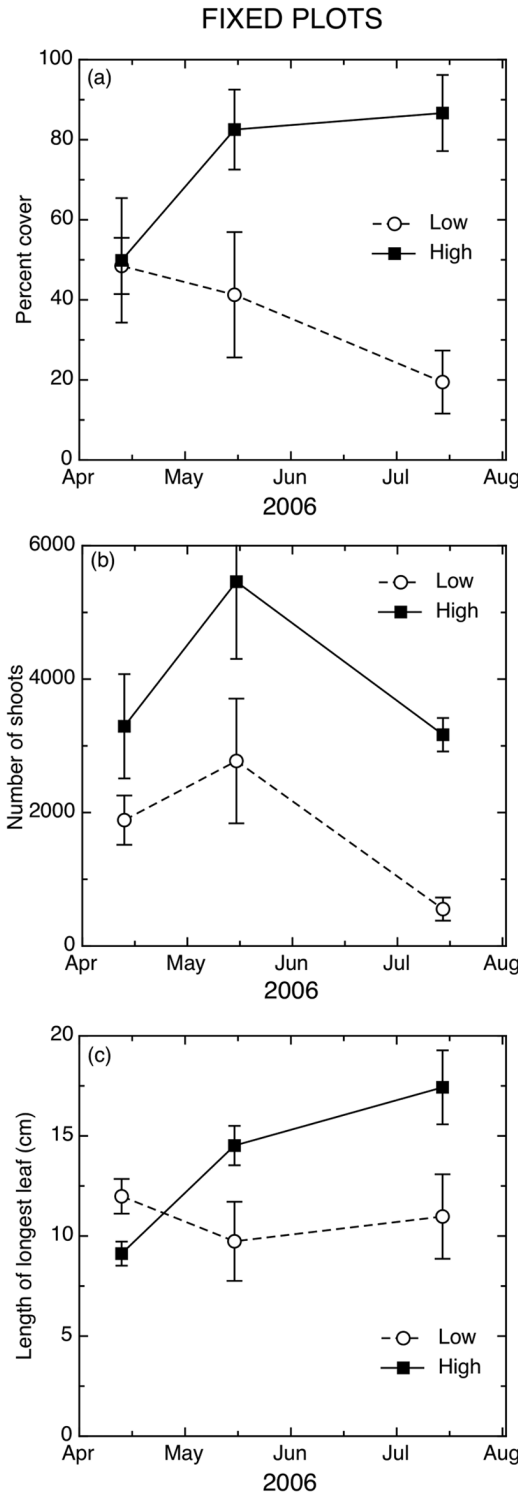
## FIXED PLOTS



FIGURE 4. Percentage cover (*a*), shoot density (*b*), and leaf length (*c*) in *Z. japonica* patches from fixed plots in upper and lower portions of the population at South Beach (*n* = 5 per tidal height). Shoot number is per m² area. Data are means ± 1 SE.

Repeated Measures ANOVA Analyses of Fixed Plot Data

| Source of Variation | df | *F* | *P* |
|---|---|---|---|
| Percentage cover | | | |
| Between subjects | | | |
| Tidal height | 1 | 18.89 | .002 |
| Error | 8 | | |
| Within subjects | | | |
| Time | 2 | 0.63 | .55 |
| Time × Tidal height | 2 | 4.50 | .028 |
| Error | 16 | | |
| Number of shoots | | | |
| Between subjects | | | |
| Tidal height | 1 | 11.64 | .009 |
| Error | 8 | | |
| Within subjects | | | |
| Time | 2 | 8.79 | .003 |
| Time × Tidal height | 2 | 0.85 | .44 |
| Error | 16 | | |
| Number of leaves | | | |
| Between subjects | | | |
| Tidal height | 1 | 0.04 | .84 |
| Error | 8 | | |
| Within subjects | | | |
| Time | 2 | 0.53 | .60 |
| Time × Tidal height | 2 | 2.28 | .13 |
| Error | 16 | | |
| Leaf width | | | |
| Between subjects | | | |
| Tidal height | 1 | 0.09 | .77 |
| Error | 8 | | |
| Within subjects | | | |
| Time | 2 | 6.29 | .01 |
| Time × Tidal height | 2 | 2.47 | .12 |
| Error | 16 | | |
| Length of longest leaf | | | |
| Between subjects | | | |
| Tidal height | 1 | 4.63 | .06 |
| Error | 8 | | |
| Within subjects | | | |
| Time | 2 | 3.68 | .049 |
| Time × Tidal height | 2 | 6.77 | .007 |
| Error | 16 | | |

There was no difference in the number of leaves per *Z. japonica* shoot between upper and lower patches (*P* = .84) (Table 1). Although there was significant variation over

time in leaf width ($P = .01$) there was no indication that leaf width differed between the two tidal heights ($P = .77$) (Table 1). The percentage of leaves with broken tips was 34% in high plots (15 of 44 leaves) and 42% in low plots (19 of 45 leaves) and was not significantly different ($G = 0.62$, $P \gg .05$).

### Transplants

The high-elevation transplants were completely gone (i.e., no tissue, including rhizome remained) when we returned to the site in May (Figure 5). The lower-elevation transplants survived throughout our sampling period (Figure 5) but were missing when we visited the site in April 2007.

The biomass production in the clipped *Z. japonica* cores in the low-elevation zone was $76 \pm 39$ mg (mean $\pm$ 1 SD) between April and May. Production from May to July was $283 \pm 206$ mg (mean $\pm$ 1 SD), which on a per-month basis (i.e., divided by 2) yields an estimate of $141 \pm 103$ mg (mean $\pm$ 1 SD) during that period. Thus, the monthly productivity of the lower-elevation transplants doubled during the later months compared with the April–May interval.

### Sediment Cores

No seeds from either species of *Zostera* were found in the 25 sediment cores.

### DISCUSSION

The distinctive gap zone between the lower edge of *Z. japonica* and the upper edge of *Z. marina* at South Beach (Figure 2) is a pattern that occurs at the majority of sites in this region (Shafer 2007). At South Beach *Z. japonica* was present (on average) from +0.05 m to +0.34 m, with a vertical distance of 0.44 m between *Z. japonica* and *Z. marina*. Although this distance is relatively small, on this gently sloping beach that translates into an average distance along the substratum of 22.2 m. This gap zone is sufficiently large that the two seagrass species do not come into direct contact at this site. Although exploitation competition for water column nutrients could
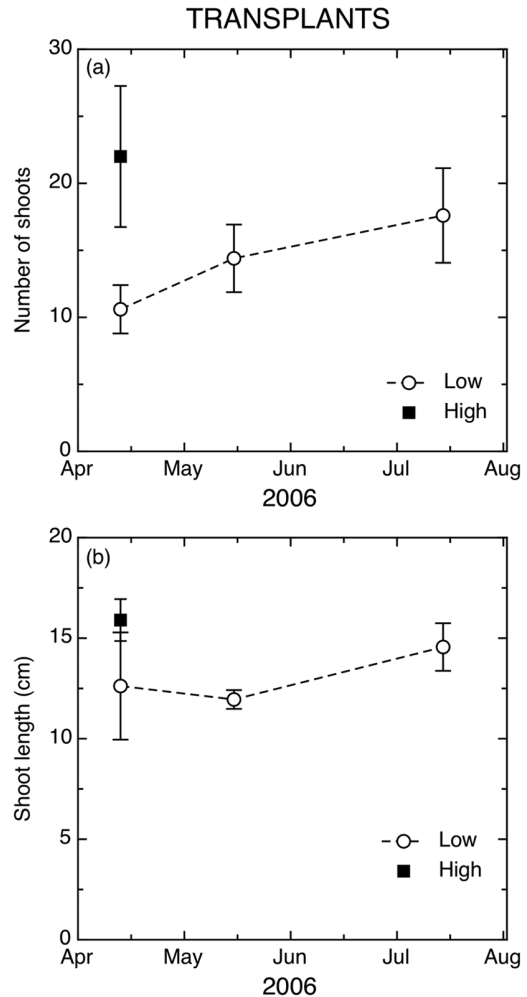


Figure 5. Performance of *Z. japonica* transplants, all of which were taken from a single patch in the center of the vertical distribution of *Z. japonica* ($n = 5$ transplants per treatment). All high-elevation transplants were gone by the May sample date. Low-elevation transplants did not survive over the winter. Data are means $\pm$ 1 SE.

still occur (Larned 2003), seagrass in this region is generally not nutrient limited (Phillips 1984), especially at relatively high-energy sites like South Beach. Therefore, we think it is unlikely that competition between the two seagrasses occurs at this site.

One goal of our study was to evaluate whether *Z. japonica* can survive above and be-

low its natural vertical distribution at South Beach. When transplanted above its existing upper limit *Z. japonica* disappeared completely (including rhizomes) within 1 month (Figure 5). In the absence of transplant controls we cannot exclude the possibility that transplant stress contributed to the mortality of these transplants. Nevertheless, one possible explanation is that the transplants were eroded from the sandy substrate by wave action. This mechanism fits with our observation that the high intertidal substratum at South Beach was very dynamic and changed considerably between our visits. However, *Z. japonica* is relatively vulnerable to desiccation (Baldwin and Lovvorn 1994, Shafer et al. 2007), and a second potential explanation is that desiccation weakened the high transplants, facilitating their removal by water motion. The alternative hypothesis that herbivory caused the mortality in this zone is inconsistent with absence of rhizome material and lack of herbivores at this site.

Transplants of *Z. japonica* into the gap zone between the two seagrass species survived, and even increased in shoot number, throughout the summer but then disappeared during the winter. Likewise, Nomme and Harrison (1991*b*) found that *Z. japonica* transplanted into the low intertidal increased in shoot density during the summer months in British Columbia. Whereas the lower limit of *Z. japonica* may be set by competition with *Z. marina* at some sites (Nomme and Harrison 1991*b*), it appears to be determined by something else at sites like South Beach where the two species do not overlap. One possibility is herbivory by birds during the winter months, when migrating and overwintering birds feed intensively on *Z. japonica* in this region (Baldwin and Lovvorn 1994). However, birds such as dabbling ducks and black brant (*Branta bernicla*) have not been observed at South Beach (S.W.-E., pers. obs.). An alternative hypothesis is that light limitation precludes long-term survival in the low intertidal (Huong et al. 2003).

Does seed limitation play an important role in structuring the distribution of *Z. japonica*? We found no seeds in our coring study and we saw no evidence of *Z. japonica*

flowering at this site. Because seed distribution within a *Zostera* population can be nonuniform (Boese and Robbins 2008) we cannot exclude the possibility that seeds were present at South Beach but not detected by our coring study. However, *Z. japonica* seeds persist in the sediment year-round and can be viable for multiple years (Bigley 1979), so we should have detected seeds if they were present, even if they were the result of flowering we have observed at this site in previous years (S.W.-E., pers. obs.). Given the complete absence of seeds it seems likely that growth of the South Beach *Z. japonica* population occurs primarily via expansion of existing patches. Fragmentation may also be a mechanism by which new patches are initiated, but it is unknown whether *Z. japonica* can generate new patches in that way, and the importance of fragmentation for seagrasses in general is debated (Ewanchuk and Williams 1996, Hall et al. 2006). Although the lack of seeds might suggest a role for dispersal limitation, the failure of long-term survival of our transplants indicates that dispersal limitation is probably not regulating the vertical distribution of *Z. japonica* at this site.

Our fixed-plot surveys clearly showed that *Z. japonica* performed better at the upper edge of its vertical distribution, compared with the lower edge (Figure 4). In addition, *Z. japonica* patches tended to be smaller and more distant from one another in the low intertidal compared with the high intertidal (Figure 3). These results collectively suggest that the high intertidal is better habitat for *Z. japonica* than is the low intertidal. One possible explanation is bioturbation (e.g., Burrowing shrimp [Dumbauld and Wyllie-Echeverria 2003]), but bioturbating organisms have not been observed at this site. Other possible reasons include herbivory, epiphyte load, and light. Aside from an occasional amphipod, we observed no herbivores in the vicinity of *Z. japonica* at this site. Thus, we think it unlikely that increased levels of herbivory in the lower intertidal can explain our results. The lack of herbivores at this site contrasts with the large number of gastropods and crustacean herbivores that

have been found in association with *Z. japonica* at some other sites in this region (Thom et al. 1995) and in its native range (Fong et al. 2000), suggesting that there is considerable intersite and interregion variation in herbivore pressure. Epiphytic algae can have important effects on *Z. japonica* in other regions of the world (Fong et al. 2000). However, the only epiphytic algae we observed on *Z. japonica* at our site were diatoms and they were never abundant, possibly due to the wave-exposed nature of this beach.

In our view the most obvious explanation for the pattern we observed is that higher light availability in the upper intertidal zone resulted in enhanced *Z. japonica* performance. Although laboratory experiments indicate that *Z. japonica* performs better when continuously submerged (Harrison 1982), in the field being continuously submerged comes at a cost of reduced access to light. To our knowledge minimum light requirements for *Z. japonica* have not been measured. However, such data are available for *Z. noltii*, a species in the same subgenus (Bigley and Barreca 1982, den Hartog and Kuo 2006) with a comparable vertical distribution. Whereas *Z. noltii* requires a minimum of 15 mol quanta $m^{-2}$ $day^{-1}$ to trigger rhizome branching (Vermaat and Verhagen 1996), *Z. marina* growth is unconstrained by light at just 7 mol quanta $m^{-2}$ $day^{-1}$ (Thom et al. 2008). Likewise, the half saturation constant ($K_m$) of *Z. noltii* is more than four times higher than that of *Z. marina* (Vermaat and Verhagen 1996). These data indicate that *Z. noltii* has much higher light requirements than *Z. marina*. To the extent that *Z. noltii* and *Z. japonica* light requirements are comparable, this provides some support for our hypothesis that light limitation may be a factor mediating *Z. japonica* performance near the lower edge of its vertical distribution.

*Zostera japonica*'s tidal height-dependent performance notwithstanding, it is currently unclear which *Zostera* species is responsible for variation among sites in the presence of the unvegetated gap zone separating the two species in the Pacific Northwest. Available data on the vertical distribution of *Z. japonica* suggest that the lower limit of this species is relatively invariant, even when gap and non-gap sites are considered (Figure 2). Conversely, *Z. marina* distribution data suggest that its upper edge is highly variable in this region (Figure 2) (Bando 2006, Gaeckle et al. 2008). A large-scale (79 sites) monitoring program in the Greater Puget Sound confirms that the upper limit of *Z. marina* is extremely variable within Washington State, ranging more than 4 m in some subregions (Gaeckle et al. 2008). Thus, we propose that *Z. marina* is the species responsible for generating the unvegetated gap zone. Specifically, we hypothesize that the gap zone occurs at sites where the upper limit of *Z. marina* is constrained (e.g., South Beach [Figure 2]; see also Boese and Robbins 2008). Regardless of whether *Z. marina* plays a key role in generating the gap pattern, an important next step to understanding its genesis is to identify how sites at which the gap is present differ from those where it is absent. No studies have addressed this issue directly, but Shafer (2007) suggested that abiotic habitat parameters may control variability among sites in the presence of the gap.

Overall our results suggest that *Z. japonica* performance is dependent on tidal height, with reduced performance lower in the intertidal. This pattern is largely consistent with prior work (Bigley and Harrison 1986, Nomme and Harrison 1991*b*, Shafer 2007). However, previous *Z. japonica* studies have focused on sites where the vertical distribution of *Z. japonica* overlaps with that of *Z. marina*. Our study provides information about the distribution and abundance of *Z. japonica* at a second, and more common (Shafer 2007), type of site: those where the two *Zostera* species do not come into direct contact.

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