A comparison of epifaunal invertebrate communities in native eelgrass Zostera marina and non-native Zostera japonica at Tsawwassen, BC

Nicole S. Knight, Carolyn Prentice, Michelle Tseng & Mary I. O'Connor

ORIGINAL ARTICLE

A comparison of epifaunal invertebrate communities in native eelgrass *Zostera marina* and non-native *Zostera japonica* at Tsawwassen, BC

NICOLE S. KNIGHT⋆, CAROLYN PRENTICE, MICHELLE TSENG & MARY I. O'CONNOR

Department of Zoology, Biodiversity Research Centre, University of British Columbia, Vancouver, Canada

Abstract
The introduction of non-native species can alter the structure of local communities and ecosystems. Although there is concern over the negative effects imposed by introduced species, positive effects are also possible. Introduced species may facilitate local resident species by providing or modifying habitat; these positive effects are sometimes overlooked, but are important for decisions about the local management of non-native species. The introduction of *Zostera japonica* to the Northeast Pacific coast is a case of a non-native foundation species that appears to expand total eelgrass habitat area, potentially facilitating local eelgrass-inhabiting species. In this study, we asked whether the non-native *Z. japonica* provides habitat for eelgrass-dwelling invertebrates that is similar to its native congener, *Z. marina*. We systematically quantified invertebrate assemblages in the two eelgrass species and quantified eelgrass characteristics that are relevant to epifaunal habitat quality (e.g. shoot density and surface area). We found that *Z. japonica* supports a greater total abundance of the same invertebrate species found in *Z. marina* meadows; however, the relative abundance of invertebrate species differed between *Z. japonica* and *Z. marina*. This result is consistent with differences in the two congeners' morphological characteristics, density of vegetative and reproductive shoots, and total blade surface area per square metre. We conclude that the expansion of total eelgrass habitat due to the introduction of *Z. japonica* appears to increase the available habitat for local epifaunal invertebrate communities.

Key words: *Facilitation, foundation species, invertebrates, non-native species, Northeast Pacific,* Zostera

Introduction

Non-native species are frequently introduced to Northeast Pacific coastal ecosystems (Wonham & Carlton 2005) and they can alter the abundance of local species through changes in resource use and species interactions (Rius & McQuaid 2009; Brenneis et al. 2011; Deudero et al. 2011). Species introductions can lead to negative effects on native communities through competition or predation, often reducing local species diversity and abundance (Hollebone & Hay 2007; Gerber et al. 2008; Byers et al. 2010; Salvaterra et al. 2013; Tanner et al. 2013). Non-natives may also increase the diversity and abundance of local species, typically by modifying or creating habitat (e.g. Wohnam et al. 2005; Rius & McQuaid 2009). Whether introduced species lead to positive or negative effects on local species

is relevant to local management decisions about the control and remediation of non-native species (Shafer et al. 2014).

The eelgrass *Zostera japonica* Ascherson & Graebner has become established in many areas of the Northeast Pacific coast from British Columbia to California, and regional management entities are increasingly considering whether the species requires management (Shafer et al. 2014). Since its establishment in North America, possibly in 1957 (Harrison & Bigley 1982), *Z. japonica* can now be found growing adjacent to or in mixed stands with its native congener, *Zostera marina* Linnaeus, in areas formerly occupied only by *Z. marina* (Baldwin & Lovvorn 1994; Shafer et al. 2014). The native *Z. marina* is an important foundation species that supports many invertebrate, fish and bird species (Baldwin & Lovvorn 1994; Lovvorn & Baldwin

1996; Thom et al. 1995; Lee et al. 2001; Seymour et al. 2002; Semmens 2008; Sutherland et al. 2013) and provides a multitude of ecosystem services, including carbon storage (Schmidt et al. 2011). Whether the non-native *Z. japonica* can provide similar ecosystem services and habitat for local fauna will help determine whether this species is managed as a problem species, or protected as a foundation species (Shafer et al. 2014).

Zostera marina and *Z. japonica* both grow in the intertidal zone; however, *Z. marina* is found predominantly in the low intertidal and subtidal zones, whereas *Z. japonica* grows higher in the intertidal zone (Baldwin & Lovvorn 1994). In the mid-intertidal zone, the two congeners may grow in mixed stands, particularly in intertidal habitats with shallow slopes (Baldwin & Lovvorn 1994; Shafer et al. 2014). *Zostera marina* and *Z. japonica* also have markedly different morphologies: the blades of *Z. marina* are longer and wider than those of *Z. japonica*, and *Z. japonica* grows in much denser stands than does *Z. marina*.

The growth of *Z. japonica* in the high intertidal zone may expand total eelgrass habitat and support greater invertebrate species richness than unvegetated sediment (Posey 1988; Ruesink et al. 2010; Shafer et al. 2014), but in eelgrass meadows comprised of both species it is still unknown whether the habitat provided by *Z. japonica* is of comparable quality to that of *Z. marina*, particularly for the invertebrate grazers that provide a key trophic link between primary production and juvenile fish. Seagrass meadows and their associated invertebrates have been shown to support much greater fish production than nearby unvegetated sediment (Edgar & Shaw 1995; Posey 1988). In addition, seagrass morphology and density have been demonstrated to affect invertebrate community composition and abundance, both within and between seagrass species (Boström & Bonsdorff 2000). Therefore, expanding or modifying eelgrass habitat could lead to shifts in energy flow throughout this ecosystem.

Here, we address the following questions: do *Z. japonica* and *Z. marina* support similar communities of epifaunal invertebrates? Do morphological characteristics or shoot density explain variation in invertebrate abundance or community composition between or within eelgrass species? To answer these questions, we quantified the abundance and diversity of invertebrates living in monospecific stands of *Z. japonica* and *Z. marina*, and we measured eelgrass morphological characteristics. We expected that the smaller and more densely growing shoots of *Z. japonica* would support a different community of invertebrates than that supported by *Z. marina*.

Materials and methods

Eelgrass and invertebrate collection

We quantified abundance and composition of eelgrass, epiphytes and epifauna at Tsawwassen, BC (49°00′N, 123°09′W) in August 2011 (Figure 1). The eelgrass meadow at Tsawwassen is a large intertidal meadow that extends over several kilometres of coastline in the Salish Sea. This region is strongly influenced by freshwater and sediment output from the Fraser River, and summertime salinity ranges from 20 to 16 ppt. *Zostera japonica* is well established at this site, although we lack records for its colonization date. *Zostera japonica* inhabits the upper intertidal zone above the *Zostera marina* meadow, and there is a mixed zone where the two species are found together at a mid-intertidal height.

To compare invertebrate assemblages between eelgrass species, we randomly chose 10 0.0625 m^2 plots (0.25 m per side; five plots for each eelgrass species). We sampled dense, monospecific stands of *Z. marina* and *Z. japonica* growing at the same tidal height, approximately 0.75 m above lower low water, large tide (LLWLT), minimizing the variation in abiotic factors associated with intertidal elevation.

From each plot, we collected eelgrass, epiphytes and epifauna at low tide. We first surveyed plots for highly mobile epifauna such as crabs and isopods. Next, we uprooted and bagged all shoots within the quadrat. We selected four shoots, one at each of the quadrat's four corners, for epiphyte quantification.
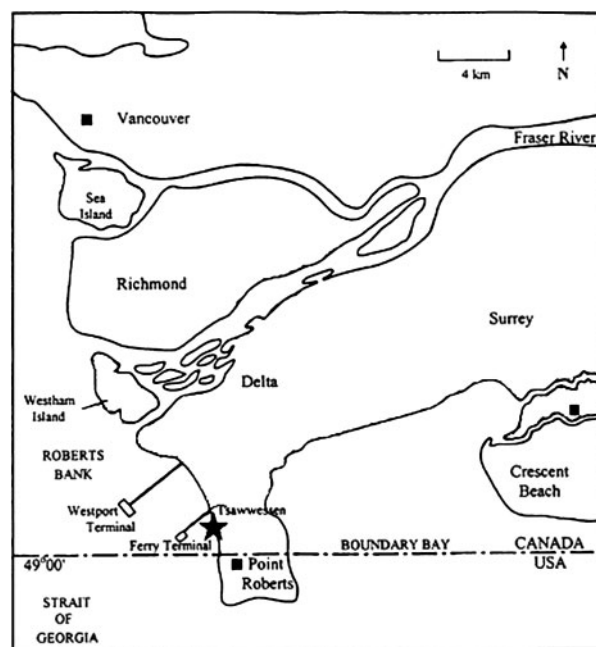

Figure 1. Map of the eelgrass sampling site in Tsawwassen, BC. Adapted from Gutsell (1995).

Sample processing

For each plot, we recorded the total number of shoots, the number of reproductive shoots, the wet and dry mass (60°C for 48 h) of the shoots, and the length and width of each blade and leaf sheath for each shoot. We calculated the blade surface area using the formula: blade length × blade width × 2. Total shoot surface area per plot was calculated by summing the blade surface area and adding the surface area of the leaf sheath of the lowermost blade. We also measured the length and width of these four shoots to calculate epiphyte mass per unit surface area of eelgrass (mg/cm^2).

In the laboratory, we agitated the *Zostera* shoots in fresh water, and carefully scraped off invertebrates and epiphytes. We passed the mixture of invertebrates, epiphytes and water through a 0.5 mm sieve and preserved invertebrates in 70% ethanol. Taxa were identified to the lowest resolution possible, typically species or genus.

Of the four shoots per plot that were collected for epiphyte quantification, we randomly chose one shoot and removed all of the epiphytes by gently scraping the length of the blades. We dried (60°C for 48 h) and weighed the epiphytes.

Data analysis

We used *t*-tests to compare blade length, blade width, total shoot density, reproductive shoot density, surface area per plot, epiphyte load (standardized to surface area), wet and dry mass of eelgrass shoots, and invertebrate abundance per plot between the two eelgrass species. In the event of unequal variances between groups, Welch's *t*-test was used.

We examined whether the variation in invertebrate abundance within eelgrass species was explained by the following eelgrass properties: total shoot density, reproductive shoot density, dry epiphyte mass (standardized to shoot surface area), shoot surface area per plot, or wet and dry mass of eelgrass shoots. To test for correlations between possible predictors and invertebrate abundance, we first visually inspected scatter plots of abundance vs. each predictor. When a correlation appeared possible, we proceeded with a formal statistical analysis. This approach reduces the likelihood of false detection by minimizing the total number of tests. Before performing parametric tests, we tested data for normality and homogeneity of variances.

We used analysis of covariance (ANCOVA) to investigate whether the relationship between invertebrate abundance and shoot surface area per plot was unique to each eelgrass species (categorical factor: eelgrass species; covariate: shoot surface area per plot). In the event that an ANCOVA showed a significant interaction effect, we used independent linear regression to quantify relationships between invertebrate abundance and predictor variables.

We characterized invertebrate assemblages by calculating Simpson's diversity index and individual-based rarefied species richness for each plot using the package vegan in R version 3.0.2 (Oksanen et al. 2013; R Core Team 2013), and compared these metrics using *t*-tests. Rarefied richness was calculated using Hurlbert's (1971) method. We performed a post-hoc analysis to determine the statistical power of the diversity and species richness tests, as well as the sample size that would be required to achieve an acceptable statistical power.

We used non-metric multi-dimensional scaling (nMDS) to determine whether invertebrate communities differed between *Z. japonica* and *Z. marina* habitats. We square root-transformed the abundance of each taxa to reduce the influence of dominant invertebrates, and created a Bray–Curtis dissimilarity matrix with the resulting data. Following this analysis, a permutational analysis of variance (PERMANOVA) was done to quantify differences in community composition, and a similarity percentages analysis (SIMPER; using Bray–Curtis dissimilarities) was performed on the square root-transformed data to determine which invertebrate species were driving differences in community composition. Multi-dimensional community composition analysis was done using the R package vegan (Oksanen et al. 2013). All statistical analyses were performed using R version 3.0.2 (R Core Team 2013) and GPower, version 3.1, for power analyses (Faul et al. 2009).

Results

Physical differences between Zostera japonica *and* Zostera marina

At our site we found distinct *Zostera marina* and *Z. japonica* densities and morphologies (Table I). *Zostera japonica* shoots were over 10 times more abundant than *Z. marina* shoots, and *Z. marina* blades were approximately twice as long and four times as wide as *Z. japonica* blades (Figure 2). Reproductive shoot density was greater in plots of *Z. japonica* by almost two orders of magnitude. However, total shoot surface area, as well as wet and dry mass of eelgrass per plot, did not differ significantly between the two species. *Zostera japonica* supported an epiphyte load (standardized to shoot surface area) approximately four times greater than did *Z. marina* at the time of sampling.

Table I. Morphological characteristics of *Zostera marina* and *Z. japonica* at Tsawwassen, BC. Measurements were taken from plots of 0.0625 m^2.

	Z. japonica mean (SD)	*Z. marina* mean (SD)	$t_{1,8}$	P
Blade length (mm)	303 (48)	608 (79)	7.38	0.0002
Blade width (mm)	1.64 (0.24)	6.36 (0.73)	13.68	$< 10^{-6}$
Total shoot density (shoots/plot)	136 (44)	11 (4)	9.65	$< 10^{-4}$
Reproductive shoot density (shoots/plot)	37.2 (27.2)	0.4 (0.9)	3.03	0.04
Shoot surface area (cm^2/plot)	3613 (1620)	5246 (2024)	1.41	0.19
Epiphyte load (mg/cm^2)	0.88 (0.41)	0.25 (0.14)	3.24	0.01
Eelgrass wet mass (g/plot)	76.0 (14.6)	70.5 (12.7)	0.64	0.54
Eelgrass dry mass (g/plot)	9.3 (2.5)	7.9 (1.8)	1.05	0.33

Invertebrate abundance

We identified and enumerated approximately 4000 epifaunal invertebrates, including representatives of 16 taxa. To our knowledge, *Monocorophium acherusicum* Costa, 1853 is the only non-native invertebrate identified in this study (Wonham & Carlton 2005; Williams 2007). However, we were unable to identify all taxa to species. Invertebrate abundance in plots of *Z. japonica* was over twice that of *Z. marina* plots ($t_{1,8} = 5.15$, $p < 0.001$; Table II). A visual inspection of the data suggested no correlation between invertebrate abundance and within-species variation in eelgrass wet and dry mass, epiphyte dry mass and shoot density.

Of the possible predictors (Table I), the only morphological eelgrass characteristic that explained variation in invertebrate abundance within eelgrass species was total shoot surface area per plot. The relationship between invertebrate abundance and total shoot surface area differed between eelgrass species (species × surface area: $F_{1,6} = 9.84$, $P = 0.02$; Figure 3). Invertebrate abundance increased with total shoot surface area for *Z. marina* ($R^2 = 0.91$, $P = 0.01$; Figure 3), but showed no significant relationship with *Z. japonica* total shoot surface area ($R^2 = 0.15$, $P = 0.28$; Figure 3).

Figure 2. Samples of *Zostera marina* (top) and *Z. japonica* (bottom), taken from Tsawwassen, BC. Specimens are shorter than the average measured lengths of 608 mm (*Z. marina*) and 303 mm (*Z. japonica*).

Invertebrate community composition

Invertebrate community composition varied between eelgrass species (PERMANOVA, $F_{1,8} = 8.95$, $P = 0.04$; Figure 4). Plots of *Z. marina* were dominated by (in order of decreasing abundance) a benthic copepod (likely from the genus *Amphiascus* or *Orthopsyllus*), *Caprella laeviuscula* Mayer, 1903 and *Mytilus trossulus* Gould, 1850; similarly, plots of *Z. japonica* were dominated by *C. laeviuscula*, *M. trossulus* and *Monocorophium acherusicum* (Table III). All of the identified invertebrate species were found on both eelgrass species (with the exception of Caridea sp., which was only seen on *Z. japonica*; Table III).

Only a handful of invertebrate species were responsible for the majority of the variation in community composition. *Monocorophium acherusicum*, *C. laeviuscula*, *M. trossulus* and *Littorina* spp. contributed most to the dissimilarity in community composition, according to the SIMPER analysis. These taxa were more abundant in plots of *Z. japonica*; abundances of many other invertebrate species, including gammarid amphipods, isopods and polychaetes, were unaffected by eelgrass species (Table III).

Despite differences in composition, invertebrate species diversity did not differ significantly between *Z. japonica* and *Z. marina* ($t_{1,8} = 0.86$, $P = 0.43$; Table II); however, the statistical power of this *t*-test was very low ($1 - \beta = 0.07$; $1 - \beta \geq 0.80$ is an acceptable statistical power; Cohen 1992). Rarefied species richness also did not differ significantly between *Z. japonica* and *Z. marina* invertebrate communities ($t_{1,8} = 1.69$, $P = 0.13$; Table II), but the statistical power of this test was also low ($1 - \beta = 0.33$). Power analyses revealed that a sample size of at least $n = 18$ would be required to achieve a statistical power ($1 - \beta$) of 0.80 when testing species richness, and that a sample size of $n = 158$ would be required to achieve a statistical power ($1 - \beta$) of 0.80 when testing species diversity. This result suggests

Table II. Characteristics of invertebrate communities found on *Zostera marina* and *Zostera japonica* at Tsawwassen, BC. Measurements were taken from plots of 0.0625 m².

	Z. japonica mean (SD)	*Z. marina* mean (SD)	$t_{1,8}$	*P*
Invertebrate abundance (/plot)	558 (145)	205 (50)	5.15	< 0.001
Simpson's index of diversity	0.83 (0.02)	0.82 (0.04)	0.86	0.43
Rarefied species richness	11.5 (0.7)	12.1 (0.5)	1.69	0.13

that any significant difference in invertebrate richness or diversity would likely be small.

Discussion

The community-level effects of non-native, habitat-forming species depend on the particular species present in the system and on the quality and distribution of habitat provided (Viejo 1999; Wonham et al. 2005; Wright & Gribben 2008). Some introduced habitat-forming species may provide habitat that is inferior to the pre-colonization substrate, resulting in reductions in resident species' survivorship and growth (e.g. Wright & Gribben 2008), whereas other non-natives can facilitate both native and non-native or invasive species (e.g. Wohnam et al. 2005). Non-native habitat-forming species that are morphologically or structurally similar to the native habitat-forming species may support comparable epifaunal communities (Viejo

1999). Facilitation of native species is most likely to occur when the introduced species increases the habitat complexity or provides a limiting resource (Rodriguez 2006). The eelgrass system comprised of the native eelgrass species *Zostera marina* and its non-native congener, *Z. japonica*, is an ideal setting in which to examine how non-native species may facilitate native species assemblages.

We found that *Z. japonica* at Tsawwassen, BC, appears to provide habitat for most epifaunal invertebrates comparable to that provided by *Z. marina*. Species diversity and rarified richness were indistinguishable between the two eelgrass species, although statistical power may have been a limitation. However, *Z. japonica* supports a greater total abundance of epifaunal invertebrates per unit area and a significantly different invertebrate community composition than does *Z. marina*. This expansion in eelgrass habitat and its associated invertebrate community could lead to an increase in resources for higher trophic levels.

It is possible that the greater abundance of invertebrates in the *Z. japonica* habitat is due to *Z. japonica*'s higher shoot density, providing greater habitat complexity than *Z. marina*: a study by Jenkins
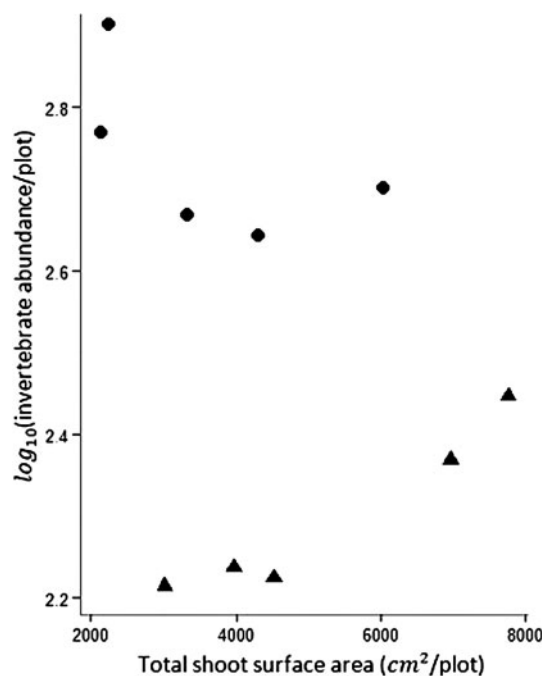

Figure 3. The relationship between total invertebrate abundance (log₁₀ (invertebrate abundance/plot)) and total shoot surface area in each plot of *Zostera japonica* (circles) and *Z. marina* (triangles). Measurements were taken from plots of 0.0625 m².
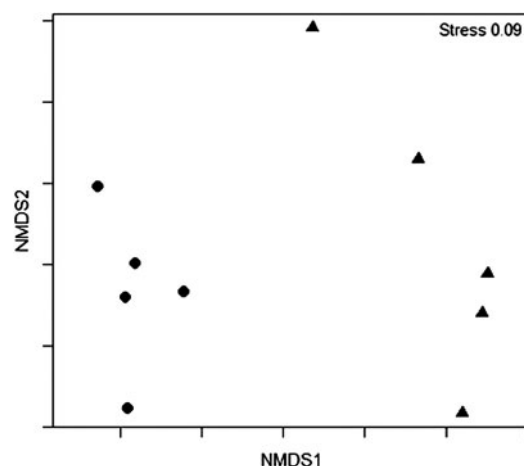

Figure 4. nMDS plot of invertebrate communities in *Z. japonica* (circles) and *Z. marina* (triangles) habitats. The plot was constructed from a Bray–Curtis dissimilarity matrix of square root-transformed invertebrate abundances. The more similar the invertebrate communities of two replicates are, the closer they are on the plot.

Table III. Average abundance of invertebrates and their standard deviations (SD) found in 0.0625 m^2 plots of *Zostera marina* and *Z. japonica* at Tsawwassen, BC.

Taxon	Species	*Z. marina* (SD)	*Z. japonica* (SD)
Crustacea	Caridea sp.	0.0 (0.0)	0.2 (0.4)
	Petidotea resecata Stimpson, 1857	14.6 (8.9)	12.8 (3.5)
	Aoroides columbiae Walker, 1898	7.8 (4.5)	11.4 (7.0)
	Monocorophium acherusicum Costa, 1853	11.0 (11.7)	98.2 (47.8)
	Photis brevipes Shoemaker, 1942	0.8 (0.8)	0.8 (0.4)
	Caprella laeviuscula Mayer, 1903	39.8 (36.0)	123.8 (78.4)
	Leptochelia sp.	15.0 (10.8)	31.4 (19.7)
	Copepod spp.	46 (21.1)	61 (42.1)
	Balanus sp.	0.4 (0.9)	0.2 (0.4)
Mollusca	*Mytilus trossulus* Gould, 1850	33.8 (19.7)	107.0 (23.6)
	Littorina spp.	10.2 (4.9)	74.4 (4.9)
	Lottia pelta Rathke, 1833	5.4 (2.6)	1.2 (1.1)
	Heterodonta spp.	0.4 (0.5)	3.6 (2.6)
Polychaeta	*Platynereis bicanaliculata* Baird, 1863	6.2 (2.9)	10.2 (9.7)
Halacaridae	Halacaridae sp.	13.6 (13.1)	20 (9.7)
Unknown	Unknown invertebrate	0.4 (0.5)	2.0 (2.0)

et al. (2002) found that increased shoot density of artificial seagrass increased invertebrate abundance. We did not see a statistically significant relationship between shoot density and invertebrate abundance within each eelgrass species, perhaps because there was relatively little variation in shoot density among plants within a single eelgrass species. Alternatively, Carr et al. (2011) found that reproductive shoots of *Z. marina* harboured a higher density of invertebrates than did vegetative shoots, likely due to their increased structural complexity. Therefore, the much greater density of flowering shoots in the plots of *Z. japonica* could also contribute to the increased invertebrate abundance.

It is also possible that the greater epiphyte availability observed on *Z. japonica* could have facilitated the greater invertebrate abundance in *Z. japonica*. However, because we did not control for the effects of grazing on epiphyte abundance, we cannot causally link epiphyte load and invertebrate abundance.

Within *Z. marina*, invertebrate abundance was positively correlated with eelgrass surface area (Figure 3). No such significant relationship was seen for *Z. japonica*. In general, we expect that increased shoot surface area would increase the amount of habitat available to invertebrate communities, increasing invertebrate abundance. It is unclear why there was no relationship between invertebrate abundance and shoot surface area for *Z. japonica*. Future studies that include a greater sampling effort are needed to confirm the relationship between invertebrate abundance and shoot surface area in *Zostera*.

Invertebrate community composition was significantly different between eelgrass species. This finding is reasonable given the high interspecific variation in shoot length, width, total shoot density, reproductive shoot density and epiphyte load between *Z. japonica* and *Z. marina* (Boström & Bonsdorff 2000). Although with our data we cannot attribute variation in invertebrate community composition to a specific morphological difference, our findings are consistent with reports that invertebrate community composition can vary with total shoot density and reproductive shoot density (Carr et al. 2011; Nakaoka et al. 2008). Specifically, Nakaoka et al. (2008) found that a subset of invertebrate species reached higher densities on reproductive shoots, whereas others did not appear to respond. In our study, differences in community composition are due to the much greater abundances of *Monocorophium acherusicum*, *Caprella laeviuscula*, *Mytilus trossulus* and *Littorina* spp. in the plots of *Z. japonica*.

Studies by Ferraro & Cole (2011, 2012) found that meadows of *Z. japonica* and *Z. marina* growing in geographically separated locations also supported significantly different invertebrate communities. However, unlike in our study, their data showed little overlap in the identities of the most dominant species. This difference in findings could be due to the difference between the two studies in the spatial proximity of the plots of *Z. japonica* and *Z. marina* sampled.

We observed that *Z. japonica* had a substantially higher proportion of reproductive shoots and a much higher epiphyte load than did *Z. marina*. These differences, observed in August, could reflect general differences between the two species, or they could reflect differences in the phenology of the native vs. non-native *Zostera*. *Zostera marina* flowers throughout the summer but peaks in May and June (personal observations, 2011 and 2012), and the total epiphyte

load on *Z. marina* varies substantially throughout the summer. Native and non-native species often differ in phenology in traits that influence the interacting species (Stachowicz et al. 2002; Wolkovitch & Cleland 2011) and it is possible that differences in phenology of flowering, and possibly epiphyte growth, between *Z. marina* and *Z. japonica* influence the invertebrate assemblages at Tsawwassen.

Our study suggests that *Z. japonica* extends the available habitat for native, eelgrass-dwelling invertebrate species during summer. Furthermore, differences in invertebrate abundance, community composition, timing of high densities of reproductive shoots, and epiphyte loads show that the two eelgrass congeners provide different qualities of habitat for some species. We believe this to be an example of a non-native foundation species facilitating the persistence of a local invertebrate community, and given the current knowledge, *Z. japonica* could be considered to extend *Z. marina*-like habitat for epifaunal invertebrates.

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