

Native clams facilitate invasive species in an eelgrass bed

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ABSTRACT: Whether the non-native seaweed *Sargassum muticum* can displace or impact native eelgrass *Zostera marina* has been debated in the literature, based on differing substrate requirements of the 2 species. Field observations in Bamfield, British Columbia, Canada, revealed that the non-native *S. muticum* successfully inhabits an eelgrass bed through colonizing siphons of the native clam *Tresus capax*. Numerical or physical facilitation of *S. muticum* into the eelgrass bed by *T. capax* may be tempered by seaweed quality or condition. We used field sampling to investigate whether seaweed condition differs between 2 attachment substrates (clam siphon and rock) as a proxy for habitat quality. Attachment substrate promoted different morphologies of *S. muticum*; individuals attached to clam siphons expressed morphologies consistent with sheltered areas compared to individuals attached to rock, which expressed wave-exposed morphologies. Habitat association with the different morphologies supported differences in the epibiont communities colonizing *S. muticum*. Further, *S. muticum* subsequently facilitated incursion of the non-native tunicates *Styela clava* and *Botrylloides violaceus* into the eelgrass bed through habitat provisioning. By facilitating 2 additional invaders, *S. muticum* enhances the level of invasion in the eelgrass bed. This non-native seaweed has the potential to disrupt the persistence of eelgrass in this system.

KEY WORDS: *Sargassum muticum* · *Zostera marina* · Non-native species · Facilitation · *Tresus capax*

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INTRODUCTION

Introduced species can change populations, communities, and ecosystems in dramatic ways over relatively short periods of time (Clavero & Garcia-Berthou 2005, Kappel 2005), and have been strongly linked to losses of biodiversity (Shurin 2000, Stachowicz et al. 2002, Báez & Collins 2008). Biological invasions in the marine environment have increased dramatically due to a number of vectors promoted by globalization and the increase of transoceanic shipping. The dominant vector for the introduction of non-native marine and estuarine species to the northeast Pacific previously was aquaculture, with imports peaking around the 1950s (Wonham & Carlton 2005), but currently the emphasis lies with shipping (Fofonoff et al. 2003).

Due to their coastal habitat, eelgrass beds are exposed to high invasion pressure, with the number of reports of introduced species in eelgrass beds globally increasing over recent decades (Williams 2007). Eelgrass beds profoundly influence the physical, chemical, and biological environments in coastal waters (Orth et al. 2006). Eelgrass beds are highly productive and important for sediment deposition, substrate stabilization, benthic oxygen production, as substrate for epiphytic seaweeds and invertebrates, and as nursery grounds for many species of economically important fish and shellfish (Williamson 2006). In British Columbia, Canada, these fish and shellfish include the commercially important Dungeness crab *Cancer magister* and Pacific herring *Clupea pallasii*.

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Despite the ecological and environmental importance of eelgrass beds, their decline has been observed in many areas of the world, i.e. Florida Bay in North America (Fourqurean & Robblee 1999), Japan (Environment Agency of Japan 2000), the European Mediterranean (Marbà et al. 2005), and Australia (Walker et al. 2006). Over the last decade, 90 000 ha of eelgrass loss has been documented, although the actual area lost is certainly greater (Short & Wyllie-Echeverria 1996). Declines have been attributed to (1) disturbance of coastal and estuarine environments, including industrial, residential, and recreational development, where impacts are most notably manifested in the near-absence of eelgrasses in industrialized ports and areas of intense human coastal development (Short & Wyllie-Echeverria 1996, Orth et al. 2006), and (2) the incursion of non-native species (Orth et al. 2006, Martínez-Lüscher & Holmer 2010).

We found the non-native seaweed *Sargassum muticum* (Yendo) Fensholt (Phaeophyceae: Fucales) colonizing an eelgrass bed at the head of Bamfield Inlet, Bamfield, British Columbia. A non-native seaweed from southeast Asia, *Sargassum muticum* was accidentally introduced to British Columbia around the 1940s with Japanese oysters *Crassostrea gigas* that were imported for aquaculture (Scagel 1956). *Sargassum muticum* is both a fouling species and an opportunist (Critchley 1983). Effective dispersal strategies, which include vegetative drift and the ability to self-fertilize, enable *Sargassum muticum* to colonize nearly any available hard substrate, including rocks in sand and mud substrates, docks, pilings, boat hulls, and other human-made structures, shells, and other seaweeds, from the lower littoral to the sub-littoral (Critchley et al. 1983)—habitat usually occupied by eelgrass. *Sargassum muticum* has proved to be a preemptive competitor whose effects are not evident initially after its introduction, making it difficult to justify a rapid response to remove it (Williams 2007). Since its introduction to the northeast Pacific, *Sargassum muticum* has been of particular concern to environmental managers, largely because it has been documented competing with a number of native seaweed taxa: *Lithothrix aspergillum* (DeWreede & Vandermeulen 1988), bull kelp *Nereocystis luetkeana* (Thom & Hallum 1990), *Gracilaria verrucosa*, *Scytosiphon lomentaria*, and the kelps *Macrocystis integrifolia* (Ribera & Boudouresque 1995), *Laminaria bongardiana*, and *Agarum* spp. (Britton-Simmons 2004).

Whether *Sargassum muticum* can displace or impact eelgrass has been debated in the literature. Druehl (1973) suggested that *S. muticum* may displace native eelgrass *Zostera marina* in British Columbia based on observations that the seaweed had become well established in habitat typically occupied by *Z. marina*. Con-

trary to this, a number of empirical studies showed that the 2 species could coexist without interference as *S. muticum* was unable to colonize the soft sediments inhabited by *Z. marina* (North 1973, Fletcher & Fletcher 1975, Norton 1977, Thomsen et al. 2006). However, den Hartog (1997) and Strong et al. (2006) showed that the 2 species can coexist in mixed substrates when eelgrass is in decline.

In the present study we found the non-native seaweed *Sargassum muticum* colonizing the distal end of siphons of the clam species *Tresus capax*. Native to the Pacific Northwest, *T. capax* is abundant in the low intertidal zone, burying to depths of 1 m in sand and mud substrates, from the lower littoral down into the sub-littoral, occurring above, in and below *Zostera marina*. *T. capax* is a filter-feeding bivalve that possesses a long (~30 cm) fused siphon, extending from the soft sediments into the overlying water column (Coan et al. 2000). The shells are flared around the siphon and individuals are unable to completely close or fully retract their siphons within their shells. At low tide, the extended siphons lie on the surface of the mud, retracting when disturbed and pulling the attached *S. muticum* down into the substrate. *T. capax* facilitates incursion of the non-native seaweed into the *Z. marina* bed through habitat provision of a solid substrate for attachment. Despite this, numerical or physical facilitation of non-native *S. muticum* into the eelgrass bed by *T. capax* may be tempered by seaweed quality or condition. We used field sampling to investigate whether seaweed condition differs between the 2 attachment substrates (*T. capax* siphon and rock) as a proxy for habitat quality. Specifically we looked at whether any morphological differences in *S. muticum* were manifested through the attachment substrate, as individuals colonizing a frequently retracting siphon were repeatedly dragged across the mud and partially buried in the sediment. We explored whether the different morphotypes of *S. muticum* expressed as a function of attachment substrate influenced the abundance and composition of the epibiont community colonizing it.

MATERIALS AND METHODS

Study site. The present study was conducted at Bamfield Marine Sciences Centre (hereinafter BMSC), on the west coast of Vancouver Island, Canada. Bamfield Inlet (48° 48.9' N, 125° 09.5' W) is highly sheltered, with low tidal flow. Large expanses of eelgrass *Zostera marina* colonizing a sandy-mud substrate characterize the lower littoral zone, extending into the sub-littoral zone. The mid-littoral zone is rock-strewn and dominated by the Pacific oyster *Crassostrea gigas* (introduced for aquaculture from Japan) and the ephemeral

green seaweed *Ulva intestinalis*. Non-native *Sargassum muticum* is sparsely distributed throughout the eelgrass bed, but forms a dense band ~2 m wide along the upper edge. At this *S. muticum*–*Z. marina* boundary, rocky substrate for attachment by the non-native seaweed is abundant. Within the eelgrass bed, the substrate is primarily soft sediments, with small rocks and shell fragments patchily dispersed throughout.

Populations of non-native *S. muticum* were surveyed during low tides in July 2008. Sampling was restricted to the *S. muticum*–*Z. marina* boundary to minimize disturbance to the eelgrass bed.

Morphometric comparisons. To determine whether morphological differences exist between *Sargassum muticum* individuals colonizing the siphons of *Tresus capax* and those colonizing rock substrates, we established a 30 m transect along the *S. muticum*–*Zostera marina* boundary during low tide, and randomly sampled *S. muticum* individuals along its length. For each individual, we noted the attachment substrate (clam siphon or rock), and measured a number of morphometric characteristics including (A) the length of the longest primary lateral (from the base of the holdfast to the distal tip), (B) the holdfast diameter, (C) the length and (D) the width of the basal axes, (E) the number of primary laterals from the holdfast, and (F) the number of air vesicles on the first branch from the base (Fig. 1). All *S. muticum* individuals attached to *T. capax* siphons were located within the top 5 cm of the siphon.

We collected 44 *Sargassum muticum* individuals: 22 attached to *Tresus capax* siphons, and 22 attached to rock substrate. These were individually bagged and transported to BMSC for quantification of the epibiont communities.

Epibionts on non-native *Sargassum muticum*. We quantified and compared the abundance of all epibionts (native and exotic) on *Sargassum muticum* individuals attached to the 2 substrates. Each *S. muticum* individual was removed from its collection bag and gently agitated in seawater to dislodge any epifauna. Epibionts were removed from the seaweed using tweezers and identified under a dissecting microscope. Colonial organisms were difficult to quantify in terms of number of individuals, so for the purpose of comparisons between substrate types, we counted each colony as 1 individual.

Statistical analyses. We used principal components analysis (PCA) to view the relationship between the morphology of *Sargassum muticum* and substrate type. Morphological differences were further explored using separate univariate ANOVAs, as was the relationship between the width and length of the *Tresus capax* siphon and all of the morphological traits measured on *S. muticum*. We used multivariate ANOVA (MANOVA) to explore whether any distributional differ-

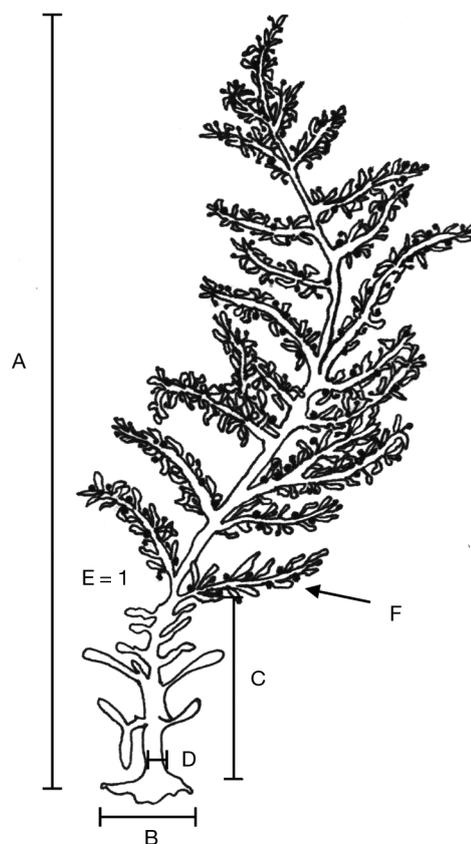


Fig. 1. *Sargassum muticum*. Morphological traits measured: (A) length of the primary lateral, (B) holdfast diameter, (C) the length and (D) the width of the basal axes, (E) number of primary lateral branches from the holdfast, and (F) number of air vesicles present on the first air branchlet from the base

ences in the epibiont species colonizing *S. muticum* were promoted by attachment substrate. Individual epibiont species associations were further explored using separate, univariate ANOVAs to indicate the significance of the response by individual species. Data were tested for normality using a Shapiro-Wilk W test, and epibiont abundance data were log-transformed. Epibionts were further separated into mobile and sessile groupings, and analyzed for effects of substrate types using a 2-factor ANOVA. Significant effects were examined using Tukey's HSD. All analyses were performed using JMP 4.0.4 (SAS Institute).

RESULTS

Morphometric comparisons

Substrate types were significantly different along the first 2 principal component (PC) axes (ANOVA: PC1: $F_{1,41} = 11.99$, $p = 0.001$; PC2: $F_{1,41} = 8.49$, $p = 0.006$).

PC1 was largely influenced by the basal portion of the seaweed: (B) the holdfast diameter, (C) the length, and (D) the width of the basal axes, and (F) the number of air vesicles on the first branch from the base. PC2 was influenced by size variables: (A) the length of the longest primary lateral and (E) the number of primary laterals from the holdfast (Table 1). That PC1 and PC2 show significant substrate differences suggests there are morphological differences independent of size. PC3 promoted no substrate differences ($F_{1,41} = 1.67$, $p = 0.20$).

To better visualize the response of each morphological trait, we plotted the average morphological response as a function of each substrate type (Fig. 2). Separate ANOVAs revealed that *Sargassum muticum* individuals attached to *Tresus capax* siphons were shorter in length (A; $F_{1,42} = 7.58$, $p = 0.009$), and had wider holdfasts (B; $F_{1,42} = 20.84$, $p < 0.0001$), longer basal axes (C; $F_{1,42} = 5.43$, $p = 0.02$), and more primary laterals (E; $F_{1,42} = 9.77$, $p = 0.003$) than individuals attached to rocks. No differences were found in the width of the basal axes (D; $F_{1,42} = 0.12$, $p = 0.73$) or the

Table 1. Principal components analysis (PCA). Variables contributing the greatest to the respective principal component (PC) axis are shown in **bold**

Variable	PC axis				
	1	2	3	4	5
(A) length of longest primary lateral	0.029	-0.572	0.743	-0.129	-0.176
(B) holdfast diameter	0.548	0.090	0.217	-0.027	-0.364
(C) length of basal axes	0.452	0.315	0.126	-0.667	0.427
(D) width of basal axes	0.449	-0.376	-0.048	0.502	0.632
(E) number of primary laterals from holdfast	-0.123	0.637	0.587	0.452	0.158
(F) number of air vesicles on first branch from base	0.528	0.137	-0.196	0.284	-0.480
Eigenvalue	1.97	1.10	1.03	0.74	0.65
% Variance	32.84	18.25	17.23	12.27	10.77

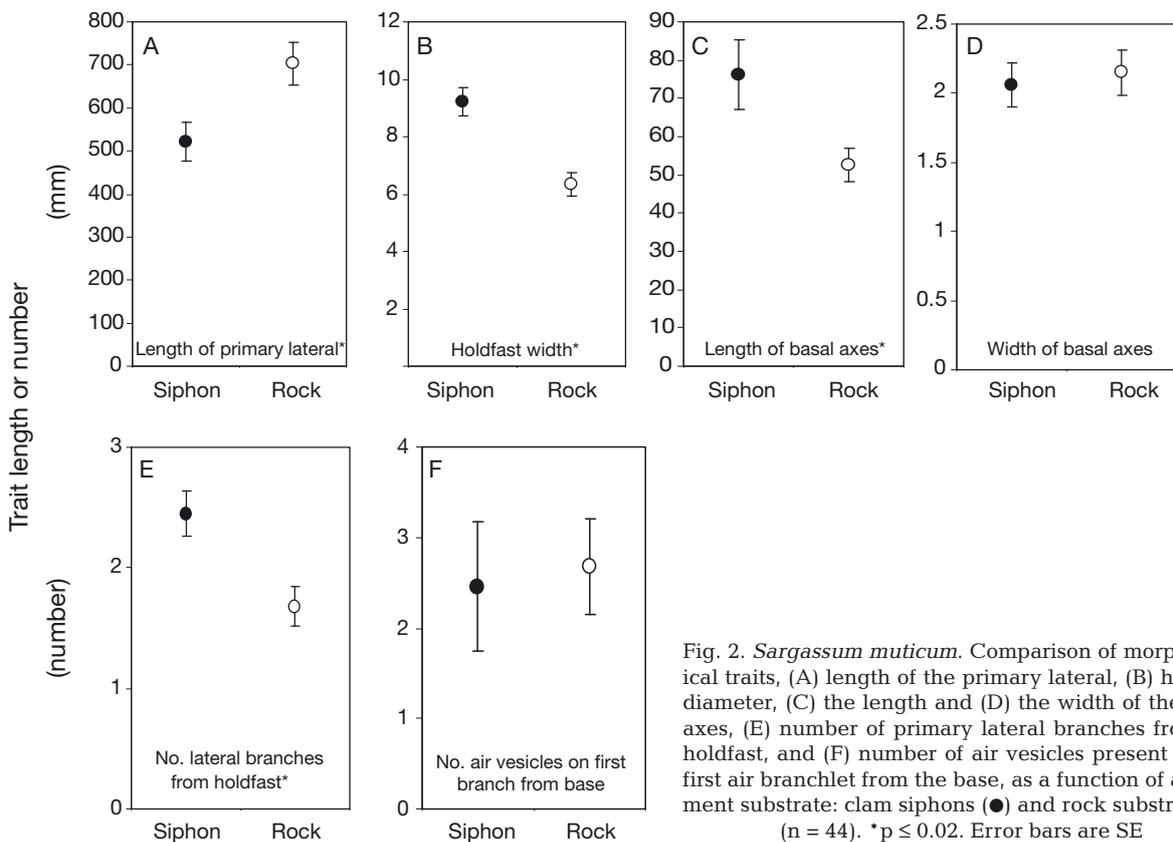


Fig. 2. *Sargassum muticum*. Comparison of morphological traits, (A) length of the primary lateral, (B) holdfast diameter, (C) the length and (D) the width of the basal axes, (E) number of primary lateral branches from the holdfast, and (F) number of air vesicles present on the first air branchlet from the base, as a function of attachment substrate: clam siphons (●) and rock substrate (○) (n = 44). *p < 0.02. Error bars are SE

number of air vesicles on the first branch from the base (F ; $F_{1,42} = 0.07$, $p = 0.80$). No relationship existed between the width or length of the *T. capax* siphon, and any of the morphological traits measured (ANOVAs: all $p > 0.11$). In addition to the 2 substrates we tested, 2 small (<13 cm) *S. muticum* individuals were found attached directly to the soft sediments that *Zostera marina* colonize. The lack of large *S. muticum* individuals attached to the soft sediment might suggest a size threshold, in which the seaweed becomes too large, or the drag created too great, to persist attached to this substrate.

Exotic facilitation

We found 2 invasive tunicate species, the colonial tunicate *Botrylloides violaceus* (Code 16 in Table 2) and the solitary tunicate *Styela clava* (Code 17), colonizing *Sargassum muticum* attached to *Tresus capax* siphons within the eelgrass bed. Neither tunicate species was found colonizing the eelgrass directly. Seventeen epibiont species from 8 phyla were found colonizing *Sargassum muticum*, 4 of which were epiphytic seaweeds (Table 2). All *Sargassum muticum* individuals sampled hosted >4 epibiont species, the most prevalent being the beach hopper amphipod *Traskorchestia traskiana* (Code 2) and juveniles of the blue mussel *Mytilus edulis* complex (Code 8).

There was a higher total abundance of epibionts on *Sargassum muticum* attached to rock than to *Tresus*

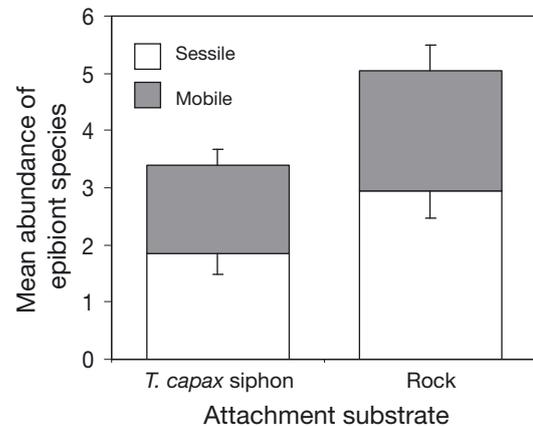


Fig. 3. Mean abundance of mobile and sessile epibiont species by attachment substrate (*Tresus capax* siphon or rock) of host seaweed *Sargassum muticum*. Error bars are SE. Epibiont species are presented in Table 2

capax siphons (2-factor ANOVA, substrate \times epibiont species: $F_{33,680} = 26.31$, $p < 0.0001$). We found distributional differences of the epibiont species on *Sargassum muticum* with substrate type (MANOVA: $F_{1,698} = 22.40$, $p < 0.0001$). When analyzed separately with individual ANOVAs, only 4 epibiont species showed significant differences in abundance with substrate type. *Sargassum muticum* attached to rock substrate had higher abundances of the 2 periwinkle species *Littorina sitkana* (Code 4; $F_{1,42} = 5.45$, $p = 0.02$) and *L. scutulata* (Code 5; $F_{1,42} = 5.67$, $p = 0.02$), and the bryozoan *Membranipora serrilamella* (Code 9; $F_{1,42} = 7.85$, $p = 0.01$; Fig. 3) than *Sargassum muticum* individuals attached to *T. capax* siphons. The exotic tunicate *Styela clava* (Code 17) was more prevalent on *Sargassum muticum* attached to *T. capax* siphons ($F_{1,42} = 4.19$, $p = 0.05$; Fig. 3). All other epibiont species showed no difference with substrate type (all $p > 0.09$), including the exotic tunicate *Botrylloides violaceus* ($F_{1,40} = 0.20$, $p = 0.66$).

We separated epibiont species based on their mobility (mobile or sessile; Table 2) as sessile species utilize *Sargassum muticum* as habitat whereas mobile species may incidentally occur there. The abundance of mobile and sessile epibionts varied with substrate (2-factor ANOVA, substrate \times mobility: $F_{3,710} = 13.74$, $p < 0.0001$) (Fig. 3). Tukey's post hoc tests revealed a higher abundance of both sessile and mobile epibionts on *S. mu-*

Table 2. Epibiont species found on *Sargassum muticum* and mobility groupings. n.a. = not available

Code	Species	Common name	Mobility
Invertebrates			
1	<i>Idotea vosnesenskii</i>	Kelp isopod	Mobile
2	<i>Traskorchestia traskiana</i>	Beach hopper amphipod	Mobile
3	<i>Lottia pelta</i>	Shield limpet	Mobile
4	<i>Littorina sitkanay</i>	Sitka periwinkle	Mobile
5	<i>Littorina scutulata</i>	Checkered periwinkle	Mobile
6	<i>Asterina miniata</i>	Bat star	Mobile
7	Unidentified polychaete	n.a.	Mobile
8	<i>Mytilus edulis</i> complex	Blue mussel	Sessile
9	<i>Membranipora serrilamella</i>	Kelp lace bryozoan	Sessile
10	Spirorbinae spp.	n.a.	Sessile
Seaweeds			
11	<i>Polyneura latissima</i>	n.a.	Sessile
12	<i>Gracilaria</i> sp.	n.a.	Sessile
13	<i>Ceramium</i> sp.	n.a.	Sessile
14	<i>Ulva intestinalis</i>	Gut weed	Sessile
Tunicates			
15	<i>Corella inflata</i>	Transparent tunicate	Sessile
16	<i>Botrylloides violaceus</i>	Violet tunicate (exotic)	Sessile
17	<i>Styela clava</i>	Club tunicate (exotic)	Sessile

ticum attached to rock than to *Tresus capax* siphons (Fig. 3). There was no relationship between the length of *S. muticum* individuals and total abundance of epibiont species ($F_{1,42} = 1.64$, $p = 0.21$).

We also found individuals of the non-native dwarf eelgrass species *Zostera japonica* at the upper fringe of the *Z. marina* bed. Despite *Z. japonica* frequently existing at the same sites as native *Z. marina* in the northeast Pacific (Britton-Simmons et al. 2010), this is, to our knowledge, the first reported occurrence of *Z. japonica* in Barkley Sound.

DISCUSSION

Because eelgrass systems are in decline in many areas of the world (Short & Wyllie-Echeverria 1996, Orth et al. 2006, Walker et al. 2006), much effort is being devoted to their conservation and restoration (Fonseca et al. 2000). Over recent decades, the number of reports of introduced species in eelgrass beds has increased (Williams 2007), but the role of introduced species in eelgrass systems has not received much attention, with some notable exceptions (dwarf eelgrass *Zostera japonica*, the seaweed *Caulerpa taxifolia*). A number of empirical studies have shown that the non-native seaweed *Sargassum muticum* and native eelgrass *Z. marina* can coexist without interference due to differing substrate requirements (North 1973, Fletcher & Fletcher 1975, Norton 1977, Thomsen et al. 2006). The present study demonstrates that *S. muticum* successfully colonized a *Z. marina* bed via a variety of mechanisms: colonizing the mixed substrate within the eelgrass bed (both rock and soft sediment directly), and uniquely, via the siphons of the native clam *Tresus capax*. Tweedley et al. (2008) reported that introduced *S. muticum* in British waters is also capable of colonizing soft sediments within eelgrass beds, suggesting that eelgrass may actually enhance the colonization of the non-native seaweed by trapping vegetative fragments and providing substrate. However, is the numerical or physical facilitation of non-native *S. muticum* into the eelgrass bed by *T. capax* tempered by seaweed quality or condition?

Effects of attachment Substrate on *Sargassum muticum* morphology

Strong phenotypic plasticity has long been recognized as a significant characteristic for colonizing or invasive species (Baker 1965, Parker et al. 2003). Wave exposure is a strong determinant of the shape of *Sargassum muticum* individuals (DeWreede 1978). Individuals inhabiting sheltered areas tend to be shorter

and bushier with more lateral branches than individuals in exposed areas, which have longer, but fewer, lateral branches. In the system we studied, the different attachment substrates (*Tresus capax* siphon or rock) promoted different morphologies of *S. muticum*. Individuals colonizing the siphons of *T. capax* exhibited morphologies consistent with a sheltered area, being shorter in length but producing more lateral branches when compared to individuals on rock substrate, which attained greater lengths, but had fewer lateral branches (Fig. 2). As all *S. muticum* individuals sampled inhabited the same sheltered area, the difference in morphologies expressed with attachment substrates are likely due to the movement associated with siphons regularly retracting into the sediment and not exposure per se. The sheltered morphology of *S. muticum* found on *T. capax* is also expressed in tide pools, where individuals are continuously submerged. It is possible that the increased submergence of *S. muticum* attached to *T. capax* siphons influences morphology. Finally, *S. muticum* individuals attached to *T. capax* siphons had a greater holdfast width (Fig. 2), which may be necessary to avoid dislodgement during siphon retraction. While *S. muticum* has the ability to persist in the water column after dislodgement and release of germlings, it lacks the ability to reattach to a substrate (Critchley et al. 1986). This suggests that *S. muticum* individuals colonizing the siphons of *T. capax* must have attached as germlings, remained attached, and developed into adults on a frequently retracting clam siphon. That the *S. muticum* individuals attached to *T. capax* were adults also suggests that the occurrence of *S. muticum* in the eelgrass bed is not ephemeral, as *S. muticum* germlings recruit in July in British Columbia (White & Shurin 2007), meaning that *S. muticum* individuals sampled during the present study were all at least 1 yr old, having persisted over the fall.

Positive interactions between non-native species

By facilitating the 2 non-native tunicate species *Styela clava* and *Botrylloides violaceus* through habitat provision of hard substrate for colonization, non-native *Sargassum muticum* enhanced the level of invasion in the eelgrass bed. Despite this, exotic epibiont species were still relatively rare, and native species dominated in abundance. Wonham et al. (2005) provided another example of a non-native species, the Asian hornsnail *Battilaria attramentaria*, facilitating invaders in an eelgrass system through habitat provision of hard substrate.

Distributional differences existed for *Styela clava*, which was more prevalent on *Sargassum muticum*

attached to *Tresus capax* siphons than to rocks, while no effects of substrate were evident for *Botrylloides violaceus*. In the system we studied, the non-native tunicates utilized *Sargassum muticum* exclusively as habitat, and no tunicates were found colonizing the eelgrass directly, although *B. violaceus* is reportedly able to grow directly on *Zostera marina* (Locke et al. 2007).

In her global review, Williams (2007) reported 13 invasive species in eelgrass beds in the northeast Pacific, which did not include either of the non-native tunicate species (*Styela clava* or *Botrylloides violaceus*) found during the present study. Invasive tunicates can alter community structure and eelgrass bed size, largely through habitat alteration and space competition. *B. violaceus* is a colonial tunicate with a sheet-like morphology, and has been observed overgrowing other sessile organisms, including mussels, barnacles, encrusting bryozoans, and solitary sea squirts (Cohen 2005). *S. clava* is a solitary tunicate which can grow in dense clumps, with densities attaining 1000 m⁻² on the east coast of Canada (DFO 2006). Both invasive tunicate species are serious pests of aquaculture, as they interfere with the settlement of oyster and mussel larvae and compete for space and food with young oysters and mussels (DFO 2006). The positive interactions between these invasive species and the potential for compounded negative effects to this eelgrass system are being investigated and will be reported separately.

In addition to the facilitation of non-native tunicates by *Sargassum muticum*, a number of native epibiont species utilize this non-native seaweed as habitat (Table 2). *S. muticum* has been described as housing a rich diversity of mobile invertebrates due to its structural complexity (Giver 1999). A variety of structural forms exist within a single individual: a discoid holdfast, cylindrical and moderately branched axes, mature leaflets that are flattened and relatively narrow, large and obovate basal leaves, and spherical air vesicles (Scagel 1973); together, these provide a structurally complex habitat for a wide variety of epibionts. A higher abundance of epibionts were found on *S. muticum* colonizing rocks than on those attached to *Tresus capax* siphons (Fig. 3), suggesting that habitat associations with the different morphologies promoted by attachment substrate support different epibiont communities. The higher total abundance of epibionts on *S. muticum* attached to rock than to *T. capax* siphons (Fig. 3) is intuitively correct, as the rock substrate provides a relatively stable substrate for attachment whereas clam siphons are frequently retracted into the sediment; however, *S. muticum* individuals attached to *T. capax* siphons exhibited shorter, bushier morphologies with more lateral branches, potentially providing more surface area for colonization.

In comparison with other studies, we found relatively few ($n = 17$) epibiont taxa on *Sargassum muticum* (80 taxa: Withers et al. 1975; 115 taxa: Giver 1999; 82 taxa: Bjærke & Fredriksen 2003). These studies might suggest that *S. muticum* is a positive addition to the local flora as it increases diversity of invertebrates through its structural complexity. However, within Barkley Sound, a study investigating the invertebrate communities associated with seaweeds revealed a low invertebrate abundance on *S. muticum* compared to native species of comparable morphology and size (Bates 2009).

Possible impacts of *Sargassum muticum* on eelgrass

While the impacts of these 3 non-native species (*Sargassum muticum*, *Styela clava*, and *Botrylloides violaceus*) on the eelgrass were beyond the scope of the present study, *Sargassum muticum* has the potential to disrupt the persistence of eelgrass in this system. The main competitive effects of *S. muticum* are shading and the preemption of space (Britton-Simmons 2006, White & Shurin 2007). *S. muticum* has perennial basal axes that persist in a vegetative state over winter and thus is poised to preempt space from eelgrass following any disturbance that results in eelgrass declines or loss, such as habitat fragmentation, eutrophication, disease, or impacts of non-native species. *Zostera marina* is unable to regain space preempted by *S. muticum*, a pattern observed in other regions (Critchley et al. 1987, Givernaud et al. 1991, den Hartog 1997). While eelgrass beds are often subject to multiple introduced species, their cumulative effects are virtually unstudied (Williams 2007). The potential for compounded negative effects of multiple invaders to this eelgrass system are currently being investigated.

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