

Native eelgrass (*Zostera marina* L.) survival and growth adjacent to non-native oysters (*Crassostrea gigas* Thunberg) in the Strait of Georgia, British Columbia

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Abstract

We investigated effects of the introduced Pacific oyster (*Crassostrea gigas*) on native eelgrass (*Zostera marina*) health on Cortes Island, British Columbia, Canada. Oysters physically alter their environment by increasing habitat complexity and altering water flow, and possibly by causing sulphide to accumulate in the sediment. Sulphide is toxic to eelgrass, and the current decline of eelgrass around Cortes Island may be a consequence of oyster population growth. While oysters and eelgrass coexist at a regional scale, eelgrass is typically absent directly seaward of oyster beds (the “below-oyster zone”) on Cortes Island. In a controlled experiment, we transplanted eelgrass plugs to below-oyster plots to determine whether this habitat is suitable for eelgrass growth. Shoot and leaf number were significantly greater over time in eelgrass-bed transplants than in below-oyster transplants. These results indicate that the below-oyster zone is unsuitable for eelgrass growth; if a causal link exists between oyster presence in the high intertidal zone and eelgrass absence directly seaward, then expansion of feral and farmed oyster beds will result in further eelgrass loss on Cortes Island.

Keywords: Canada; invasive oyster species; seagrass; sulphide; transplant.

Introduction

Non-native species have invaded marine habitats worldwide. Many of these invasions have proven detrimental to native species, either directly through processes such as predation and competition, or indirectly through habitat modification (Carlton and Geller 1993, Carlton 1996, Reusch and Williams 1998, Crooks 2001, Branch and Steffani 2004, Ross et al. 2004). Many successful marine invaders alter the physical conditions of their new habitat. These changes may lead to exclusion of native species

(Lodge 1993, Jones et al. 1997, Coleman and Williams 2002, Grosholz 2002). For example, the invasive alga *Caulerpa taxifolia* (Vahl) C. Ag. off the coast of France creates a homogeneous substratum matted with extensive rhizoids, leading to the decline of the native fish *Mullus surmuletus* (L.), which is unable to forage among the dense vegetation (Levi and Francour 2004). The Asian date mussel *Musculista senhousia* (Benson) modifies habitat by forming extensive mats that prevent deposit-feeding invertebrates from accessing sediment (Reusch and Williams 1998, Mistri 2003). The Mediterranean mussel *Mytilus galloprovincialis* (L.) forms dense beds on South African shores, excluding native limpets from rock surfaces (Branch and Steffani 2004).

Another ecosystem engineer, the Pacific oyster (Ostreidae: *Crassostrea gigas* Thunberg), was introduced to coastal British Columbia, Canada from Japan for aquaculture in the 1920s. Feral populations of the Pacific oyster established throughout the Strait of Georgia when unusually warm water temperatures in 1932 and 1958 allowed successful spawning, and strong oceanic currents aided dispersal (Quayle 1964, 1969). Today, feral and farmed populations spawn most years in late summer, although natural spawning is considered an insufficiently reliable source of spat for shellfish aquaculture (Quayle 1988, BCSGA 2003). The Pacific oyster is cultured in British Columbia using one of two methods: off-bottom tray culture or beach culture (BCSGA 2003). In the tray culture method, oysters are placed on large trays, which are suspended from rafts or long lines in deep water (Quayle 1988, BCSGA 2003). In beach culture, oysters are grown directly on the sediment in the intertidal zone (Quayle 1988, BCSGA 2003). The shellfish aquaculture industry in British Columbia has increased oyster production from 5500 t in 2000 to over 7500 t in 2005, and plans to increase production to over 14,000 t in the near future (BCSGA 2003, Wilson 2003, DFO 2006). This increase in the proliferation of farmed populations, along with rising global sea surface temperatures increases the likelihood of future major breeding events that would likely result in further range expansion of feral oysters.

A potential consequence of increased feral oyster distribution is the loss of native eelgrass (*Zostera marina* L.) beds. Oysters and eelgrass coexist at a regional scale in coastal British Columbia and the American Pacific Northwest, with oysters inhabiting the high-intertidal zone and eelgrass found in the low-intertidal to shallow subtidal zone (Dumbauld and Wyllie-Echeverria 2003, J.R. Kelly personal observations). However, coexistence is not observed at a fine scale; eelgrass is not found directly adjacent to oysters or in areas of former oyster culture, and eelgrass-free patches in the low-intertidal zone often

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correspond with oyster beds directly landward (Everett et al. 1995, J.R. Kelly personal observations). In addition, the presence of farmed oysters has been correlated with decreased eelgrass abundance (Waddell 1964, Everett et al. 1995, Griffin 1997). This distribution suggests consistent impacts of oyster beds on eelgrass; however, the mechanisms behind these observed distributions are poorly understood and remain speculative (Everett et al. 1995, Griffin 1997).

The Pacific oyster differs from British Columbia's native oyster (*Ostrea lurida* Carpenter) in being larger and faster-growing, and having a higher filtering capacity and the ability to ingest a wider range of particle sizes (Quayle 1964, 1988). These characteristics make it both an ideal aquaculture organism and an ecologically significant invader. One potential pathway of interaction is that the presence of Pacific oyster affects eelgrass beds through accumulation of toxic levels of sulphide in sediments. The large quantity of organic matter added to the sediment by oysters in the form of feces and pseudofeces is associated with hypoxic sediment conditions, which promote the growth of sulphate-reducing bacteria (Ingold and Havill 1984, Castel et al. 1989, Nugues 1996, Sorokin et al. 1999, de Zwaan and Babarro 2001, Kaiser 2001).

These bacteria release sulphide, which is associated with reduced photosynthesis and growth in eelgrass (Goodman et al. 1995, Holmer and Bondgaard 2001). Sediment sulphide concentration under cultured bivalves can be more than 100 times higher than at reference sites (Dahlback and Gunnarsson 1981, Grant et al. 1995). Eelgrass is highly susceptible to sulphides, showing decreased photosynthetic activity and slower growth at elevated sulphide concentrations (Goodman et al. 1995, Holmer and Bondgaard 2001, Holmer et al. 2005). Through promotion of a sulphide-rich substratum, Pacific oyster beds (cultured or feral) may be linked to local eelgrass loss.

Eelgrass beds are characterized by high primary productivity, sediment stability, habitat complexity, reduced wave action and protection from predators for resident fauna (Orth et al. 1984, Phillips 1984, Everett et al. 1995, Trianni 1996, Coleman and Williams 2002, Duarte 2002). On the Pacific coast of North America, eelgrass beds act as nurseries for juveniles of many commercially and ecologically important organisms such as salmonids and crabs, and as egg attachment sites for herring (Orth et al. 1984, Griffin 1997, Murphy et al. 2000, Wyllie-Echeverria et al. 2003). Zooplankton and detritus trapped in eelgrass beds by reduced current velocity serve as food

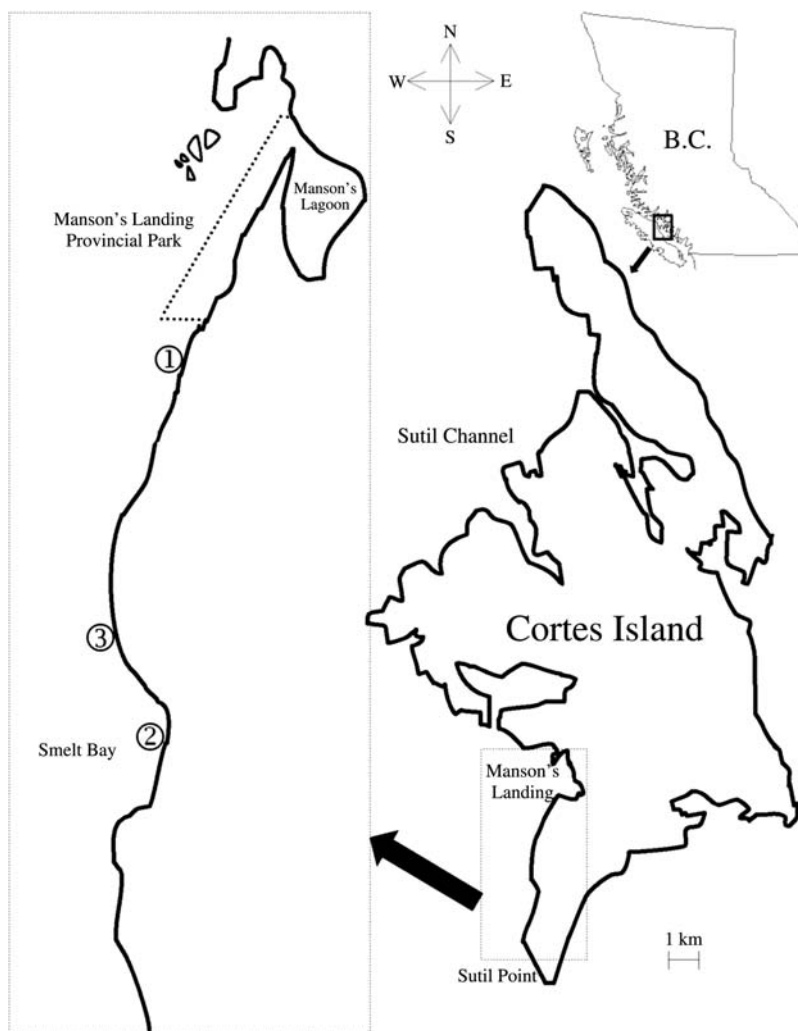


Figure 1 Map of Cortes Island with detail of study site locations. B.C.=British Columbia.

for juvenile fish and invertebrates (Griffin 1997). Infaunal organisms are protected from predators by eelgrass root structure (Reise 1985), while eelgrass leaves provide refuge for juvenile crabs and myriad other motile epifaunal organisms (Orth and van Montfrans 1982, Fernandez et al. 1993). A shift from eelgrass-dominated to oyster-dominated tidal flats results in a significant reduction in habitat quality for many species, leading to changes in community composition. For instance, fish and decapod predation on macrofauna is higher in tidal flats dominated by oysters than in those dominated by eelgrass (Reise 1985, Castel et al. 1989), and overall benthic macrofauna abundance is reduced in oyster-dominated habitats, due to the accumulation of hypoxic sediments (Castel et al. 1989). Abundance and diversity of fish and swimming macroinvertebrates are significantly higher in eelgrass beds than in below-oyster areas, and assemblages of epibenthic plants and macroalgae differ significantly between eelgrass beds and below-oyster areas (Kelly et al. in press).

Transplants of propagated seagrasses have been used around the world to combat seagrass loss, but success of such restoration efforts depends on identifying and mitigating the original cause of loss as well as taking into account the functional changes present in the system following seagrass loss (Homziak et al. 1982, Harrison 1987, 1990, de Jonge et al. 1996, Reusch and Williams 1998, Peralta et al. 2003). Few experiments testing the ability of eelgrass to survive near oysters have been published (e.g., Waddell 1964). This investigation was con-

ducted to test the hypothesis that conditions below oyster beds are inhospitable to eelgrass.

Materials and methods

Study sites

All study sites were located on the southwestern coast of Cortes Island, British Columbia, Canada (50°4' N, 124°56' W) (Figure 1). Each eelgrass transplant site consisted of an area immediately below an oyster bed (the "below-oyster" zone), and the eelgrass bed adjacent to this area (Figure 2). Substantial recreational boat traffic was present in July and August at site 1 (see Figure 1) due to proximity to Manson's Bay and the government dock at Manson's Landing Provincial Park. Site 1 was located in the low-intertidal zone below a feral oyster bed. Beach-culture oyster farms are present south of site 1, while eelgrass beds are found along the shore north and south of site 1. Sites 2 and 3 (Figure 1) were located in Smelt Bay, north of Smelt Bay Provincial Park. Eelgrass is found in large patches throughout Smelt Bay. A feral oyster bed was located in the high-intertidal zone above site 2, and a beach-culture oyster farm was located in the high-intertidal zone above the below-oyster zone at site 3. No oysters were present in the high-intertidal zone directly above the eelgrass beds.

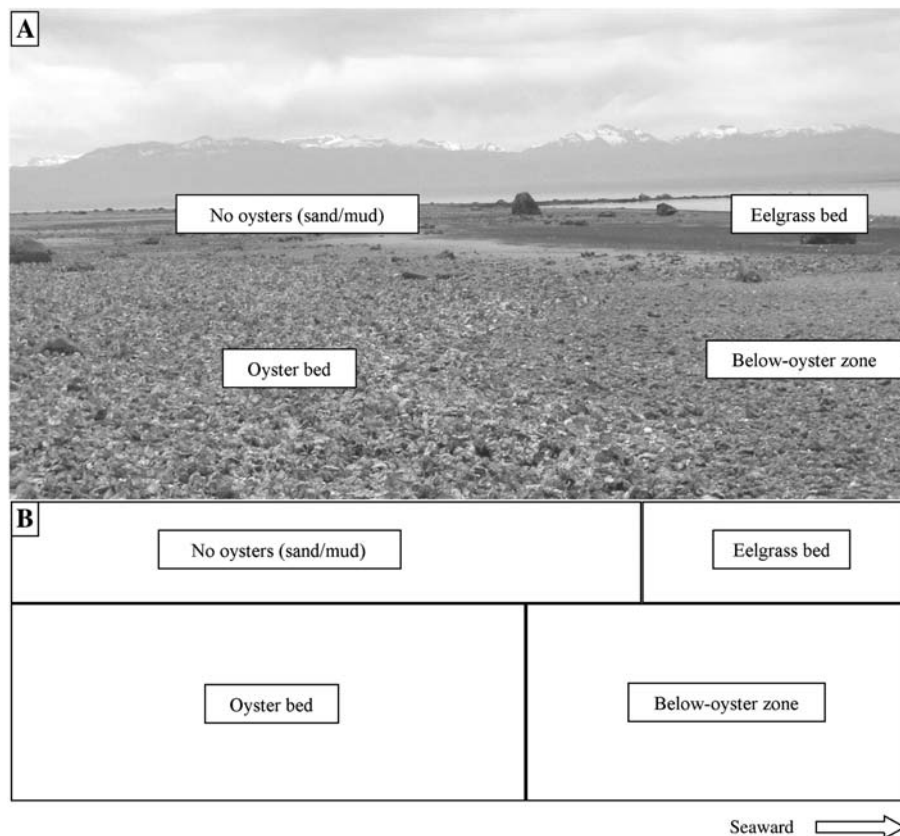


Figure 2 Study site layout.

(A) Physical relationship of below-oyster zone to oyster bed and eelgrass bed. (B) Schematic diagram of below-oyster zone, oyster bed and eelgrass bed.

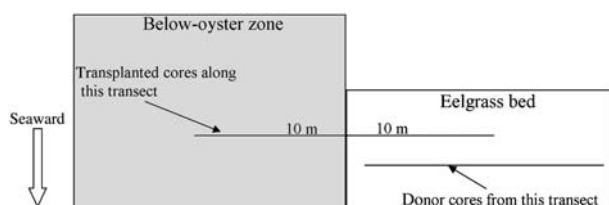


Figure 3 Schematic diagram of eelgrass transplant experiment (not to scale).

Eelgrass transplants

We placed a 20 m transect parallel to shore at each study site so that 10 m of the transect were in the eelgrass bed and the other 10 m were in the below-oyster zone (Figure 3). The transect line was placed as high as possible within the *Zostera marina* zone to maximize accessibility and proximity to the oyster bed.

Every 1 m along the transect line, we excavated a 15 cm deep hole using a 10 cm diameter PVC pipe (Phillips 1990). We took cores of *Zostera marina* (15 cm deep, 10 cm in diameter) from randomly-chosen points along an additional line located about 2 m seaward from the 20 m transect line, and used these cores to fill the holes along the 20 m transect line (Figure 3). Original sediment from donor cores was kept intact for transplanting (Phillips 1990). Wire-stemmed flags marked the center of each transplant.

We counted the number of shoots (leaf bundles) and individual leaves in each transplant by placing a 10 cm diameter plastic ring around the transplanted core, using the flag as a guideline for positioning in order to ensure a standardized enumeration method for subsequent sampling occasions. Shoot and leaf counts were recorded immediately after transplanting, and at five subsequent sampling occasions for site 1, four subsequent sampling occasions for site 2, and two subsequent sampling occasions for site 3. Each transplant site was digitally photographed at each sampling interval in order to document changes in relative abundance of a green alga (*Ulva* sp.) over time. Relative abundance of *Ulva* was cat-

egorized as follows: no visible *Ulva*; scattered *Ulva* not forming a continuous mat; a thin (<5 mm), translucent layer of *Ulva* forming a continuous mat; or a thick (>5 mm), opaque layer of *Ulva* forming a continuous mat.

Statistical methods

Number of shoots and leaves in eelgrass-bed transplants and below-oyster transplants were compared over time using the linear mixed model procedure in the SAS 8.2 software package (SAS 2001). A first-order autoregressive structure with heterogeneous variances was used for the model following significant ($p < 0.05$) results for Levene's test for homogeneity of variances (Roy 2006).

Results

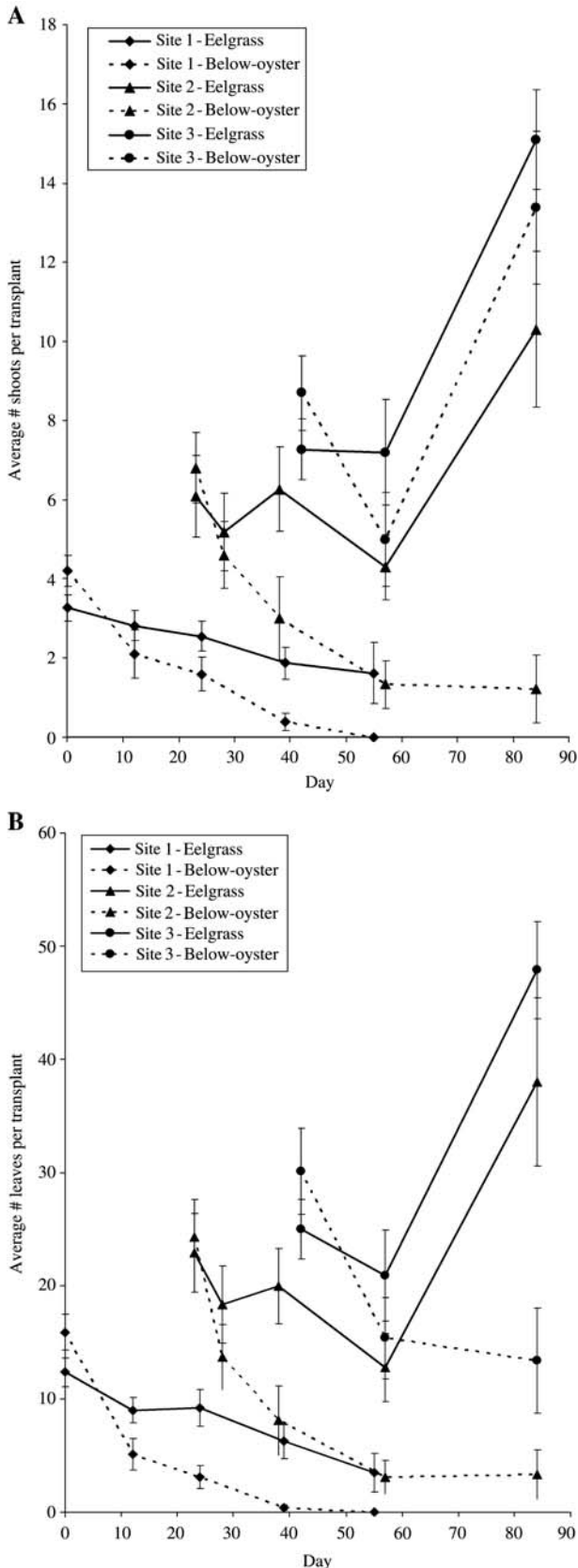
Eelgrass transplant

A preliminary linear mixed model analysis of all sites showed a significant interaction of site and treatment (shoots: $F_{1,59} = 46.19$, $p < 0.0001$; leaves: $F_{1,59} = 51.45$, $p < 0.0001$); subsequent analyses were therefore carried out separately for each site. Over time, the number of shoots and leaves in cores transplanted within eelgrass beds were significantly greater than in cores transplanted to below-oyster zones at all sites (Table 1). While number of leaves per transplant in below-oyster transplants decreased over the course of the experiment, number of leaves per transplant in eelgrass bed transplants increased over time. Mean number of shoots and leaves per transplanted core declined until the end of July in both treatments at all sites (Figure 4A,B). The eelgrass bed at site 1 appeared to have experienced substantial physical damage (likely due to boat traffic) between 15 July and 31 July, as density of *Zostera marina* was drastically reduced intertidally and appeared somewhat reduced subtidally. Observations at site 1 were discontinued after 31 July, when all plots in the below-oyster zone were completely devoid of eelgrass

Table 1 Results of linear mixed model analysis for each eelgrass transplant site.

Site	Effect	Measure	F	p
1	Treatment	Shoots	$F_{1,19} = 8.46$	0.0090
		Leaves	$F_{1,19} = 18.90$	0.0003
	Time	Shoots	$F_{4,68} = 13.70$	<0.0001
		Leaves	$F_{4,68} = 29.81$	<0.0001
	Time×treatment	Shoots	$F_{4,68} = 3.67$	0.0091
		Leaves	$F_{4,68} = 6.10$	0.0003
2	Treatment	Shoots	$F_{1,19} = 6.87$	0.0168
		Leaves	$F_{1,19} = 7.95$	0.0109
	Time	Shoots	$F_{4,72} = 6.33$	0.0002
		Leaves	$F_{4,72} = 10.62$	<0.0001
	Time×treatment	Shoots	$F_{4,72} = 7.33$	<0.0001
		Leaves	$F_{4,72} = 9.45$	<0.0001
3	Treatment	Shoots	$F_{1,19} = 5.73$	0.0271
		Leaves	$F_{1,19} = 6.41$	0.0203
	Time	Shoots	$F_{2,32} = 11.56$	0.0002
		Leaves	$F_{2,32} = 13.40$	<0.0001
	Time×treatment	Shoots	$F_{2,32} = 13.67$	<0.0001
		Leaves	$F_{2,32} = 14.87$	<0.0001

and very few shoots remained in the eelgrass-bed transplants (Figure 4A,B). In August, the number of shoots and leaves had recovered completely in the eelgrass bed transplants at sites 2 and 3. The only increase in below-oyster transplants was in the number of shoots observed at site 3 (Figure 4A,B).



The abundance of green algae (*Ulva* sp.) varied over time and among sites, but over the course of the summer, slightly more *Ulva* was present near below-oyster zone transplants than near eelgrass bed transplants (Table 2). Thick mats of *Ulva* were present in the below-oyster zone at site 1 in late June, and in the eelgrass bed at site 2 in early July (Table 2).

Discussion

Results of the eelgrass transplant experiment indicate that the below-oyster zone is a poor habitat for eelgrass; oyster presence in the high-intertidal zone was correlated with low eelgrass growth rates in the low-intertidal zone, suggesting that oysters may contribute to eelgrass loss below oyster beds. Over the course of the eelgrass transplant experiment, leaf number increased in cores transplanted to eelgrass beds and decreased in cores transplanted below oyster beds. After an initial decrease in shoot density in all eelgrass transplants, those transplanted to an eelgrass bed experienced a more rapid increase than those transplanted to the below-oyster zone.

The initial decrease in leaf count and shoot density for all eelgrass transplants may have been due to transplanting stress, or transplants may have coincided with other factors contributing to eelgrass decline. Annual variation in eelgrass abundance occurs due to changes in nutrient availability, temperature, turbidity and salinity as well as physical disturbances (Phillips 1984, Kentula and McIntire 1986). Because eelgrass typically dies back in fall and winter and grows dramatically in spring and summer, it is unlikely that initial decreases in leaf count and shoot density were due to seasonal growth patterns (Phillips 1984, Kentula and McIntire 1986).

The dramatic changes in algal cover that were observed in eelgrass beds and below-oyster areas may have affected eelgrass health; heavy algal cover was likely sufficient to reduce light for photosynthesis, while light to moderate algal cover may have provided protection from desiccation at low tide. Hauxwell et al. (2001) found that heavy macroalgal cover (>9 cm canopy height) caused a decrease in eelgrass shoot density, while eelgrass density under lighter algal cover (2 cm canopy height) did not differ from algae-free eelgrass plots.

Harrison (1987) found that *Zostera marina* seedlings took at least a year from transplanting to reach peak shoot density, because of the time required to recover

Figure 4 (A) Change in average number of shoots per transplant over time in eelgrass and below-oyster zones. Solid lines represent eelgrass bed transplants; dotted lines represent below-oyster transplants. ♦ indicates site 1 transplants, ▲ indicates site 2 transplants, and ● indicates site 3 transplants. (B) Change in average number of leaves in eelgrass transplants over time in eelgrass and below-oyster zone. Solid lines represent eelgrass bed transplants; dotted lines represent below-oyster transplants. ♦ indicates site 1 transplants, ▲ indicates site 2 transplants, and ● indicates site 3 transplants. Means ± SE, n = 10.

Table 2 Relative abundance of *Ulva* sp. at eelgrass transplant sites.

	Site 1		Site 2		Site 3	
	Eelgrass bed	Below-oyster zone	Eelgrass bed	Below-oyster zone	Eelgrass bed	Below-oyster zone
June	6th: - 18th: ++ 30th: +	6th: + 18th: +++ 30th: +++	29th: +	29th: +	N/A	N/A
July	15th: - 31st: +	15th: - 31st: +	4th: +++ 14th: +	4th: ++ 14th: +	18th: +	18th: +
August	N/A	N/A	2nd: + 29th: +	2nd: ++ 29th: ++	2nd: + 29th: -	2nd: + 29th: -

(-) indicates no visible *Ulva*; (+) indicates scattered *Ulva* not forming a continuous mat; (++) indicates a thin (<5 mm) continuous mat of *Ulva*; (+++) indicates a thick (>5 mm) continuous mat of *Ulva*. Site 1 observations were discontinued on 31 July because all plots in the below-oyster zone were completely devoid of eelgrass. N/A, not applicable.

from transplant shock and re-establish roots. The short duration of this experiment precluded attainment of peak shoot density; however, the initial post-transplanting decline was more pronounced in eelgrass transplanted to the below-oyster zone at all sites, and recovery of eelgrass transplanted to the below-oyster zone was significantly poorer than that of cores transplanted in the eelgrass bed at sites 2 and 3. Longer-term monitoring of eelgrass transplants in both eelgrass beds and below-oyster zones may provide further insight into this issue.

The results of this study provide insight into interactions between introduced oysters and native eelgrass. Eelgrass tends to grow in sheltered and low energy coastal areas also considered ideal for beach culture of oysters. As the oyster aquaculture industry continues to expand, such interactions as those documented here may occur throughout coastal British Columbia and the American Pacific Northwest (Everett et al. 1995, Simenstad and Fresh 1995, Griffin 1997). The eelgrass transplant experiment employed seagrass restoration protocols common in conservation projects (Harrison 1990, Phillips 1990) and demonstrated their ineffectiveness for restoring *Zostera marina* below oyster beds on Cortes Island. Therefore, the best strategy for minimizing the effects of oyster aquaculture on native eelgrass may be to limit beach-culture leases to areas where eelgrass has been historically absent.

Globally, seagrasses face many anthropogenic threats in addition to the effects of introduced oysters. Substantial losses of seagrass have been documented in Australia (Kendrick et al. 2002), along the east coast of the USA (Short and Burdick 1996), and along the west coast of North America in Washington state (Wyllie-Echeverria et al. 2003) and British Columbia, Canada (Wright 2002). A variety of human-induced disturbances such as dredging, eutrophication from agricultural runoff, and industrial waste spills, as well as natural disturbances such as extreme weather conditions, grazing and sediment resuspension, have been cited as causes of seagrass declines (Short and Wyllie-Echeverria 1996, Wright 2002, Wyllie-Echeverria et al. 2003). The cumulative effects of such factors, in addition to the planned increases to shellfish aquaculture, could exacerbate eelgrass loss in British Columbia and the American Pacific Northwest. Further research into the mechanisms responsible for eelgrass absence below oyster beds is required, as it is

likely that many interactive effects contribute to the interplay between eelgrass and oysters.

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