The influence of burrowing thalassinid shrimps on the distribution of intertidal seagrasses in Willapa Bay, Washington, USA

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Abstract

Two species of seagrasses frequently co-occur with extensive thalassinid shrimp populations and aquaculture operations in the intertidal zone of estuaries along the west coast of North America. Although thalassinid shrimp are known to be strong bioturbators and affect both aquaculture operations and benthic intertidal community structure, few studies have investigated shrimp–seagrass interactions. Application of the pesticide carbaryl to control shrimp populations for oyster aquaculture in Willapa Bay, Washington provided us with an experimental tool to investigate one such interaction. We found that the seagrass *Zostera japonica* colonized areas where ghost shrimp (*Neotrypaea californiensis*) had been removed via carbaryl application. We applied carbaryl to small (900 m^2) experimental plots and compared seagrass colonization on these to that on control plots where shrimp remained abundant (100 m^{-2}). The cumulative proportion of *Z. japonica* seeds and sprouts was slightly higher in the surface layer of treated plots (presumably due to the lack of shrimp bioturbation distributing them to depth), but seedling abundance was not significantly different between treated (no shrimp) and untreated control plots when they first emerged in early spring. As the season progressed however, and shrimp became more active, fewer seedlings survived in the untreated areas, and those that did survive grew much more slowly than those in the treated plots. We suspect that this was due to the effects of shrimp bioturbation and either light limitation (shoots that survived were much smaller) or direct burial and loss. Although it is an introduced plant, the natural distribution of *Z. japonica* is high in the intertidal zone and it is often separated from its congener *Zostera marina* by an expansive sandflat that is dominated by the ghost shrimp *N. californiensis* in west coast estuaries. The treatment of intertidal oysterbeds with carbaryl clearly reduces abundance of shrimp in this zone and we documented the same pattern of seagrass colonization on a commercial oyster bed and lack of seagrass in an adjacent unsprayed area. Density of native seagrass *Z. marina* shoots was also enhanced in plots treated with carbaryl, but only at lower tidal elevations or in intertidal pools where it could survive. We believe the removal of shrimp will

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continue to broaden the distribution of *Z. japonica* in Washington coastal estuaries where carbaryl use is permitted and add an interesting perspective to this controversial management issue.
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1. Introduction

Two species of seagrasses frequently occur in estuaries along the west coast of North America in the same intertidal zone and alongside extensive thalassinid shrimp populations and oyster aquaculture operations—*Zostera marina* L. and *Zostera japonica* Acherson and Graebner. *Z. marina* is a native seagrass and is the most cosmopolitan, occurring from Baja California through Alaska (Den Hartog, 1970; Phillips and Menez, 1988; Wyllie-Echeverria and Phillips, 1994). *Z. marina* typically inhabits the low intertidal and shallow subtidal zones from about +1.8 to −6 m MLLW, its growth being limited by aerial exposure at the upper end (Phillips, 1984) and generally by light availability at the lower end, particularly in shallow turbid coastal estuaries in Washington, Oregon and California (Zimmerman et al., 1991; Bulthuis, 1994; Thom and Rumrill, 2000). These conditions lead to a "fringe type" vertical distribution pattern (Koch and Beer, 1996). A congener, the intertidal seagrass *Z. japonica* was first observed as an introduced species along the west coast of North America in Willapa Bay in 1957 (Phillips and Shaw, 1976; Harrison and Bigley, 1982), presumably having been shipped with oysters *Crassostrea gigas* Thunberg from Japan. This seagrass quickly expanded its range, possibly with multiple introductions, and now occupies extensive areas in estuaries from southern British Columbia to Coos Bay in Oregon (Posey, 1988; Wyllie-Echeverria and Phillips, 1994). *Z. japonica* typically inhabits the upper and mid intertidal range above *Z. marina* (+1.5 to +3.0 m MHHW), although the two have a shared boundary where they interact and *Z. japonica* can affect the native species growth (Nomme and Harrison, 1991; Merrill, 1995). In the northern part of its introduced range *Z. japonica* is predominantly an annual with high seed production (Harrison, 1979, 1982), but this plant also spreads by rhizomes and behaves as a perennial during warm years in northern locations and in coastal estuaries like Willapa Bay (Thom, personal communication).

Temperate seagrass systems are broadly viewed as a vital resource in most nearshore coastal regions because they have been shown to be highly productive, providing structure and refuge habitat for many species of fish and invertebrates, food for migratory waterfowl such as black brant, and spawning substrate for other fish like Pacific herring (Heck et al., 1994; Baldwin and Lovvorn, 1994a,b; Simenstad, 1994; Wilson and Atkinson, 1995; Perkins-Visser et al., 1996; Jenkins et al., 1997). Due to this importance, the negative impacts of many human mediated disturbances to seagrass beds such as dredging, propeller and mooring scars, nutrient enrichment, trampling, and shading from over-water structures have also been broadly studied (Onuf, 1994; Sargent et al., 1995; Shafer, 1999; Burdick and Short, 1999; Wear et al., 1999; Eckrich and Holmquist, 2000). Although scallop dredging and clam raking have been shown to damage seagrass beds (Peterson et al., 1987; Short and Wyllie-Echeverria, 1996), oyster cultivation and other aquaculture activities which take place on the west coast of the USA have received slightly less scrutiny (Simenstad and

Fresh, 1995) and historically been afforded protection due to the economic value of this industry to local communities. Aside from harvest practices, traditional ground culture of oysters is also generally perceived to have less impact on the benthic environment than other aquaculture practices, in part because oysters were historically present in these estuaries.

While conducting an oyster aquaculture experiment in Willapa Bay, Washington, we noticed an intriguing pattern in the distribution of *Z. japonica* due to one culture practice, the application of the pesticide carbaryl (1-napthyl-*n*-methyl carbamate, Sevin®) to kill thalassinid burrowing shrimp on intertidal oyster beds. These shrimp soften the substrate with their burrowing activity causing oysters to sink into the substrate or be covered by silt and die (see Feldman et al., 2000 for a review of the pesticide application practice and its environmental consequences). One year after carbaryl had been applied, *Z. japonica* had clearly colonized the tideflat and was more abundant in treated strips where burrowing shrimp had been removed (Fig. 1). This type of result had been reported previously by oystergrowers and is not surprising, since thalassinid shrimps are known to cause bioturbation which may have a negative effect on seagrass (Suchanek, 1983). We were interested, however, in the mechanism involved in this seagrass–shrimp interaction and therefore conducted another experiment with carbaryl which provided us an excellent experimental tool for removing the shrimp. Our objective was to determine whether seeds were dispersed by shrimp to depths beyond which they could successfully sprout, or whether bioturbation itself limited seagrass growth in untreated areas, either via burial of shoots once they had sprouted or perhaps increased turbidity and reduced light affecting seedling growth. For management

Fig. 1. An experiment conducted to examine the effects of the pesticide carbaryl injected into the intertidal sediment in strips to control burrowing shrimp resulted in a distinct pattern in seagrass (*Z. japonica*) distribution 1 year after pesticide application.

purposes, we also wished to document that this process was occurring on a larger scale in Willapa Bay, since Harrison (1987) found that the opposite could also be true, i.e. seagrass expansion prevents burrowing shrimp establishment in Boundary Bay, British Columbia.

2. Materials and methods

This study was conducted in Willapa Bay, a relatively shallow 260 km^2 embayment on the coast of Washington State, USA ($46°40'$N, $124°02'$W, Fig. 2). There are important areas of intertidal seagrass (both *Z. japonica* and *Z. marina*) present in this estuary (Hedgpeth and Obrebski, 1981; Hazen, 1996; Thom and Rumrill, 2000), where more than 50% of the state's oysters and about 15% of oysters in the USA are produced (Willapa Alliance, 1998).

We treated two sets of plots with the pesticide carbaryl at a location just east of the Washington Department of Fish and Wildlife (WDFW) field station in Nahcotta, Washington during July 1994 using a commercial hand sprayer at the standard permitted rate of 9 kg ha^{-1}. These plots were located in an area dominated by the ghost shrimp *Neotrypaea californiensis* Dana (200 burrows m^{-2}, approximately 100 shrimps m^{-2}) adjacent to a nearby *Z. japonica* bed (Fig. 2). The experiment was part of a larger study designed to examine the potential for utilizing a thick layer of shell to create a habitat unsuitable for burrowing shrimp and act as a foundation for oyster culture, but we present only those results from non-shelled plots. A set of eight small (64 m^2) plots (untreated mud, treated mud, four plots per treatment) were arranged in a randomized block design (Fig. 2). Two large (900 m^2) un-replicated plots were used to test spatial scale effects. Unfortunately, most of the detailed seagrass observations were initially made on these large plots (February–May), but we also collected data from the replicated plots from June to August 1995. We ran post-hoc comparisons of variance in these two data sets to determine whether the data gathered from the large plots, while not representing true independent treatments, were representative for the site. Finally, samples were taken from a much larger commercial oyster bed sprayed with carbaryl during 1996 to document whether a similar pattern occurred on a larger scale and elsewhere within the system. We sampled along two transects perpendicular to the shore in an oysterbed located off of Goose Point along the Palix River channel (Fig. 2) during May 1997, 1 year after treatment.

2.1. Seagrass measurements

Samples were taken at five monthly intervals from February to June in each large plot. Five measurements were taken along each of six transects spaced 5 m apart utilizing a randomly picked starting coordinate. The number of *Z. japonica* sprouts and shrimp burrow openings were counted in a 0.25 m^2 quadrat placed at each sampling location. One randomly selected location on each transect was sampled using a 25 cm diameter core to each of two depth intervals (0–10 and 10–20 cm) during February to estimate biomass (Ott, 1990). Samples were sieved (0.5 mm pore mesh size) and sorted for seagrass seeds and sprouts. Shoots were sampled at one randomly selected location on each transect in April and June by removing sediment and whole plant specimens (e.g. shoots, roots and rhizomes) within a 0.1 m^2 area. Samples were rinsed in the lab, leaves were measured to the nearest 0.1 mm in length and
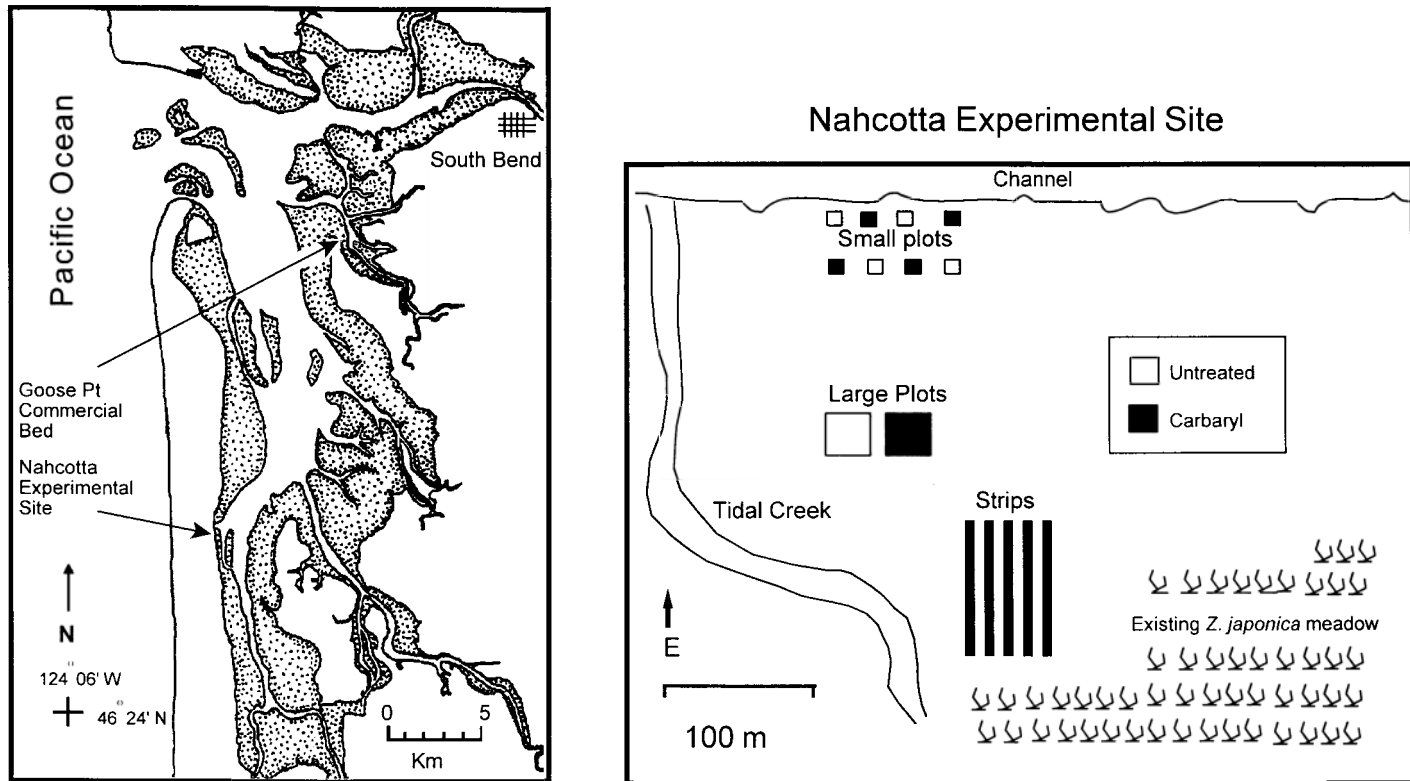
Nahcotta Experimental Site

Fig. 2. Map of Willapa Bay, Washington showing the experimental location near the town of Nahcotta and the site of the larger oyster bed just north of Goose Point that was sprayed with carbaryl in 1996 and sampled for seagrass 1 year later. Also shown is a detail of the experimental design at the Nahcotta site where two large plots and a set of eight small plots were arrayed close to an existing seagrass (*Z. japonica*) meadow and the strips shown in Fig. 1.

each composite sample was dried and weighed (60 °C for 48 h). A separate set of samples was taken in April from the nearby established bed where some *Z. japonica* was present throughout the previous winter. Finally a set of eight samples using a 25 cm diameter core was taken along a transect progressing from this established *Z. japonica* bed (see Fig. 2) to an untreated area in February 1997 to compare seed viability at depth (10–20 cm) with that at the surface (0–10 cm). Seeds were sorted and placed in separate petri dishes. The seed coats were removed and seeds immersed in a solution of 0.5% tetrazolium chloride. Dishes were placed in the dark for 24 h at room temperature, after which the seeds were removed and color of the radicle and hypocotyl recorded (methods after Conacher et al., 1994).

Each of the small 64 m^2 plots was sampled monthly during spring 1995, but *Z. japonica* measurements were only made sporadically from June to August. Nine locations were systematically sampled within each plot. Vegetative shoots were counted and percent cover estimated in a 0.25 m^2 quadrat placed at each location.

At the largest scale, *Z. japonica* was sampled along two 200 m transects located in an active oyster growing area north of Goose Point in May 1997. One transect crossed a commercial oyster bed that had been treated with carbaryl during July 1996 and one transect was located adjacent to this bed in an area that had not been treated. Shrimp burrow openings and seagrass shoots were counted in a 1 m^2 quadrat placed at 10 m intervals along each transect. All shoots within each of two selected 1 m^2 areas (at approximately the 120 m location where shoots were most abundant) were excavated, returned to the laboratory and measured.

3. Results

3.1. Seed and sprout distribution with depth

Z. japonica began to sprout at the Nahcotta site in February, 1995. We found seeds but no sprouts in preliminary samples taken near the end of January (three samples/plot). Samples taken from the large plots in February revealed what appears to be a pattern of equal distribution of both seeds and young sprouts with depth in the untreated plot, and possibly more seeds and sprouts near the surface in the carbaryl treated plot (Fig. 3). Neither of these differences in mean density was significant (ANOVA, $P = 0.69$ and 0.12 for seeds and sprouts, respectively; parametric statistics reported hereafter assume independent observations, see comparison with true replicate plots below), but the trends seemed important so we also examined the proportion of seeds and sprouts in the surface layer. Again there was no significant difference, but the cumulative proportion of seeds and sprouts at the surface was significantly greater in the treated plot (ANOVA on arcsine transformed data, $P < 0.05$).

3.2. Shoot development

There was no statistical difference in the number of individual shoots observed at the surface in February with an average of 4.4 shoots m^{-2} in the untreated plot and 1.3 shoots m^{-2} on the treated plot (Fig. 4). By March, however, the difference was significant with more

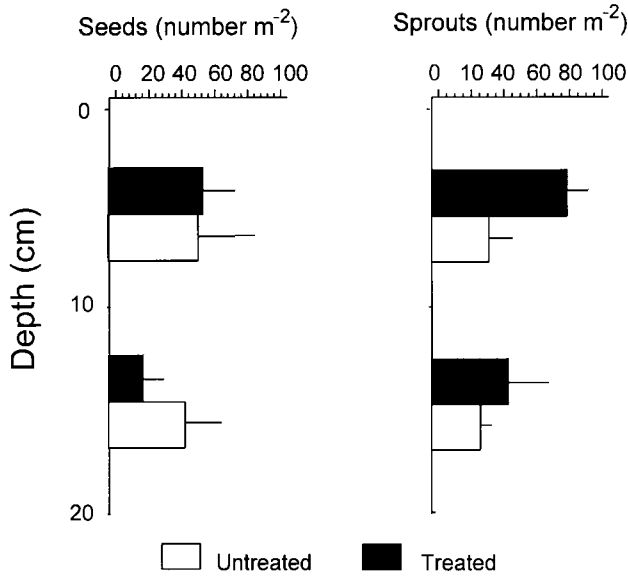Seeds (number m^{-2})   Sprouts (number m^{-2})

Fig. 3. Distribution of *Z. japonica* seeds (left) and sprouts (right) with depth, in the plot treated with carbaryl (shaded) vs. an untreated plot (open) when sampled in February (lines represent 1 S.E.). While there appears to be relatively more seeds at depth in the untreated plot, there are no statistically significant differences.
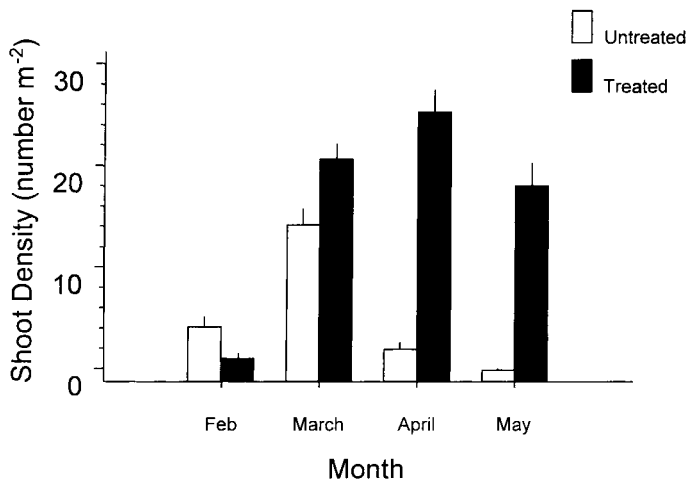
Fig. 4. Average density of *Z. japonica* shoots (number m^{-2}) observed in a plot treated with carbaryl vs. that in an untreated plot by month (lines represent 1 S.E.). Note that the density is similar in February and March just after germination, but declines sharply in April on the untreated plot.
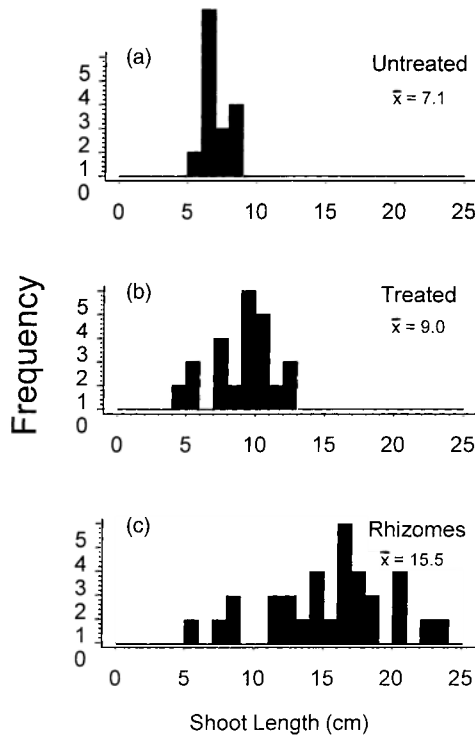
Fig. 5. *Z. japonica* shoot length in the untreated plot (a) vs. the treated plot (b) and the nearby area where shoots had developed from rhizomes (c) measured in April.

shoots present on the treated than the untreated plot (21 shoots m^{-2} versus 14 shoots m^{-2}, Student's t-test, $P < 0.005$). This difference became even more marked in April and May (Fig. 4). A significant difference in the length frequency distribution of individual shoots measured in April (Kolmogorov Smirnov test, $P = 0.004$), suggests that not only were there more shoots per unit area, but some shoots were longer on the treated than untreated plots (Fig. 5). Average shoot length was not significantly different, but shoots from both treated and untreated plots were significantly shorter than those that had returned from underground rhizomes in the nearby established *Z. japonica* bed (ANOVA, $P < 0.001$, see Fig. 2 for location). Shoot biomass per unit area was significantly less in the untreated area than in the treated area and both were significantly less than that in the nearby area where shoots had returned from rhizomes (4, 52, and 182 mg m^{-2} dry weight, respectively). By June, it was difficult to find any remaining shoots in the untreated area ($\bar{x} = 0.8$ shoots m^{-2}) and those that remained were unbranched, while in the treated area, density was even higher ($\bar{x} = 66.8$ shoots m^{-2}) because multiple branched shoots had formed on rhizomes ($\bar{x} = 6.7$ branched shoots per rhizome).

A similar result was evident in the small replicated plots. By June the number of developed shoots was significantly greater ($\bar{x} = 33.6$ shoots m^{-2}) on treated plots than untreated plots

where few shoots remained ($\bar{x} = 2.0$ shoots m^{-2}; Student's t-test, $P < 0.001$). This pattern was also evident in July and August as percent cover estimates for *Z. japonica* reached 26% in the treated plots and remained below 1% in the untreated plots. Variance ratio tests comparing shoot counts from the large plots and smaller replicated plots in June (ratio = 1.03, $P > 0.50$), and percent cover estimates in July (ratio = 0.22, $P > 0.50$), indicated no significant difference between the variances observed in these measurements of the seagrass population at our site. While not conclusive, this lends support to the results observed in the larger plots reported above.

3.3. Seed viability

Seeds sampled along a transect progressing from an area with well established *Z. japonica* present to an untreated area in February 1997 were more abundant next to the established seagrass bed, but there was no significant difference in seed abundance between depths
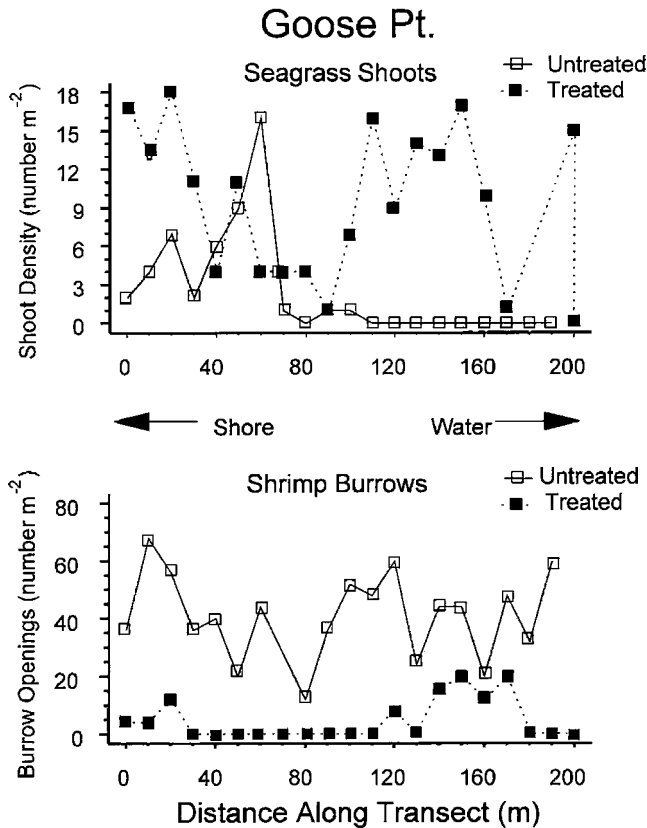

Fig. 6. Density of seagrass shoots along a transect from shore to the water (left to right) located in a treated oysterbed (dashed line, top) vs. a nearby untreated area (solid line), 1 year after treatment. Burrowing shrimp (*N. californiensis*) burrow densities are also shown for each transect, respectively (bottom).

($\bar{x} = 37.6$ seeds m^{-2} at 0–10 cm versus 32.7 seeds m^{-2} at 10–20 cm, Student's t-test, $P > 0.70$). There was however, a difference in the proportion of viable seeds, with fewer viable seeds at depth ($\bar{x} = 4\%$ at 10–20 cm versus $\bar{x} = 44\%$ at 0–10 cm, Student's t-test, $P = 0.02$).

3.4. Commercial oysterbed

Burrowing shrimp (*N. californiensis*) were moderately abundant on a transect located adjacent to a commercial oysterbed that had been treated with carbaryl in 1996 ($\bar{x} = 40.5$ burrows m^{-2}), but had been successfully removed from most of the treated bed ($\bar{x} = 4.5$ burrows m^{-2}, Fig. 6, bottom). Seagrass (*Z. japonica*, but *Z. marina* presence was noted) displayed the opposite trend with shoots present at moderate density on the treated bed (1–17 shoots m^{-2}, $\bar{x} = 9.5$ shoots m^{-2}), but conspicuously absent in the adjacent untreated area except close to shore (Fig. 6, top). The number of leaves per plant was significantly higher on the treated bed (Student's t-test, $P < 0.001$; Fig. 7a), but neither the average shoot length, nor the overall length distribution of shoots was significantly different (Fig. 7b).
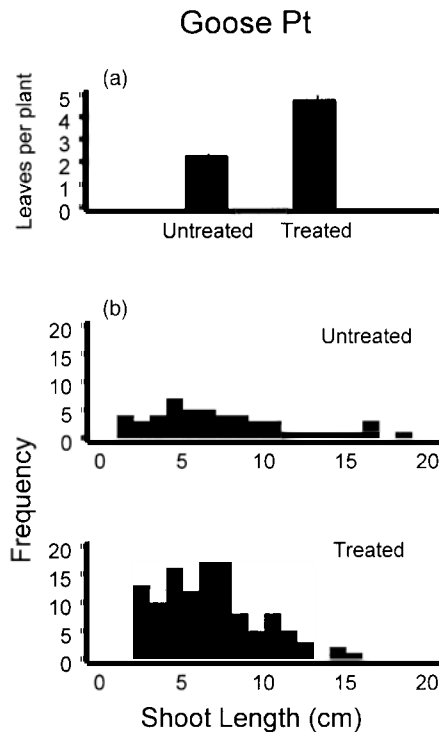

Fig. 7. Number of leaves per plant for *Z. japonica* collected along two transects located in a treated oysterbed vs. a nearby untreated area (a). Significantly more leaves were found on plants in the treated area, however shoot length was not significantly different (b) (lines represent 1 S.E.).

4. Discussion

The pattern we observed of enhanced density of seagrass in areas where thalassinid burrowing shrimp had been experimentally removed, was not unexpected given the documented ability of these strong bioturbators to influence the structure of benthic communities (Brenchley, 1981; Bird, 1982; Posey, 1986; Posey et al., 1991; Dumbauld et al., 2001). Bioturbation by polychaetes was first reported to influence seagrass by Reise (1985) and a negative interaction due to sediment re-working confirmed for the lugworm *Arenicola marina* (Phillipart, 1994) while a potential positive effect due to seed entrapment was shown for *Clymenella torquata* (Luckenbach and Orth, 1999). Suchanek (1983) transplanted the tropical seagrass, *Thalassia testudinum*, into regions of high and low densities of thalassinid shrimp (*Neotrypaea* spp.) and found a dramatic deterioration of the seagrass in the high density treatment. This "amensalism" was attributed to either reduced light for photosynthesis or the plants being physically smothered by sediment ejected from the shrimps burrow. Harrison (1987) showed a similar long term reduction in shoot density for *Z. japonica* when it was transplanted into a dense colony of *N. californiensis* in British Columbia, Canada. However, Harrison also documented decreased shrimp abundance in areas where *Z. japonica* and *Z. marina* had colonized the tideflat after a causeway was built. The difference in our case was that the seagrass *Z. japonica* colonized our experimental areas, not via transplanting or by rhizome expansion, but by seed dispersal and survival.

We suspected that the shrimp would cause seagrass seeds to be distributed to depths beyond which they could successfully sprout and survive. Burial below the surface of the sediment may be a pre-requisite for survival, decreasing losses from predation (Wigand and Churchill, 1988; Fishman and Orth, 1996) and enhancing sprouting success (Hootsmans et al., 1987; Moore et al., 1993; Wyllie-Echeverria et al., 2003). Some disturbance via movement amongst sand grains enhances the potential for incising the seed coat (Loques et al., 1990) which also enhances sprouting success. However, Bigley (1981) found highest germination rates at the anaerobic–aerobic interface and reduced germination success for *Z. japonica* seeds below 12 cm depth, because hypocotyls failed to reach the surface. Together these observations suggest a fairly narrow depth range for optimal survival. The seeds we found at 10–20 cm depth were less viable, but they were only slightly so and the mean density of seeds at depth was not significantly different between treated and untreated plots in February (Fig. 3). Although the proportion of seeds and sprouts together was significantly higher in the surface layer in the treated plots where shrimp had been removed (again in February), seedlings that had already sprouted were equally abundant in treated plots and untreated plots in both February and March (Fig. 4). As the season progressed and shrimps became more active, fewer sprouts survived in the untreated areas (Fig. 4), and those that did survive grew more slowly than those in the treated plots (Fig. 5). We suspect that this was due to the effects of shrimp bioturbation and either light limitation (shoots that survived were much smaller, Fig. 5) or direct burial and loss. Thus it appears that seedling survival is important for recruitment from the seed bank and while shrimp may cause some seed loss and decreased germination success, the effect of bioturbation on seedling survival, in part due to the coincident timing of shrimp activity and sprouting in early spring, is more important at the population level.
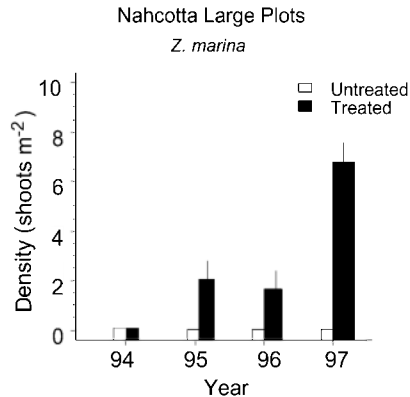
Fig. 8. Comparison of the density of *Z. marina* shoots found on the treated plot vs. the untreated plot from experiment initiation in 1994–1997 (lines represent 1 S.E.). No shoots survived on the untreated plot while *Z. marina* continued to increase on the plot treated with carbaryl.

During most recent years, *Z. japonica* has behaved as a perennial in Willapa Bay, but expands by both seed dispersal and underground rhizomes (Dumbauld, personal observation). Although it is an introduced plant, its natural distribution is high in the intertidal zone and it is often separated from its congener *Z. marina* by an expansive sandflat that is dominated by the ghost shrimp *N. californiensis*. The treatment of intertidal oysterbeds with carbaryl clearly reduces abundance of shrimp in this zone (WDOE and WDF, 1992; Dumbauld et al., 1997), and our data indicate that this in turn enhances seagrass abundance via the mechanism described above (Fig. 6). We found that the density of native seagrass (*Z. marina*) shoots was also enhanced in the experimental plot treated with carbaryl (Fig. 8), but *Z. marina* was found predominantly in pools of water at the tidal elevation where our plots were located. We suspect, therefore, that carbaryl treatment for burrowing shrimp control in Willapa Bay and Grays Harbor also enhances the distribution of *Z. marina*, since culture operations and this seagrass overlap extensively (oysters are typically fattened closer to the 0 m tide level). Visual observation of maps depicting seagrass distribution in estuaries along the Oregon coast, where carbaryl is not used for shrimp management, suggest that although *Z. japonica* has dramatically expanded its distribution since its introduction, it either remains separated from *Z. marina* by a stretch of open mudflat, presumably dominated by ghost shrimp (Yaquina Bay, Dewitt and Young, personal communication) or occurs in the upper less saline portion of the estuary where ghost shrimp are less abundant (Tillamook Bay, 1995; Coos Bay, Oregon Department of Land Conservation and Development, 1998; Strittolt and Frost, 1995). *Z. japonica* currently has a much broader distribution in Willapa Bay, particularly, as we observed, in those areas where ghost shrimps have been removed (Hazen, 1996; Dumbauld, personal observation) but also in less saline areas where shrimps were never present.

Both burrowing shrimp control and exotic species introduction are controversial management issues (Carlton and Geller, 1993; Feldman et al., 2000). The present policy for seagrass management in Washington State and elsewhere in the United States is based on the recog-

nized importance and ecological value of seagrass habitat as support for fish and wildlife (Phillips, 1984; Fresh, 1994; Hershman and Lind, 1994; Wyllie-Echeverria and Thom, 1994; Wyllie-Echeverria et al., 1995). The regulatory system is based on protection of this value and "no net loss" due to the negative impacts of development. Aquaculture practices are generally perceived to have less negative impacts than over-water structures, dredging, filling, etc. and have historically been protected due to their high social and economic value, particularly in Washington State. In the case of seagrass impacts, off-bottom culture (Everitt et al., 1995) and harvest activities like mechanical harvest (Wadell, 1964), are perceived to have the greatest negative impact, but only off-bottom culture has been regulated to date in Washington State. The practice of spraying the pesticide carbaryl on oyster beds to control burrowing shrimp continues to raise environmental concerns due to perceived impacts to non-target organisms (Feldman et al., 2000), but in this case we have shown that this practice likely enhances seagrass distribution in Washington's coastal estuaries and as such would be viewed as a beneficial practice if the no net loss policy were the only concern. Because Willapa Bay is a primary feeding area for resident and migratory waterfowl, the expanded distribution of *Z. japonica* will certainly benefit dabbling ducks and brant as it did in Boundary Bay, B.C. (Baldwin and Lovvorn, 1994a,b).

Finally, though exotic species are generally expected to have negative impacts, there is currently no policy distinction between *Z. marina* and *Z. japonica* in Washington state (Pawlik and Olson, 1995), even though little data exists on the relative value of *Z. japonica* habitat versus open mudflat or *Z. marina* habitat (but see Posey, 1988). Clearly, policy and regulation must be flexible enough to encompass habitat issues on a much broader estuarine and perhaps regional scale, while recognizing the tradeoffs involved with individual practices on a smaller scale. We hope that our study gives perspective on one aquacultural practice that influences seagrass habitat in the Pacific Northwest.

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