Padilla Bay
National Estuarine Research Reserve

Technical Report No. 12

THE EFFECT OF *ZOSTERA JAPONICA* ON THE GROWTH OF *ZOSTERA MARINA* IN THEIR SHARED TRANSITIONAL BOUNDARY

Glenn G. Merrill

June 1995

Publication No. 95-68

The Padilla Bay National Estuarine Research Reserve is one of the reserves in the National Estuarine Research Reserve System. One of the purposes of the Reserve is to facilitate research and monitoring at Padilla Bay to provide information for the conservation and management of the nation's estuaries, in particular greater Puget Sound and other estuaries in the Pacific Northwest. The Padilla Bay National Estuarine Research Reserve assists the dissemination of this information from research and monitoring by publishing a Reprint Series and a Technical Report Series.

The **Reprint Series** includes research grant reports, out of print agency reports and student reports dealing with the Padilla Bay estuary. Reports are reprinted without revision or editing. Final reports for research grants and Masters Theses should be treated as unpublished data and should not be cited without permission of the author(s).

The **Technical Report Series** includes articles, reports of research projects, data reports, bibliographies and reviews dealing with the Padilla Bay estuary.

Communications concerning receipt or exchange of Technical Reports or Reprints or submission of manuscripts should be directed to the Research Coordinator at Padilla Bay National Estuarine Research Reserve. Communications concerning the content of reports and reprints should be directed to the author(s).

Padilla Bay National Estuarine Research Reserve
10441 Bayview-Edison Road
Mount Vernon WA 98273-9668
(360)428-1558

Padilla Bay National Estuarine Research Reserve is managed by the Shorelands and Environmental Assistance Program, Washington State Department of Ecology, in cooperation with the Estuarine Reserves Division, National Oceanic and Atmospheric Administration (NOAA), U.S. Department of Commerce. The preparation of this document was financially aided through a grant to the Washington State Department of Ecology with funds obtained from NOAA/Office of Ocean and Coastal Resource Management, and appropriated for Section 306 or 315 of the Coastal Zone Management Act of 1972, as amended.

WASHINGTON STATE DEPARTMENT OF ECOLOGY

NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION
NOAA
U.S. DEPARTMENT OF COMMERCE

18

Padilla Bay National Estuarine Research Reserve
Technical Report No. 12

THE EFFECT OF *ZOSTERA JAPONICA* ON THE GROWTH OF *ZOSTERA MARINA* IN THEIR SHARED TRANSITIONAL BOUNDARY

Glenn G. Merrill
School of Marine Affairs
University of Washington

June 1995

Bibliographic citation: Merrill, Glenn G. 1995. The effect of *Zostera japonica* on the growth of *Zostera marina* in their shared transitional boundary. Washington State Department of Ecology, Padilla Bay National Estuarine Research Reserve, Mount Vernon, Washington. 16 pp. Padilla Bay National Estuarine Research Reserve Technical Report No. 12.

Padilla Bay National Estuarine Research Reserve
Shorelands and Water Resources Program
Washington State Department of Ecology

1043 Bayview-Edison Road
Mount Vernon WA 98273

Table of Contents

ABSTRACT

Merrill, G. G. 1995. The effect of *Zostera japonica* on the growth of *Zostera marina* in their shared transitional boundary. Washington State Department of Ecology, Padilla Bay National Estuarine Research Reserve, Mount Vernon, Washington. 16 pp.

A field research project was initiated during the summer of 1994, in the intertidal flats at Padilla Bay, Washington to gain preliminary information on the effect of the non-indigenous seagrass *Zostera japonica* on the growth of the native seagrass *Zostera marina* in their shared transitional boundary. The study measured the leaf growth and new shoot recruitment of 28 individual *Zostera marina* plants in the presence and absence of *Zostera japonica*. Leaf growth and shoot recruitment were measured at two week intervals from 10 July 1994 to 24 August 1994. The results of this research show that *Zostera japonica* inhibited the leaf growth and shoot recruitment of *Zostera marina* during the latter half of the study. This research is important in that it suggests competitive interaction between the species, and it provides a basis for further investigation into the interaction of these two species.

INTRODUCTION

The native seagrass, *Zostera marina*, serves a wide range of important ecological functions in Pacific Northwest estuaries, including sediment stabilization, feeding and nursery habitat for economically important bird and fisheries species, and as a substrate for highly productive epiphytic algal communities (Simenstad et al. 1979, Phillips 1984, Borum 1985, Castell et al. 1989, Thom 1990, Bulthuis 1991, Baldwin and Lovvorn 1994, Simenstad 1994). However, the ecological functions of *Zostera marina* may be adversely affected by the introduction of the non-indigenous seagrass *Zostera japonica* (Harrison 1987, Posey 1988, Nomme and Harrison 1991a, 1991b).

Zostera japonica was first recorded in Willapa Bay, Washington, in 1957 (Posey 1988, Harrison 1982). *Zostera japonica* was probably introduced by the oyster industry in Washington State which used to bring live stock of Japanese oysters into Samish Bay and Willapa Bay in the early part of this century (Harrison 1976, Phillips and Shaw 1976, Harrison and Bigley 1982). *Zostera japonica* was probably used a packing material for the stock and when the stock were removed, the *Zostera japonica* was dumped in the bays and most likely established itself via seed (Harrison 1976, Phillips and Shaw 1976, Harrison and Bigley 1982). *Zostera japonica* has spread rapidly throughout the estuaries of the Pacific Northwest and is common along the coast from southern British Columbia, Canada, to as far south as Coos Bay, Oregon (Bigley and Barreca 1982, Thom and Hallum 1990, Posey 1988).

Zostera japonica is similar in appearance to the native *Zostera marina*. However, it is typically smaller, grows as an annual, and reproduces primarly from overwintering seeds (Harrison 1982, Phillips 1984, Nomme 1989, Nomme and Harrison 1991a, 1991b). *Zostera japonica* grows principally in the upper intertidal and mid-intertidal regions, overgrowing previously unvegetated mudflats and growing in mixed beds with *Zostera marina* in the mid-intertidal region (Nomme and Harrison 1991a, 1991b, Posey 1988, Harrison 1987). *Zostera japonica* composes a substantial portion of the total seagrass cover in Padilla Bay, Washington (Thom 1990, Bulthuis 1991).

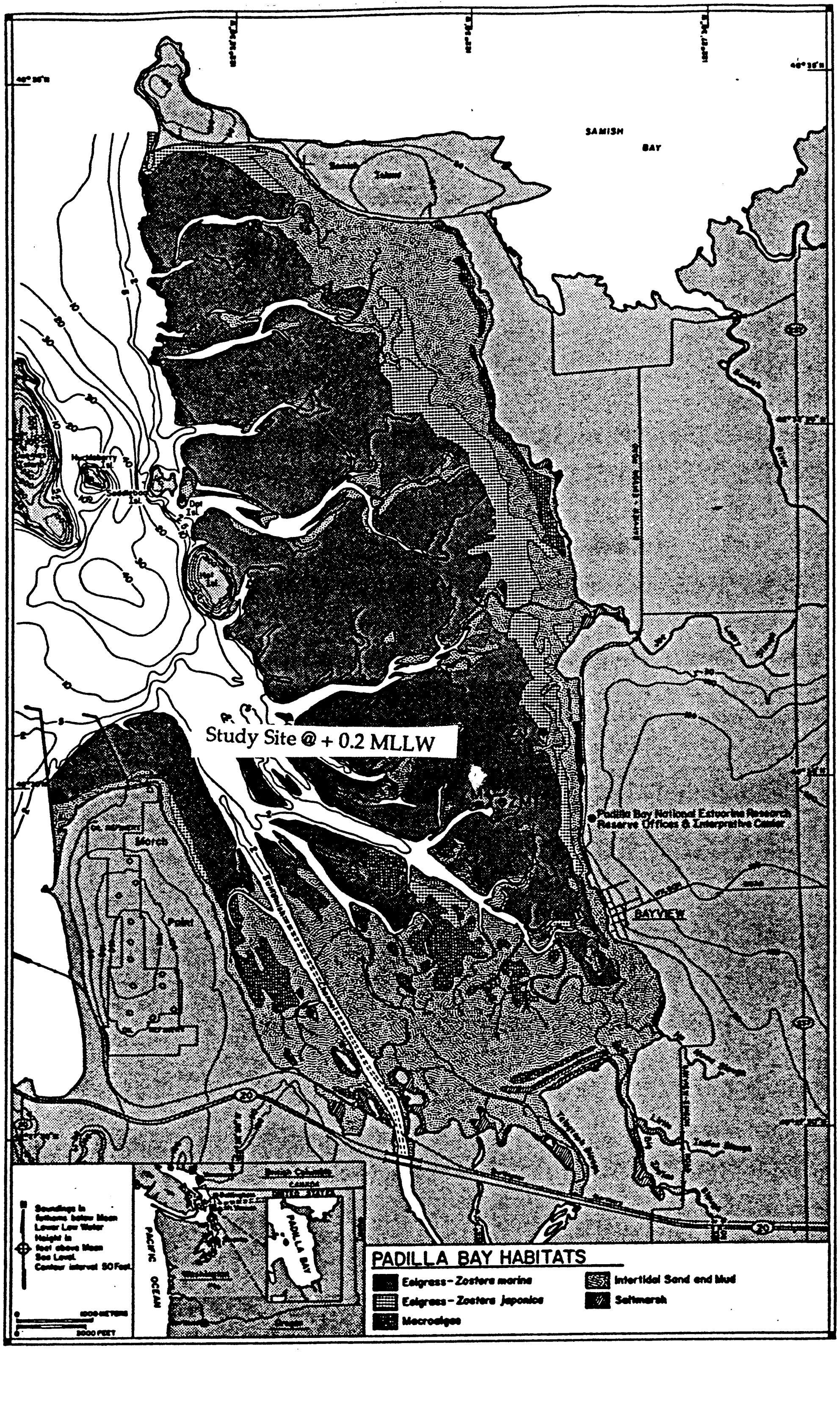
Research conducted in the Pacific Northwest indicates that *Zostera japonica* alters the infaunal community structure of overgrown mudflats (Harrison 1987, Posey 1988), and it may also affect the growth of the native *Zostera marina* (Nomme and Harrison 1991a, 1991b).

Experiments conducted in British Columbia, Canada, by Harrison and Nomme (1991a, 1991b) indicate that there is a significant difference in growth patterns of both *Zostera marina* and *Zostera japonica* when growing in mixed beds versus monospecific beds. However, these results do not clarify whether these differences in growth could be attributed to some form of competitive interaction or are due to other factors (Harrison and Nomme 1991a, 1991b). The intent of this project is to test the potential effects of*Zostera japonica* presence on *Zostera marina* growth *in situ*. To test this ecological linkage, individual *Zostera marina* plants growing in a *Zostera japonica* bed were randomly selected to observe their leaf elongation rates and shoot recruitment rates in the presence and absence of *Zostera japonica*.

MATERIALS AND METHODS

The design is a completely randomized field design (Peterson and Peterson 1979). The research site was at 0.2 meters MLLW elevation in an area of heavy *Zostera japonica* cover (>80% macrophyte cover) (Figure 1). Twenty-eight *Zostera marina* plants were marked by thin strips of flagging tape tied around the rhizome of the plant. The plants were isolated from each other by a minimum of 1.5 meters and originally had a minimum of three shoots per plant greater than 0.4 cm in diameter measured at the base of the shoot.

Figure 1: Location of study site in Padilla Bay National Estuarine Research Reserve. Summer 1994.



14 of the plants were randomly selected to have all *Zostera japonica* removed by above-ground weeding from an area equal to or greater than 50cm x 50 cm centered around the attachment point of the red flagging tape around the rhizome. Sixteen experimental and 14 control plants were initially tagged, but two experimental plants were lost before the first sampling. Embroidery scissors were used to clip the *Zostera japonica* just above the substrate surface in the experimental plots. The other 14 plants served as controls and no *Zostera japonica* was removed. However, the substrate was disturbed by "massaging" the area around the plants in the control plots to replicate the turbulence cause by above-ground weeding in the treatment plots. The 28 *Zostera marina* plants were monitored for leaf growth and shoot recruitment during each low tide series which occurred every two weeks for a ten week period.

Leaf growth was measured by piercing the largest shoot in each plot with a thin sewing needle (< 0.5 mm diameter) just above the blade emergence zone, defined as the point where the leaves are no longer bundled together. The change in position of the needle scar from the blade emergence zone indicates the amount of new growth in the individual leaf (Dennison 1990). Typically, three leaves per shoot can be measured using this technique. Due to the possible effects of weathering, senescence, or fragmentation in *Zostera marina* leaves, the two outer leaves were not measured (Dennison 1990). The amount of growth of the two largest inner leaves were measured and averaged to obtain a value for the entire plant. The shoots marked by piercing were always near the center of the plot, the thickest diameter of the centermost shoots was pierced for the second and fourth data series. This reduced the possible deleterious effects of plant growth from piercing, but maintained consistency in the size and location of shoots marked (Dennison 1990). Measurements were taken every low tide series, occurring approximately every 13 days.

Shoot density was measured by counting all *Zostera marina* shoots greater than 0.4 cm diameter in a 50 cm x 50cm quadrat centered around the rhizome marked by the flagging tape. The quadrat was aligned to the same compass direction (0°N) for each sampling so as to ensure the area within the quadrat was the same for each measurement.

T-tests were performed to evaluate treatment effects. Because the t-test assumes homogeneity of variances between treatments, an F-test was first conducted on variances (Rholf and Sokal 1981). Where significant heterogeneity of variance was observed, a t-test for non-equal variances was used (Microsoft Corporation 1993). For leaf growth, observations for different sampling dates were not independent, so a Bonferroni correction was used (Rohlf and Sokal 1981), thus, p=.05 was corrected to p=.0125 for four observations.

Additionally, regression analysis was performed on the initial and final shoot densities of the *Zostera marina* to determine if the observed shoot recruitment patterns were due to differences in the initial shoot density of the plants. A test of assumption for regression analysis indicated the variance in initial shoot density between the control and treatment plots were normally distributed, and variances were homogeneous.

The final *Zostera marina* shoot densities in the experimental and control plots were analyzed graphically using a best-fit linear trendline (Microsoft Corporation 1993). This analysis indicated any potential differences in shoot recruitment trends between the experimental and control plots.

RESULTS

Statistical analysis of these results indicate that *Zostera japonica* removal plots showed significantly higher mean leaf growth for the last two data sampling series(07 August, 20 August). The first two data sampling series, (10 July, 07 August), showed higher mean leaf growth in the treatment plots, but it was not statistically significant (Table 1 & Figure 2).

Table 1: Leaf growth (mean ± SEM) of *Z. marina* in *Z. japonica* removal and control plots. n=14.

	------------- Leaf Growth (cm)-----------		
Date	*Zj* removal	Control	Corrected t-test (p)a
10 July '94	25.95 (± 1.59)	22.41 (± 1.77)	0.074 ns
24 July '94	27.23 (± 1.80)	22.34 (± 1.67)	0.028 ns
08 Aug. '94	25.25 (± 1.36)	19.52 (± 1.48)	0.002 **
20 Aug. '94	25.03 (± 1.19)	16.37 (± 1.44)	<.001 ***

a Bonferroni correction for four values used (p = 0.0125)

Table 2: Shoot density (mean #/plot ± SEM) of *Z. marina* in *Z. japonica* removal and control plots. n=14.

	---------Shoot Density (#/plot)---------		
Date	*Zj* removal	Control	Corrected t-test (p)
Initial	6.71 (± 1.28)	6.00 (± 0.94)	0.328 ns
Final (b)	15.86 (± 4.16)	9.50 (± 1.43)	0.086 ns
Init.-Final (b)	9.14 (±3.32)	3.36 (± 0.80)	0.043 *

b T-test for homogeneous variance was used.

Table 3: Regression analysis of final shoot density on initial shoot density of *Z. marina* in *Z. japonica* removal and control plots. n=14.

Tmt.	Slope (± SEM)	Intercept (± SEM)	Adj. R^2	df	F value
Control	1.219 (± 0.264)	2.186 (± 1.818)	0.607	13	<0.001 ***
Zj removal	3.067 (± 0.342)	-4.738 (± 2.780)	0.859	13	<0.001 ***

Tmt.	p value (slope)	p value (intercept)	Mean Sq.	Mean Sq. Error
Control	< 0.001 ***	0.250 (ns)	237.656	11.153
Zj removal	< 0.001 ***	0.112 (ns)	2774.194	34.260

Figure 2: Leaf growth (mean ± SEM) of *Zostera marina* in *Zostera japonica* removal and control plots. n=14.

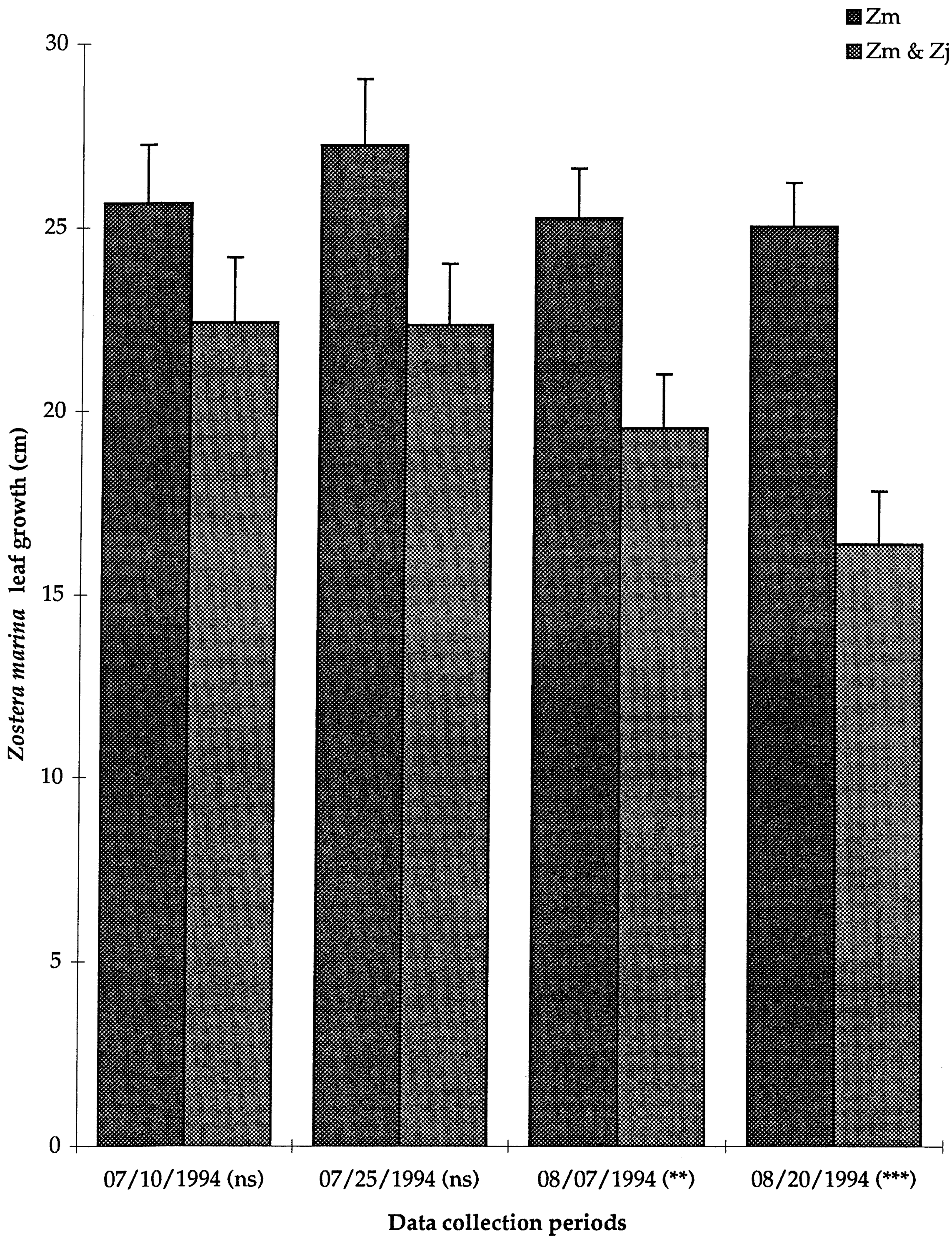


Figure 3: Shoot density (mean no./plot ± SEM) of *Zostera marina* shoots in *Zostera japonica* removal and control plots. n=14.

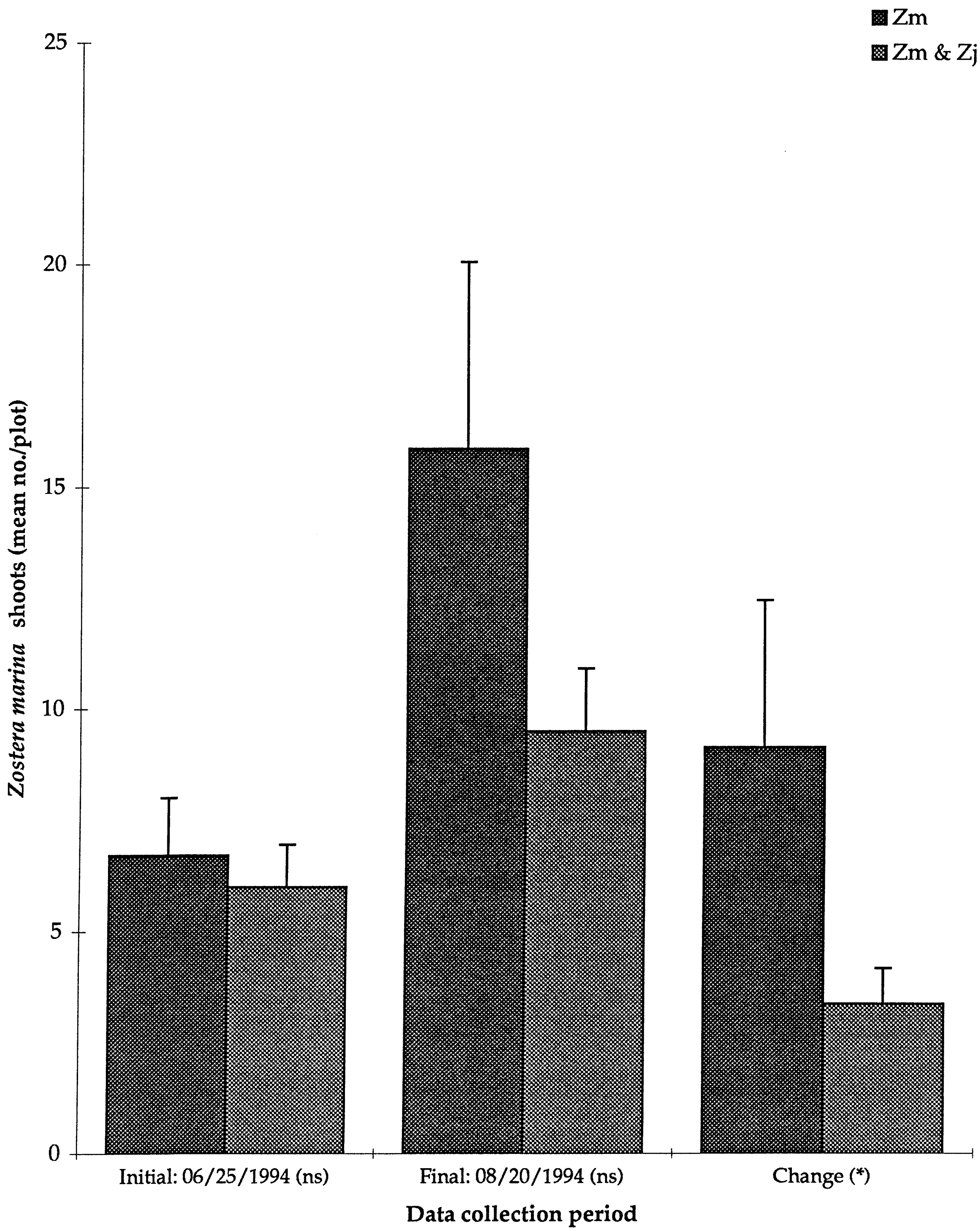
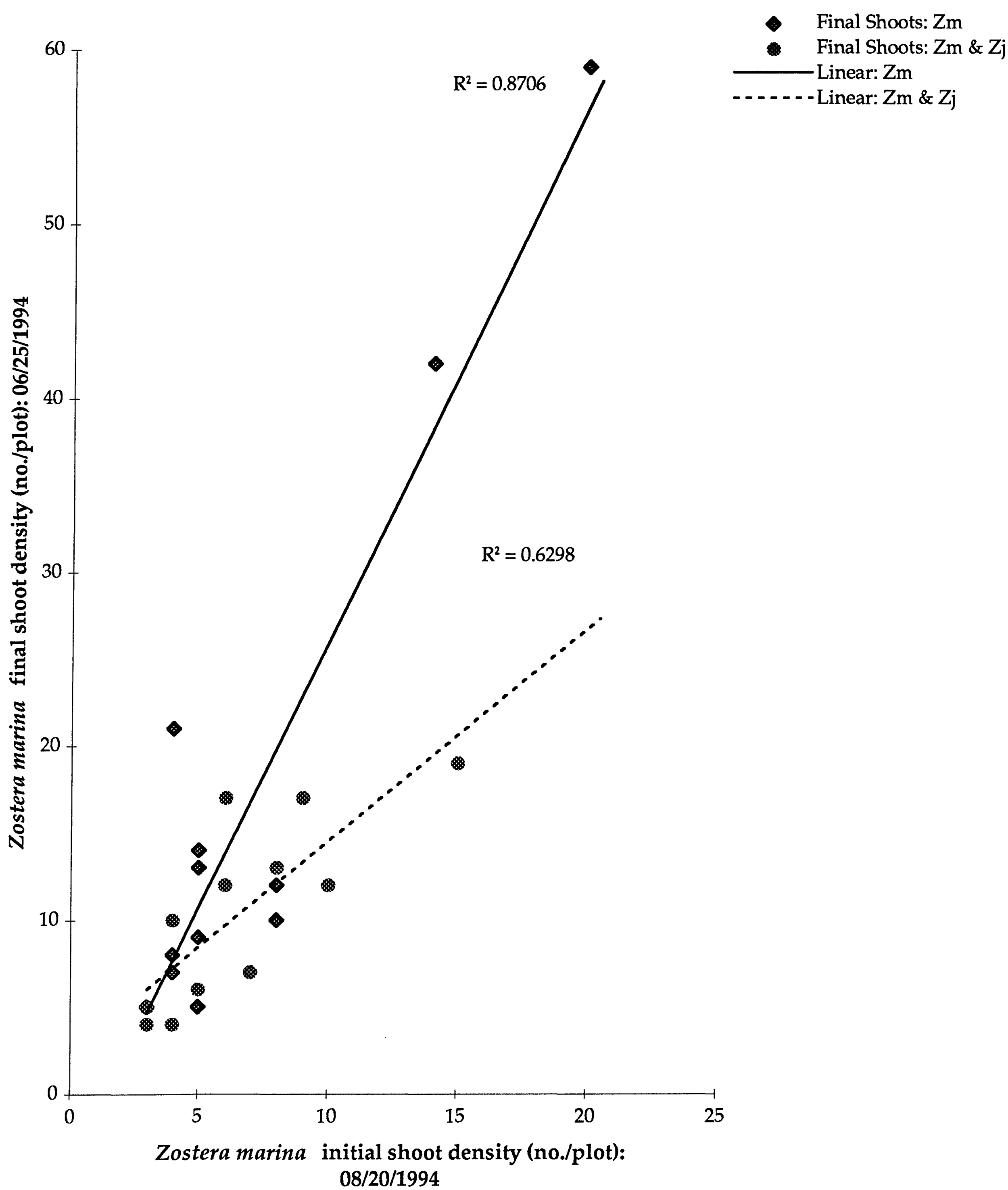


Figure 4: Best-fit trendline analysis of final shoot density of *Zostera marina* in *Zostera japonica* removal and control plots. (Linear fit). n=14.



The *Zostera japonica* removal plots showed significantly higher shoot density than the control plots at the end of the sampling period (Table 2, Figure 3). These results indicate that *Zostera japonica* inhibits leaf growth and shoot recruitment of *Zostera marina*. The lack of significant effects on the growth of *Zostera marina* in the first two sampling series may be due to a lag in treatment effects. The change in mean shoot density from the start to the end of data collection in the *Zostera japonica* removal plots was significantly higher than in the control plots (Table 2 & Figure 3). Shoot density in the treatment and control plots were not significantly different at the start of the study (Table 2).

Regression and trendline analyses of final *Zostera marina* shoot density in the experimental plots showed a reasonably strong linear recruitment trend (Adj. R^2=0.859: Table 3 & Figure 4). This indicates that larger initial shoot densities in *Zostera japonica* removal plots recruit a greater number of shoots after treatment. Regression and trendline analyses of final *Zostera marina* shoot density in the control plots did not show such a clear linear recruitment trend (R^2=0.607: Table 3 & Figure 4). This indicates that the shoot recruitment pattern in the control plots is not as strongly affected by the initial shoot density.

DISCUSSION

The results obtained during the 1994 summer season indicate that the removal of *Zostera japonica* resulted in enhanced leaf growth and shoot recruitment in individual *Zostera marina* plants. The data from the leaf growth measurements show a clear trend of higher growth in the treatment plots, statistically significant during the last two sampling periods. The trends observed in the data (Tables 1 & 2, Figures 2 & 3) indicate there may be a lag in the effects of *Zostera japonica* weeding on the growth of *Zostera marina,* but this cannot be conclusively stated from these data.

The statistics on shoot density support the data on leaf growth, but with a greater degree of variability, suggesting *Zostera japonica* inhibits the growth of large individuals of *Zostera marina* where they coexist, and the removal of *Zostera japonica* allows increased shoot recruitment in the samples observed (Table 2 & 3, Figures 3 & 4). This is potentially important for restoration activities as the presence of *Zostera japonica* could inhibit the re-establishment of *Zostera marina.* The strong linear shoot recruitment trend observed in the experimental plots suggests that restoration efforts with *Zostera marina* may be more successful with the removal of *Zostera japonica* and the use of larger transplant units. The *Zostera marina* surrounding the study area died back considerably during the 1992-1993 growing season, and much of the former range of the *Zostera marina* was colonized by *Zostera japonica* (D. Bulthuis, pers. comm. 1994). The cause of this die-back in unknown, but the continued presence of *Zostera japonica* may affect the re-establishment of the native eelgrass given the results on leaf growth and shoot recruitment provided by this study.

These results are consistent with the findings of Nomme and Harrison (1991a, 1991b) that indicated significant differences in growth between monospecific and mixed beds of the two seagrasses. However, these studies did not conclude that *Zostera japonica* inhibited *Zostera marina* growth and interspecific competition was not explicitly tested (Nomme and Harrison 1991a, 1991b).

This study was conducted in only one locale within one embayment and was restricted both in sampling period and sampling duration, thereby limiting the ability to generalize these results to other regions in the Padilla Bay system, other embayments, or subtidal populations. Additionally, this study examined only above-ground indicators and the growth of rhizomes and roots should be considered in future competition experiments. However, this study provides a basis for future comparisons and should be expanded in both sample size and sampling period to provide a more complete treatment of interspecific interactions.

This study does not seek to uncover the specific factor which may be limiting *Zostera marina* growth, but nutrient limitation, decreased light availability, or species associated with *Zostera japonica* may be contributing factors (den Hartog 1970, Wetzel and Neckles 1986, Nomme 1989, Harrison 1993, Williams and Ruckelshaus 1993, Neckles et al. 1994). Future studies should attempt to address the specific factors which may be limiting *Zostera marina* growth in these zones.

In particular, experiments should be performed to test the nutrient uptake rates of *Zostera marina* and *Zostera japonica*. By understanding how nutrients (especially nitrogen and phosphorus) are utilized by the plants, one can compare rates of nutrient uptake in both *Zostera marina* and *Zostera japonica* in monospecific and mixed species habitats and correlate this to growth patterns. Such an experiment would best be conducted in situ, however, the difficulty of accurately delivering nutrients to the plants can confound the data (Kenworthy and Fonseca 1992, Murray et al. 1992, Williams and Ruckelshaus 1993). Further exploration of the competitive interaction between these two species could clarify and define an important component in the food web interactions involved in the *Zostera marina, Zostera japonica* system. Such findings could have significant ecological and economic implications for the coastal resources of the Pacific Northwest.

ACKNOWLEDGEMENTS

Sincere thanks and appreciation are due to Dr. Annette Olson for her warm encouragement and assistance in study design, statistical analysis, and editing; to Lorraine McNeely who provided assistance and encouragement in the field; to the Padilla Bay National Estuarine Research Reserve for awarding me a Padilla Bay Research Assistantship in Estuarine Science and Coastal Zone Management which provided funding; to Dr. Doug Bulthuis, Sharon Riggs, and the staff of the Padilla Bay National Estuarine Research Reserve for assistance in siting and designing the study and the use of equipment; to Kate Wing who assisted with statistical analysis; and to the staff of the Still Life Café in Fremont who provided free coffee and nourishment during the writing of this study.

The preparation of this report was financially aided through a grant to the Washington State Department of Ecology with funds obtained from NOAA/Office of Ocean and Coastal Resource Management, and appropriated for Section 306 of the Coastal Zone Management Act of 1972, as amended.

LITERATURE CITED

Baldwin, J.R., and J.R. Lovvorn. 1994. Expansion of seagrass habitat by the exotic *Zostera japonica* and its use by dabbling ducks and brant in Boundary Bay, British Columbia. *Mar. Ecol. Prog. Ser.* **103**: 119-127.

Bigley, R.E., and J.L. Barreca. 1982. Evidence for synonymizing *Zostera americana* den Hartog with *Zostera japonica* Aschers. and Graebn. *Aquatic Botany* **4**: 349-356.

Borum, J. 1985. Development of epiphytic communities on eelgrass (*Zostera marina*) along a nutrient gradient in a Danish estuary. *Mar. Biol.* **87**: 211-218.

Bulthuis, D.A. 1991. Distribution of habitats and summer standing crop of seagrasses and macroalgae in Padilla Bay, Washington, 1989. Washington State Department of Ecology, Padilla Bay National Estuarine Research Reserve Technical Report No. 2., Mount Vernon, Washington. 35 pp.

Castell, J., P.J. Labourg, V. Escaravage, I. Auby, M.E. Garcia. 1989. Influence of seagrass beds and oyster parks on the abundance and biomass patterns of meio- and macrobenthos in tidal flats. *Estuar. Coast. shelf Sci.* **28**: 71-85.

Dennison, W.C. 1990. "Leaf production," in *Seagrass Research Methods* eds. R.C. Phillips & C.P. McRoy, UNESCO. NY. 168 pp.

Harrison, P.G. 1976. *Zostera japonica* (Aschers. and Graebn.) in British Columbia, Canada. *Syesis.* **9**: 359-360.

Harrison, P.G. 1982. Seasonal and year-to-year variations in mixed intertidal populations of *Zostera japonica* Aschers. and Graebn. and *Ruppia maritima* L.S.L. *Aquatic Botany* **14**: 357-371.

Harrison, P.G. 1987. Natural expansion and experimental manipulation of seagrass (*Zostera* spp.) abundance and the response of infaunal invertebrates. *Estuar. Coast. Shelf Sci.* **24**: 799-812.

Harrison, P.G. 1993. Variations in demography of *Zostera marina* and *Zostera noltii* on an intertidal gradient. *Aquatic Botany* **45**: 63-77.

Harrison, P.G. and R. E. Bigley. 1982. The recent introduction of the seagrass *Zostera japonica* Achers. and Graebn. to the Pacific coast of North America. *Can J. Fish Aquat. Sci.* **39**: 1642-1648.

den Hartog, C. 1970. The seagrasses of the world. Amsterdam. North-Holland Pub. Co.

Kenworthy, W.J., and M.S. Fonseca. 1992. The use of fertilizer to enhance the growth of transplanted seagrasses *Zostera marina* L. and *Halodule wrightii* Achers. *Jour. Exp. Mar. Biol. Ecol.* **163**: 141-161.

Microsoft Corporation. 1993. Microsoft Excel User's Guide: Version 5.0. Cambridge, MA. 786 pp.

Murray, L., W.C. Dennison, W.M. Kemp. 1992. Nitrogen versus phosphorus limitation for growth of an estuarine population of eelgrass (*Zostera marina* L.). *Aquatic Botany* **44**: 83-100.

Neckles, H.A., E.T. Koepfler, L.W. Haas, R.L. Wetzel, R.J. Orth. 1994. Dynamics of epiphytic photoautotrophs and heterortrophs in *Zostera marina* (eelgrass) microcosms: Responses to nutrient enrichment and grazing. *Estuaries* **17**: 597-605.

Nomme, K. 1989. "Interactive biology of two seagrasses, *Zostera marina* L. and Zostera *japonica* Achers. & Graebn." Unpublished thesis. Department of Botany, University of British Colombia.

Nomme, K. and P. G. Harrison. 1991a. A multivariate comparison of the seagrasses *Zostera marina* and *Zostera japonica* in monospecific versus mixed populations. *Can J. Bot./J. Can. Bot.* **69**: 1984-1990.

Nomme, K. and P. G. Harrison. 1991b. Evidence for interaction between the seagrasses *Zostera marina* and *Zostera japonica* on the pacific coast. *Can J. Bot./J. Can. Bot.* **69**: 2004-2010.

Peterson, C. H. and N. M. Peterson. 1979. The ecology of intertidal flats of North Carolina: a community profile. National Coastal Ecosystem Team. USFWS, US Dept. of Interior.

Phillips, R. C. 1984. The ecology of eelgrass meadows in the Pacific Northwest: a community profile. (FWS/OBS-84/24). U.S. Fish Wildlife Service.

Phillips, R. C. and R. F. Shaw. 1976. *Zostera noltii* Hornem. in Washington, U.S.A. *Syesis* **9**: 355-358.

Posey, M.H. 1988. Community changes associated with the spread of an introduced seagrass, *Zostera japonica*. *Ecology* **69**: 974-983.

Rohlf, F. J. and R. R. Sokal. 1981. Statistical tables. San Francisco. Freeman Co.

Simenstad, C.A. 1994. Faunal associations and ecological interactions in seagrass communities of the Pacific Northwest coast. in Seagrass Science and Policy in the Pacific Northwest: Proceding of a seminar series. S. Wyllie-Echeverria, A.M. Olson, M.J. Hershman eds. (SMA 94-1). EPA 910/R-94-004. 11-18.

Simenstad, C.A., B.S. Miller, C.F. Nyblade, K. Thornbugh, L.J. Bledsoe. 1979. Food web relationships of northern Puget Sound and Strait of Juan de Fuca: a synthesis of the available knowledge. Interagency Energy/Environment Research and Development Report. DOC EPA-600/7-79-259.

Thom, R.M. 1990. Spatial and temporal patterns in plant standing stock and primary production in a temperate seagrass system. *Bot. Mar.* **33**: 47-510.

Thom, R. M. and L. Hallum. 1990. Long-term changes in the areal extent of tidal marshes, eelgrass meadows and kelp forests of Puget Sound. Report to Office of Puget Sound, Region 10, U.S. Environmental Protection Agency, Seattle, Washington by Univ. Washington, fisheries Research Institute (FRI-UW-9008). 92 pp. Seattle, Washington.

Wetzel, R.L., and H.A. Neckles. 1986. A model of *Zostera marina* L. photosynthesis and growth: Simulated effects of selected physical-chemical variables and biological interactions. *Aquat. Bot.* **26**: 307-323.

Williams, S.L., and M.H. Ruckelshaus. 1993. Effects of nitrogen availability and herbivory on eelgrass (*Zostera marina*) and epiphytes. *Ecology* **74**: 904-918.