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Kirk P. Dietz
Washington Maritime National Wildlife Refuge Complex
715 Holgerson Road
Sequim, WA 98382

360-457-8451

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Kirk P. Dietz
Washington Maritime National Wildlife Refuge Complex
715 Holgerson Road
Sequim, WA 98382

360-457-8451

Oysters and Aquaculture Practices Affect Eelgrass Density and Productivity in a Pacific Northwest Estuary

Author(s): Heather M. Tallis, Jennifer L. Ruesink, Brett Dumbauld, Sally Hacker and Lorena M. Wischart

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OYSTERS AND AQUACULTURE PRACTICES AFFECT EELGRASS DENSITY AND PRODUCTIVITY IN A PACIFIC NORTHWEST ESTUARY

HEATHER M. TALLIS,^{1*} JENNIFER L. RUESINK,¹ BRETT DUMBAULD,² SALLY HACKER³ AND LORENA M. WISEHART³

¹University of Washington, Biology Department, Box 351800, Seattle, Washington 98195; ²Hatfield Marine Science Center, 2030 S.E. Marine Science Drive, Newport, Oregon 97365; ³Oregon State University, Department of Zoology, 3029 Cordley Hall, Corvallis, Oregon 97331

ABSTRACT The presence of bivalves and bivalve aquaculture can have positive and negative impacts on seagrass and associated benthic communities. Some oyster (*Crassostrea gigas*) aquaculture methods recently have been restricted to reduce benthic disturbance and protect native eelgrass (*Zostera marina*) in West coast (USA) estuaries. We argue that aquaculture, like all food production systems, involves tradeoffs with natural systems, but that the magnitude of those tradeoffs depends on the ecological details of the production system. Capitalizing on oyster aquaculture farms as large scale “manipulations” in Willapa Bay, WA (USA), we explored three different oyster aquaculture methods (mechanical harvest or “dredged” on-bottom, hand picked on-bottom and long line off-bottom). We found that both the biological (oyster-eelgrass interactions) and physical (disturbance or structure) components of aquaculture led to changes in the eelgrass population. Eelgrass density declined with oyster density in all aquaculture areas, likely as a result of direct competition for space. Eelgrass relative growth rate, plant size, and production did not change with oyster density. However, all eelgrass measures were affected by aquaculture, and the type and magnitude of impacts varied among eelgrass measures and aquaculture methods. Throughout the bay, eelgrass in long line areas occurred at densities indistinguishable from nearby uncultivated areas, but in 2004, eelgrass in long line areas was smaller (32%) and had lower production per area (70%). Cultivating oysters in dredged or hand picked beds increased eelgrass growth rates slightly, but led to lower eelgrass density (70% and 30%, respectively), plant size (32%, both cases), and production (70%, both cases). In a large scale simulated mechanical harvest experiment, the temporal response of eelgrass density varied dramatically by site, ranging from 1 to >4 y. If eelgrass impact reduction, rather than avoidance, is identified as the management goal, the degree of tradeoff between eelgrass habitat and oyster production can be minimized by managing aquaculture methods or oyster planting densities, depending on the eelgrass measure of interest. Explicit management goals and appropriate eelgrass habitat indicators must be developed before our findings can be used to suggest best management practices for intertidal aquaculture in the Pacific Northwest.

KEY WORDS: species interactions, food security, management, Willapa Bay, Washington, *Crassostrea gigas*, eelgrass, oysters, aquaculture

INTRODUCTION

As marine fisheries decline, aquaculture is emerging as one of the most likely means of supporting increasing demands for seafood (DeFur & Rader 1995). The impacts of intensive, single-species aquaculture on native marine communities depends on the community’s resilience to disturbance (Simenstad & Fresh 1995) and the type and intensity of aquaculture practices (Folke & Kautsky 1992). Existing information shows a wide spectrum of ecosystem response to aquaculture, from severe ecosystem stress (Folke & Kautsky 1992) to enhanced biodiversity and production (Pillay 1992). It is critical to understand the nature of aquaculture-ecosystem interactions as the demand for aquaculture products increases and natural components of estuaries ideal for aquaculture fall under greater regulatory protection.

Oyster aquaculture is an important industry in the United States and operations often overlap with ecologically significant, native eelgrass (*Zostera marina* L.) communities. However, management issues are complex given the mixed effects aquaculture can have on eelgrass populations. Filter feeding bivalves can enhance seagrass growth and size (Reusch et al. 1994, Peterson & Heck 2001a, 2001b), but these positive interactions have been described in nonaquaculture settings. Studies of aquaculture itself generally show negative interactions (Everett et al. 1995; but see Wisehart et al. 2007), and

harvest of wild shellfish can also reduce seagrass (Fonseca et al. 1984, Peterson et al. 1987, Orth et al. 2002, Neckles et al. 2005). Bivalve aquaculture has the potential to interact with seagrass through several mechanisms. Bivalves themselves may interact with seagrass by altering multiple physical, chemical or biological properties and functions of the system. The direction and magnitude of these interactions can depend on the density of bivalves or the component of seagrass growth measured. For instance, eelgrass (*Zostera marina*) shoot growth rates were higher in middensity mussel beds in San Diego Bay, USA, but rhizome growth rates were lower at high mussel densities (Reusch & Williams 1998).

Higher seagrass production in the presence of bivalves may be driven directly by disturbance and higher nutrient availability and indirectly by greater light availability. The disturbance that bivalves can create by abrading or breaking seagrass blades may release individuals from intraspecific light competition, a mechanism well recognized in the plant-herbivore literature (e.g., Carpenter 1981, McNaughton 1985), but largely unexplored in seagrass systems. Bivalves produce pseudofeces and feces that can enrich the sediment or water column with organic or inorganic nutrients (Bertness 1984, Reusch et al. 1994, Reusch & Williams 1998) and release seagrass from nutrient limitation (Reusch et al. 1994, Peterson & Heck 2001b, Newell et al. 2002). Bivalves may indirectly release seagrass from light limitation (Thom & Albright 1990) by removing phytoplankton from the water column (Newell & Koch 2004; for submerged

*Corresponding author. E-mail: htallis@stanford.edu

aquatic vegetation see Phelps 1994), or by indirectly reducing epiphyte loads on seagrass by capturing epiphyte propagules or providing a predation refuge for epiphyte grazers (Williams & Ruckelshaus 1993, Peterson & Heck 2001a, Duffy et al. 2001). The relative importance of the nutrient enhancement mechanism and the water filtration mechanisms is likely mediated by larger scale physical factors (tidal flushing, bay residence time, etc.) and the level of nutrient limitation (as influenced by natural processes or anthropogenic inputs).

Aquaculture can also interact with seagrass through disturbances associated with harrowing, dredging, raking, leveling, planting oysters and treatment with carbaryl (an arthropocide used to kill burrowing shrimp, reduce bioturbation, and thus potentially enhance eelgrass, Dumbauld & Wyllie-Echeverria 2003) or through the installment of structures such as those used for long lines and racks (Everett et al. 1995, Simenstad & Fresh 1995, Rumrill & Poulton 2004). Three different aquaculture methods are common in Willapa Bay and are the focus of this study. The off-bottom long line method involves stringing oysters on polypropylene lines approximately 0.5m above the substrate between stakes. These "long lines" can slow water flow and lead to higher local sedimentation rates (Everett et al. 1995). Anecdotal evidence suggests that blades of eelgrass caught on the oysters or lines during low tide may desiccate and break, decreasing eelgrass cover (Simenstad & Fresh 1995). The remaining two types of aquaculture involve planting oysters directly on the substrate. Oysters are then harvested either by hand or by mechanical harvester or "dredge." Eelgrass bed damage has been observed after bivalve planting or harvest in diverse sites worldwide (Fonseca et al. 1984, De Jonge & De Jonge 1992, Everett et al. 1995). In the Pacific Northwest, the magnitude of disturbance associated with dredge harvesting is perceived to be more severe than with hand harvesting (Simenstad & Fresh 1995), though differences in eelgrass response among methods have not been quantified.

In this study, we explored tradeoffs between oyster aquaculture and eelgrass productivity in a Pacific Northwest estuary (Fig. 1) where nearly 10% of all United States oysters are produced (Ruesink et al. 2006). In particular, we measured growth, density and biomass (plant size) of eelgrass exposed to three different oyster aquaculture methods at a number of sites in Willapa Bay, WA, USA. Pacific oyster (*Crassostrea gigas*) aquaculture is an important industry in Washington worth USD \$30 million in 1995 (Simenstad & Fresh 1995). The Pacific oyster, introduced from Japan in the 1920s, grows well in low intertidal and near-subtidal areas that also harbor native eelgrass. These oysters occupy a higher tidal range than their native predecessor, *Ostrea conchaphila*, which was largely overharvested in Willapa Bay by 1900 (Ruesink et al. 2006). Impacts on eelgrass are regulated by federal statute in the U.S. (Clean Water Act Section 404, Rivers and Harbors Act Section 10 implemented by the US Army Corps of Engineers) and also by individual states under "no net wetland loss" and other policies. Any federal permit (e.g., dredge or fill permits) triggers a requirement for Endangered Species Act (ESA) and Essential Fish Habitat (EFH) consultation with other federal agencies (United States Fish and Wildlife, National Oceanic and Atmospheric Administration, 2005) concerned with critical habitat issues for species like some salmonids along the west coast.

Impacts of oyster aquaculture on eelgrass could lead to restrictions of the type or amount of aquaculture allowed under

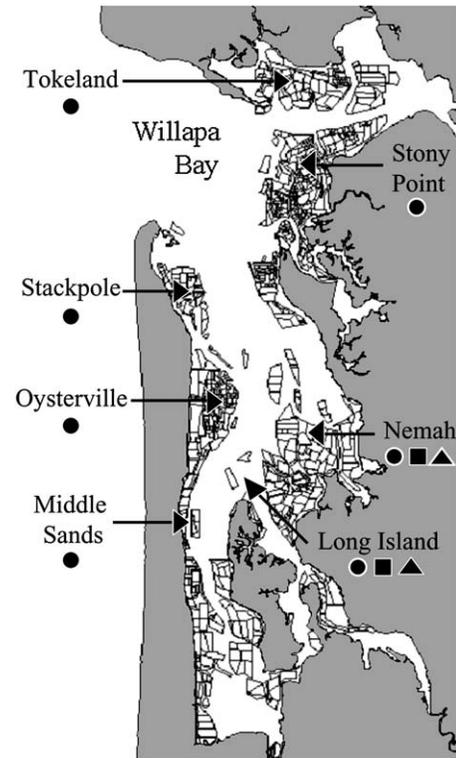


Figure 1. Willapa Bay, WA. Areas outlined in gray are aquaculture beds leased by oyster growers for oyster production. General regions of the bay are named. Symbols represent regions that were included in the 2002–2004 density survey (circles), growth studies (squares) and dredge experiment (triangles).

these regulations, particularly in estuaries used as habitat by a species listed as threatened or endangered under ESA. However, the relationship between aquaculture and eelgrass has not been described for most aquaculture practices in this region (but see Everett et al. 1995, Rumrill & Poulton 2004, Wisheart et al. 2007), making management decisions and design of best management practices for aquaculture challenging. It is crucial to understand how biological communities respond to oyster aquaculture if management is to succeed in sustaining oyster production and ecosystem function.

As part of a multiorganizational study to assess the role of oyster aquaculture in west coast estuarine ecosystems, we present the first quantitative assessment of variation in eelgrass metrics under multiple aquaculture methods. A major advance was our ability to quantify tradeoffs and distinguish how eelgrass density and growth respond to oysters (the ecological component) and to aquaculture methods (the human component) as independent factors in this aquaculture system.

MATERIALS AND METHODS

Study Sites

Willapa Bay is an estuary with extensive tideflats and large tidal exchange (Hickey & Banas 2003). About 20% of the intertidal area contains oyster aquaculture beds (Feldman et al. 2000; Fig. 1). Aquaculture methods are distributed throughout the bay, though explicit mapping of different practices has not been completed. The native eelgrass, *Zostera marina*, occurs at

and below mean lower low water throughout the bay, and the introduced eelgrass *Zostera japonica* has established on large expanses of higher intertidal areas (Thom et al. 2003, Ruesink et al. 2006). Several sites distributed around the bay were used for different components of this study (Fig. 1). Tidal heights of individual aquaculture or uncultivated beds varied from -0.8 to $+0.3$ m MLLW.

Density Surveys

We measured eelgrass and oyster percent cover and eelgrass shoot density (all in 0.25m^2 quadrats) during the summers of 2002 to 2004 to identify trends with aquaculture across several spatial scales and years. Eelgrass and oyster percent cover were estimated by eye, no individuals were counted for this measure. Individual eelgrass shoots were counted for eelgrass density measures. The 2002 survey included sites throughout the bay (27 beds, 2–6 beds per site, 4–5 beds per culture type, except 13 uncultivated beds; Fig. 1). ‘Beds’ are areas delineated by oyster growers and treated with a single aquaculture method. Beds that we sampled have likely been in cultivation for over 100 y (Collins 1892). The role of environmental variability was tested by grouping sites into north and midbay. This grouping was chosen based on distinct rotation times prescribed in the two regions for both types of on-bottom aquaculture. Hand picking and dredging are used in both parts of the bay, but aquaculture areas in the North bay include fattening beds where oysters are placed on-bottom for shorter periods (on the order of months). Midbay beds are planted for longer periods (on the order of years), so that general disturbance patterns are different between the two bay regions. Long lines generally remain in place for several years between planting and harvest in both regions.

Each bed was surveyed along three parallel transects with observations (30–78 depending on bed size) recorded at 10 m intervals along transects (for total transect lengths from 300–780 m depending on bed size). Each location in the bay (e.g., Stackpole, Nemah, etc.) was treated as a sampling site such that any bed within that location could serve as a replicate. Beds were not revisited sequentially in locations used in all 3 y to avoid temporal dependence of measures. In 2003, a subset of sites was used to provide a fully factorial sampling design (all aquaculture types present at each site). This survey was carried out at three sites (Stackpole, Nemah, Long Island) with the same transect sampling design (1 bed of each culture type per site, 330–350 m long transects). The final survey (2004) focused on the two midbay sites sampled in 2003, where we could find replicate beds of each culture type within sites. This was preferred for the growth survey, which was paired with this density survey. We measured eelgrass density in three beds of each aquaculture type per site, with 20 observations per bed.

Dredge Experiment

We conducted a large scale harvest dredge experiment at two sites (Nemah and Long Island; Fig. 1) located in the midbay. The experimental unit consisted of three treatments: eelgrass beds planted with oysters (single planting at least 6 y prior to dredging) and dredged (dredge + oysters), eelgrass beds without oysters that were dredged (dredge) and undredged, unplanted eelgrass beds (control). We marked off three 0.33 ha (1 acre) plots at each site in August 2000. We recorded eelgrass shoot

density (0.25m^2 quadrats along a diagonal transect in each plot, $n = 20$) in each bed twice (August 2000, March 2001) to test for predredge differences. A commercial oyster grower then conducted experimental harvest operations from March 13–17, 2001. The sites were resurveyed for density measures in May 2001, July 2001, August 2002, July 2003, April 2004 and May 2005.

Eelgrass Production Surveys

Eelgrass biomass production is the integrated result of three attributes: the density of eelgrass shoots (shoots m^{-2}), relative shoot growth rate ($\text{g g}^{-1} \text{d}^{-1}$) and shoot size (g aboveground biomass plant^{-1}). In May 2004, we surveyed eelgrass density and growth across beds subjected to different aquaculture methods at two sites (Nemah and Long Island; Fig. 1) in the midbay. At each site, we examined three replicate beds of each of four types (dredged ground culture, hand picked ground culture, long line culture, and uncultivated areas). For density, we counted eelgrass shoots in 20 randomly-placed 0.25m^2 quadrats; for growth, we marked five groups of five plants in each bed. Eelgrass growth was measured by puncturing two parallel holes in each shoot 1 cm above the leaf sheath with a hypodermic needle (Zieman 1974). All above ground tissue was collected 3–4 days later. Blades were separated into new and old biomass, using marks on outer nongrowing leaves as reference. Nongrowing blades were discarded. Plant tissue was then dried to a constant weight (65°C), and both new and old biomass per plant were measured. Biomass-corrected plant growth, or relative growth rate, was calculated as the ratio of new to old biomass divided by the number of days between marking and collecting plants. We used the total biomass of growing blades above the leaf sheath (a consistent underestimate of total aboveground g plant^{-1}) as our measure of overall plant size. Eelgrass production per area was calculated as the product of eelgrass density and new biomass production per shoot ($\text{g shoot}^{-1} \text{d}^{-1}$).

Statistics

For all survey data, we considered our ‘‘samples’’ to be bed averages of density and growth metrics. Eelgrass percent cover and oyster percent cover were arcsine square root transformed and eelgrass shoot density and productivity were log transformed to improve normality of residuals. For each analysis, we developed a suite of statistical models to examine the relationship between eelgrass and the following predictor variables: bed type, oyster density, year, and region or site, including all main effects and interactions. We were specifically interested in differences among aquaculture methods. This was achieved by comparing models that represent all possible combinations of methods because we had no *a priori* reason to rule out any pairings of aquaculture methods. The coding of methods selected in the best models reveals which methods are different. For example, if the model with eelgrass and hand-picked areas coded as the same method is selected, then there is no difference between these two methods.

We identified the best models with an information theory approach (Akaike’s information criterion, AIC) (Burnham & Anderson 1998), which balances model complexity (number of predictor variables, or k) and model fit. This approach is becoming the preferred alternative to hypothesis testing in

ecology (Johnson & Omland 2004). We calculated AIC corrected for small sample size (AICc) for all possible models, and standardized these to the best fit model (ΔAICc). We considered all models with $\Delta\text{AICc} \leq 3.0$ to have essentially identical explanatory power, and given the large number of models considered in each case, we report only those models with strong support ($\Delta\text{AICc} \leq 3.0$). Parameter weights, similar to partial R^2 values in multiple linear regression, give a sense of the importance of each predictor variable. Parameter weights (wAICc) were calculated for each main effect by adding the normalized likelihoods of every model including that parameter (Burnham & Anderson 2004), and we report in particular those parameters that appeared in most of these best fit models (wAICc > 0.5).

Eelgrass density and oyster density were measured for three years, whereas eelgrass growth measures were gathered only in 2004. For density measures, we considered three main effects: bed type, year and region of the bay. We examined all models with main effects and their two-way interactions (234 models) that were not over-parameterized for our sample size ($n = 63$ in all cases) for their ability to describe variation in eelgrass shoot density and oyster density.

In the initial model selection, we found that oyster density varied with bed type, but that this was mainly driven by low oyster density in uncultivated beds, as expected. Therefore, we could not distinguish the independent roles of oysters themselves and aquaculture practices with respect to eelgrass. However, there was substantial overlap in oyster density among aquaculture methods, so it was possible to examine oyster density and aquaculture method as independent factors in an analysis of cultivated beds only. Models were built from aquaculture method (again considering all possible combinations), oyster density, bay region and year as main effects and their two-way interactions (392 models not over-parameterized for $n = 41$).

We took a similar approach for eelgrass growth, which was measured at two sites in the midregion of Willapa Bay in 2004. Dependent variables were eelgrass shoot size (g above ground biomass shoot⁻¹), relative growth rate (g g⁻¹ d⁻¹), and above-ground production (g m⁻² d⁻¹), and possible predictors were aquaculture method, site and their interaction (41 models, $n = 25$). As above, we identified differences among aquaculture methods by building models with all possible combinations of treatment coding. Oyster density again varied with aquaculture method, driven by the low density of oysters in uncultivated beds. We were able to examine aquaculture method and oyster density separately in cultivated beds only, by testing models with aquaculture method, oyster density and site (as main effects plus two-way interactions; 57 models, $n = 19$ beds).

Results from the harvest dredge experiment were analyzed with repeated measures ANOVA for each site. Differences among treatments at each time point were then assessed with simple ANOVA and *post hoc* Tukey-Kramer comparisons. Given the scale of these experimental manipulations, we were unable to replicate dredge treatments within a site, so our samples within treatments are "pseudoreplicates," and therefore any differences among beds may be caused by spatial variation in factors other than those we manipulated. Nonetheless, results were instructive for preliminary interpretations of the direct effects of dredge harvesting and assessing the ability of dredged beds to recover to predisturbance conditions.

RESULTS

Eelgrass and oyster density both varied by aquaculture method, as well as by year and region of the bay (Table 1, Fig. 2). Across all aquaculture methods, eelgrass density was higher in the midbay in 2002 (mid: 36 ± 21 SD shoots m⁻²; north: 21 ± 17 SD shoots m⁻²) and highest overall in 2003 (north: 43 ± 32 SD shoots m⁻²; mid: 40 ± 12 SD shoots m⁻²; for comparison, 2004 mid: 26 ± 17 SD shoots m⁻²). Year-to-year variation is confounded with the fact that measurements were made on different beds each year. Based on AIC, statistical interactions provided sufficient additional explanatory power to offset increased model complexity in some cases (Table 1), but interactions were relatively weak (Table 2).

Both on-bottom aquaculture methods (hand picked and dredge) had lower eelgrass densities than uncultivated areas (Fig. 2a). Although site differences were important, uncultivated areas had three times more eelgrass than nearby dredged beds. Model selection results were less clear for long line beds. Long line practices were associated with eelgrass densities higher than dredged areas, but indistinguishable from hand picked or uncultivated areas (Table 1).

Oyster cover was, not surprisingly, higher in aquaculture beds than in uncultivated areas (Fig. 3a). Dredged and hand-picked beds had the highest average oyster cover (>15%). Oyster cover in long lines was lower than in other aquaculture methods, although numbers of oysters are likely more similar than we represent because long line oysters grow in three-dimensional clumps and we measured percent cover in two dimensions. Across cultivated and uncultivated beds, oyster cover was low in general, and regional cover patterns varied by year (north bay, 2002: $12 \pm 16\%$ SD; 2003: $13 \pm 13\%$; midbay, 2002: $11 \pm 10\%$; 2003: $10 \pm 13\%$; 2004: $14 \pm 15\%$ SD).

A key interest in interpreting the results of the density surveys is to understand how much of the variation in eelgrass density with aquaculture method is related to the presence of oysters versus the physical changes associated with cultivation practices. We explored this issue with all three years of survey data by looking at cultivated beds only. In this analysis, eelgrass density varied with both oyster cover (Fig. 3b) and aquaculture method (Fig. 2a), in addition to bay region and year (Table 3). Eelgrass density declined with oyster cover. Although oyster cover varied with aquaculture method (Fig. 3a), in all cases, the negative relationship with eelgrass density held (Fig. 3b).

Interpreting all eelgrass density analyses together, we found that long-lines and hand-picking tend to have smaller effects on eelgrass density than dredging. There was no clear link between oysters, aquaculture structures and eelgrass density in long line areas. However, oysters and aquaculture structures corresponded with lower eelgrass density in hand-picked and dredged beds.

When all bed types were considered, our measures of eelgrass growth (2004) all varied with site and aquaculture method (Table 1), with the interaction between these predictors being important, but weak (Table 4). Surprisingly, eelgrass relative growth rates were faster in dredged and hand picked beds than in uncultivated areas (Fig. 2b). It was not clear whether eelgrass relative growth rates in long lines were more similar to those in other aquaculture areas or to uncultivated eelgrass beds (Table 1, Fig. 2a). In contrast, all aquaculture areas had smaller plants (above-ground biomass) and lower production than uncultivated areas (Table 1, Fig. 2c, d). On average, plant size was

TABLE 1.

Model selection results for eelgrass survey across all bed types. Eelgrass density and oyster density (measured in 2002 to 2004) varied with all main effects tested (bay region, year, aquaculture method). Other eelgrass metrics, measured only in 2004, also varied with all main effects tested (site, aquaculture method). Aquaculture method differences were determined by considering all possible combinations of methods in the model selection. For example, DHL.E in a model below codes for method differences between uncultivated areas (E) and all aquaculture methods (D = dredge, H = hand picked, L = lines), with no difference among aquaculture methods. Only models with ΔAICc values ≤ 3.0 are reported here. AICc = small sample size corrected Akaike's Information Criterion. ΔAICc = AICc standardized to best model. $w\text{AICc}$ = model weight. $n = 63$ for oyster and eelgrass density, $n = 25$ for all other measures.

model	k	AICc	ΔAICc	r^2
Relative Growth Rate ($\text{g g}^{-1} \text{d}^{-1}$)				
Site + DHL.E + Site*DHL.E	5	-74.31	0.00	0.37
Site + LE.HD + Site*LE.HD	5	-73.10	1.21	0.34
LE.H.D	3	-72.61	1.70	0.15
Shoot Size (g aboveground biomass)				
Site + DHL.E	4	-117.42	0.00	0.51
Site + DHL.E + Site*DHL.E	5	-114.98	2.44	0.52
Production ($\text{g m}^{-2} \text{d}^{-1}$)				
Site + DHL.E	4	-49.07	0.00	0.70
Site + DHL.E + Site*DHL.E	5	-47.09	1.97	0.71
Eelgrass Density (shoots m^{-2})				
Bay + Year + LE.H.D + Bay*Year	6	-19.89	0.00	0.41
Bay + Year + LE.H.D + Bay*Year + Bay*LE.H.D	7	-19.66	0.23	0.43
Bay + LE.H.D	4	-17.80	2.09	0.34
Bay + Year + LE.H.D + Bay*Year + Year*LE.H.D	7	-17.72	2.17	0.41
Bay + Year + D.HE.L + Bay*Year	6	-17.25	2.63	0.39
Bay + Year + LE.H.D + Bay*Year + Bay*LE.H.D + Year*LE.H.D	8	-17.20	2.68	0.43
Oyster Density (% cover)				
DHL.E	3	-237.10	0.00	0.57
Year + DHL.E	4	-236.15	0.95	0.58
LE.HD	3	-235.71	1.40	0.56
Bay + DHL.E	4	-235.46	1.64	0.57

32% lower in aquaculture areas, and production was 70% lower (Fig. 2c, d).

Eelgrass growth also varied by site in 2004. Eelgrass plants were larger at Long Island ($0.37 \pm 0.1 \text{ g biomass plant}^{-1}$) and collectively produced more biomass ($0.90 \pm 0.61 \text{ g m}^{-2} \text{d}^{-1}$) than plants at Nemah ($0.26 \pm 0.1 \text{ g biomass plant}^{-1}$, $0.42 \pm 0.44 \text{ g m}^{-2} \text{d}^{-1}$). Overall, the mean relative growth rate was $0.14 \text{ g g}^{-1} \text{d}^{-1}$, indicating that the growing portions of eelgrass increase in biomass by 14% daily in spring.

To assess the independent roles of oysters and aquaculture methods, we examined aquaculture areas only. Oyster density (range = 1–66% cover) was not a predictor in any of the selected models, indicating that eelgrass density, relative growth rate, plant size and production were not affected by oysters themselves (Table 3, 4). As in the full suite of aquaculture methods, eelgrass relative growth rate was fastest in dredged areas (Fig. 2b). Dredged beds also had higher eelgrass biomass per shoot than hand picked beds, whereas the association of long line beds is again unclear (Fig. 2c). Finally, hand picked beds had higher eelgrass production per unit area than dredged beds (Fig. 2d).

The impact of our experimental dredge treatments varied over time (time*treatment: Long Island $\text{df} = 14$, $F = 6.15$, $P < 0.0001$; Nemah $\text{df} = 14$, $F = 2.34$, $P < 0.01$). Pretreatment average eelgrass density was 51 shoots m^{-2} on all 6 plots, with no significant difference among treatments at either site in August 2000 (Fig. 4, Long Island $\text{df} = 2,27$, $P = 0.77$; Nemah $\text{df} = 2,27$, $P = 0.06$). However, just prior to the dredge treatment in March 2001, eelgrass density was already significantly lower in eelgrass beds planted with oysters at both sites (Long Island $\text{df} = 2,57$, $P < 0.01$; Nemah $\text{df} = 2,57$, $P < 0.001$). These differences persisted immediately after the experimental harvest operation, however counts were equally low on the dredged eelgrass beds (Fig. 4), indicating that the harvest operation had a significant effect at both sites (date: 4/2001; Long Island $\text{df} = 2,57$, $P < 0.001$; Nemah $\text{df} = 2,57$, $P < 0.001$). The sites showed very different initial response magnitudes and recovery times. Eelgrass cover immediately dropped ~42% and 56% on the dredged and dredged + oyster treatments respectively at Long Island, but only ~15% and 24% on these same treatments at Nemah (Fig. 4). Eelgrass density increased 31% and 9% on the control plots at Long Island and Nemah sites, respectively, over

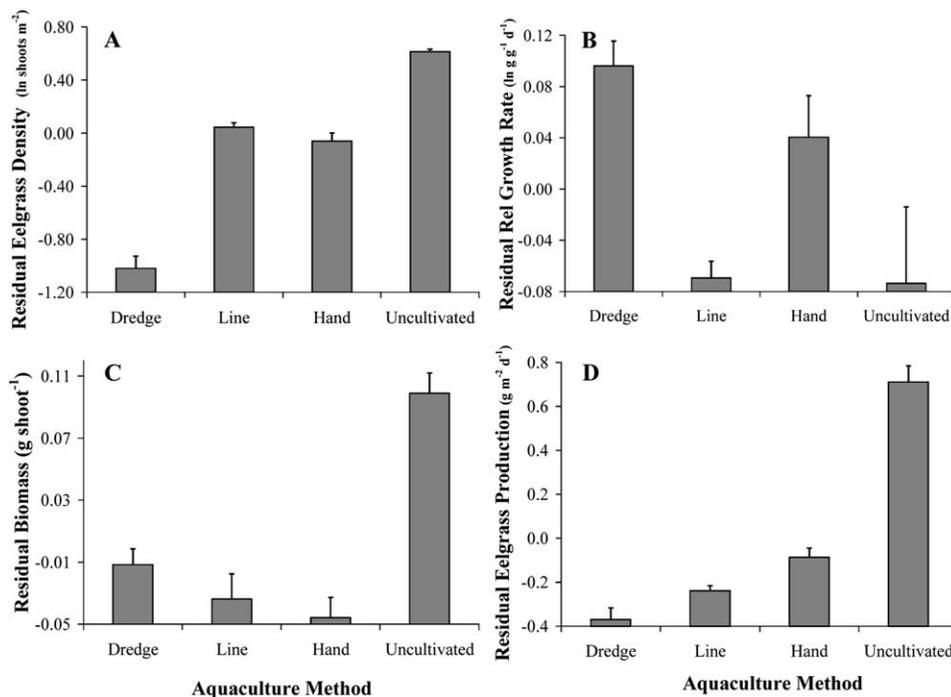


Figure 2. Bed type (aquaculture type) affected all eelgrass measures. Plots show residuals of regressions with other important variables identified in model selection (A = residuals of bay region and year, B, C, D = residuals of site). Hand picked and dredged beds had higher relative growth rates (B) than eelgrass beds. Other treatment differences were supported but unclear in model selection (Table 1). Eelgrass density represents 2002–2004 data, all other responses were measured in 2004 only. Error bars = SE.

the same period. In addition, differences among treatments persisted at Long Island much longer than at Nemah. Treatments at Nemah had similar eelgrass densities after approximately one year (date: 5/2002, $df = 2,57$, $P = 0.75$), whereas the dredged + oyster bed at Long Island still had significantly less eelgrass than the other two treatments four years after the initial disturbance (date: 5/2005, $df = 2,57$, $P = 0.05$).

DISCUSSION

Three years of surveys in actively managed oyster aquaculture areas in Willapa Bay, WA (Fig. 1), revealed that oysters (*Crassostrea gigas*) and aquaculture methods had identifiable and distinct impacts on eelgrass (*Zostera marina*) density and growth. Most of the relationships were negative, though the direction and magnitude varied depending on the eelgrass parameter and aquaculture method considered. For example, we found lower eelgrass density corresponding with higher oyster cover in all aquaculture areas (Fig. 3b), even though overall oyster density varied by aquaculture method (Fig. 3a). Eelgrass densities were lower under oyster culture, however eelgrass growth rates were higher in hand picked and dredge harvested areas, suggesting positive impacts on the relative growth rate of eelgrass (Fig. 2b). On average, plants in dredged and hand picked beds grew ~15% faster (relative to their size) than plants in uncultivated areas. The effect of long lines was unclear (Fig. 2b), with model selection suggesting that growth rates in this aquaculture type were similar to hand picked and dredged areas or uncultivated areas (Table 1).

The negative and positive effects of aquaculture on eelgrass are likely caused by the direct disturbance of aquaculture and

the indirect response of plants to that disturbance. Three interrelated effects of aquaculture are likely to be responsible for the lower eelgrass densities we report. First, the direct effects of oyster harvesting (hand picking or dredging) reduces the density of eelgrass via breakage of shoots and rhizomes. The dredge implement and steel mesh bag physically overturn the sediment, cut eelgrass blades or rhizomes or entangle whole plants, removing blades and rhizomes with oysters (Wadell 1964, Dumbauld pers. obs.). Although eelgrass does grow back in the beds over time (both via rhizomes and seeds; Wisheart et al. 2007), densities may not reach those of uncultivated beds within the typical harvest cycle (~3 y) (Fig. 4). Second, oysters use space in direct competition with eelgrass. Eelgrass shoots cannot grow in areas occupied by shell, so direct space competition could lower eelgrass density. In a similar case, an interstitial species of bivalve that makes extensive byssal mats rendered the sediment surface impenetrable and inhibited eelgrass rhizome elongation (Reusch & Williams 1998). Finally, bivalves can also mechanically damage eelgrass (Reusch et al. 1994), a process that has been observed (Simenstad & Fresh 1995), but not quantified. Eelgrass fronds that desiccate on oyster shells can break off and repeated breakage could reduce shoot size (Fig. 2c) and eventually lead to shoot death and lower density.

Higher growth rates of eelgrass in oyster beds are likely related to lower eelgrass density rather than the direct effect of oysters *per se*. Eelgrass growth is generally light limited in this region (Thom & Albright 1990, Wisheart et al. 2007), so lower eelgrass densities in dredged and hand picked beds (Fig. 2a) may release individual plants from intraspecific competition, increasing light levels, and leading to higher relative growth rates. The other possibility that we cannot reject is that oysters

TABLE 2.

Variable weights calculated across models for 2002–2004 eelgrass density in all areas, and in aquaculture areas only (uncultivated areas excluded). A variable weight = 1.00 indicates that a factor is present in all models that describe variance in the response variable well. Weights were averaged when more than one aquaculture method coding was selected in the best model set.

Parameter	Eelgrass Density	Oyster Density
All Treatments		
Aquaculture Method	1.00	1.00
Bay	0.95	0.38
Year	0.83	0.39
Aquaculture Method*Year	0.21	0.10
Bay*Aquaculture Method	0.49	0.14
Bay*Year	0.75	0.03
Aquaculture Areas (Uncultivated areas excluded)		
Oysters	0.99(-)	
Aquaculture Method	1.00	
Year	0.63	
Bay	0.84	
Aquaculture Method*Year	0.15	
Oysters*Aquaculture Method	0.36	
Bay*Year	0.43	
Bay*Aquaculture Method	0.18	
Oysters*Bay	0.28	
Oysters*Year	0.13	

increase eelgrass growth through increased nutrients from fecal production (Reusch et al. 1994, Peterson & Heck 2001b, Newell et al. 2002) or through increased water filtration (Newell & Koch 2004). The latter is more likely given that light, not nutrients, is probably the limiting growth factor in Willapa Bay and other estuaries in the region (Thom & Albright 1990; Wiseshart et al. 2007). This is an interesting pattern whose mechanism warrants further exploration.

Eelgrass biomass and production data show that the slightly higher growth rates in disturbed areas were largely overshadowed by lower density and plant size (Fig. 2a, c). Compared with uncultivated areas, we found 70% fewer eelgrass plants in dredged beds, and 30% fewer in hand picked beds (Fig. 2a). In addition, aboveground biomass of individual shoots (measured in 2004) was consistently 32% lower in all aquaculture areas, showing no variation among aquaculture methods (Fig. 2c). Production, the measure that integrates eelgrass density, size (biomass) and relative growth rates, also varied strikingly and consistently across aquaculture methods (Fig. 2d). All aquaculture areas were ~70% less productive than uncultivated areas. In other words, when the cumulative effects of oyster aquaculture (oysters and practices) are considered, higher growth rates in dredged, and perhaps hand picked beds are cancelled out by lower plant densities and size in these areas. As a result, all current aquaculture methods have equal, and relatively large impacts on plant size and eelgrass production.

Most research to date in West coast estuaries has shown that eelgrass is less dense within aquaculture than at similar tidal elevations outside aquaculture areas. Environmental conditions (sediment type, flow), harvest decisions such as when and how often, and the life-history traits of eelgrass are likely to influence the magnitude of aquaculture impact, but does this context-specificity alter the relative ranks of different aquaculture

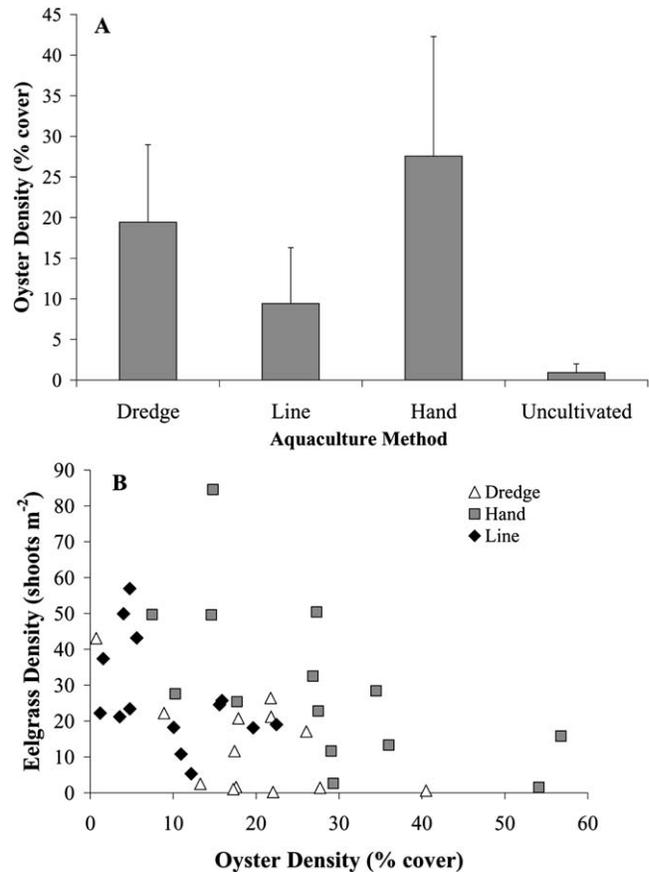


Figure 3. (A) Dredged and hand picked beds had higher oyster density than eelgrass areas. Other treatment differences were supported but unclear in model selection (Table. 1). (B) Eelgrass density declined with oyster cover in all aquaculture types in all years (overall $R^2 = 0.17$). Error bars = SD.

practices? Some studies have shown higher impacts from long lines than we found in our bay-wide survey: oyster stake culture in an intertidal eelgrass meadow in Coos Bay reduced eelgrass cover by 75% relative to nearby controls (Everett et al. 1995), and in a small subset of beds in Willapa Bay, densities were ~60% lower in both long lines and dredged beds relative to uncultivated areas (Wiseshart et al. 2007). Our bay-wide survey, which showed eelgrass in long lines to be intermediate between (and indistinguishable from both) uncultivated and dredged beds, was more consistent with Humboldt Bay, CA, where eelgrass density declined at lower line spacing but was still within the range of densities observed at reference sites throughout the bay (Rumrill & Poulton 2004). Our results from dredged aquaculture show smaller effects on eelgrass than in Humboldt Bay, where previously documented long-term losses approached 96% (Waddell 1964). We were unable to find other records of hand-picking to know whether eelgrass density in these areas tends to group with that in dredged beds or occur at higher density. There are also few records of measures besides eelgrass density.

Given the variability in response of different eelgrass measures to different aquaculture methods, it is clear that two

TABLE 3.

Model selection results for 2004 eelgrass growth measures and all years of eelgrass density measures in aquaculture areas only. Eelgrass density varied with all main effects tested (oyster density, bay, year, aquaculture method). All other measures only varied with site and aquaculture method, though oyster density was considered as a main effect. $n = 41$ for eelgrass density, $n = 19$ for all other measures. Labels as in Table 1.

Model	k	AICc	$\Delta AICc$	r^2
Relative Growth Rate ($g\ g^{-1}\ d^{-1}$)				
Site	3	-88.55	0.00	0.38
Site + D.HL	4	-85.81	2.74	0.40
Shoot Size (g aboveground biomass)				
Site	3	-88.55	0.00	0.38
Site + D.HL	4	-85.81	2.74	0.40
Site + H.D.L	4	-85.64	2.91	0.39
Site + H.DL	4	-85.64	2.91	0.39
Production ($g\ m^{-2}\ d^{-1}$)				
Site	3	-42.63	0.00	0.34
Site + H.DL	4	-42.40	0.24	0.44
Site + D.HL	4	-42.10	0.54	0.43
Site + H.DL + Site*H.DL	5	-41.82	0.82	0.53
Site + H.D.L	4	-40.78	1.85	0.39
Eelgrass Density (shoots m^{-2})				
Oysters + Bay + Year + H.DL + Bay*Year	7	-6.33	0.00	0.52
Oysters + Bay + Year + D.HL + Bay*Year	7	-5.73	0.60	0.52
Oysters + Bay + H.DL	5	-5.69	0.64	0.44
Oysters + H.DL	4	-5.54	0.79	0.41
Oysters + Bay + H.DL + Oysters*Bay	6	-5.06	1.27	0.47
Oysters + Bay + D.HL	5	-5.05	1.28	0.44
Oysters + Bay + Year + D.HL + Bay*Year + Oysters*D.HL	8	-4.94	1.39	0.54
Oysters + Bay + D.HL + Oysters*D.HL	6	-4.69	1.64	0.47
Oysters + Bay + Year + H.DL + Oysters*Bay + Bay*Year	8	-4.53	1.80	0.54
Oysters + D.HL	4	-4.50	1.83	0.39
Oysters + Bay + Year + H.DL + Bay*Year + Oysters*H.DL	8	-4.36	1.97	0.54
Oysters + Bay + D.HL + Oysters*Bay + Oysters*D.HL	7	-4.11	2.22	0.50
Oysters + Bay + H.DL + Oysters*Bay + Bay*H.DL	7	-3.99	2.34	0.50
Oysters + D.HL + Oysters*D.HL	5	-3.90	2.43	0.42
Oysters + Bay + H.DL + Oysters*Bay + Oysters*H.DL	7	-3.67	2.66	0.49
Oysters + Bay + Year + H.DL + Oysters*Year + Bay*Year	8	-3.63	2.70	0.53
Oysters + Bay + H.DL + Oysters*H.DL	6	-3.60	2.73	0.45
Oysters + Bay + Year + H.DL	6	-3.42	2.91	0.45
Oysters + Bay + Year + H.DL + Bay*Year + Bay*H.DL	8	-3.37	2.96	0.53

critical questions need to be addressed before managers considering aquaculture can use our findings: (1) Which eelgrass measure(s) are most representative of the eelgrass habitat

characteristics desired? and (2) What level of that measure(s) is required to maintain functioning habitat for the species or functions of interest? The answers to these questions may

TABLE 4.

Variable weights calculated across models for all eelgrass growth parameters and oyster density measured in 2004. Units and formatting as in Table 2.

Parameter	Shoot Size	Relative Growth Rate	Production	Oyster Density
All Treatments				
Aquaculture Method	0.60	0.79	0.77	1.00
Site	0.42	0.28	0.24	0.73
Site*Aquaculture Method	0.01	0.06	0.01	0.70
Aquaculture Areas (Uncultivated areas excluded)				
Oyster Density	0.23	0.22	0.26	
Aquaculture Method	0.22	0.22	0.49	
Site	0.95	0.95	0.93	
Site*Aquaculture Method	0.03	0.03	0.14	
Oyster Density* Site	0.05	0.05	0.07	
Oyster Density*Aquaculture Method	0.01	0.00	0.04	

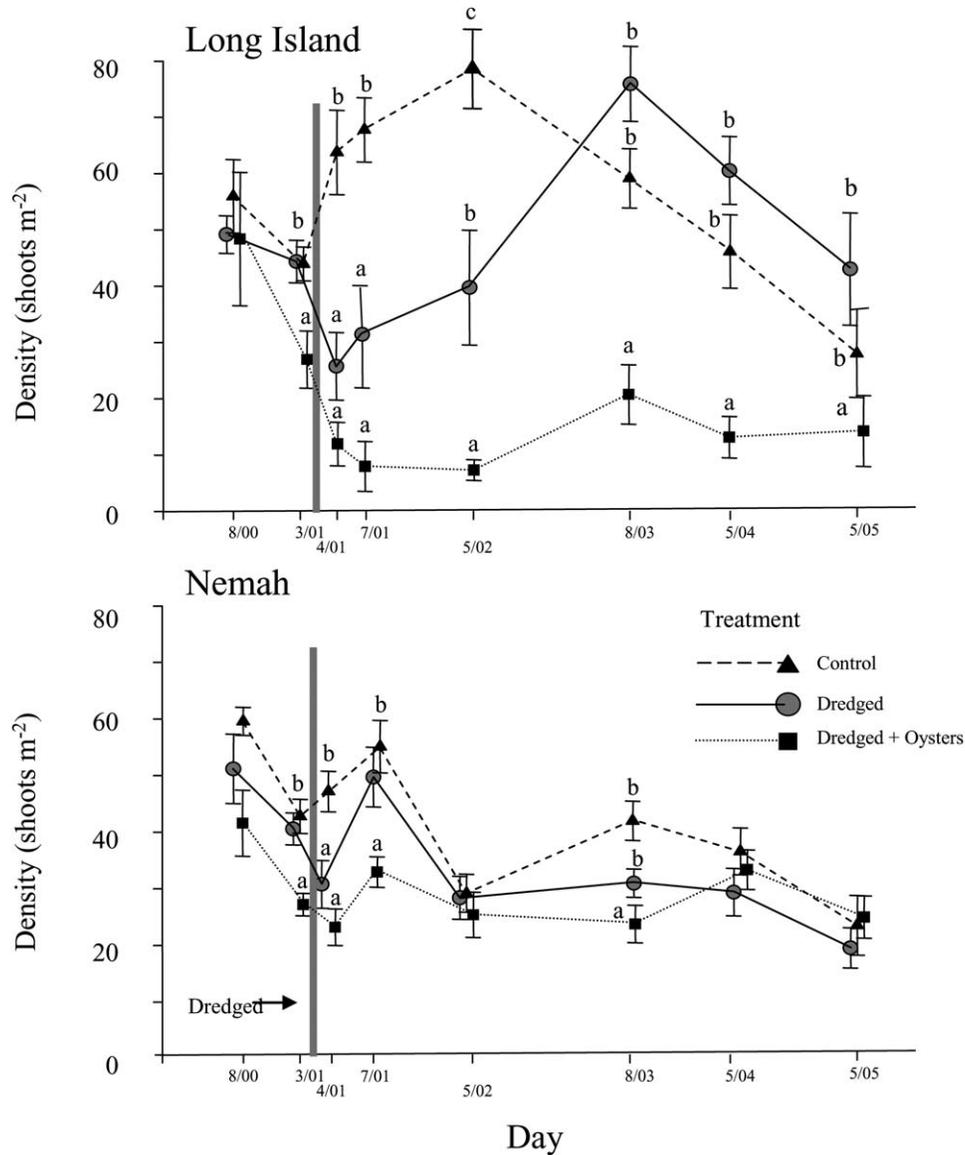


Figure 4. Eelgrass density patterns at two experimental dredge sites (top panel = Long Island, bottom panel = Nemah). Dredging occurred in March 2001. Eelgrass density declined after dredging in dredged (circles) and dredged with oysters (squares) treatments relative to controls (triangles). Nemah treatments recovered much more quickly than those at Long Island. Different letters indicate significantly different values. Error bars = SE.

change with the species of interest (e.g., salmon versus migratory birds), but our results emphasize the need to explore the implications of different management objectives. For instance, if the objective is to maximize salmon habitat, which eelgrass measure best represents the structure that migrating smolts use for predator avoidance and feeding? If the best measure is eelgrass density and uncultivated areas provide the best habitat, then our findings suggest that long line beds may provide similar value. In this case, impacts could be minimized by selecting particular aquaculture methods or reducing oyster planting densities because eelgrass density responds to both of these components of oyster aquaculture. However, if the best measure of habitat is eelgrass production, because for example detritus produced fuels upper trophic levels, then we would conclude that all areas used for aquaculture under current practices provide less habitat than uncultivated areas, and the effects

cannot be mitigated by changing planted oyster densities or selecting one of the currently used aquaculture methods. Finally, if the goal of management is to minimize impacts on eelgrass within aquaculture areas rather than avoiding impacts entirely, then harvesting oysters by hand-picking would likely be a preferred alternative, where eelgrass growth rates were high and density and production were higher than in dredge harvested beds (Fig. 2 a, b, d).

Our dredge experiment showed that minimizing impacts on eelgrass may also be a matter of timing. Here we add a third question for management consideration: (3) When does the species of interest occupy the habitat, and for how long? Experimental dredging led to large, immediate declines in eelgrass cover (Fig. 4). However, eelgrass cover recovered much faster in experimentally dredged beds at one site than the other. In other estuaries, recovery after disturbance often occurs

through vegetative branching, because eelgrass seed dispersal capabilities are limited (Orth et al. 1994), germination rates are low (Orth et al. 1994, Wisehart et al. 2007) and seedling mortality is high (Duarte & Sand-Jensen 1990, Olesen & Sand-Jensen 1994, Ramage & Schiel 1999, Wisehart et al. 2007). In Willapa Bay, seedling densities can be high ($>5 \text{ m}^{-2}$ on dredged beds; Wisehart et al. 2007), so sexual reproduction also appears to contribute to resilience after eelgrass is disturbed. Treatment effects were no longer detectable at our Nemah site after one year, whereas dredged beds with oysters at Long Island still had depleted eelgrass four years after treatment (Fig. 4). Although we cannot provide an explanation for this difference in recovery rate, muddier sediments at Long Island (Richardson et al. 2007) may have led to more severe disturbance during dredging (Dumbauld, pers observation), or conditions may be more favorable for growth at Nemah. The important conclusions from this preliminary study are that the immediate and long term magnitude of impacts from dredge harvesting can show dramatic spatial variation. The quick recovery at Nemah suggests that research to understand the reason for site differences could help identify areas where infrequent dredging could be compatible with relatively dense eelgrass.

We show that tradeoffs exist between oyster aquaculture and native eelgrass populations. None of the existing aquaculture methods in this region can be conducted whereas avoiding all impacts on eelgrass. Oysters can be cultivated using long lines with the least impact on eelgrass density, but eelgrass biomass (shoot size) and production will decline (as will eelgrass seed recruitment, Wisehart et al. 2007). Similarly, growing oysters in dredged or hand picked beds can increase eelgrass growth rates, but leads to lower eelgrass density, shoot size and production. If impact reduction, rather than avoidance, is identified as the management goal, our findings show that the degree of tradeoff between eelgrass habitat and oyster production can be mediated by the aquaculture method used.

Oyster aquaculture has been practiced in Willapa Bay for over 100 y (Collins 1892), and yet all aquaculture beds still had some eelgrass present (Fig. 2a). Further, oyster aquaculture today may be taking place in areas that historically did not contain native eelgrass but now do because burrowing shrimp

have been removed (Dumbauld & Wyllie-Echeverria 2003). Future work needs to focus on identifying the eelgrass measures that best represent species or community-specific indicators of critical habitat, and on describing critical thresholds beyond which the probability of species persistence changes. These approaches should take a landscape perspective, considering all habitats in a given estuary, including oysters themselves, and their value to species of concern. Emerging work in this area suggests that oyster beds and uncultivated eelgrass areas provide comparable structural habitat for small infaunal benthic and epibenthic organisms including Dungeness crab less than one year old, whereas differences in habitat value may occur for larger, more mobile organisms like Dungeness crab more than a year old (Rumrill & Poulton 2004, Hosack et al. 2006, Holsman et al. 2006). Context is also important because eelgrass abundance and population status vary dramatically on local, regional and global scales (Short & Wyllie Echeverria 1996) and aquaculture impacts need to be considered along with other factors affecting overall eelgrass health. These and other aspects of the tradeoffs between estuarine habitat and aquaculture are in the early stages of scientific exploration (Rumrill & Poulton 2004, Hosack et al. 2006). Ultimately, all work in this arena must be applied to decisions in the context of specific management goals.

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