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Bivalve aquaculture and eelgrass: A global meta-analysis

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ABSTRACT

The marine, intertidal zone is the optimal environment for eelgrass (*Zostera* spp.) and bivalve aquaculture. Eelgrass is a valuable and protected nearshore habitat. It is important to understand how bivalve aquaculture interacts with eelgrass to support the sustainable development of this globally expanding industry. This study provides a comprehensive understanding of the positive and negative effects of bivalve aquaculture on eelgrass by conducting the first quantitative, global meta-analysis of aquaculture-eelgrass studies. A literature review resulted in 125 studies that met established criteria for inclusion in this analysis. The meta-analysis determined: (1) how eelgrass responds to on-bottom and off-bottom bivalve aquaculture, (2) how these responses vary between regions and specific grow-out methods, and (3) the resilience of eelgrass after harvesting disturbances. On-bottom culture (laying directly on the sediment potentially including predator exclusion devices) corresponded to significant increases in eelgrass growth and reproduction, and a decrease in density and biomass. Off-bottom culture (e.g., longline and suspended bag) resulted in significant decreases in eelgrass density, percent cover, and reproduction. Results support a space-competition hypothesis for on-bottom culture and provide limited support for light limitation in off-bottom culture, although other mechanisms of interaction are potentially occurring as well. A US west coast case study revealed regional differences in eelgrass responses, including a more negative trend in eelgrass density from off-bottom culture, and a neutral effect on reproduction from on-bottom culture (relative to neutral and positive trend, respectively, in the average of all other studies). Eelgrass densities recovered after all harvest methods, however mechanical harvest methods created greater initial impact and longer recovery times than manual harvest methods. The time-period over which observations were reported was an important variable that was not included in the analysis but could influence these results. These analyses suggest the response of eelgrass to bivalve aquaculture varies depending on eelgrass characteristics, grow-out approaches, and harvesting methods, with potential regionally specific relationships. Questions remain, regarding how this dynamic relationship between eelgrass and aquaculture habitat relates to ecological functions and services in the nearshore environment.

1. Introduction

Eelgrass (*Zostera* spp.) has physiological and substrate requirements similar to those of cultivated bivalves (class Bivalvia), resulting in overlapping distributions and causing concerns over the expansion of aquaculture in coastal estuaries (Cullen-Unsworth and Unsworth, 2013; Seitz et al., 2014). Eelgrass is a valuable nearshore habitat that provides numerous ecosystem services and functions, such as primary productivity, nursery habitat, sediment stabilization, predator refuge, and carbon sequestration (Jackson et al., 2001; Duarte, 2002). Despite its ecological importance, widespread threats to eelgrass habitats are well documented (Lotze et al., 2006; Orth et al., 2006) and analyses suggest declines in many eelgrass populations (Waycott et al., 2009, but see Shelton et al., 2017). Interactions between eelgrass and bivalve aquaculture have been proposed as a potential driver of eelgrass declines (Rumrill and Poulton, 2004, Tallis et al., 2009, but see Forrest et al., 2009, Dumbauld and McCoy, 2015). However, interactions between bivalve aquaculture and nearshore marine communities remain poorly understood and are challenging to summarize across studies due to variation in experimental design, species being cultured, grow-out methods, harvest and maintenance disturbance regimes, scale of development, and local environmental conditions. Qualitative reviews

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have summarized existing studies (Dumbauld et al., 2009; Forrest et al., 2009), but they have not determined which trends are supported by the weight of the data, accounting for differences in experimental design, variation, and sample size.

Molluscan shellfish aquaculture (of which bivalves account for the vast majority) is an expanding, global industry that produced 16 million tonnes (US$19 billion) from marine and coastal habitats of America, Africa, Asia, Europe, and Oceania in 2014 (FAO, 2016). Bivalves (clams, oysters, mussels, and scallops) are grown in the nearshore marine environment, using a variety of grow-out and harvesting methods. Grow-out methods range from on-bottom (growing shellfish directly on the substrate, sometimes including predator exclusion devices) to off-bottom methods suspending bivalves above the sediment, including long lines, racks, stakes, and bags. Bivalves are harvested using manual (hand, rake, and hoe) and mechanical methods (digging, dragging, dredging, and sediment liquefaction). Cultivation and harvesting methods are often selected based on regional practices, substrate type, scale of operations, and environmental conditions. As regional management entities develop and evolve their aquaculture policies, there is an increasing request for a mechanistic understanding of how individual bivalve aquaculture practices influence eelgrass presence as well as eelgrass service and functions (Costa-Pierce and Bridger, 2002; National Research Council, 2010a; Coen et al., 2011).

The commercial cultivation of bivalves has coexisted with eelgrass for 100's of years, and bivalves have been harvested from these environments for 1000s of years prior (Mackenzie et al., 1997). Interactions between bivalve aquaculture and eelgrass exist, yet there is little established consensus on the overall trends and underlying mechanisms explaining how aquaculture and eelgrass interact (as reviewed in Dumbauld et al., 2009, Forrest et al., 2009, National Research Council, 2010a). Off-bottom culture can lead to light limitation (shading), potentially limiting eelgrass density, growth, productivity, and canopy structure (Burdick and Short, 1999, Rumrill and Poulton, 2004, Wisehart et al., 2007, but see Forrest et al., 2009). Conversely, increased sediment stabilization and wave attenuation from the addition of aquaculture-related structure could facilitate increased eelgrass percent cover and density (as reviewed in Dumbauld et al., 2009, McKindsey et al., 2011). On-bottom grow-out methods are hypothesized to compete for space with eelgrass, with potential to decrease eelgrass density (Tallis et al., 2009; Wagner et al., 2012). Increased eelgrass reproductive effort is an established response to disturbance, although the response of asexual versus sexual reproductive effort is less well understood (Alexandre et al., 2005; Cabaco and Santos, 2012; Ruesink et al., 2012). In eutrophic conditions, plankton-grazing bivalves can increase water clarity and, indirectly, enhance eelgrass growth (Newell, 2004). A combination of varying environmental conditions and cultivation methods can influence direct and indirect interactions between bivalve aquaculture and eelgrass, making the mechanism of interaction difficult to identify (Olesen and Sand-Jensen, 1994; Booth and Heck, 2009; Yang et al., 2013).

Multiple literature reviews have summarized existing studies on bivalve aquaculture and eelgrass interactions, but have not been able to provide insight on the weight of often-conflicting evidence (Dumbauld et al., 2009; National Research Council, 2010b; Coen et al., 2011; Mach et al., 2015; Herbert et al., 2016). A quantitative meta-analysis of shellfish aquaculture-ecological interactions can provide quantitative generalizations based on combining the data from independent studies (Englund et al., 1999). Meta-analyses have been broadly used in ecology and can be applied to aquaculture studies that follow an experimental design, including controls, treatments, and replicates (Hedges et al., 1999). Meta-analyses provide a formal method for combining information across studies and as a result can overcome limitations of variations in response metrics, scales of response, within study sample sizes, and levels of uncertainty. These analyses calculate a mean effect size for a given aquaculture-eelgrass interaction across multiple studies, accounting for inter-study heterogeneity, to identify shared responses among studies. Meta-analysis has the advantage over qualitative summaries that sum the number of studies supporting or refuting a hypothesis, in that it has statistical power, is less biased, and accounts for differences in study precision (Hedges and Pigott, 2001). Disadvantages to this approach include publication and research bias (e.g., significant findings are more likely to be published), incomplete data reporting (i.e., not reporting sample size and variance), lack of independence in effect size estimates, and bias in selecting studies to include in the analysis (Englund et al., 1999; Gurevitch and Hedges, 1999).

To provide essential knowledge for resource managers and the shellfish industry, we perform the first global meta-analysis of eelgrass-shellfish aquaculture interactions. We focus on three specific components: (1) how eelgrass responds to on-bottom and off-bottom shellfish aquaculture; (2) how these responses vary between grow-out gear types and region; and (3) the resilience of eelgrass after harvesting disturbances. Within these analyses, we test the hypotheses of light limitation caused by off-bottom shellfish aquaculture and space competition caused by on-bottom shellfish aquaculture. Finally, we use a US west coast case study to determine if regional patterns in aquaculture-eelgrass relationships are consistent with global averages.

2. Methods meta-analysis

2.1. Literature review & study selection

We conducted a literature review in the Web of Science using the following terms, where an asterisk symbol indicates any group of characters can be added to the end of that word:

1. eelgrass OR seagrass* OR zostera
2. AND aquaculture OR culture* OR harvest* OR cultivat* OR farm*
3. AND shellfish OR clam* OR Ruditapes OR oyster* OR crassostrea OR Ostreidae OR mussel* OR mytilus OR geoduck* OR Panopea OR scallop OR bivalv*

Of the resulting list of publications, we selected studies that examined the relationship between eelgrass and shellfish, reported original data, had a study design that included a treatment and control, and reported uncertainty (standard error or standard deviation). Most studies included in our analysis related to cultured shellfish. We added a few that experimentally manipulated shellfish-eelgrass interactions outside of an aquaculture setting to increase our sample size (e.g., Reusch et al., 1994; Reusch and Williams, 1998). We used "Web Plot Digitizer" (http://arohatgi.info/WebPlotDigitizer/app/ accessed Oct. 25, 2017) to extract data from figures when they were not provided in the paper. When selecting publications to include in this study, we were as inclusive as possible to avoid introducing bias to the analysis (Englund et al., 1999).

We first divided studies into two disturbance types for separate analysis: those that examined how eelgrass responds to shellfish presence/absence, and studies that examined the response of eelgrass to shellfish harvest. We then separated these studies into six categories of eelgrass response metrics to maximize sample size: density, biomass, growth, percent cover, reproduction, and structure (Table 1, Supplementary Table A.1). The structure metric includes physical characteristics of eelgrass, such as blade width, leaf area, and height (Table 1). If a study reported data from multiple eelgrass response categories (e.g., eelgrass biomass and density), we included all the data, as each eelgrass response category was analyzed in a separate model. If a study reported multiple eelgrass metrics that fell under the same eelgrass category (e.g., eelgrass structure), we selected the one metric that was the most inclusive from that study (e.g., leaf area instead of leaf width or height). If a study included multiple treatment locations, we included all sites (accounting for the lack of independence by including "study" as a random effect in the analysis). If a study had multiple treatment levels

Table 1
The six eelgrass response metrics used in the meta-analysis and their corresponding eelgrass characteristics as they were reported in the literature.

Eelgrass response metric	Eelgrass characteristic
Density	Density
	Abundance
	Terminal shoot density
Biomass	Biomass
	Above-ground biomass
	Biomass ratio
	Shoot biomass
Structural	Blade width
	Canopy height
	Height
	Leaf area
	Leaf area index
	Leaf length
	Leaf width
	Number leaves
	Sheath length
	Shoot height
	Shoot size
	Leaf size
Percent cover	Percent cover
Growth	Growth
	Growth rate
	Leaf growth rate
	Shoot growth
	New leaf tissue
Reproduction	Density reproductive shoots
	Flowering shoots
	Reproductive effort
	Reproductive shoots
	Seed production
	Seed density
	Branching frequency
	Rhizome growth
	Rhizome biomass
	Rhizome diameter
	Rhizome internode length

(e.g., multiple levels of longline spacing, nutrient concentrations, or light availability) we selected the conditions that matched realistic local conditions where possible (often identified within the study). In studies that included multiple shellfish densities, we selected treatments of higher but realistic densities to better identify possible trends in eelgrass responses.

We restricted the eelgrass biomass category to above-ground biomass as we had limited data on below-ground biomass and reason to expect that metric would react differently to shellfish aquaculture (Yang et al., 2013). The eelgrass reproduction response metric included data on sexual and asexual reproduction, although we found limited data on the latter. While there is evidence that these metrics can respond differently to shellfish aquaculture (e.g., Ruesink et al., 2012), we kept both metrics to maximize sample size and found no change in overall significance of results when removing asexual reproduction. In the shellfish presence/absence analysis, we only used the final time point of reported time series to avoid issues of data dependence and focus on the longer-term trends in eelgrass. We included full time series data on the separate harvest–recovery analysis and as part of the length of study analysis described below. We only used studies that reported a non-zero variance in order to use the inverse variance weighting method described below.

2.2. Data preparation

The eelgrass response data were standardized using natural log-transformed response ratios (lnRR) to calculate effect size and variance (Eq. (1): Hedges et al., 1999)

$$\mathrm{lnRR} = \ln\left(\frac{\overline{X}_T}{\overline{X}_C}\right) \tag{1}$$

here, $\overline{X}_T$ is the mean treatment response metric for eelgrass that co-occurs with bivalve aquaculture and $\overline{X}_C$ is the mean control response metric for eelgrass in undisturbed eelgrass beds, within a given study. The lnRR measures proportionate change between treatment and control groups such that positive values indicate higher values of the response variable (e.g., eelgrass density) in the experimental (bivalve aquaculture) treatments relative to the control treatments (eelgrass beds). Negative lnRR values indicate the experimental treatments had lower values than the control treatments. Values close to zero indicate little or no effect. If a treatment mean and treatment standard deviation equaled zero, we created new non-zero treatment values by multiplying the control mean and control SD by 0.1 to produce a low but valid number for lnRR calculations.

Variance (v) of the lnRR from a given study (k) is calculated using the standard deviation (sd), sample size (n), and mean response from the treatment ($\overline{X}_T$) and control ($\overline{X}_C$) (Eq. (2): Hedges et al., 1999).

$$v_k = \frac{sd_T^2}{n_T * \overline{X}_T^2} + \frac{sd_C^2}{n_C * \overline{X}_C^2} \tag{2}$$

We used mixed effect models in the meta-analysis to estimate the mean effect size in each analysis (Hedges et al., 1999; Koricheva et al., 2013). The random effect accounts for between study variation (residual heterogeneity). Studies were weighted by their variance to account for unequal sample sizes and variance. Studies with higher levels of replication, and thus more precise, were more heavily weighted and contributed relatively more to the overall mean lnRR of an eelgrass response metric. Following the random effects meta-analysis approach, the lnRR from each study (k) was multiplied by a weight (w) of the inverse of the sum of within study variance (v_k) and between study variance ($\hat{\sigma}^2$), as obtained from the mixed effect model (Eq. 3: Lajeunesse, 2011, Koricheva et al., 2013).

$$w_k = \frac{1}{v_k + \hat{\sigma}^2} \tag{3}$$

The weighted means of the individual studies were then used to estimate the grand mean effect size across all studies in the models described below. Final mean lnRR estimates were back-transformed to provide mean percent change for each gear/region/eelgrass response category ($-(100 - (\exp(lnRR) * 100))$).

2.3. Shellfish presence/absence analysis

We used a meta-analytic approach to estimate the mean and variance of the distribution of effect sizes obtained from these shellfish-eelgrass studies (Hedges et al., 1999). The mean effect size of interactions between shellfish presence and the six eelgrass response metrics were calculated using mixed effect models in the Metafor package in the R programming environment (Viechtbauer, 2010, R Core Team, 2016). Each eelgrass response metric (biomass, growth, percent cover, density, reproduction, and structure) was modeled separately. In these models, “study” was included as the random effect to account for data obtained from multiple locations within some studies (20–40% of the studies used in each metric-specific model). The percent cover model did not include any studies with multiple treatment locations and was modeled without the random effect. First, we tested the overall effect of shellfish aquaculture on eelgrass by grouping all gear types and regions together. We then examined whether eelgrass response metrics varied between on-bottom culture (oysters and clams on/in the sediment with no associated predator exclusion devices) and off-bottom culture (oysters in longlines, stakes, racks, and suspended bags), including the on- and off-bottom grow-out category as a fixed effect. To determine if regional differences influence shellfish-eelgrass interactions, we included two regional categories based on sample size: US west coast (i.e.,

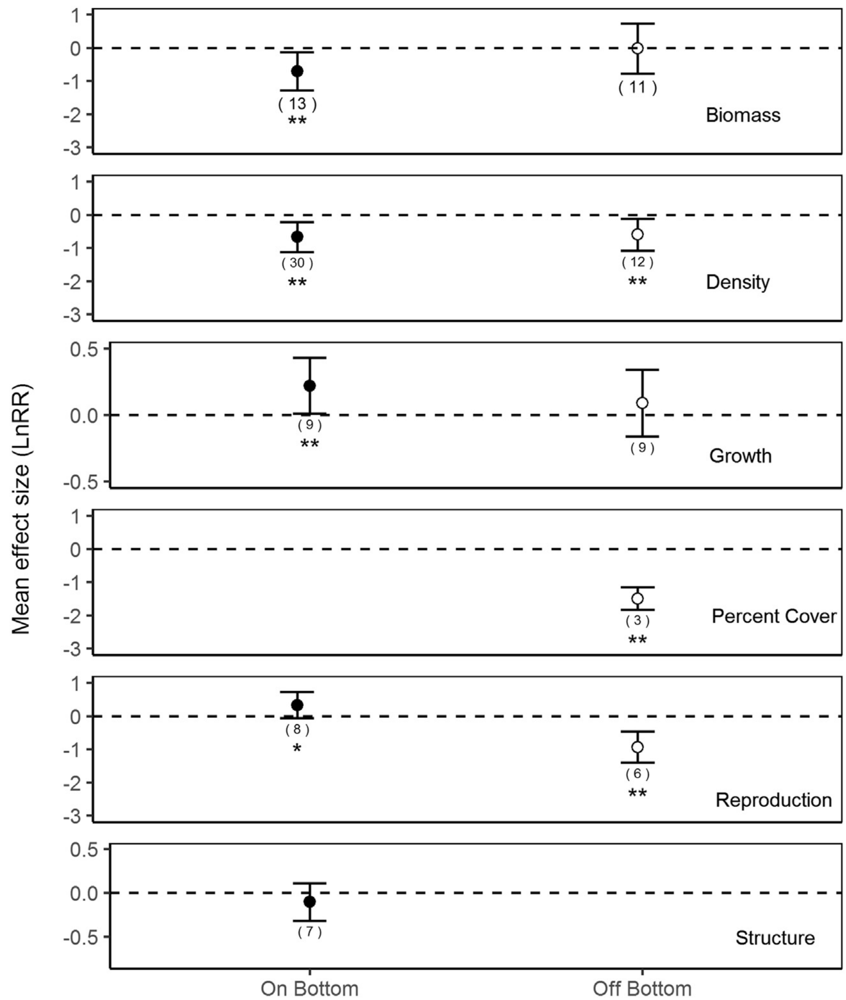

Fig. 1. The mean effect (95% confidence intervals) of on-bottom and off-bottom bivalve aquaculture on separate analyses of eelgrass biomass, density, growth, percent cover, reproduction, and structure. Sample size is in parenthesis and significance is indicated by * (< 0.1) or ** (< 0.05). The zero dashed line indicates no effect.

the Pacific coasts of Washington, Oregon, California states, Puget Sound, WA, and three studies from the west coast of Canada, and Mexico) and Global (the remaining studies excluding the US west coast). A third analysis examined eelgrass responses to various on- and off-bottom gear types. Results were only reported if the subgroup had a sample size of three or more studies. We considered results significant at a p value less than 0.1.

2.4. Harvest disturbance analysis

Studies identified as having a harvest disturbance were included in a separate analysis. We used mixed effect models to analysis change in eelgrass density over time (post-harvest). We used the same weighted, lnRR effect size and variance calculations described above, but this time included all time points in the published time series. In this analysis the random effect was “study” accounting for the measurement of eelgrass density at multiple time points within the same study. We restricted this analysis to the eelgrass density response metric, as sample size was limited for the other eelgrass response metrics across numerous harvest methods. Harvest methods were divided into Manual (hand, hand blade, hoe, and rake) and Mechanical (digging, dragging, dredging, sediment liquefaction) groups for analysis. We determined recovery as the time when there was no difference (lnRR = 0) between treatment (eelgrass in a site harvested for shellfish) and control (undisturbed eelgrass). We log-transformed time (days) to account for the large range in time scales across studies and harvest methods. We used an ANOVA test to determine significant differences between the manual and mechanical harvest groups slope and intercept.

2.5. Sensitivity analysis

Two potential biases in meta-analyses includes publication bias, in which non-significant studies are less likely to be published, and the disproportionate contribution of an individual study (Gurevitch and Hedges, 1999). We calculated Rosenberg's fail-safe numbers ($\alpha = 0.05$) in each analysis to determine the number of non-significant results required to change the significance of the meta-analysis (Rosenberg, 2005). Rosenberg's approach was selected over the more traditional Rosenthal method, as it better suits the meta-analytical framework by using weighted calculations and is applicable to mixed effect models (Rosenberg, 2005). A larger fail-safe number would indicate low publication bias and greater robustness of the results. To identify any disproportionate contributions from individual studies, each study was ranked by its weight (higher weights contribute relatively more to the overall mean effect size). The analyses were rerun to determine if the model significance changed when the three highest weighted effect sizes were individually removed. The assumption of normality was checked using quantile-quantile (Q-Q) plots (Zuur, 2009).

We analyzed the potential temporal effect of study length on each category of eelgrass responses (lnRR estimates) using generalized mixed effect models, assigning days-since-disturbance (log transformed) as a fixed effect and study as a random effect. Observations from all time points were included in this analysis.

3. Results

The initial literature search produced 1404 publications, 31 of which fit the criteria outlined above. These 31 papers included 125 studies that could be analyzed separately, based on different eelgrass response metrics (Table 1, Table A.1). Here we report results as lnRR, such that positive values indicate higher values of the response variable (e.g., eelgrass density) in the experimental (bivalve aquaculture) treatments relative to the control treatments (eelgrass beds). Negative lnRR values indicate the experimental treatments had lower values than the control treatments, and values close to zero indicate little or no effect.

Eelgrass response to on-bottom culture (no associated gear or predator exclusion devices) and off-bottom culture (e.g., longline and suspended bag) varied by response metric (Fig. 1, Table 2). On-bottom culture showed a 25% increase in eelgrass growth ($p < 0.05$), a 39% increase in reproduction ($p < 0.1$), a 51% decrease in eelgrass biomass ($p < 0.1$), and a 49% decrease in density ($p < 0.1$). Off-bottom culture resulted in 45% decrease in eelgrass density ($p < 0.05$), 78% decrease in percent cover ($p < 0.05$), and 61% decrease in reproduction ($p < 0.05$). The remaining responses of eelgrass metrics to on- and off-bottom culture were not significantly different from zero or lacked adequate sample sizes for analysis.

Broad regional differences explain some of the trends in on-bottom/off-bottom culture – eelgrass interactions (Fig. 2, Table 2). Sample sizes restricted our regional separation into two groups: the US west coast (the Pacific coasts of Washington, Oregon and California states, Puget Sound, WA, and one study from British Columbia, Canada), and the Global group (excluding the US west coast studies) (Table A.1). The US west sub-region and the remaining global region differed in two metrics. Off-bottom culture on the US west coast decreased eelgrass density by 50% ($p < 0.05$), relative to a neutral interaction in the global group, and on-bottom culture had a neutral effect on reproduction, relative to a 50% increase in the global group ($p < 0.1$).

Specific aquaculture gear types explained significant variation of eelgrass responses within on- and off-bottom categories, however, our analysis categories were again restricted by sample size (Fig. 3, Table 2). The lack of gear (i.e. no predator exclusion devices) used in on-bottom culture had a neutral effect on all eelgrass categories except density (45% decrease, $p < 0.05$) and growth (25% increase, $p < 0.05$). Longline gear also had a negative effect on eelgrass density (44% decrease, $p < 0.05$). Suspended bag gear type had a neutral effect across all eelgrass response categories ($p > 0.1$).

Manual harvesting methods (hand, hand blade, and hoe) had less initial impact on eelgrass density than mechanical methods (digging, dredging, sediment liquefaction, and dragging) (χ^2 (1, N = 65) = 5.6, $p < 0.01$, Fig. 4). Mechanical harvesting resulted in average initial decrease in eelgrass density lnRR of -5.18 (99% decrease), while manual harvesting resulting in an average initial decrease of -0.84 (57% decrease). Eelgrass density had a positive slope in both categories implying post-harvest recovery (Fig. 4) .

4. Sensitivity analysis

There were no changes in model significance when the three highest weighted studies were individually removed from each analysis (on/off bottom, on/off bottom and region, and gear type), showing no disproportionate influence of a specific study. The Rosenberg fail-safe numbers were relatively high for eelgrass density and growth (N = 3783, N = 1275, respectively), and moderate for eelgrass biomass (N = 282), percent cover (N = 112), reproduction (N = 260), and structure (N = 203).

All six eelgrass response metrics significantly varied with the length of time between the initial time of shellfish presence and sampling time

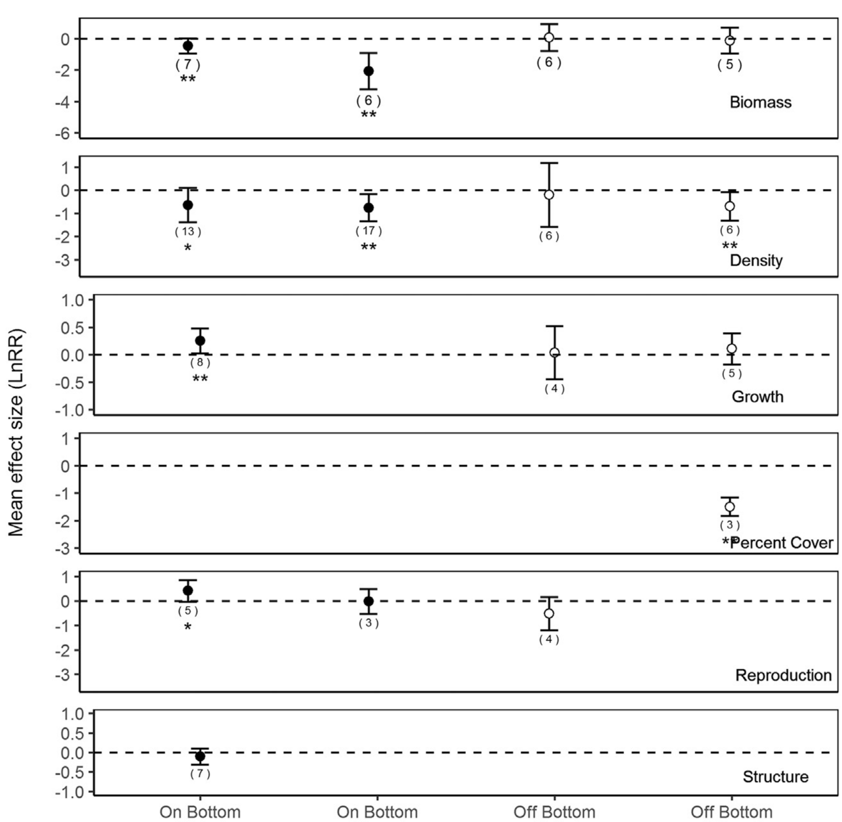

Fig. 2. The mean effect (95% confidence intervals) of on-bottom (black circles) and off-bottom (white circles) bivalve aquaculture on the US west coast relative to the Global region (all other studies not in the US west coast group), on separate analyses of eelgrass biomass, density, growth, percent cover, reproduction, and structure. Sample size is in parenthesis and significance is indicated by * (< 0.1) or ** (< 0.05). The zero dashed line indicates no effect.

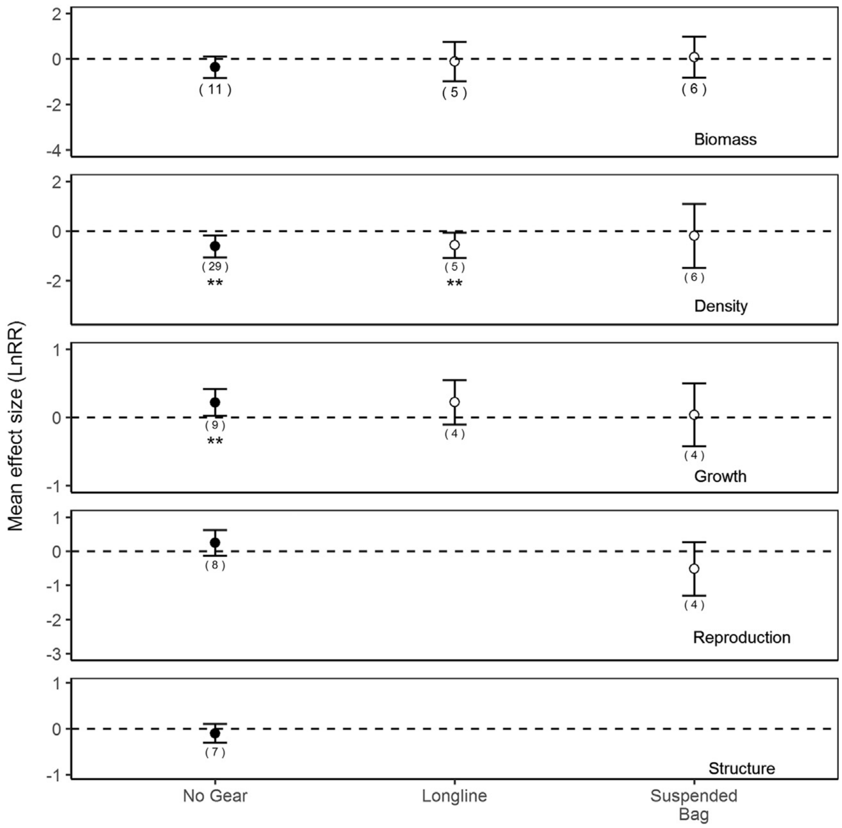

Fig. 3. The mean effect (95% confidence intervals) of no gear (on-bottom, black circle) relative to longline and suspended bag gear types (off-bottom, white circle) on separate analyses of eelgrass biomass, density, growth, percent cover, reproduction, and structure. Sample size is in parenthesis and significance is indicated by * (< 0.1) or ** (< 0.05). The zero dashed line indicates no effect.

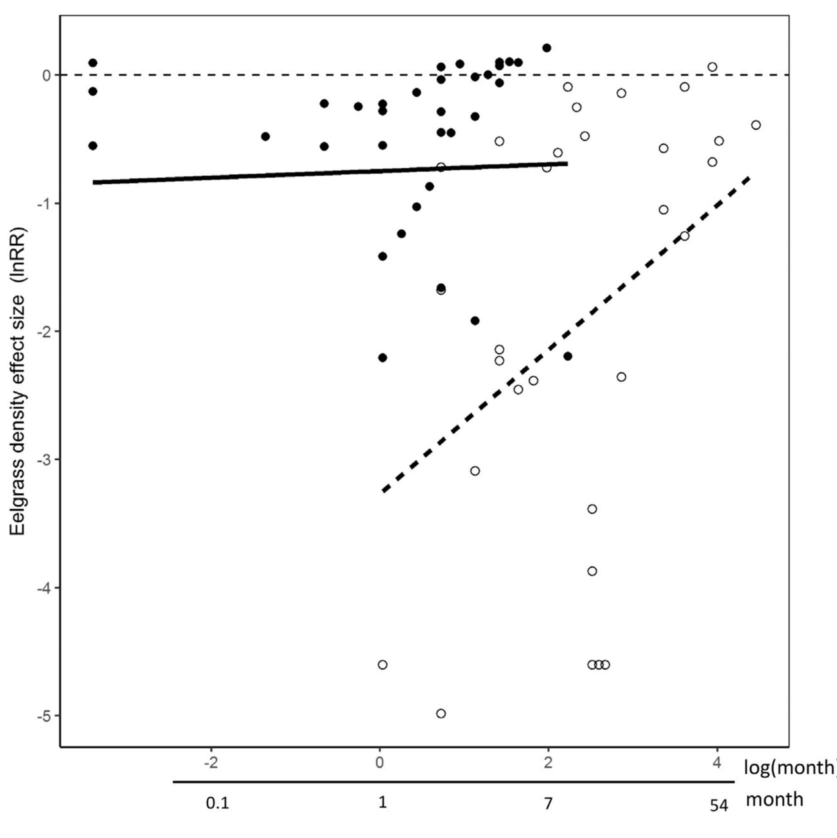

Fig. 4. Changes in eelgrass density (lnRR) in time (log month) after bivalve harvest disturbance. Harvest methods are divided into manual (closed circles and solid line: hand, hand blade, hoe, rake) and mechanical (open circles and dashed line: dragging, dredging, digging, and sediment liquefication).

Table 2
Summary of significant ($p < 0.1$) percent changes in eelgrass response metrics due to presence of shellfish aquaculture (as shown in Figs. 1–3). Eelgrass metrics increased (blue), decreased (orange), had no significant change (yellow) or had inadequate sample size for analysis (NA; gray).

	% Change in Eelgrass Response Metric					
Grow-out method & Region	Density	Percent Cover	Growth	Biomass	Structure	Reproduction
On Bottom						
All Regions	-48.91	NA	24.83	-50.60		39.46
No Gear	-46.20	NA	24.65			
Global	-47.20	NA	28.63	-36.57		51.66
US West	-53.11	NA	NA	-87.31	NA	
Off Bottom						
All Regions	-45.12	-77.58			NA	-60.66
Longline	-43.67	NA			NA	NA
Suspended Bag		NA			NA	
Global		NA			NA	
US West	-50.17	-77.58			NA	NA

($p < 0.001$; Table A.2). Eelgrass growth and structure lnRR values increased over time and eelgrass density, biomass, reproduction, and percent cover lnRR values decreased over time. These trends do not speak to lnRR magnitude, meaning eelgrass density could have a mean positive lnRR response but still have negative slope over time, or vice versa. All regions and gear types were grouped together to obtain adequate sample size, acknowledging that variation exists within these groups as described above. We did not use these temporal relationships to detrend our original lnRR data, as sample size was too limited across eelgrass metrics, gear types, and time steps to develop robust relationships.

5. Discussion

Eelgrass has variable responses to shellfish aquaculture depending on the characteristic of eelgrass being measured, the use of on-bottom or off-bottom grow-out methods, geographic region, and gear type. Off-bottom grow-out methods negatively affected eelgrass density, percent cover, and reproduction. On-bottom grow-out methods decreased eelgrass density and biomass, and increased eelgrass growth and reproduction. Varying eelgrass responses to on-bottom versus off-bottom shellfish culture suggest alternative mechanisms underlying these relationships. Differences between the US west coast and the remaining Global group suggest that regional environmental conditions or aquaculture practices can influence these cultured bivalve-eelgrass relationships. Neutral trends in eelgrass response metrics could reflect a neutral impact or be due to averaging across many environmental conditions and bivalve densities, potentially masking locally significant positive or negative trends. The temporal nature of these impacts are not analyzed in this study (except for density response to harvest), however shellfish cultivation has coexisted with eelgrass for 100s of years in many locations implying these impacts are not permanent.

Bivalves and eelgrass have the potential to compete spatially at high shellfish densities. On-bottom culture with no predator exclusion gear resulted in a decrease in eelgrass density, an increase in growth, and neutral effects on biomass, reproduction, and structure. A decrease in eelgrass density from on–bottom culture supports the space competition hypothesis (Tallis et al., 2009; Wagner et al., 2012) and the inverse relationship that can exist between eelgrass density and biomass (Yang et al., 2013). In conditions where shellfish are competing with eelgrass for space but not for other resources (e.g., light), decreased eelgrass density can result in competitive release of remaining eelgrass shoots and enhance growth (Olesen and Sand-Jensen, 1994). Site-specific studies have observed increases in shoot length and clonal branching, which may be masked by the broad grouping, and neutral results of our eelgrass reproduction and structure response categories (Kelly and Volpe, 2007; Vinther et al., 2008; Tallis et al., 2009; Ruesink and Rowell, 2012).

Off-bottom shellfish aquaculture (e.g., longlines and suspended bags) has the potential to negatively impact eelgrass through light limitation, improve the eelgrass environment via sediment stabilization and wave attenuation, or have a neutral effect on the eelgrass bed (as reviewed in Dumbauld et al., 2009, Forrest et al., 2009). The meta-analysis supported mean negative (eelgrass density, percent cover and reproduction) and neutral (biomass and growth) effects of off-bottom culture on eelgrass response metrics. The negative/neutral eelgrass responses to suspended culture lends weight to the light attenuation mechanism of interaction over the benefits of habitat modification. Site-specific suspended culture studies have documented neutral and decreased eelgrass densities and percent cover, while increased spacing of gear can reduce negative effects (Everett et al., 1995; Crawford et al., 2003; Rumrill and Poulton, 2004; Wisehart et al., 2007; Skinner et al., 2014). The lack of consensus on off-bottom-eelgrass interactions in the literature suggests a more complex interaction, reflecting multiple mechanisms, environmental conditions, and gear spacing and design (Rumrill and Poulton, 2004; Dumbauld et al., 2009). Eelgrass reproductive efforts tends to increase when eelgrass is disturbed, including asexual branching to fill gaps and sexual seed production for rapid recruitment after major disturbances (Cabaco and Santos, 2012; Ruesink et al., 2012; Yang et al., 2013; Thom et al., 2014). Off-bottom culture correlated with a negative response in eelgrass reproduction in this study, at odds with the trends found in individual studies described below. The unexpected result could be due to the averaging of asexual and sexual reproductive metrics across multiple types and levels of disturbance (within the off-bottom culture category) or the time frame of measurements after disturbance. Finally, habitat modification may not have been supported in this study due to our requirement that studies have an eelgrass reference site present nearby, thus not allowing for the possibility that eelgrass could recruit into shellfish beds where it had not existed previously.

Regional differences in growing practices and environmental conditions can influence the response of eelgrass to bivalve aquaculture. Along the US west coast, off-bottom culture negatively influenced eelgrass density, whereas this effect was neutral elsewhere, and on-bottom culture had a neutral effect on reproduction on the US west coast while this effect was positive elsewhere. The difference in eelgrass density response is partially explained by an increased representation of longline studies in the US west coast region. The meta-analysis results show longlines negatively impacted eelgrass density, whereas suspended bag (more represented in the global region) had a neutral effect on eelgrass density. The difference in eelgrass' reproductive response could indicate a greater disturbance caused by on-bottom culture in the global region relative to the US west coast (Cabaco and Santos, 2012; Yang et al., 2013; Thom et al., 2014). Averaging across a variety of environmental conditions in the Global region may contribute to the larger confidence intervals and neutral responses of eelgrass biomass, density, reproduction, and growth to off-bottom culture. The global studies included in our meta-analysis range in turbidity, temperature, water levels, nutrient levels, salinity, light limitations, and *Zostera* spp. which can influence growth, biomass, and reproduction (Yang et al., 2013; Thom et al., 2014; Hitchcock et al., 2017). Conversely, spring-summer environmental conditions in estuaries along the US west coast (NE Pacific Ocean) are characterized by relatively lower temperature, nutrient-rich, higher salinity, upwelled water from the California Current (Hickey and Banas, 2003).

Bivalve harvest method and intensity influence the initial impact and final recovery time of eelgrass density. Mechanical harvest practices (e.g., dredging) had the largest initial impact and required the longest time for recovery, potentially due to the removal or destruction of above and below ground eelgrass biomass. Longer return times for mechanical methods could also be explained by their potential for use in harvesting of larger sites, resulting in a larger area to be repopulated from an intact eelgrass source population that is farther away. Manual methods of harvest can be more spatially targeted, have less impact on the eelgrass rhizomes beneath the surface, and result in a faster recovery time (Cabaco et al., 2005; Wootton and Keough, 2016). Manual harvesting would imply a smaller area of disturbance, leaving intact eelgrass closer to the disturbed area (e.g., gap edges) and more quickly able to recolonize (Ruesink et al., 2012). Eelgrass reproductive effort can also influence recovery time, varying between clonal branching (asexual) and seed production (sexual) (e.g., Plus et al., 2003; Boese et al., 2009). Disturbance type, intensity, and frequency can influence the resilience of intertidal communities, but return time might not be the most appropriate metric for monitoring the health of eelgrass habitat after a disturbance (Short and Wyllie-Echeverria, 1996). Eelgrass recovery time assumes a stable state ecosystem as the point of return and not a dynamic equilibrium with cumulative stressors and disturbances (Gunderson, 2000). In the latter context, which better suits the marine environment, the resilience and persistence of an eelgrass bed may be better measured by its retention of ecological services and function (Thom et al., 2012). Eelgrass density has established relationships with certain ecological functions, including ability to trap sediment, primary productivity and contribution to the detrital food web (Koch, 2001; Duarte et al., 2010). There is less consensus, and more species-specific differences, on the relationships between eelgrass density and habitat value for fish, invertebrate, and infaunal communities (Turner et al., 1999; Bostrom and Bonsdorff, 2000; Blackmon et al., 2006; Hosack et al., 2006; Hirst and Attrill, 2008; Semmens, 2008; Dumbauld et al., 2015; Gross et al., 2018).

Understanding the trends in eelgrass responses to bivalve aquaculture is an important step in sustainably managing bivalve aquaculture. The benefits of a meta-analysis include the discovery of general trends that outweigh the underlying variability present in individual studies. While these meta-analyses results are not intended to supersede regionally specific studies, they may be helpful in informing best practices to locations where individual studies are not yet available. Some sources of variability that we could not account for in these analyses included the spatial and temporal scale of disturbance, for example, the size of aquaculture plots in each study and whether individual sites were repeatedly planted and harvested or were being disturbed for the first time. Accounting for study length (time since shellfish planting) has the potential to change some of these results (e.g., Dumbauld and McCoy, 2015). In addition, a greater number of studies from different regions would enable us to examine the potential influence of ocean conditions on the responses of eelgrass metrics to shellfish aquaculture.

Shellfish have been farmed in and around eelgrass for over a century and it is clear that shellfish aquaculture does not preclude eelgrass. However, as demonstrated by our study, there can be temporary changes in certain eelgrass characteristics. To account for these potential changes on the US west coast, resource managers follow avoid, minimize, and mitigate protocols outlined in federal and state management documents (e.g., NOAA Fisheries West Coast Region, 2014, US Army Corps of Engineers Seattle District, 2015). These documents currently recommend that any new farms avoid impacts to eelgrass by placing a buffer around eelgrass, or including an unvegetated perimeter in the eelgrass bed definition, and avoid working in those areas. If avoidance is not possible, such as on existing farms, impacts should be minimized (e.g., minimizing the number of workers or boats used in areas with eelgrass). If disturbance cannot be avoided or minimized then mitigation is recommended. The US west coast data analyzed in this meta-analysis were mostly collected from farms working within this management context. Best management practices continue to evolves. For example, there is a condition for Endangered Species Act coverage in Washington, USA, that oyster longlines and flipbags must be spaced laterally at 10 feet intervals in fallow areas that have been colonized by eelgrass to minimize potential impacts of shading (NOAA Fisheries 2016). Additional topics that would inform this discussion include spatial management, landscape perspectives, and connecting changes in eelgrass response metrics (e.g., density) to ecological function.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.aquaculture.2018.08.046.

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