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RECIPROCAL INTERACTIONS BETWEEN BIVALVE MOLLUSCS AND SEAGRASS: A REVIEW AND META-ANALYSIS

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ABSTRACT Both seagrasses and bivalve molluscs act as ecosystem engineers in marine systems by forming habitat or modifying environmental conditions. They also have the potential for reciprocal interactions when colocated, through a wide variety of potential mechanisms involving different directions in effect. Pathways mediated by biogenic structure could be facilitative through protection from predation or bioturbators, or by harboring beneficial interactors, or alternatively could result in competition for space or reduced food supply. Other pathways mediated by biological activity could positively link autotrophic roles of seagrass and heterotrophic roles of bivalves, but excessive organic matter production or nutrient release could be damaging. Published studies were compiled for a meta-analysis of field experiments testing bivalve response to seagrass (25 studies) and *vice versa* (11 studies), as well as for surveys of bivalves in and out of seagrass (39 studies). In experiments, seagrass improved bivalve survival, and bivalves at high cover reduced seagrass density, but seven other response metrics showed no consistent change. In surveys of particular bivalve species, densities were 1.6 times higher in seagrass than out of seagrass. This augmentation did not differ by body size but was especially pronounced in some functional groups, especially lucinid and solemyid bivalves harboring sulfide-oxidizing bacteria. Weak overall directional effects of colocation of seagrass and bivalves reflect weak effects in some individual studies, for instance because of low densities in soft-sediment systems, as well as strong but inconsistent effects because different pathways of interaction dominate. Therefore, generalizations about the outcome of interactions between these two ecosystem engineers when they are colocated cannot be made, although coexistence is typically enabled by weak or positive interactions. Further work is needed, especially outside of some well-studied regions, to explore the specific mechanisms and spatiotemporal scales enabling seagrasses and bivalves to coexist because there are many pathways at work.

KEY WORDS: bivalves, molluscs, seagrass

INTRODUCTION

Seagrasses and bivalves are ecosystem engineers in shallow marine waters, creating habitat structure and modifying abiotic conditions and resource availability (Gutiérrez et al. 2011). Yet their environmental effects are unlikely to be functionally equivalent because of differences in architecture, chemical composition, flexibility, and trophic level. Seagrasses frequently are managed for protection and restoration (van Katwijk et al. 2016), whereas bivalves additionally are targets for aquaculture and fishing (Beninger & Shumway 2018, Bersosa Hernández et al. 2018). Because the two taxonomic groups often co-occur on soft sediments, interventions on the part of one taxon potentially affect the other, such as facilitation during joint restoration (Gagnon et al. 2020). How do these two ecosystem-engineering taxa reciprocally interact? This quantitative review summarizes evidence from field experiments testing bivalve–seagrass interactions, in either direction, as well as surveys of bivalves inside and outside seagrass habitats.

Seagrass could affect bivalves negatively or positively through several pathways, including both structural attributes of seagrass and its biological activity as a primary producer (Fig. 1A). Furthermore, a single pathway may have different effects depending on functional traits of the bivalve. In general, epifaunal invertebrates respond positively to aboveground structure provided by seagrass, whereas infaunal invertebrates may be inhibited (Stoner 1980). Aboveground structure could be particularly beneficial for surface-dwelling or epifaunal bivalves under high-flow conditions where structure increases

sediment stability, protects them from dislodgment, and does not result in long water residence times.

In some pathways, seagrass structure modifies trophic interactions of bivalves (Fig. 1A). Considering top-down effects, structure can exclude predators or reduce their foraging effectiveness both above- and belowground (e.g., Reise 1977, Peterson 1982). For instance, thin-shelled and surface-dwelling bivalves reached greater densities in seagrass than mud habitats (Glaspie & Seitz 2017), and vegetation shifted communities from endobenthic to epibenthic because of providing habitat and protecting from predation above sediment (Bouma et al. 2009). Alternatively, predators might be attracted to seagrass, enhancing the strength of top-down effects (Lowe et al. 2019). From the bottom-up effect, seagrass structure characteristically reduces water flow and food delivery (e.g., current speeds reduced by half; Fonseca et al. 2019), which could stunt bivalve growth or condition, although particulate matter may also be enhanced in seagrass beds (Judge et al. 1993, Ruesink et al. 2019). Through this bottom-up pathway, responses of bivalves could depend on the functional group, with vegetation harming filter feeders through reduced food delivery, but favoring deposit feeders through organic matter accretion (Bouma et al. 2009). In another study, deposit feeders were more abundant outside than in vegetation (Glaspie & Seitz 2017), emphasizing that functional group responses may be context-dependent. An emerging paradigm is for seagrass to foster bivalve survival but reduce growth (Carroll & Peterson 2013).

Another species interaction that may drive bivalve response to seagrass is through an intermediate bioturbator species. Bivalves could be facilitated not only by seagrass directly but also by seagrass' ability to exclude bioturbators. Accordingly, sandflats in the Knysna estuary (South Africa) without bioturbating

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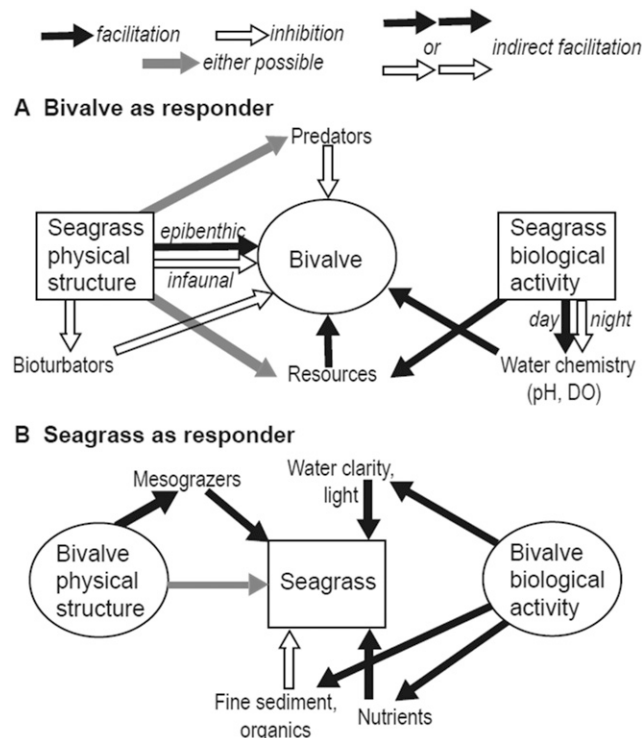


Figure 1. Pathways of interactions among ecosystem engineers, distinguishing roles of physical structure, and biological activity. (A) Seagrass effects on bivalves. Explaining the grey arrows, predators and resource delivery are generally considered to be reduced in seagrass (inhibition), but counterexamples exist (facilitation). (B) Bivalve effects on seagrass. Explaining the grey arrow, bivalves may outcompete seagrass for space (inhibition), but structure could improve colonization of early life stages (facilitation). Indirect effects derive from two sequential arrows in a pathway of interaction.

shrimp had as many or more macrofauna relative to nearby seagrass (Barnes & Barnes 2014).

Unlike the inconsistent predicted effects of seagrass structure on bivalves, most pathways involving biological activity of seagrass are expected to be facilitative (Fig. 1A). Primary production can enhance secondary production, as indicated by the suggestion that flagellates consumed by oysters were supported by “the decomposition of a vast amount of eelgrass” (Imai et al. 1950). In daytime, oxygen released from seagrass photosynthesis is available for bivalve respiration, and drawdown of carbon dioxide could improve pH. Nevertheless, whether conditions for calcification are improved or primarily made more variable by seagrass remains an open avenue of research (Kowek et al. 2018). Lucinid and solemyd bivalves are particularly likely to show a trophic facilitation by seagrass because of organic matter enrichment and sediment sulfide that their symbiotic gill bacteria use, shunting some of the energetic benefit to their host (Reynolds et al. 2007, van der Heide et al. 2012).

The reciprocal interaction, in which bivalves are the effector and seagrass the responder species, likewise provides both facilitative and negative pathways that could govern the overall interaction (Fig. 1B). Space occupied by bivalves is unavailable to seagrass, a negative effect that may appear primarily at high bivalve densities (Wagner et al. 2012). Beyond spatial

interference, structural aspects of bivalves could benefit seagrass. Structure could catch seeds or anchor seagrass at early life stages, especially in high-flow conditions, or harbor invertebrates that remove epiphytes from seagrass. Biological activities of bivalves are expected to modify water or sediment conditions in ways that benefit seagrass, for instance by particle filtration, thereby improving water clarity and light availability, or by nutrient release; however, biodeposits that fertilize plant growth may become detrimental to seagrass in excess, including reduced growth rate from sulfide toxicity or competitive epiphytes (Vinther & Holmer 2008).

In any particular bivalve–seagrass (or seagrass–bivalve) interaction, the outcome reflects the relative importance of a variety of pathways (Fig. 1). This meta-analysis intends to move beyond single cases to understand the weight of evidence across multiple bivalve–seagrass systems. The expectations are given as follows:

- (1) Among experiments comparing bivalves in treatments with and without seagrass, seagrass will generate more positive responses in bivalve survival (predator protection) than growth (resource restriction) and will facilitate two functional groups in particular: clams with sulfur-oxidizing gill bacteria (lucinids and solemyds) and epibenthic bivalves that would otherwise have no structural protection.
- (2) In the reciprocal interaction, for experiments comparing seagrass in treatments with and without bivalves, spatial interference will reduce seagrass density, but improved sediment or water properties from bivalves will have positive effects on demographic rates.
- (3) Among observational studies of bivalve densities in and out of seagrass, seagrass will facilitate particular taxonomic and functional groups as identified in prediction 1 (trophic mutualism and protection), and effects of seagrass structure will differ by body size (e.g., smaller body sizes being able to live in spaces within rhizome mats).

MATERIALS AND METHODS

Inclusion Criteria for Meta-Analysis

The following search terms were used in Web of Science to find articles published throughout 2019: (seagrass* or eelgrass* or Zostera or Posidonia or Halophila or Cymodocea or Enhalus or Thalassia or “sea grass”) and (bivalv* or shellfish or cockle* or mussel* or clam* or oyster* or scallop* or geoduck*). Of 1,112 publications, 70 contained data relevant to this meta-analysis. No additional relevant publications appeared in the review or synthesis articles identified by these search terms (Fig. 2). Data were extracted from figures using “Web Plot Digitizer” (<https://apps.automeris.io/wpd/Version 4.2>) when data were not available in text or tables. Raw data were accessed for some results visualized as boxplots or symbol area (e.g., Ruesink et al. 2014).

Meta-Analysis of Manipulative Studies

Manipulative studies were required to have a treatment in which bivalves and seagrass were colocated, and a reference in which only the responding taxon was present. Studies in which recruitment was measured in and out of the effector taxon were included, although these were not strictly manipulative because

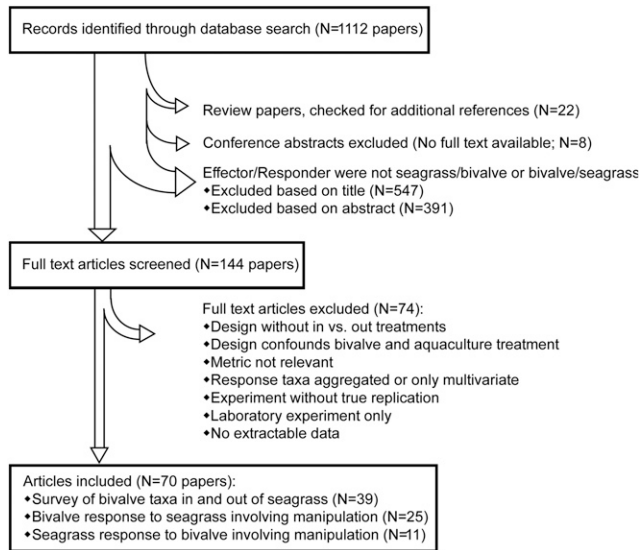


Figure 2. Flow diagram for identification and screening of articles used in meta-analysis. Two publications included both seagrass and bivalves as responders (Reusch & Chapman 1995, Tsai et al. 2010). Three publications included both observational and manipulative components to study bivalve response to seagrass (Peterson 1982, Reusch & Williams 1999, Ruesink et al. 2014).

neither the effector nor responder was added or removed by the researchers. Study designs were checked for true replication, which eliminated some studies where multiple plots were tracked in and out of one large patch of the effector taxon; if this design was established at multiple sites, sites were considered samples to calculate a grand study mean and SE. Studies that had artificial treatments (i.e., artificial seagrass and empty shells), involved bivalve aquaculture methods, or concerned habitat edges, instead of presence/absence of the effector, were excluded.

Many different response metrics were recorded across studies, which were categorized as growth, size, density, survival, and recruitment. Diet, isotope, physiological, or transcriptome responses were not included. Studies often reported more than one measurement for each metric (i.e., growth per day and size corrected growth per day), but only one measurement per metric was retained. For duplicate metrics, the most prevalent measure based on the hierarchy in Table 1 was retained. Treatment conditions were considered to include both seagrass and bivalve, colocated, whereas reference conditions contained only the responder taxon. From each article, mean, measure of dispersion [SD, SE, or confidence interval (CI)], and sample size were extracted for the responder taxon in both treatment and reference conditions. Duration since the beginning of the experiment was recorded, including any repeated measures during the experiment. All studies included information about site location and effector/responder species identity, and for some, effector density was quantified. These values were subsequently used to calculate standardized effects as Hedges' d with a small sample size correction (sometimes referred to as Hedges' g , Gurevitch et al. 1992, Viechtbauer 2010).

$$d = \frac{\bar{Y}_e - \bar{Y}_c}{S} J$$

$$S = \sqrt{\frac{(n_e - 1)s_e^2 + (n_c - 1)s_c^2}{n_e + n_c - 2}}$$

$$J = 1 - \frac{3}{4(n_e + n_c - 2) - 1}$$

Here, $\bar{Y}_e$ and $\bar{Y}_c$ are treatment and reference means. S is a pooled SD including treatment (n_e) and reference (n_c) sample sizes and treatment (s_e) and reference (s_c) SD. J is a correction factor that removes small sample size bias. Values overlapping zero are nonsignificant, negative values indicate inhibition, and positive values indicate facilitation.

TABLE 1.
Responses measured in studies of reciprocal seagrass–bivalve interactions.

Response metric	Seagrass	Bivalve
Density	Shoots per area % Cover	Individuals per area Biomass per area % Cover
Size	Leaf length per shoot Aboveground mass per shoot Leaf width per shoot Leaf area per shoot	Maximum linear shell dimension Tissue mass Other linear shell dimension (e.g., oyster length and clam height) Tissue mass per shell dimension (condition)
Growth	Increment (leaf length, mass, and area) per shoot per time Size-standardized increment per time (relative growth rate) Increment (mass) per ground area per time	Increment in maximum linear shell dimension per time Increment in total mass per time Increment in other linear shell dimensions per time Specific growth per time: increment in ln-transformed linear shell dimension
Survival	No publications	Proportion remaining Number remaining
Recruitment	Seeds germinating per area Asexual branching per area or per shoot	Individuals settling per area

Responses within a metric category are listed from most to least common, and a more common response was selected for use in meta-analysis if several within a category were measured on the same individuals in the same study.

Separate meta-analyses were performed for each category of response metric in seagrasses and bivalves, using the *metafor* package in *R* version 3.5.2 (Viechtbauer 2010, R Core Team, 2017). The meta-analysis included 25 bivalve response studies and 11 seagrass response studies (Fig. 2, Appendix 1), with two studies of reciprocal effects germane to both. No publication bias was found via funnel plot asymmetry in Egger's regression tests in bivalve responses ($t_{81} = 1.05$, $P = 0.30$) or seagrass responses ($t_{44} = -1.88$, $P = 0.07$). Many studies reported repeated measures, but only the final duration was used in the main analysis, which is a standard practice in ecological meta-analyses (Gurevitch et al. 1992). Based only on final samples, overall effect size was estimated for each response metric category in a linear mixed-effects model with study as a random effect. In addition, all time points and all metrics were included in a linear mixed-effects model with duration as a fixed effect and study as a random effect. A separate meta-analysis was carried out for seagrass density response, including only the five studies with information about bivalve density, which was considered a fixed effect. Studies that reported densities of bivalves as individuals per area were converted to percent cover (density multiplied by individual shell area) to make all densities comparable.

Surveys of Bivalves In and Out of Seagrass

Surveys of macrofauna at nearby sites in and out of seagrass were compiled for densities of bivalve taxa (see Appendix 1). Two studies reported biomass per area [Reise et al. 1994 (*Mya arenaria* only), Ortiz et al. 2003], and the remainder reported the number per area. Studies were not suitable if they reported only richness, total bivalve abundance (e.g., Skilleter et al. 2007, Armenteros et al. 2018), or community-level multivariate analyses. No studies involved manipulation of seagrass, and most lacked true replication of each habitat type. Variance was not taken into consideration. In two studies, bivalves in and out of seagrass were compared temporally because seagrass appeared or disappeared (Rueda et al. 2009, Do et al. 2011). Surveys across a range of seagrass densities were excluded, unless unvegetated samples were included in this range, and then samples above 50% seagrass cover were used to calculate mean bivalve density in seagrass (Reusch & Williams 1999, Prado et al. 2014, Lohrer et al. 2016). Several surveys compared bivalves colocated with different seagrass species with a single bare site, in which case a single mean density was calculated in seagrass (Eklöf et al. 2005, Katsanevakis & Thessalou-Legaki 2009, Ferraro & Cole 2011, 2012). Two publications covered a lucinid bivalve at a single site with multiple seagrass species (Rattanachot & Prathep 2015, 2016) but became just a single point in the analysis. For surveys with several bare sites, the bare site at a similar depth and in close proximity to seagrass was selected, or—when sand and mud seemed otherwise equally valid for comparison with seagrass—mean density across bare sites was calculated (Ferraro & Cole 2007).

The response variable in this analysis was calculated on a species-specific basis and, in a few cases, at the level of taxonomic family (Eklöf et al. 2005) or functional group (Glaspie & Seitz 2017). A log response ratio was used as a metric of effect size, specifically calculating $\log_{10}$ ratio of abundance in seagrass relative to out of seagrass. If the bivalve taxon was absent from one of the habitats, the lower value was set to one and the higher

value augmented by one before calculation of the log response ratio. When it was necessary to combine several time points or spatial samples to generate one log response ratio, densities were averaged before calculating the log response ratio. In total, 105 unique species-by-site combinations were available from 39 publications. These log response ratios were used in a linear model with fixed effects of (log) body size, functional group, and their interaction. Body size was based on typical shell lengths of collected specimens. Functional groups were based on taxonomy and trait databases: epibenthic (at least some portion of shell extending above sediment); shallow (<5 cm into the sediment); deep (generally >10 cm into the sediment, including commensals in burrows); and mutualists (Lucinidae and Solemyidae with symbiotic sulfur-oxidizing gill bacteria). Likelihood ratio tests (LRT) comparing to a simpler model were used to decide whether these fixed effects were statistically significant.

Data Availability

Quantitative data extracted from each field experiment and comparative study, as well as sources for functional traits, are archived (doi:10.17632/yj45zcnxbp.1).

RESULTS

Meta-Analysis of Manipulative Studies

Experiments included 12 bivalve species responding to five seagrass species in terms of density (seven cases), growth (19), recruitment (10), size (17), and survival (30). Reciprocally, four seagrass species responded to eight bivalve species in terms of density (16), growth (19), recruitment (3), and size (8), but not survival. Overall, experimental studies were not well-distributed across the globe because most experiments were performed in the United States (Fig. 3).

Among all response metrics, only survival of bivalves was significantly affected by experimental colocation with seagrass, with seagrass generally improving bivalve survival (Table 2, Fig. 4). Density, growth, recruitment, and size showed no difference with colocation, regardless of whether seagrass or bivalves were responding. When all metrics were combined for an overall effect size, no significant effect appeared in either direction of the reciprocal bivalve–seagrass interaction (Table 2). When additional samples before the end of experiments were included, along with duration as a fixed effect, the seagrass effect on bivalves did not change with duration (effect size = -0.001 , $z = -1.28$, $P = 0.2$, Fig. 5A), but duration had a negative effect on seagrasses in the presence of bivalves (effect size = -0.001 , $z = -2.53$, $P = 0.01$, Fig. 5B). Excluding time points greater than 500 days did not change the statistical outcome (effect size = -0.002 , $z = -2.14$, $P = 0.03$). Seagrass density responded negatively to increased bivalve density (effect size = -0.02 , $z = -3.17$, $P = 0.002$, Fig. 6), although this appeared to be driven by one high-density case.

Surveys of Bivalves In and Out of Seagrass

Based on the grand mean log response ratio, bivalves were 1.6 times more abundant in than out of seagrass ($\log_{10}$ (in/out) = 0.215 ± 0.096 SE, $t_{1,104} = 2.24$, $P = 0.03$). Bivalve response to seagrass did not show any significant interaction

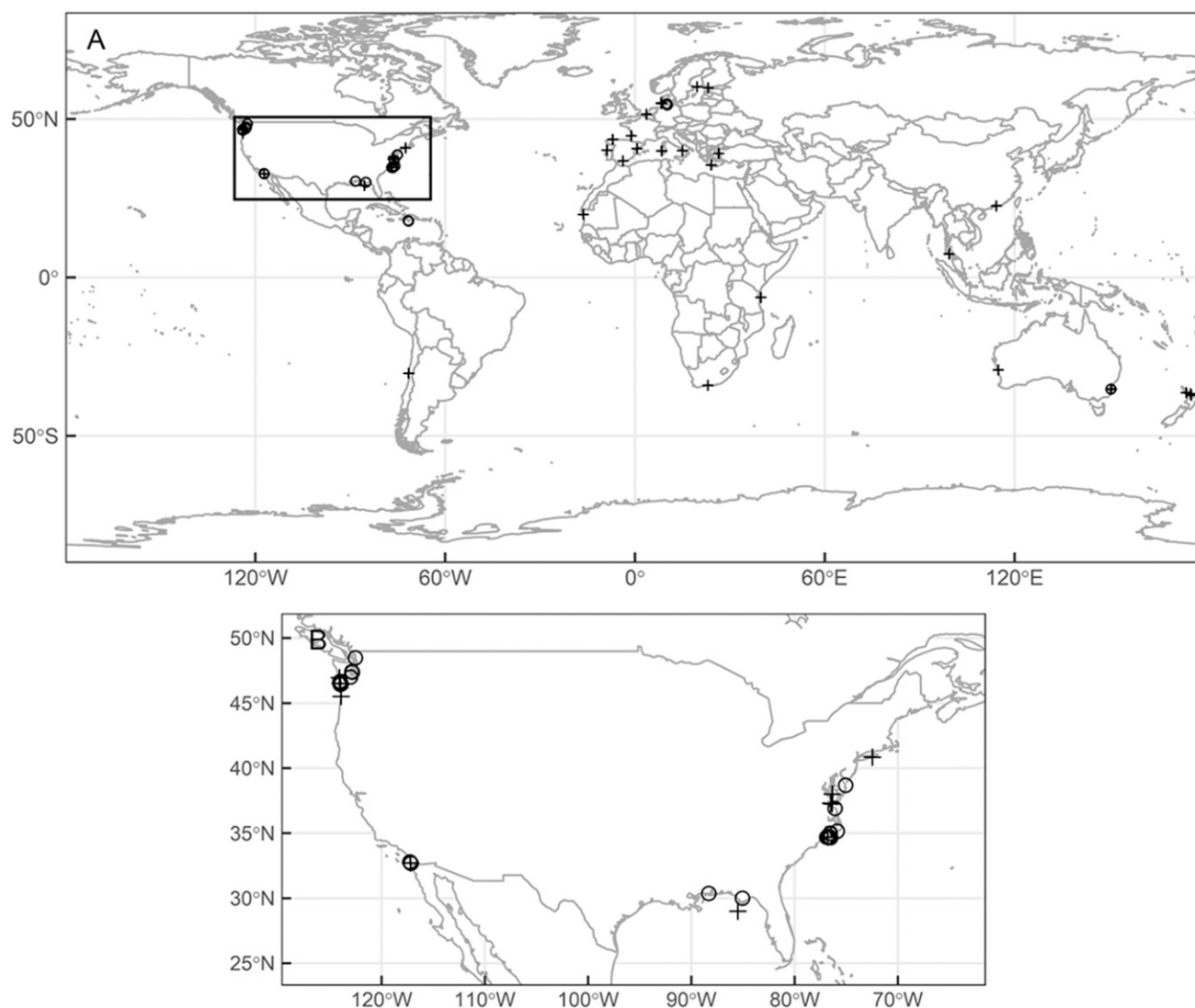


Figure 3. Map of study sites, (A) global, (B) United States. Experiments used in the meta-analysis are represented by open circles, and surveys are represented by crosses. Experimental studies are concentrated in North America. Surveys are more widespread than experiments.

between body size and functional group (LRT $F_{3,97} = 0.15$, $P = 0.93$), nor a significant main effect of body size (LRT $F_{1,100} = 0.94$, $P = 0.33$). Response to seagrass differed by functional group (LRT $F_{3,101} = 6.0$, $P = 0.0008$), primarily because almost all cases of mutualists (lucinid or solemyid clams) showed substantially greater densities in than out of seagrass (Fig. 7). Seagrass clearly facilitated mutualists [$\log_{10}(\text{in/out}) = 1.376 \pm 0.353 \text{ SE}$, $t_{1,8} = 3.9$, $P = 0.005$] and nonsignificantly augmented epibenthic bivalves [$\log_{10}(\text{in/out}) = 0.350 \pm 0.176 \text{ SE}$, $t_{1,24} = 1.99$, $P = 0.059$]. Shallow burrowers were overall not responsive to seagrass [$\log_{10}(\text{in/out}) = 0.019 \pm 0.120 \text{ SE}$, $t_{1,53} = 0.16$, $P = 0.88$], nor were deep burrowers [$\log_{10}(\text{in/out}) = 0.024 \pm 0.246 \text{ SE}$, $t_{1,16} = 0.10$, $P = 0.92$].

DISCUSSION

The present review detected minimal evidence of consistent reciprocal interactions between bivalves and seagrasses with some notable exceptions. Bivalves had higher survival in

seagrasses in experimental studies (hypothesis 1) and greater abundances of some functional groups in seagrass habitats (hypothesis 3), and seagrass showed some evidence of negative effects of spatial competition from bivalves at high cover (hypothesis 2) and appeared more negatively affected by bivalves over time; however, generalizations about the outcome of interaction between these two ecosystem engineers when they are colocated cannot be made, but rather require case-specific information. This conclusion follows from the weak overall effect sizes, although particular studies and metrics can reveal strong facilitative (Irlandi & Peterson 1991, Irlandi 1996, Goshima & Peterson 2012) or negative interactions (Booth & Heck 2009, Wagner et al. 2012). The results of the present review are reassuringly similar to another recent review that casts a wider net to evaluate plant–bivalve interactions (Gagnon et al. 2020). They, 225 publications covering not just seagrass but also mangroves, salt marsh, and freshwater plants, were evaluated in a vote-counting approach to determine the percentage of studies with positive, negative, mixed, or only nonsignificant

TABLE 2.
Meta-analysis of bivalve responses to seagrass and seagrass responses to bivalves.

Metric	Bivalve response			Seagrass response		
	Effect size	Z	P	Effect size	Z	P
Density	0.54	1.81	0.07	−0.26	−1.19	0.2
Growth	0.58	0.54	0.6	0.24	1.88	0.06
Recruitment	−0.001	−0.003	0.9	−0.02	−0.03	0.9
Size	−0.35	−0.75	0.5	0.02	0.05	0.9
Survival	0.90	2.07	0.04*	No data		
Overall	0.46	1.81	0.07	0.10	0.67	0.5

Effect sizes from mixed effects models are reported for metrics of density, growth, recruitment, size, and survival in experimental manipulations with and without the effector species.

responses. These 225 publications provided 491 studies, of which 316 (64%) involved seagrasses. Overall, positive interactions occurred in 51% of studies and negative in 25%, with pathways similar to those suggested in Figure 1. Among seagrass–bivalve studies, those with epibenthic and sulfide-oxidizing bivalves were especially prone to positive interactions (Gagnon et al. 2020). As Gagnon et al. (2020) noted, they were restricted to a vote-counting approach because of the wide variety of methods applied in the studies in their review, for instance, both colocated and spatially distinct arrangements of plants and bivalves, modern and paleontological time frames, and laboratory and field studies. Of the 34 publications suitable for the quantitative meta-analysis reported here, 20 overlapped with Gagnon et al. (2020), and for surveys, the number overlapping was 19 of 39. Therefore, only about half of the articles in the present review were previously covered by Gagnon et al. (2020), with the present review also smaller because of stricter inclusion criteria for meta-analysis. The present review expands on Gagnon et al. (2020) by using a quantitative meta-analytic approach and highlights the different responses (survival, growth, reproduction, and density) that could occur in a reciprocal interaction.

Comparison of the present review with others covering seagrass and marine animals also helps focus on lessons learned here. One widely examined ecological effect of biogenic habitats is their provision of nursery habitat, specifically defined when juveniles, rather than adults, are found in the habitat (Beck et al. 2001). Seagrasses provide nursery habitat for a wide variety of fish and invertebrates through aboveground structure (Heck et al. 2003, McDevitt-Irwin et al. 2016), but no examples of bivalves appeared in these reviews, probably because of the sedentary lifestyles of bivalves that preclude moving out of seagrass as adults. Because these reviews of nursery habitat included no bivalve responses, there is no overlap with the present evaluation of bivalve–seagrass interactions. Whereas juvenile fish and invertebrates generally were enhanced in seagrass nursery habitat, the results here showed bivalve enhancement by seagrass was primarily driven by species with sulfide-oxidizing bacteria (Fig. 7). Bivalves may not be consistently facilitated because many live infaunally or create their own structure and are less dependent on aboveground structure than mobile species in the water column. Another prior meta-analysis found that density and demography of seagrasses were

generally negatively affected by bivalve shellfish aquaculture (Ferriss et al. 2019). Of 28 publications reviewed by Ferriss et al. (2019), five included field experiments without aquaculture gear and in small planted plots, and these experiments also appear in the present review addressing bivalve effects on seagrass. The generally negative effects of farming bivalves in seagrass (Ferriss et al. 2019) were not evident in the present review addressing the species interaction alone, without aquaculture gear or disturbance from farming.

The wide variety of potential mechanisms involved in reciprocal interactions between seagrasses and bivalves underpins a lack of consistency in whether these interactions are facilitative, negative, or neutral. For example, some pathways of interaction may be positive and other pathways may be negative creating an overall net neutral effect (see Fig. 1). In principle, biological activity tends to exert positive effects reciprocally, but these magnitudes could be quite small (Bruno et al. 2003). In addition, the relative importance of negative and positive interactions could shift with spatial scale. For example, endangered pen shells in the Gulf of Oristano (Italy) reached highest density in the region of the gulf without seagrass (Addis et al. 2009), but at smaller scales, were denser in seagrass than in interspersed sand patches (Coppa et al. 2019). Meanwhile, space competition occurs at small spatial scales as well as recruitment facilitation (Mikkelsen et al. 2004). At larger scales, facilitation of seagrass by bivalves may be mediated through filtration or wave attenuation and improved water clarity, with evidence primarily from models (Newell & Koch 2004, Smith et al. 2009). Thus, although the current review deliberately focuses on consequences of collocation (i.e., plot or quadrat scale), seascape-level considerations of distance to edge, patch size (Bowden et al. 2001, Mills & Berkenbusch 2009), and habitat composition of the neighborhood are needed. Gagnon et al. (2020) found more positive effects between bivalves and plants when they were in adjacent areas than when colocated.

Density of the effector species can play a large role in how another species responds to their presence. Effector density was often not provided in published studies so could not be applied as a predictor in the full meta-analysis, except for the effect of bivalve density on seagrass density, but it is reasonable to expect that interaction strength could vary with density. In some studies, low-density outplants were a method that was deliberately used to avoid space competition (Valdez et al. 2017). In other studies, density treatments were explicitly tested; Booth and Heck (2009) showed that seagrass density and growth responded more negatively to higher oyster density treatments. In the future, studies on seagrasses and bivalves should consider a range of densities, rather than comparing just presence/absence of effector species.

The articles included in the meta-analysis of bivalve–seagrass interactions included many different treatments (e.g., patch size, density, tidal height, and cages), which likely increases variability in outcome both within and among studies. Laboratory and mesocosm studies were not included in this meta-analysis but were less common than field studies. The overall findings of the meta-analysis are most applicable to the United States, especially Washington state and the Carolinas, where most of the experiments were performed. Further experimental research is needed, especially in the tropics. Some

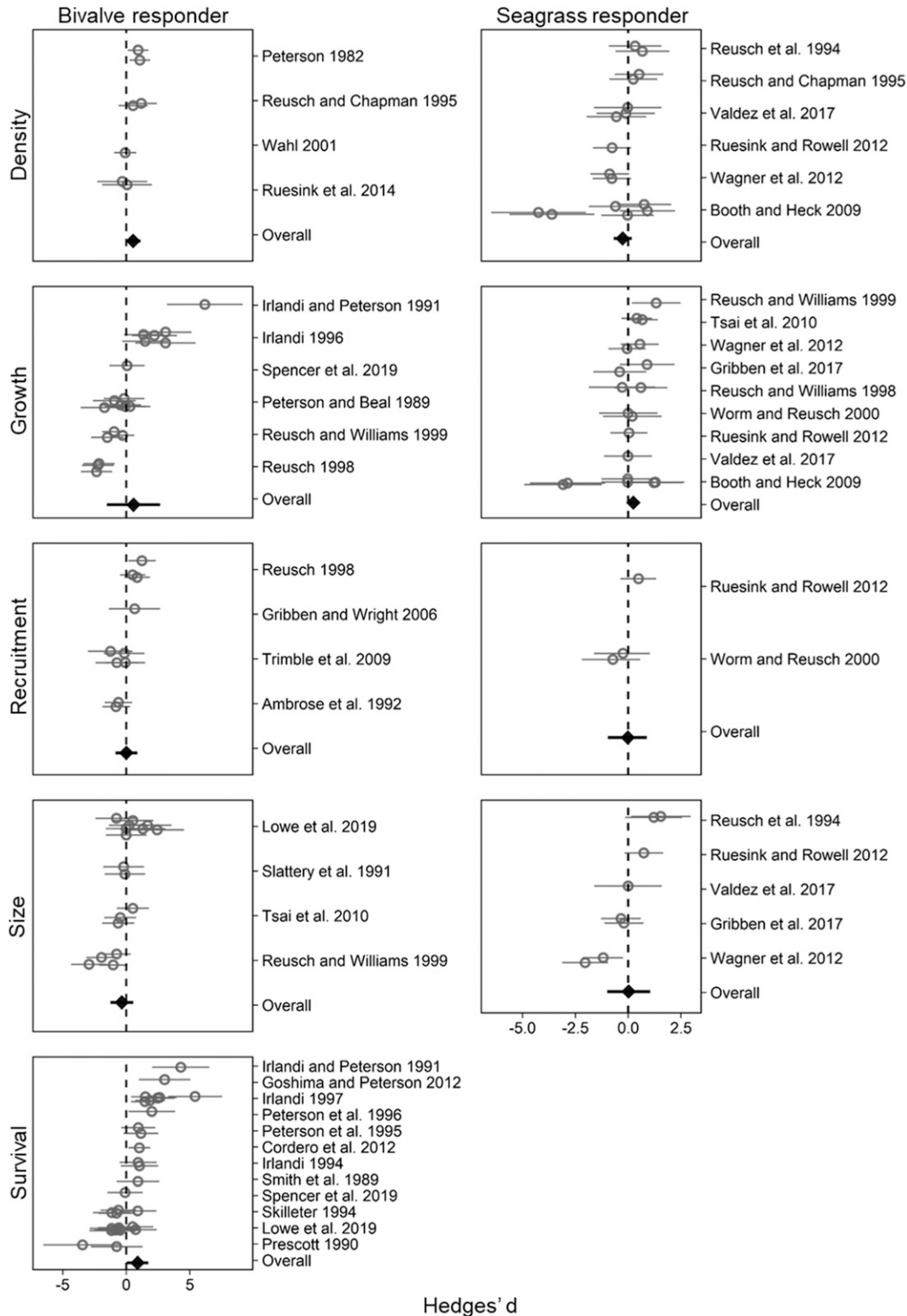


Figure 4. Responses of bivalves to seagrasses (left) and /seagrasses to bivalves (right), with studies ordered within each panel from facilitative to inhibitory interactions. Studies with multiple points reflect multiple experimental treatments (e.g., density, cages, etc.). Responses are given as mean effect sizes (Hedges' d) and 95% CI for density, growth, recruitment, size, and survival. Seagrasses and bivalves have little overall directional effect on each other in experimental studies.

metrics were much better represented than others, for example, there were no experimental data on the survival of seagrasses and very little on seagrass reproduction when colocated with bivalves; these metrics warrant further investigation. This

review did not cover chemical or genetic metrics, where pathways mediated by the trophic facilitation of consumers by primary producers might be revealed, for instance in tissue nutrient or stable isotope ratios (Hori et al. 2019, Lowe et al. 2019).

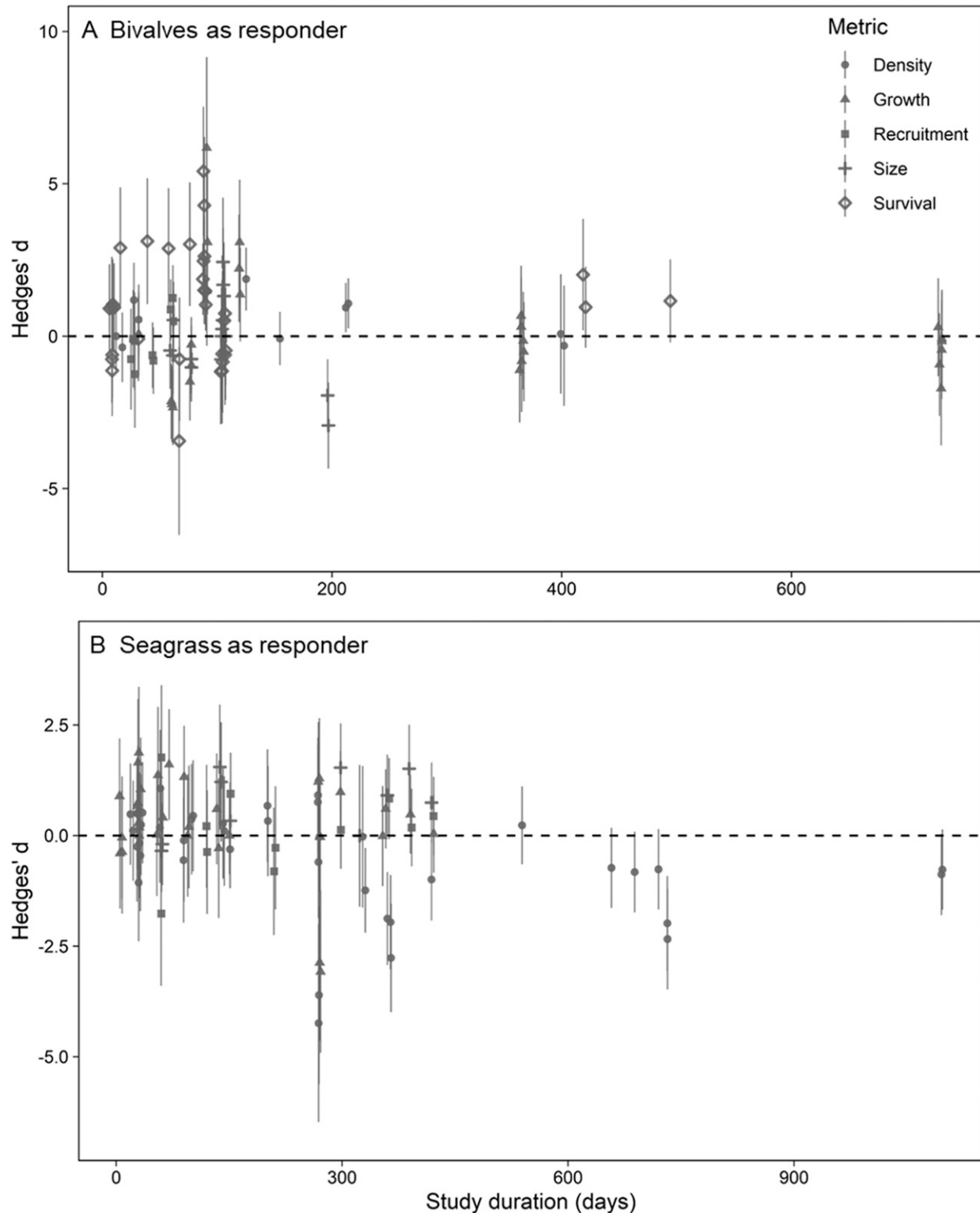


Figure 5. Responses in seagrass-bivalve experiments according to study duration. Responses are given as mean effect sizes (Hedges' d) and 95% CI, points are slightly jittered. Few studies included measurements after more than a year. For studies with multiple time points, all were included in this figure and analysis. (A) Bivalves show no change in effect sizes over time. (B) Seagrass shows a slight negative effect of bivalves on seagrass responses over time.

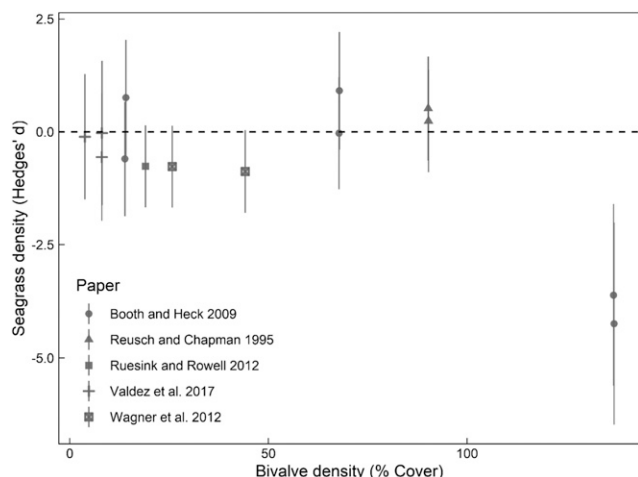


Figure 6. Seagrass density across treatments differing in bivalve density, showing a slight decrease in seagrass density with increased bivalve density. Responses are given as mean effect sizes (Hedges' d) and 95% CI.

Substantial sampling effort has gone into reporting bivalves across seagrass-vegetated and unvegetated habitats because surveys were more prevalent than experiments (Fig. 2). Yet the survey dataset only accommodated studies with species-specific data, so missed cases reporting bivalve diversity or a multivariate response, as well as publications of macrofauna that did not distinguish the bivalve component. Habitat specialists have been defined when species are at least 2.5 times more abundant in one habitat than another (Barnes & Hamylton 2013). Based on this criterion, of the 105 bivalve species in a seagrass-bare comparison at a site, 39 were generalists, 40 were seagrass specialists, and 26 were bare specialists. Yet particular species often showed different results in different sites, for instance *Limecola balthica* (L.) was generalist (four of six cases) or bare-specialist (two of six cases), and *Cerastoderma edule* (L.) was generalist (two of five cases), seagrass-specialist (two of five cases), or bare-specialist (one of five cases). Most species (48 of 66, 73%) were recorded at only a single site so were not possible to evaluate for consistent patterns of habitat association within a species. Nevertheless, disparate patterns within species emphasize the value of case-specific exploration of the magnitude and direction of seagrass-bivalve effects.

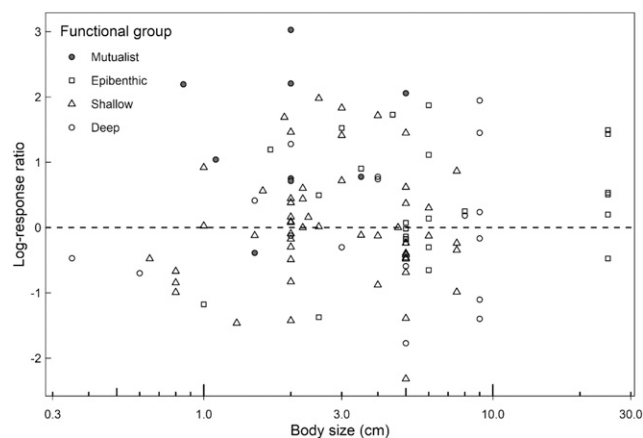


Figure 7. Density of bivalves in seagrass relative to bare sand or mud, as $\log_{10}$ (abundance in/abundance out). Bivalves differed in functional traits of body size, position in sediment, and presence of mutualistic sulfide-oxidizing bacteria in gills. Analysis included 105 data points (unique site and species combination) from 39 publications.

Weak overall directional effects of collocation of seagrass and bivalves likely stem from the variety of mechanisms by which these biogenic habitat formers can affect each other, or from low densities in soft-sediment systems. Differences in species responses to the effector may also change with shared evolutionary history. In estuaries, many species of bivalves and some seagrasses have been moved beyond their native range creating new interactions between species pairs (Ruesink 2018), but nonnative species were considered in four of 39 surveys, insufficient to use as a predictor. Meanwhile, lucinid bivalves are considered seagrass mutualists with strong shared evolutionary history (Reynolds et al. 2007) and showed the strongest positive association. Further work is needed to explore the specific mechanisms and spatiotemporal scales enabling seagrasses and bivalves to coexist because there are many pathways at work.

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APPENDIX 1: MANIPULATIVE STUDIES AND SURVEYS

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Studies included in meta-analysis of manipulative experiments testing bivalve–seagrass interactions in either direction. Scientific names as listed by the authors.

Reference	Sites(s), geoposition *denotes that sites were true replicates	Effector species	Responder species	Response metric category
Ambrose et al. 1992	Cape Lookout, NC N34.7125, W76.8195	<i>Zostera marina</i> , <i>Halodule wrightii</i>	<i>Argopecten irradians</i>	Recruitment
Booth & Heck 2009	Point aux Pines, AL N30.371, W88.313	<i>Crassostrea virginica</i>	<i>H. wrightii</i>	Density, growth
Hernández Cordero et al. 2012	Lynnhaven rivers system, Chesapeake Bay, USA N36.904, W76.089	<i>A. irradians</i>	<i>Z. marina</i>	Survival
Goshima & Peterson 2012	Pine Knoll Shores, NC N34.704, W76.811	<i>H. wrightii</i>	<i>Mercenaria mercenaria</i>	Survival
Gribben & Wright 2006	Sponge Bay and Yooralla Bay, New South Wales, Australia* S35.26231, E150.4467	<i>Zostera capricorni</i>	<i>Anadara trapezia</i>	Recruitment
Irlandi & Peterson 1991	Back Sound, NC N34.689, W76.565	<i>Z. marina</i> , <i>H. wrightii</i>	<i>M. mercenaria</i>	Survival
Irlandi 1994	Oscal Shoal, NC N34.70221, W76.5858	<i>Z. marina</i> , <i>H. wrightii</i>	<i>M. mercenaria</i>	Survival
Irlandi 1996	Cape Lookout and Oscar shoal, NC* N34.683, W76.55 Bottle Run and Middle Marsh, NC* N34.685, W76.583 Caple Lookout, NC N34.66, W76.518	<i>Z. marina</i> , <i>H. wrightii</i>	<i>M. mercenaria</i>	Growth
Irlandi 1997	Bottle Run, NC N34.67, W76.58 Middle Marsh, NC N34.694, W76.607 Oscar Shoal, NC N34.702, W76.586	<i>Z. marina</i> , <i>H. wrightii</i>	<i>M. mercenaria</i>	Survival
Lowe et al. 2019	Willapa Bay, WA N46.454, W123.921 Willapa Bay, WA N46.433, W124.997 Willapa Bay, WA N46.628, W124.034 Padilla Bay, WA N48.481, W122.528	<i>Z. marina</i>	<i>Ostrea lurida</i> , <i>Crassostrea gigas</i>	Size

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Reference	Sites(s), geoposition *denotes that sites were true replicates	Effector species	Responder species	Response metric category
Peterson & Beal 1989	Cape Lookout, NC N34.66, W76.53	<i>Z. marina</i> , <i>H. wrightii</i>	<i>M. mercenaria</i>	Growth
Peterson 1982	Bogue Sound, NC N34.69, W76.896	<i>H. wrightii</i>	<i>M. mercenaria</i> , <i>Chione cancellata</i>	Density
Peterson et al. 1995	Carteret County, NC N34.69556, W76.68972 Northern Region, NC N35.15056, W75.87472	<i>Z. marina</i>	<i>M. mercenaria</i>	Survival
Prescott 1990	Bogue Sound, NC N34.7, W76.76667	<i>H. wrightii</i>	<i>Argopecten irradians</i>	Survival
Reusch & Chapman 1995	Friedrichsort, Baltic Sea, Germany N54.389, W10.19 Moltenort, Baltic Sea, Germany N54.38389, W10.20111	<i>Z. marina</i> , <i>Mytilus edulis</i>	<i>Mytilus edulis</i> , <i>Z. marina</i>	Density
Reusch & Williams 1998	Harbor Island, CA N32.72.361, W117.1886	<i>M. senhousia</i>	<i>Z. marina</i>	Growth
Reusch & Williams 1999	Harbor Island, CA N32.72.361, W117.1886 Sail Bay, CA N32.79056, W117.25 Coronado, CA N32.68056, W117.1517	<i>M. senhousia</i> , <i>Z. marina</i>	<i>Z. marina</i> , <i>M. senhousia</i>	Growth, size (bivalve)
Reusch 1998	Kiel Bight, Baltic Sea, Germany N54.683, W10	<i>Z. marina</i>	<i>Mytilus edulis</i>	Growth, recruitment
Reusch et al. 1994	Friedrichsort, Baltic Sea, Germany N54.389, W10.19	<i>M. edulis</i>	<i>Z. marina</i>	Density, size
Ruesink & Rowell 2012	South Puget Sound, WA N47.3666, W122.8147	<i>Panopea generosa</i>	<i>Z. marina</i>	Density, growth, recruitment, size
Skilleter 1994	Brown Creek, NC N34.99611, W76.55722 Luckens, NC N34.95861, W76.56917	<i>Ruppia maritima</i>	<i>Mya arenaria</i> , <i>Macoma balthica</i>	Survival
Slattery et al. 1991	MA, NJ, NC, Northeast, USA* N39, W74	<i>Z. marina</i> , <i>H. wrightii</i>	<i>M. mercenaria</i>	Size
Smith et al. 1989	Core Sound, NC, N34.0667, W76.53333	<i>Z. marina</i>	<i>A. irradians</i>	Survival
Spencer et al. 2019	Washington, USA* N47, W123	<i>Z. marina</i>	<i>P. generosa</i>	Survival, growth
Trimble et al. 2009	Willapa Bay, WA N46.66667, W124	<i>Z. marina</i>	<i>C. gigas</i> , <i>Ruditapes philippinarum</i>	Recruitment
Tsai et al. 2010	Leadbetter Point, WA N46.60893, W123.0357	<i>Zostera japonica</i> , <i>R. philippinarum</i>	<i>R. philippinarum</i> , <i>Z. japonica</i>	Size (bivalve), growth (seagrass)
Valdez et al. 2017	Mission Creek, WA N47.4238, W122.8748	<i>O. lurida</i>	<i>Z. marina</i>	Density, growth, size
Wagner et al. 2012	Peterson Station, WA N46.482, W123.997 Mill Channel, WA N46.504, W124.008	<i>Crassostrea gigas</i>	<i>Z. marina</i>	Density, growth, size
Wahl 2001	Kiel Bight, Baltic Sea, Germany N54.68222, W10.01667	<i>Z. marina</i>	<i>M. edulis</i>	Density
Worm & Reusch 2000	Friedrichsort, Baltic Sea, Germany N54.383, W10.2	<i>M. edulis</i>	<i>Z. marina</i>	Growth, recruitment

Studies included in surveys of bivalve density in and out of seagrass. (Taxonomy follows World Register of Marine Species.)

Reference	Sites(s), geoposition	Seagrass species (*non-native)	Bivalve species (*non-native)
Addis et al. 2009	Gulf of Oristano, western Sardinia, Italy N39.9167, W8.4833	<i>Posidonia oceanica</i> , <i>Cymodocea nodosa</i>	<i>Pinna nobilis</i>
Barnes & Barnes 2014	Knysna estuary, South Africa S34.0583, E23.0667	<i>Zosterella capensis</i>	<i>Arcuatula capensis</i>
Bologna & Heck 1999	St Joseph Bay, USA N29.0 W85.5	<i>Thalassia testudinum</i>	<i>Argopecten irradians</i>
Bouma et al. 2009	Ritthem, Westerschelde estuary, Netherlands N51.45, E3.65	<i>Zostera noltii</i>	<i>Cerastoderma edule</i> , <i>Limecola balthica</i>
Carroll et al. 2008	Shinnecock and Quantuck Bays, Long Island, USA N40.842 W72.4783	<i>Zostera marina</i>	<i>Mercenaria mercenaria</i>
Coppa et al. 2010	Gulf of Oristano, western Sardinia, Italy N39.87, E8.44	<i>Posidonia oceanica</i>	<i>Pinna nobilis</i>
de Paz et al. 2008	Eo estuary, Spain N43.5, W7.0167	<i>Zostera noltii</i>	<i>Cerastoderma edule</i> , <i>Loripes lucinalis</i>
Do et al. 2011	Banc d'Arguin, Mauritania N44.6667, W1.1667	<i>Z. noltii</i>	<i>Cerastoderma edule</i> , <i>Scrobicularia plana</i> , <i>Ruditapes philippinarum*</i> , <i>Abra segmentum</i> , <i>Mytilus edulis</i>
Donnarumma et al. 2018	South Italy N40, E15	<i>Posidonia oceanica</i>	<i>Fabulina fabula</i> , <i>Glans trapezia</i> , <i>Loripinus fragilis</i> , <i>Lucinella divaricata</i> , <i>Moerella donacina</i> , <i>Striarca lactea</i> , <i>Thracia villosioscula</i>
Eklof et al. 2005	Unguja Island, Zanzibar, Tanzania S6.3167, E39.8	<i>Thalassia hemprichii</i> , <i>Cymodocea serrulata</i> , <i>Enhalus acoroides</i>	Lucinidae, Mytilidae, Pinnidae, Mactridae, Cardiidae
Ferraro & Cole 2007	Willapa Bay, USA N46.5, W124.0	<i>Z. marina</i>	<i>Clinocardium</i> spp.
Ferraro & Cole 2011	Grays Harbor, USA N46.95, W124.08	<i>Z. marina</i> , <i>Zostera japonica*</i>	<i>Macoma</i> spp., <i>L. balthica</i>
Ferraro & Cole 2012	Tillamook Bay, USA N45.52, W123.92	<i>Z. marina</i> , <i>Z. japonica*</i>	<i>Cryptomya californica</i> , <i>Clinocardium nuttallii</i>
Glaspie & Seitz 2017	Lynnhaven, York, Mobjack in Chesapeake Bay, USA N37.26, S76.38	<i>Z. marina</i>	Deep-burrowing suspension feeders, thin-shelled surface dwellers
Glaspie et al. 2018	Chesapeake Bay, USA N38.0, W76.35	<i>Z. marina</i>	<i>Tagelus plebeius</i>
Henseler et al. 2019	Åland Islands, Finland N60.15, E19.64	<i>Z. marina</i>	<i>Mya arenaria*</i> , <i>Cerastoderma glaucum</i> , <i>Mytilus edulis</i> , <i>L. balthica</i>
Honkoop et al. 2008	Banc d'Arguin, Mauritania N19.8737, W16.3083	<i>Zostera noltii</i>	<i>Senilia senilis</i> , <i>Loripes lucinalis</i> , <i>Dosinia hepatica</i>
Katsenevakis & Thessalou-Legaki 2007	Souda Bay, Crete, Greece N35.4833, E24.1167	<i>Cymodocea nodosa</i> , <i>Halophila stipulacea</i>	<i>Pinna nobilis</i>
Lee et al. 2001	Lai Chi Wo, Crooked Harbor, Hong Kong N22.5333, E114.2667	<i>Z. japonica</i>	<i>Arcuatula senhousia</i>
Lohrer et al. 2016	Tapora Bank, Kaipara Harbour, NZ S36.3928 E174.2919	<i>Zostera muelleri</i>	<i>Austrovenus stutchburyi</i> , <i>Macomona liliana</i>
McKinnon et al. 2009	St George's Basin, NSW, Australia S35.1833, E150.6	<i>Halophila ovalis</i>	<i>Anadara trapezia</i> , <i>Laternula gracilis</i> , <i>Spisula trigonella</i> , <i>Tapes conspersus</i> , <i>Macomona deltoidalis</i> , <i>Hiatula alba</i>
Meysick et al. 2019	Hanko Peninsula, SW Finland N59.8167, E23.15	<i>Z. marina</i>	<i>Limecola balthica</i> , <i>Cerastoderma edule</i>
Ortiz et al. 2003	Tongoy Bay, Coquimbo, Chile S30.25, W71.5167	<i>Heterozostera tasmanica</i>	<i>Argopecten purpuratus</i>
Peterson 1982	Bogue Sound, USA M34.7, W76.8	<i>Halodule wrightii</i>	<i>M. mercenaria</i> , <i>Chione cancellata</i>
Prado et al. 2014	Alfacs Bay, Spain N40.6108, E0.6569	<i>Cymodocea nodosa</i>	<i>Pinna nobilis</i>
Rainer & Wadley 1991	Seven Mile Beach, Australia S29.1833, E114.8833	<i>Halophila ovalis</i> , <i>Syringodium isoetifolium</i> , <i>Heterozostera tasmanica</i>	<i>Solemya</i> sp.
Rattanachot & Prathep 2015	Haad Chao Mai National Park, Thailand N7.3833, E99.3333	<i>Halophila ovalis</i> , <i>Thalassia hemprichii</i> , <i>Cymodocea rotundata</i>	<i>Rugulucina vietnamica</i>

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Reference	Sites(s), geoposition	Seagrass species (*non-native)	Bivalve species (*non-native)
Rattanchot & Prathep 2016	Haad Chao Mai National Park, Thailand N7.3833, E99.3333	<i>Halophila ovalis</i> , <i>Thalassia hemprichii</i> , <i>Cymodocea rotundata</i>	<i>Rugulucina vietnamica</i>
Reise et al. 1994	Konigshafen, Sylt, Germany N55.0414, E8.4144	<i>Zostera noltii</i> , <i>Z. marina</i>	<i>Limecola balthica</i> , <i>Cerastoderma edule</i> , <i>Mytilus edulis</i> , <i>Mya arenaria</i> *
Reusch & Williams 1999	San Diego Bay, USA N32.71, W117.19	<i>Z. marina</i>	<i>Arcuatula senhousia</i> *
Rueda et al. 2009	Canuelo Bay, Alboran Bay, Spain N36.7417, E3.7934	<i>Z. marina</i>	<i>Moerella distorta</i> , <i>Anomia ephippium</i> , <i>Chamelea gallina</i> , <i>Polititapes aureus</i> , <i>Spisula subtruncata</i> , <i>Kurtiella bidentata</i> , <i>Fabulina fabula</i> , <i>Solemya togata</i> , <i>Nucula nitidosa</i> , <i>Peronaea planata</i> , <i>Thracia villosioscula</i> , <i>Donax venustus</i> , <i>Flexopecten flexuosus</i> , <i>Parvicardium scriptum</i> , <i>Abra alba</i> , <i>Ervilia castanea</i> , <i>Pitar rudis</i> , <i>Glycymeris nummaria</i>
Ruesink et al. 2014	Willapa Bay, USA N46.5, W124.0	<i>Z. marina</i> , <i>Z. japonica</i> *	<i>Ruditapes philippinarum</i> *, <i>M. arenaria</i> *
Sanmartí et al. 2018 Seitz et al. 2005	Alfacs Bay, Spain N40.6108, E0.6569 York river, Chesapeake Bay, USA N37.3, W76.5	<i>Cymodocea nodosa</i> <i>Z. marina</i>	<i>Loripes lucinalis</i> <i>L. balthica</i>
Strasser et al. 1999	Sylt-Romo Bight, Germany N54.83, E8.33	<i>Zostera</i> spp.	<i>M. arenaria</i> *
Tsatiris et al. 2018	Geras Gulf, Lesvos Island, Greece N39.09, E26.49	<i>Posidonia oceanica</i>	<i>Pinna nobilis</i>
van Houte-Howes et al. 2004	Whangamata, NZ S37.1854, E175.8627 Wharekawa, NZ S37.109, E175.88 Whangapoua, NZ S36.7386, E175.6533; S36.735, E175.6407	<i>Zostera capricorni</i>	<i>Austrovenus stutchburyi</i> , <i>Macomona liliana</i> , <i>Linucula hartvigiana</i> , <i>Arthritica bifurca</i>
Verdelhos et al. 2014	Mondego estuary, Portugal N40.1333, W8.8333	<i>Zostera noltii</i>	<i>Scrobicularia plana</i>
Wright et al. 2007	St George's Basin, NSW, Australia S35.1833, E150.6 Burrill Lake, NSW, Australia S35.4, E150.45	<i>Halophila ovalis</i> , <i>Z. capricorni</i>	<i>Anadara trapezium</i>