Annotated Bibliography

Assessment of ecological function and interactions of oyster culture and eelgrass

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1. Boardman, F.C., E.R. Subbotin, and J.L. Ruesink. 2023. Nekton use of co-occurring aquaculture and seagrass structure on tidal flats. Aquaculture Environment Interactions 15: 307–321. https://doi.org/10.3354/AEI00467.

In Willapa Bay, WA, the authors evaluated the effects of different Pacific oyster aquaculture methods on nekton (fish and mobile invertebrate) communities across a gradient of eelgrass (*Zostera marina*). Three categories of oyster culture were sampled: no culture, on-bottom culture, and off-bottom culture (longlines or flipbags). For each of the oyster culture categories, sampling also occurred across three levels of eelgrass (no eelgrass, sparse eelgrass, or dense eelgrass) to compare the nekton communities supported by these different structured habitat types, and investigate community response when oyster aquaculture and eelgrass overlap. Nekton data was collected two ways, by using a modified beach seine, as well as deploying GoPro cameras. Eelgrass and nekton data were collected in spring and summer to capture seasonal differences in habitat-use. The complete sampling scheme was repeated across six regions in Willapa Bay.

Findings from this work reveal that some taxa use eelgrass and off-bottom culture similarly, while other taxa are eelgrass specialists. A third set of taxa primarily use habitats lacking vertical structure, either with on-bottom culture or on unstructured mudflat. The effects of the overlapping structured habitats were additive, meaning that taxa associated with both habitats were present when overlapping. This work concludes that eelgrass and oyster culture habitat support distinct communities and generally, oyster aquaculture within eelgrass is not detrimental to the habitat value of eelgrass for nekton.

2. Boardman, F.C., and J.L. Ruesink. 2023. Taxon-Specific Habitat and Tidal use by Birds in an Oyster Culture Estuary. Journal of Shellfish Research 42: 525–531. https://doi.org/10.2983/035.042.0316.

In Grays Harbor, WA, the authors studied shore and waterbird use of oyster longline, eelgrass and mudflat habitats. Sampling was conducted using GoPro cameras that were deployed in the intertidal during ebbing tides and collected during the flood. Cameras were programmed to take photos once per minute during the deployment. Two sites, each with the three habitat types, were sampled in the spring and late summer/early autumn. The bird communities shifted throughout sampling, as they included migratory shorebirds.

Of the six focal taxa, black-bellied plover, American crow, and dunlin were positively associated with eelgrass and/or longlines—whereas dunlin, dowitcher, and gulls were positively associated with the ebb or flood periods (as water passed through the sampling area). This work concludes that taxa use of intertidal habitat mosaics (in this case: eelgrass, mudflat, oyster longlines), is taxaspecific, with some taxa associated with higher structured habitats, including oyster culture, while taxa other are more affected by tidal activity.

3. Boardman, F.C., and J.L. Ruesink. 2025. Eelgrass (*Zostera marina*) Recovery Affected by Disturbance Timing on Mechanically Harvested Oyster Culture Beds. Estuaries and Coasts. https://doi.org/10.1007/s12237-024-01454-4.

The authors studied eelgrass recovery following large-scale disturbances from the mechanical harvest of oysters. Sampling was conducted in Willapa Bay, WA, on six consecutive bottom-culture beds used for the commercial production of Pacific oysters. The oyster beds were mechanically dredged on a rotating schedule to harvest and maintain beds; this process is damaging to co-occurring eelgrass, by pulling out or damaging shoots. The authors sampled in spring, summer and fall for three years, measuring shoot density, seedling density, branching rates, and in the fall, proportion of shoots originated from seed. The times of disturbance were categorized based on local eelgrass phenology into early growing season (EGS; January-April), late growing season (LGS; May-September) and non-growing season (NGS; October-December).

At 200 and 400 days post-disturbance, beds disturbed during EGS were estimated to have greater than double the vegetative shoot density of beds disturbed during LGS. EGS disturbance also resulted in a higher contribution of new shoots from seedlings, relative to LGS disturbance, with up to 71% of shoots occurring from seed. This paper concludes that seeds play a significant role in eelgrass recovery, particularly during EGS disturbance, and that targeting EGS for mechanical harvest can support the resilience of eelgrass co-occurring in oyster culture beds.

4. Garcia, M.S., K. Houle, A. Suhrbier, B. Hudson, J. L. Ruesink. 2025. Estuarine community response to longline spacing in intertidal oyster culture. Aquaculture Environment Interactions. doi.org/10.3354/aei00497.

This study experimentally tests the effects of oyster longline spacing on eelgrass, nekton (fish and decapods) and epifaunal communities, as well as epiphyte load. The experiment was set up across two sites in Willapa Bay, WA, with 30 x 30 m blocks of longlines arranged (1) in a gradient of densities, and (2) with packed lines that allow a constant line density across treatments while altering aisle width. Spacing for the first design ranged from 0.56-1.25 m, while the second design included 2, 3 and 4-pack line spacing. Sampling of all factors occurred 3-4 times between spring of 2023 and spring of 2024 (oysters measured twice), 9+ months after the experimental plots were established.

Across the two-year crop cycle, eelgrass density was negatively related to oyster density, however this effect was mitigated by increasing aisle width from line-packing. Oyster shell height and condition were not affected. Epifaunal load increased with aisle width, but epifauna and epiphytes were not significantly affected otherwise. Nekton communities and abundance were not significantly affected overall, however caution should be taken when interpreting the nekton, epiphyte and epifauna results due to limited sample sizes. This work concludes that setting up longlines at a lower density and/or clustering lines to increase aisle width can limit negative impacts of oyster culture on eelgrass density.

5. Houle, K., K. Page, F.C. Boardman, and J.L. Ruesink. *In Prep.* Nekton use of flip bag oyster aquaculture co-located with native eelgrass (*Zostera marina*) beds in Washington state, USA.

This study examines nekton use of oyster flip bag farms co-occurring with native eelgrass beds. The sampling took place across three Washington state estuaries, with three sites in Willapa Bay, two sites in Samish Bay and one site in Hood Canal, for a total of six sites. At each site, four habitat types were examined: flip bags/eelgrass, flip bags/mudflat, eelgrass only and mudflat only. Nekton were sampled with two methods, by using a modified beach seine, as well as by deploying GoPro cameras to collect video data. Both methods were used during spring and summer. Analyses examined taxa richness, abundance and community composition of nekton, as well as a focal behavioral analysis of shiner perch.

Results varied seasonally and with sampling method, reflecting seasonal changes in species assemblage as well as sampling biases associated with the different methods (e.g. under sampling cryptic taxa with videos or under sampling highly mobile fish while seining within structured habitats). Both habitat types were determined to affect community composition and increase abundance and taxa richness, according to at least one sampling method and season combination. In the spring, eelgrass had a stronger effect on nekton compared to flipbags. Neither eelgrass nor flip bags had a significant effect on shiner perch behavior, likely due to sample size. The authors conclude that both flipbags and eelgrass shape nekton community composition. While the effects seem to be additive when the habitats overlap, eelgrass had stronger effect sizes than flipbags during the spring and also had more associated taxa overall.

6. Hull, W., E. Subbotin., J.L. Ruesink. 2025. Sediment burial caused by bioturbating shrimp negatively affects juvenile oyster survival and size. Marine Ecological Progress Series. https://doi.org/10.3354/meps14831.

Hull at al. (2025) examined the effects of burrowing shrimp, *Neotrypaea californiensis,* on juvenile Pacific oysters in Grays Harbor and Willapa Bay, WA. Sampling across 31 sites, they evaluated how burrowing shrimp control sediment properties (proportion organic material, mud content, and penetrability) and how oyster size and survival respond to shrimp density directly or indirectly, via shrimp-altered sediment properties. At all sites samples of shrimp and sediment properties were taken in triplicate, and juvenile oysters on seeded cultch were outplanted. Shrimp density was sampled with a 5-core method using a clam gun. Oysters were outplanted in April 2022 and collected in August 2022, then measured for survival and size. Additionally, in August 2024, the authors measured 24 hr sediment ejection rates within tubes over (1) shrimp burrow within shrimp bed, (2) no burrow within shrimp bed, and (3) no burrow within shrimp removed area at 24 sites.

Results from Hull et al. reveal that the burrowing shrimp primarily affect oyster mortality and size via sediment deposition, or burial, as opposed to negative impacts from modification of sediment characteristics. Shrimp were negatively associated with mud and organic content, but positively associated with penetrability, however these characteristics did not affect oyster mortality or size. The authors reported 100% mortality of oysters with shrimp densities above 50 per m^2, as well as deposition of sediment from burrows averaging 28.9 mL/day. Together, this data suggests that the primary mechanism that burrowing shrimp decreases survival and growth in juvenile oysters is via burial, which is particularly extreme at higher shrimp densities.

7. Lewis, N.S., B.A. McIntyre, J.L. Ruesink, F.C. Boardman, and B.R. Dumbauld. 2025. Spatiotemporal dynamics of eelgrass (*Zostera marina*), oyster aquaculture, and channel-fringing habitat provided to managed nekton species throughout a US Pacific Coast estuary. Estuaries and Coasts. *In Review.*

Lewis et al. (*In Review*) used estuary-wide orthoimagery of Willapa Bay, WA, to determine the distribution of active oyster aquaculture and eelgrass, including in areas of overlap. A 0.25 pixel resolution orthoimagery was collected using a Vexcel UltraCam Falcon P from a fixed-wing aircraft (13,600 ft altitude) during low-tide on June 22, 2020. Simultaneous ground truthing was conducted to train habitat classification of the imagery. Delineations of shellfish aquaculture methods and species were also determined. This study utilized a subset of the nekton data from Boardman et al. 2023 (above) to evaluate the habitat use by Dungeness crabs and English sole in channel fringing areas (<25 m from channel).

Overall, eelgrass covered an estimated 5,551 ha, while active oyster aquaculture encompassed approximately 3,096 ha of intertidal area (996 ha of which contained eelgrass). The habitat use analysis revealed that bottom culture facilitated generally higher densities of Dungeness crab and English sole than both off-bottom aquaculture and areas without aquaculture, whereas no density differences were found between habitats with and without eelgrass. Eelgrass coverage, classified from orthoimagery, was higher within bottom culture beds harvested by hand compared to those harvested mechanically. Among culture methods, off-bottom culture contained the greatest coverage of eelgrass (Willapa Bay, WA).

8. Ruesink, J. L., K. Houle, E. Beck, F. C. Boardman, A. Suhrbier, and B. Hudson. 2023. Intertidal Grow-Out Technique, Not Eelgrass (*Zostera marina*), Influences Performance of Pacific Oysters (*Magallana gigas*). Aquaculture Research 2023. https://doi.org/10.1155/2023/6621043.

In Washington state, Ruesink et al. investigated how juvenile Pacific oysters perform when grown in different methods and across a gradient of eelgrass densities. Oysters were outplanted within on-bottom culture (juvenile oysters on cultch or in baskets) and off-bottom culture (longlines or flipbags) across three eelgrass habitat types: no eelgrass, sparse eelgrass and dense eelgrass. The study design was replicated across 10 sites in Washington state, including Willapa Bay, Samish Bay and Hood Canal. Oysters were outplanted in June 2020 and measured for survival, size, and condition at three and nine months after outplanting.

The authors found that overall, culture method, specifically on-bottom or off-bottom, had a much greater impact on oyster performance than the amount of eelgrass present. Off-bottom oysters outperformed bottom-cultured oysters in survival, size and condition during the summer, and in survival through the winter. Eelgrass effects were slight and only at the 9-month results, showing a negative effect of dense eelgrass on survival and a positive effect of sparse eelgrass on shell height. The authors conclude that the presence of eelgrass is unlikely to reduce the yield of oysters, and that growing oysters with off-bottom methods has a much greater effect on oyster performance.

9. Ruesink, J.L., K. Houle, K.J. Kroeker, B.R. Dumbauld, F.C. Boardman, N.S. Lewis, B.A. McIntyre, A.D. Suhrbier, and B. Hudson. 2024. Intraspecific variation in resilience traits of eelgrass across intertidal stress gradients and oyster aquaculture methods. Frontiers in Marine Science, https://doi.org/10.3389/fmars.2024.1427595.

Across the U.S. West Coast, eelgrass was studied to evaluate resilience traits across two stressors, emersion (air exposure) and oyster culture (bottom culture and off-bottom culture). Resilience has two components, (1) resistance (ability to persist through disturbance/stress) and (2) recovery (ability to recover following disturbance/stress). Here, Ruesink et al. measured resistance traits (above-ground size, rhizome storage) and recovery traits (flowering, branching, and rhizome extension rates) of eelgrass to evaluate response to stressors, coastwide. Data was collected in WA (Samish Bay, Hood Canal, Grays Harbor, Willapa Bay), OR (Tillamook Bay) and CA (Humboldt Bay, and Tomales Bay), with WA and OR data including both emersion and overlapping oyster culture as factors; only intertidal elevation (emersion) was evaluated in CA.

The results for resistance traits revealed that plant sizes were generally reduced in both bottom culture, off-bottom culture and higher intertidal elevations, where smaller above-ground mass may improve resistance to these stressors. Examining recovery traits, there was no effect of bottom culture on flowering or internode length, while in off-bottom culture, there were shorter internodes. Off-bottom culture tended to decrease ($P=0.058$) the stress response (flowering) associated with higher elevations. The authors conclude that generally the effects of emersion and oyster culture as stressors is additive for eelgrass (i.e. they cause similar responses from eelgrass traits), with limited evidence that off-bottom culture may reduce stress responses at higher intertidal elevations.

10. Spurr, R., J.L. Ruesink, K. McDonald, and P. Bloch. *In Review*. Aerial imagery reveals interannual change in eelgrass (*Zostera marina*) cover associated with shellfish aquaculture and intertidal stressors.

Spurr et al. reports four case studies of eelgrass and shellfish aquaculture interactions using aerial imagery by small unmanned aerial vehicles (sUAV). Case studies captured disturbance or stressor events in Willapa Bay and Samish Bay, WA, and two events in Humboldt Bay, CA. The four case studies are summarized as follows.

(1) Case Study 1, in Willapa Bay, monitored the effect of an oyster shell hummock (as part of on-bottom culture methods) on immediately surrounding eelgrass. The hummock

was 307 m^2 and was established recently before the first set of May/June images. While eelgrass in reference areas remained stable from 2021 to 2023, the eelgrass in the 2 m buffer zone around the hummock decreased from 61% cover to 25% cover.

(2) Case Study 2, in Samish Bay, tracked eelgrass cover in and out of oyster longlines before and after a June 2021 low tide extreme heat event. Imagery was taken pre-heat wave (April 2021), and in the years following (July 2021, July 2022, July 2023). While the initial eelgrass coverage was higher in sites without longlines, following the heat wave, eelgrass coverage was reduced to 1-2% at all mid and high tidal elevations, regardless of longline presence. The low tidal elevation site (no longlines) was the least damaged site with the fastest recovery. However, the mid and high tidal elevation sites within longlines recovered eelgrass coverage similarly and at a faster rate than the mid tidal elevation site without longlines.

(3) Case Study 3, in Humboldt Bay, found that propeller scars showed an initial reduction in eelgrass coverage (35%) compared to reference areas (54%), but that one and two years following damage, the eelgrass coverage was higher within the propeller scar impact areas (Y1: 64%, Y2: 77%) than reference areas (Y1: 48%, Y2: 64%).

(4) Case Study 4, also in Humboldt Bay, found that eelgrass percent cover in longlines was initially similar or slightly lower (57%) than reference area (70%), but that following a 2022/2023 winter storm event, eelgrass was a higher coverage within longlines (38%) than on the reference tidal flat (7%) by May 2023.

The authors conclude that these case studies provide examples of how oyster aquaculture can have negative or positive effects on eelgrass, and possibly offer protection or promote resilience during and following extreme events. Spurr et al. also conclude that sUAV is an effective monitoring tool for seagrass-shellfish aquaculture interactions over a large geographic area.

11. Toft, J.D., J.R. Cordell, J.N. Kobelt, B. Oxborrow, B.R. Dumbauld, K. Houle, B. Hudson. *In Prep.* Fish Diet Response to Eelgrass and Oyster Aquaculture along the Pacific Coast, USA.

Toft et al. (*In Prep)* analyzed gut contents of fish collected in eelgrass, oyster aquaculture, and unvegetated mudflat habitats in WA (Samish Bay, Hood Canal, Grays Harbor and Willapa Bay) and OR (Tillamook Bay). Diets from 288 fish were evaluated, from the three sample years, five estuaries, and six fish species. Staghorn sculpin and shiner perch were the most sampled species. Prey mass, source (epifauna vs. infauna) and prey assemblage were analyzed from gut content samples.

Prey mass did not differ between eelgrass and aquaculture habitats. However, gut content analysis showed that fish ate more infaunal prey at aquaculture habitats and more epifaunal prey in eelgrass habitats. Harpacticoid copepods were the most abundant epifaunal prey, consumed primarily by smaller fish in eelgrass. The infaunal prey were primarily other crustaceans such as tanaids and corophiid amphipods, and bivalves. Overall, while there were some dietary differences provided by eelgrass and oyster aquaculture habitat, there was also significant overlap (WA and OR).

12. Veggerby, K. B., M. D. Scheuerell, B. L. Sanderson, and P. M. Kiffney. 2023. Stable isotopes reveal intertidal fish and crabs use bivalve farms as foraging habitat in Puget Sound, Washington. Frontiers in Marine Science 10: 1–10. https://doi.org/10.3389/fmars.2023.1282225.

In Puget Sound, WA, Veggerby et al. used isotope analysis to examine the dietary sources for nearshore fish and crabs that were collected within and outside of Pacific oyster flipbag culture. Fish and crab species were collected at three sites (low farm activity, high farm activity, and no farm activity sites) using seine nets and crab pots, and lethally sampled for isotope analysis. Shiner perch, three-spine stickleback, staghorn sculpin, juvenile flatfish, Dungeness crab and shore crab were collected for analyses within oyster culture and in adjacent eelgrass habitats. Snails from the different habitat types at each site were used to establish benthic isotope baselines, while Pacific oyster gutballs were used to determine water column isotope baselines. Isotopic analysis is used to compare the isotopic ratios of consumers to that of possible diet sources, providing data on dietary makeup.

Results from this study showed different diet source proportions for each species, with staghorn sculpin and shiner perch having the greatest diet contribution from oyster culture habitat, while both crab species had the greatest contribution from seagrass habitats. Flatfish had similar contributions from pelagic, eelgrass and farm habitats. This study concludes that nearshore species use oyster flipbags as foraging habitats, with some species primarily foraging in oyster culture habitats, while others rely on eelgrass habitats.

In Prep Manuscripts Not Included (July 2025):

Kroeker, K.J., S. Johnson, J. Quick-Cleveland, J.L. Ruesink, F.C. Boardman, B. Dumbauld, K. Houle, B. Hudson, K. McDonald, R.S. Meyer. *In Prep.* Fish use of oyster aquaculture habitats: an environmental DNA survey.

McDonald, K., F.C. Boardman, K. Houle, B. Hudson, and J.L. Ruesink. *In Prep*. Structural elements and neighborhood mosaic influence nekton community similarity across habitat gradients.

Bloch, P. and K. McDonald. *In Prep*. Mapping and Monitoring Eelgrass Using Unmanned Aerial Vehicles in the Pacific Northwest.