

Spatial planning for shellfish aquaculture and seagrasses in US West Coast estuaries: considerations for adapting to an uncertain climate

Brett R. DUMBAULD^{*1}, Jennifer L. RUESINK^{*2}, and George G. WALDBUSSER^{*3}

Abstract: Shellfish aquaculture has been an important contributor to the local economy of several communities along the US West Coast for almost 100 years and in most of the estuaries where it occurs it has coexisted with the native seagrass (eelgrass, *Zostera marina*). Eelgrass provides numerous ecosystem services including nursery habitat for juvenile fish and invertebrates, but is declining in many locations worldwide, and is therefore now protected by no net loss provisions in US laws and regulations. We have studied the interaction between oyster aquaculture and eelgrass at both the local process scale and at the estuarine landscape scale in Willapa Bay, Washington. While there are important differences, most US West coast estuaries like Willapa Bay are small relative to the nearby coast, experience less riverine influence during the summer growing season and have shorter residence times than estuaries where oysters are cultured on eastern edges of continents, and the majority of culture takes place in intertidal areas. The ecology of eelgrass and cultured Pacific oysters as well as their role as habitat is thus directly influenced by bathymetry and proximity to the coastal ocean. We summarize studies on the interaction between eelgrass and oyster culture at local scales, present data that suggest culture practices are important to consider, but the cumulative interaction is not necessarily negative for eelgrass at the estuarine landscape scale in Willapa Bay. We also briefly summarize studies on the influence of sea level rise (SLR) and sea water chemistry (ocean acidification, OA), two projected changes in climate that are expected to occur over a broader spatial and longer temporal scale. SLR is projected to enhance the presence and interaction of eelgrass with oyster aquaculture in Willapa Bay, though this effect was mostly driven by bathymetry in our simplistic model and landward eelgrass expansion could be restricted elsewhere. OA has already influenced oyster culture especially in commercial hatcheries where it changes aragonite saturation state and the ability of larval oysters to deposit shell. Evidence for direct effects of carbonate chemistry in estuaries like Willapa Bay is more equivocal due to complex interactions, yet still related to the proximity of cold upwelled ocean water which likely influences natural spawning on this coast. The presence of eelgrass may also buffer water chemistry at least over short time scales, but this is less likely to directly affect survival of juvenile than larval oysters and instead eelgrass may impact juvenile oyster growth via this and other mechanisms. These physical effects of structure also influence conspecific eelgrass plants and appear to be more important than water chemistry feedbacks.

Recent initiatives to expand shellfish aquaculture in US west coast estuaries have received increased regulatory scrutiny due in large part to this interaction with eelgrass. Our review suggests that a permit process that simply evaluates and prevents direct negative effects of oyster culture on eelgrass at small spatial and immediate temporal scales would greatly and perhaps unnecessarily restrict expansion of culture operations. A broader adaptive approach could be employed that considers bathymetric and along estuary gradients that affect both of these resources and the services they provide, especially given projected future climate.

Key words: oyster aquaculture, sea level rise, ocean acidification

2018年8月31日受理 (Accepted on August 31, 2018)

^{*1} Agricultural Research Service, U.S. Dept. of Agriculture, Hatfield Marine Science Center, Newport, OR 97365, U. S. A.

^{*2} Department of Biology, University of Washington, Seattle, WA 98195, U. S. A.

^{*3} College of Earth, Ocean and Atmospheric Sciences, Oregon State University, Corvallis, OR 97365, U. S. A.
E-mail: brett.dumbauld@ars.usda.gov

Introduction

Seagrasses and Oyster Aquaculture in US West Coast estuaries

Oyster aquaculture became an important contributor to local US West coast economies when the Pacific oyster *Crassostrea gigas* was introduced in the early 1900's and largely replaced the native oyster *Ostrea lurida*, which had been extensively fished commercially and mostly overharvested or succumbed to other factors including pollution (Blake and Ermgassen, 2015; Dumbauld *et al.*, 2011; Kirby, 2004; Polson and Zacherl, 2009; Steele, 1964). Pacific oysters were cultured and harvested from leased and privately owned estuarine tidelands, and the industry relied on juvenile seed oysters shipped from Japan through the late 1970's when local hatchery production of oyster larvae succeeded (Chew, 1984). Though the extent and interaction between these resources has only recently been actively quantified at large scales (Dumbauld and McCoy, 2015), these aquaculture operations have coexisted for almost 100 years with the native seagrass (eelgrass, *Zostera marina*), which grows on some of these tidelands. Eelgrass provides numerous ecosystem services including habitat for some fish and invertebrates (McDevitt-Irwin *et al.*, 2016), but seagrasses are threatened and declining in many locations worldwide (Waycott *et al.*, 2009). Seagrass habitat has been protected by no net loss provisions in US laws and regulations since the late 1970's, but recognition of this wide-scale seagrass loss, as well as increasing threats to and declining populations of other important species that utilize eelgrass as habitat, has heightened concern resulting in re-evaluations of permits for existing aquaculture operations and new restrictions for expanded culture (NMFS, 2017). Reef forming bivalves like oysters are now also widely recognized to provide valuable estuarine habitat and this reef habitat is also threatened (Beck *et al.*, 2011; Zu Ermgassen *et al.*, 2012). Though oysters raised in aquaculture are not generally allowed to establish reefs, they still provide three dimensional structure and this service has mostly not yet been recognized for Pacific oysters by US west coast managers. This is in part because the oysters are introduced and cultured in US west coast estuaries by humans

and thus viewed by scientists and managers as a threat to native habitats like seagrass, despite recent recognition of the omnipresent and embedded role of humans and cultural aspects involved in crafting a sustainable future for these estuarine systems and the role of aquaculture in in both the US and Japan (Broitman *et al.*, 2017; Carpenter *et al.*, 2009; Mizuta and Vlachopoulou, 2017).

West Coast estuaries function

While there are important exceptions like the Salish Sea in Washington State, most U.S. West coast estuaries are small relative to the extensive spatial extent of the nearby open coastline. Willapa Bay, which is the single largest cultured oyster production site in the US and the third largest estuary on this coast has only a 358 km² signature (**Fig.1**), which roughly equals the size of the James River sub-estuary in Chesapeake Bay, which is the largest estuary on the US East Coast with an 11,600 km² signature. It is further dwarfed by the Seto Inland Sea in Japan which has a 23,204 km² area. The spatial footprint of the oyster culture industry in this estuary is also relatively small (1,764 ha of active culture) on 12,384 ha of privately deeded and leased oyster grounds representing about 58 % of the intertidal area in the estuary (Dumbauld and McCoy, 2015). Estuaries like Willapa Bay also experience less riverine influence during the summer months and have shorter residence times than estuaries where oysters are present on eastern edges of continents (Hickey and Banas, 2003), and the majority of oyster culture takes place across broad intertidal mudflats the which represent about 58 % of the estuarine area. This relatively shallow bathymetry and lack of a strong salinity gradient result in well mixed water column, with often turbid conditions driven primarily by surface winds at least during spring and summer. The US west coast is also adjacent to the California current ecosystem, an eastern boundary upwelling system so estuaries are subject to seasonal events where nutrient rich, high pCO₂ water is transported to the surface and episodic intrusions into these estuaries can significantly lower saturation state and pH (Feely *et al.*, 2010; Hauri *et al.*, 2013). This physical context clearly influences the distribution and ecology of both cultured Pacific

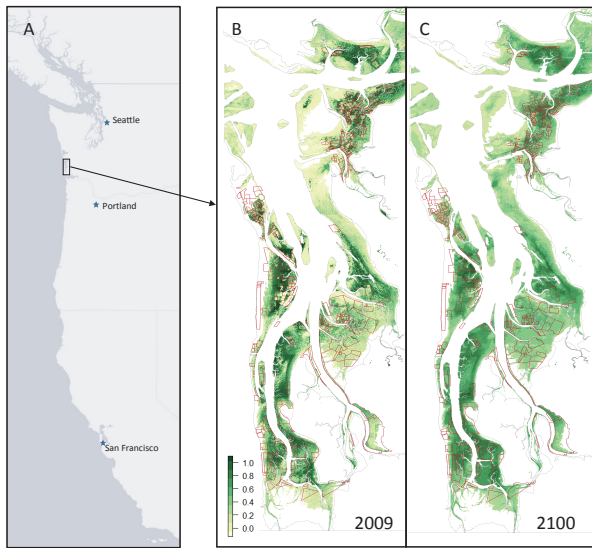


Fig. 1. A) Willapa Bay is the second largest estuary along the US West Coast, south of the Salish Sea west of Seattle, but is small relative to the extent of the nearby coast that greatly influences its hydrography. B) Eelgrass (*Z. marina*) coverage across the tidelflat in Willapa Bay based on aerial photography in 2009 and C) the predicted probable densities of eelgrass at year 2100 for the most conservative sea level rise scenarios (RCP 2.6 with 2.0 mm yr⁻¹ sediment accretion) using boosted regression tree models. Numbers on the colorbar correspond to the probability of *Z. marina* presence (zero to 100 %) within - 1.5 and 1.2 meters elevation relative to MLLW for each pixel in the image. Shellfish aquaculture beds are overlaid in red.

oysters and eelgrass in these estuaries, as well as the interaction between them and the role that both of these resources play as habitat for other fish and invertebrates. Natural disturbances due to wind and sediment movement are a regular feature in these soft sediment dominated systems (Norkko *et al.*, 2010). In some cases this context already directly influences management. For example Pacific oyster growth is clearly modulated by the distribution of phytoplankton as food and Willapa Bay and growers have long adapted to this by moving oysters from beds located near the southern end of this estuary to beds that are closer to the ocean where food supply is greater and the oysters successfully “fatten” for market (Banas *et al.*, 2007).

These larger spatial scales and gradients become important considerations when evaluating the

influence of sea level rise (SLR) and sea water chemistry (ocean acidification, OA), two projected changes in climate that are expected to occur over a broad spatial and long temporal scale in these systems. Current management of eelgrass and oysters in the US is largely focused on regulations that stipulate conditions or types of activity that can occur at relatively small scales. While there is a nationwide permit issued for shellfish aquaculture (Nationwide permit 48; ACOE, 2016), it nonetheless stipulates activities that can occur at individual sites and considers no net loss of seagrass at this or even a smaller (individual plant) spatial scale. This is also typically the scale used to evaluate success for seagrass restoration or mitigation for loss. The temporal scale is also relatively short with the year that the permit is issued most often used as the baseline reference and permit lifetime is perhaps up to 5 years over which reference conditions must be re-established or loss mitigated.

Here we briefly review existing data on both eelgrass and oysters as habitat features in Willapa Bay as the single most important US west coast estuary for oyster production and then discuss how these two future changes in climate might be addressed at a broader “seascape” scale. Our intent is to broaden the discussion about the interaction between shellfish aquaculture and eelgrass to this seascape scale and at least contemplate using a longer temporal scale to better define goals and perhaps adaptively manage these two resources over time to meet them. This exploration is consistent with ecosystem-based management in the US and the Japanese concept of *Satoumi*, though the latter explicitly includes a bottom-up social contract with local resource users (Mizuta and Vlachopoulou, 2017). We pose and attempt to address the following questions:

1. How much does the presence of oyster aquaculture affect eelgrass at the broad seascape scale?
2. How do effects differ by culture practice, and are they chronic or transitory from one year to the next?
3. What are the consequences of projected climate change to seagrass at the seascape scale and what should the baseline be? Is no net loss of seagrass based on a single contemporary date a useful

management target?

4. How would management outcomes differ if projected temporal changes to both eelgrass and aquaculture at the seascape scale were incorporated?

Methodology

Methods for collecting data on shellfish aquaculture and seagrass at broad spatial scales differ from those used in most small experimental scale studies. Detailed methods for the studies we conducted in Willapa Bay can be found in Dumbauld and McCoy (2015) and Graham *et al.* (unpublished manuscript, available from the authors), but in general involved the use of aerial color infrared photos (1:20,000) of Willapa Bay taken in 2005, 2006, and 2009. An on ground survey to truth the original photos and collect additional data was conducted in 2006-7 where 4,238 individual locations at intersection points of a 200 m x 200 m grid across the estuarine tideflat were visited and data collected on seagrass cover that would be recognizable in the photographs. This data along with other characters that would help quantify habitat at this seascape scale (oyster shell cover, burrowing shrimp and other benthic fauna burrows, macroalgal cover, sediment composition) were recorded into a Trimble Geo XT ® mapping grade GPS system. The 0.25 m color infrared photos were geo rectified and we extracted mean values for each color band in a 5 m radius around each of the ground survey points to develop a model to predict the probable cover of *Zostera marina* for each pixel in the imagery. All data was imported into R (R Development Core Team, 2015) for analyses. We then created models to predict the relationship between on ground density and color bands and used this to predict probable density of eelgrass for each pixel (mean of 1 m by 1 m values) in the aerial imagery. The photo extracted cover was then used as the actual cover and distribution of *Z. marina* for each year. Spatial data layers for aquaculture were built using data gathered from interviews with individual shellfish farmers including location, species, bed type, and harvest method for each of 458 beds. For most analyses we then created a 5 x 5 m raster layer for presence/absence of oysters and limited this to the 282 active beds with >

90 % culture above + 1.2 m MLLW.

Once these spatial data layers for eelgrass as the dependent variable and shellfish aquaculture (the primary independent variable of interest) were created, the next step involved constructing models to describe the effects of other physical and biotic factors that might influence eelgrass presence quite apart from the effect of aquaculture. This step necessarily involves assembling or collecting spatial data for these factors at this scale. In our case these data included tidal elevation (digital elevation model DEM raster created by measuring this during the ground survey with a Trimble ProXr® unit and combining with existing LiDAR data for the upper intertidal), distance to the estuary entrance (cumulative cost distance m), Euclidean distance to the nearest channel with water present in the aerial photos (m), cumulative wave stress (calculated using average wind speed and direction measured at Toke Pt. in 2009, fetch distance, and tide stage), and salinity using a model based on the 5th quantile of wet season salinity measured at 5 long term monitoring locations in the estuary. Each of these factors was resampled to a 5 x 5 m grid for further analyses and we extracted data from a set of random points outside of aquaculture. We initially used general additive models (GAM's), but have since increased predictive performance using boosted regression tree models (BRT's, Elith *et al.*, 2008), which also model interactions among predictor variables and enable improved internal cross-validation to evaluate effects on eelgrass outside of culture areas. We then similarly extracted eelgrass data from a set of random points across the entire estuarine tideflat for each of the 3 years and compared predicted and observed amounts of eelgrass in areas with aquaculture which were then summed to assess effects.

Finally we evaluated the potential effects of climate change on shellfish aquaculture and seagrass at the estuary scale in Willapa Bay. The effects of sea level rise (SLR) were examined by applying offsets to the DEM to represent 4 local SLR scenarios and predict eelgrass coverage for several scenarios at 3 future endpoints (years 2030, 2050 and 2100) using the same spatial data layers described above. While we have not yet developed spatial layers that allow us to evaluate the more complex effects of enhanced CO₂

and other changes to seawater chemistry, we review data collected along the estuarine gradient in Willapa Bay that could potentially be used in such an analysis. Seawater samples were either collected at discrete sampling locations along an estuarine gradient (details in Ruesink *et al.*, 2015; Ruesink *et al.*, 2018a) or at a single location over a broad temporal scale (Hales *et al.*, 2017) and related to either plankton samples (for oyster larvae) from the same locations, oyster and seagrass data collected at nearby locations, or optimal conditions for oyster larvae based on results of detailed laboratory studies. In both cases discrete seawater samples were analysed for two components of the carbonate chemistry system (dissolved inorganic carbon and the partial pressure of carbon dioxide ($p\text{CO}_2$)) at Oregon State University (Bandstra *et al.*, 2006; Barton *et al.*, 2012). These values were then used to calculate other parameters of the seawater chemistry system like aragonite and carbonate saturation that directly influence oyster larval growth and survival (Waldbusser *et al.*, 2015).

Results and Discussion

Previous research on the interaction between oyster culture and eelgrass in Willapa Bay conducted mostly at a small experimental scale (< 20 m² plots), but in some cases up to the shellfish culture bed scale (10 - 75 ha) suggests that:

1 - Eelgrass density declines with oyster density in all intertidal oyster aquaculture areas. This is mostly a threshold function and either due to competition for space where > 20 % shell cover results in less eelgrass (Wagner *et al.*, 2012) and/or shading and light in the case of off-bottom longline oyster culture (Ruesink *et al.*, 2009; Rumrill and Poulton, 2004; Wisehart *et al.*, 2007).

2 - Harvest disturbance significantly affects eelgrass density. Density is lowest in mechanically harvested beds especially right after harvest, but eelgrass growth is slightly greater in these areas and recovery is site specific ranging from 1- 4 years (Tallis *et al.*, 2009)

3 - Eelgrass relative growth rate, plant size, and therefore production are affected by oyster aquaculture, but these effects are variable and not always negative (Tallis *et al.*, 2009). Effects

thus depend on culture method and location. Bivalves have been shown to enhance seagrass growth indirectly via nutrient biodeposition and/or filtering and clearing water which changes the light environment. While oysters were shown to perform both of these services in Willapa Bay (Wagner *et al.*, 2012; Wheat and Ruesink, 2013), neither mechanism seemed important at the locations studied because background nutrient conditions were not limiting and the local light environment was more influenced by water flow and sediment. This in turn influenced shoot density resulting in self-shading which also influenced seedling success (Wisheart *et al.*, 2007; Yang *et al.*, 2013).

Our initial seascape scale study revealed that eelgrass declined slightly over the 3 years we modeled its presence in Willapa Bay, but oyster aquaculture reduced the overall eelgrass presence by less than 1.5 % in any single year (Dumbauld and McCoy, 2015). The general additive model we used to predict eelgrass distribution outside of aquaculture only explained about 50 % of the variation in eelgrass distribution which was likely due to the limited set of variables for which we had spatial data at this scale. Distance to the estuary mouth and tidal elevation were the most significant factors, but these variables were likely only proxies for mechanistic factors like temperature, nutrient availability, flow, and turbidity as they influenced available light discussed above and shown to be important at the local scale. Mixed effects models that considered culture practices revealed that harvest method influenced eelgrass presence, but not type of bed (e.g., oysters raised on longlines, beds only used for small oyster seed, or beds only used for larger oysters to fatten). Results were variable but beds that were mechanically harvested tended to have chronically less eelgrass present than those harvested by hand, yet even these beds had an average of 92 – 99 % of the predicted eelgrass cover present with clear temporal recovery trends across years. Many individual beds had well over the predicted amount of eelgrass present suggesting that aquaculture could enhance eelgrass presence at the seascape scale, perhaps by removing bioturbators or stabilizing substrate.

Separate examinations of eelgrass biometrics along the estuarine gradient in Willapa Bay at least in part

confirm these seascape scale patterns. Shoot size, density and above ground biomass varied seasonally (responding to daylength and perhaps temperature), but also with tidal elevation (usually with larger less dense shoots found at lower elevation; Ruesink *et al.*, 2010). Shoot density and above ground biomass also declined from the mouth of the estuary to the upriver end at the same tidal elevation (Ruesink *et al.*, 2015). There were however no consistent trends in relative growth of individual plants along these gradients, and short term reciprocal transplant experiments suggest that plant size and branching are plastic, while life history strategy of source plants (e.g., presence of flowering shoots and seedlings) was more persistent (Ruesink, 2018b). Seedling survival has also been shown to vary along stressor gradients (Yang *et al.*, 2013).

Temporal change

Eelgrass currently covers about 27 % of the tideflat in Willapa Bay and about 43 % of its distribution overlaps with commercial oyster aquaculture which covers about 15 % of the tideflat. Taking a broader temporal view, we also evaluated the potential effects of sea level rise (SLR) as one aspect of a changing climate on this eelgrass oyster aquaculture interaction. Rising global mean sea level will result in changes in water depth in estuaries, but these projections are specific to the region and system given tectonic shifts and sediment accretion/erosion. We modeled seagrass distribution and the interaction with aquaculture in Willapa Bay using two representative rates (4 mm and about 8 mm yr⁻¹, IPCC pathways 2.6 and 8.5 respectively) for three temporal endpoints (2030, 2050, and 2100) and adjusted for expected tectonic uplift and sediment accretion. In addition to elevation, we used the same additional parameters (salinity, distance to mouth, distance to channel, cumulative wave stress) and boosted regression tree models to describe current and future distributions of eelgrass. We could not predict change for these other parameters, but using a boosted regression tree allowed for model cross-validation. Results suggest as much as a 36 % increase in eelgrass cover by 2100 with similar or even greater proportional increases on oyster aquaculture beds. Mean coverage among all beds is projected to increase from 41 % (current)

to 44 – 52 % in 2100 and this will occur on as many as 325 beds representing 70 % of all beds (4,195 ha, **Fig.1**). This will represent challenges for the shellfish growers including potential impacts to oyster growth and ability to efficiently harvest product, but also potential regulatory constraints. We have not used similar models to hindcast this interaction for conditions that occurred before Pacific oysters were introduced to Willapa Bay in the 1800's, but historical maps suggest that native oysters (*Ostrea lurida*) once occupied about 17 % of the low intertidal and shallow subtidal area. Based on estimated tidal elevations alone the suitable area for eelgrass is estimated to have been about 3,139 ha (Borde *et al.*, 2003) in the 1850's. We estimated there would have been about a 45 % overlap with these oysters albeit at a mostly lower tidal elevation than today's culture operations, and today eelgrass exists as a monotypic meadow in many of those locations where native oyster beds have not returned.

Large scale temporal changes in seawater carbonate chemistry (ocean acidification, OA) are also expected to influence both seagrasses and shellfish and their interaction in US West Coast estuaries (Feely *et al.*, 2016; Feely *et al.*, 2010; Waldbusser and Salisbury, 2014). Changes to the carbonate mineral saturation state have been shown to negatively affect the acid base balance, biocalcification, and metabolism of oyster larvae (Waldbusser *et al.*, 2015). Because seasonal upwelling of nutrient rich low pCO₂ acidified water is a regular feature in nearshore coastal waters of the California Current ecosystem, episodic intrusions of this water into estuaries where shellfish hatcheries use it have already caused significant issues for the commercial aquaculture industry and practices to mitigate these losses have already been adopted (adding buffering agents and adjusting times when water is drawn, Barton *et al.*, 2015). In contrast, due to their efficient uptake of aqueous CO₂ for photosynthesis, seagrasses are expected to increase in productivity with rising levels in the environment and therein may also have the potential to mitigate effects of this chemistry on other organisms like shellfish (Hendriks *et al.*, 2014; Pacella *et al.*, 2018).

Estuarine water chemistry is however highly variable over both relatively short (daily, diel) and long term (seasonal, annual) temporal scales and

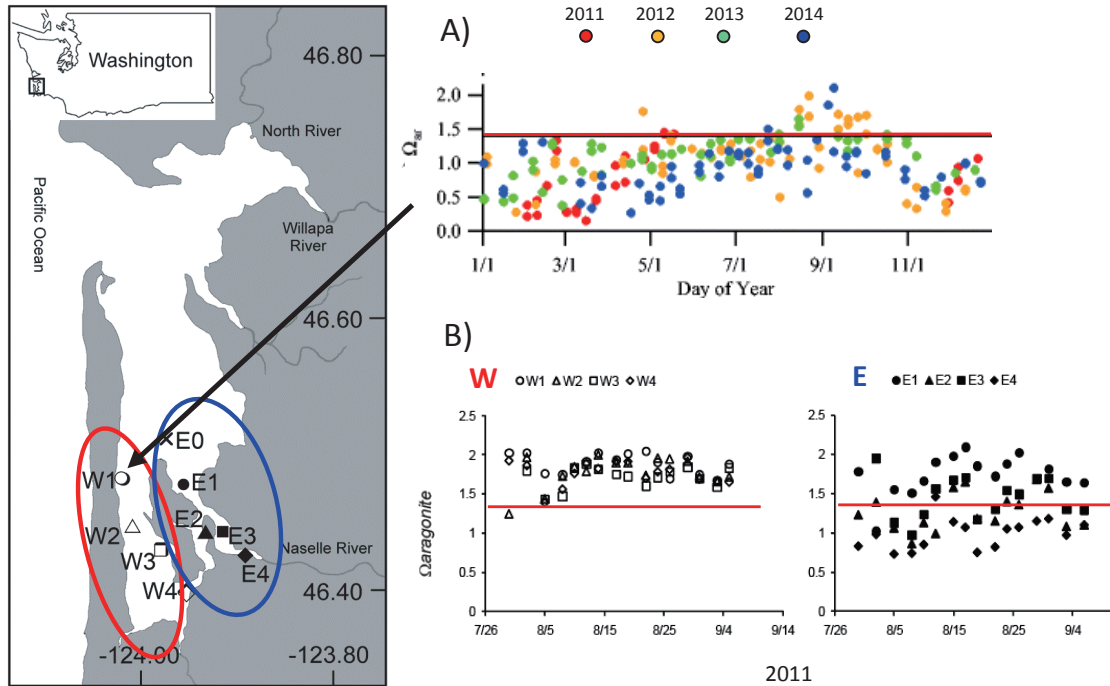


Fig. 2. Seawater carbonate chemistry measured at locations south of the fattening/recruitment line in Willapa Bay, Washington. Shown here are A) aragonite mineral saturation state calculated from observed temperature, salinity, TCO_2 and pCO_2 at Nahcotta in 2011 – 2014 (modified from Hales *et al.*, 2017) and B) aragonite mineral saturation state calculated from the same parameters measured at discrete locations along the western side of the estuary (left graph, red circle) and east side (right graph, blue circle) in 2011 (modified from Ruesink *et al.*, 2018a). Also denoted (red horizontal line) is the threshold for acute effects on oyster larvae.

along spatial estuarine gradient scales within each system. In Willapa Bay as salinity declined and temperature increased along a gradient from the mouth to the Naselle River at the southern end of the estuary, aqueous CO_2 increased and pH was reduced on a single cruise and one point in time during the summer (Ruesink *et al.*, 2015). These parameters were much more variable, especially at both mouth and river endpoints when continuously measured with moored instruments at single locations over the course of a summer month. A strong influence of upwelling events was evident near the estuary mouth, whereas consistent tidal variation in pH occurred near the river endpoint. Less variation was observed at locations near mid-bay, and there were clear differences between conditions in the eastern (Naselle River) and western (Nahcotta) arms of the estuary (Ruesink *et al.*, 2018a). As expected large seasonal fluctuations were observed in temperature, salinity, alkalinity, and TCO_2 over the course of a year

at a Nahcotta mooring with some variation between years. pCO_2 and pH varied less over the season than these other parameters and aragonite saturation state was decoupled from them, suggesting there was a very short window during summer when conditions would be favorable for oyster larval development (Fig.2A, Hales *et al.*, 2017). There were again differences between the western and eastern half of the estuary with aragonite saturation state generally exceeding critical minimums measured in the laboratory on the western, but not eastern side (Fig.2B, Ruesink *et al.*, 2018a).

The direct effects of water chemistry on eelgrass and oyster larval survival and settlement at the population level in the field are more difficult to assess due to the presence of and inability to control multiple other factors/stressors, so results to date are more equivocal. Nonetheless while tissue carbon measured in eelgrass blades increased at eight stations along the estuarine gradient and this

was coincident with depleted C-13 reflecting water carbon chemistry gradients, production (relative growth rate) did not vary and instead seemed to be more related to sediment organic content and wave exposure (Ruesink *et al.*, 2015). This is consistent with recent measurements which suggest that eelgrass has the capacity to achieve similar productivity across much broader ocean basin and latitudinal scales, despite marked differences in morphometric characteristics (Ruesink *et al.*, 2018b). Oyster larvae are most responsive to augmented CO₂ and reduced aragonite saturation in the laboratory as they cross two important and relatively short physiological transitions; initial shell formation and metamorphosis/settlement when metabolic energy allocation is crucial (Pan *et al.*, 2015; Waldbusser *et al.*, 2015). They are however subject to widely varying conditions over their 2-3 week larval period in the estuary. As noted above, aragonite saturation state was lower on the eastern more river influenced side of the southern end of Willapa Bay versus the western side when examined during three separate summers. Survival of four cohorts of Pacific oyster larvae tracked simultaneously over these 3 summers was similar between these two sides and subsequent settlement generally higher on the eastern side where aragonite chemistry was less favorable (Ruesink *et al.*, 2018a). This decoupling of population level effects from water chemistry conditions could have been due to the fact that aragonite saturation conditions on both sides were very close to, but on average above the ~ 1.4 threshold for acute effects established for risk assessments based on laboratory results (Ekstrom *et al.*, 2015), that favorable conditions were present during the critical windows or because a multitude of other factors such as temperature, advection, predation, etc. were responsible. Larval condition may also reflect a “carryover” effect from adult brooding conditions and lipid stores in eggs and thus not tie directly to stresses present during the larval period (Barton *et al.*, 2015; Hettinger *et al.*, 2012).

Eelgrass has also recently been hypothesized to potentially mitigate the negative effects of ocean acidification on bivalves by ameliorating water chemistry via photosynthesis and CO₂ uptake during the day at least at very local scales (Washington State Blue Ribbon Panel on Ocean Acidification,

2012; Hendriks *et al.*, 2014). Although respiration at night produces an asymmetrical diel signal for this effect and there is little research on whether the most sensitive bivalve larval stages benefit at this short temporal scale, recent studies suggest that post settlement growth and survival of juvenile oysters is enhanced in eelgrass (WADNR, 2017; Smith, 2016). It is however yet unresolved whether this effect can be attributed solely to water chemistry and distinguished from the effects of other factors like reduced flow in seagrass which results in less sediment but enhanced desirable phytoplankton food intake (Lowe, unpublished). Reduced flow also reduces settlement of fouling organisms that potentially compete with oysters for space and food and also alters the abundance of bivalve predators.

Perhaps most relevant on the broader temporal and estuary wide spatial scales we consider here however is recognition that both of these resources are likely not responding to average conditions and the window of favorable conditions continues to shift and narrow as atmospheric CO₂ concentration continues to rise (Hales *et al.*, 2017; Pacella *et al.*, 2018). Thus variation about the average and favorable windows of carbonate “weather” in both time and space could be important considerations when considering mitigating and adapting to future climate. Organisms may also have the ability to adapt over time to local conditions, but recognizing where these conditions occur outside of the laboratory and beyond the experimental scale at individual sites will be important.

Conclusions and Management Considerations

Initiatives to expand shellfish aquaculture in US West coast estuaries have received regulatory scrutiny due to interactions with eelgrass, but our research in Willapa Bay, an important estuary for oyster culture on the US West Coast, suggests that context and scale are very important considerations.

While significant small scale and short term temporal effects due to harvest method occur, oyster aquaculture only reduced eelgrass presence in Willapa Bay by less than 1.5 % at the seascape scale and more eelgrass was present than predicted in many aquaculture areas.

Oysters have coexisted with eelgrass in the seascape for a long time in Willapa Bay though the distribution of both across the tidal elevation gradient has changed. Unlike other locations where eelgrass is threatened by eutrophication and other anthropogenic disturbance, our models predicted a 3 – 11 % increase of eelgrass coverage within Willapa Bay oyster aquaculture beds by 2021 given projected sea level rise.

US West Coast shellfish hatcheries have already adapted and modified practices in response to changes in carbonate chemistry that routinely exceed average global conditions projected to occur in the future due to their size and proximity to upwelling conditions along this eastern ocean boundary. This creates a distinct estuarine gradient and temporal variability in conditions that make it difficult to attribute changes in natural oyster spawning and larval settlement to changes in water chemistry. While the long term average trend is for acidified conditions, oysters may be more responsive to extremes and the range of conditions, which in turn must be evaluated along these estuarine gradients where eelgrass seems less directly affected, but the mitigative effects it has on shellfish growth and survival could be important.

References

- ACOE, 2016: U.S. Army Corps of Engineers Decision Document Nationwide Permit 48.
- Banas N. S., Hickey B. M., Newton J. A., and Ruesink J. L., 2007: Tidal exchange, bivalve grazing, and patterns of primary production in Willapa Bay, Washington, USA. *Mar. Ecol. Prog. Ser.*, **341**, 123-139.
- Bandstra L., Hales B., and Takahashi T., 2006: High-frequency measurement of seawater total carbon dioxide. *Mar. Chem.*, **100**, 24-38.
- Barton A., Hales B., Waldbusser G. G., Langdon C., and Feely R. A., 2012: The Pacific oyster, *Crassostrea gigas*, shows negative correlation to naturally elevated carbon dioxide levels: Implications for near-term ocean acidification effects. *Limnol. Oceanogr.*, **57**, 698-710.
- Barton A., Waldbusser G. G., Feely R. A., Weisberg S. B., Newton J. A., Hales B., Cudd S., Eudeline B., Lang. J., Jefferds I., King T., Suhrbier A., and McLaughlin K., 2015: Impacts of Coastal Acidification on the Pacific Northwest Shellfish Industry and Adaptation Strategies Implemented in Response. *Oceanography*, **28**, 146-159.
- Beck M.W., Brumbaugh R. D., Airoidi L., Carranza A., Coen L. D., Crawford C., Defeo O., Edgar G. J., Hancock B., Kay M. C., Lenihan H. S., Luckenbach M. W., Toropova C. L., Zhang G. F., and Guo X. M., 2011: Oyster reefs at risk and recommendations for conservation, restoration, and management. *Bioscience*, **61**, 107-116.
- Blake B. and Ergmussen P. S. E. Z., 2015: The History and Decline of *Ostrea Lurida* in Willapa Bay, Washington. *J. Shellfish Res.*, **34**, 273-280.
- Borde A. B., Thom R. M., Rumrill S., and Miller L. M., 2003: Geospatial habitat change analysis in Pacific Northwest coastal estuaries. *Estuaries*, **26**, 1104-1116.
- Broitman B. R., Halpern B. S., Gelcich S., Lardies M. A., Vargas C. A., Vásquez-Lavín F., Widdicombe S., and Birchenough S. N. R., 2017: Dynamic Interactions among Boundaries and the Expansion of Sustainable Aquaculture. *Front. Mar. Sci.*, **4**. doi.org/10.3389/fmars.2017.00015
- Carpenter S. R., Mooney H. A., Agard J., Capistrano D., DeFries R. S., Diaz S., Dietz T., Duraipapp A. K., Oteng-Yeboah A., Pereira H. M., Perrings C., Reid W. V., Sarukhan J., Scholes R. J., and Whyte A., 2009: Science for managing ecosystem services: Beyond the Millennium Ecosystem Assessment. *Proc. Natl. Acad. Sci. U.S.A.*, **106**, 1305-1312.
- Chew K. K., 1984: Recent advances in the cultivation of molluscs in the Pacific United States and Canada. *Aquaculture*, **39**, 69-81.
- Dumbauld B. R., Ruesink J. L., Trimble A. C., and Kauffman B. E., 2011: The Willapa Bay oyster reserves in Washington State: Fishery collapse, creating a sustainable replacement, and the potential for habitat conservation and restoration. *J. Shellfish Res.*, **30**, 71-83.
- Ekstrom J. A., Suatoni L., Cooley S. R., Pendleton L. H., Waldbusser G. G., Cinner J. E., Ritter J., Langdon C., van Hooidek R., Gledhill D., Wellman K., Beck M. W., Brander L. M., Rittschof D., Doherty C., Edwards P. E. T., and Portela R., 2015: Vulnerability and adaptation of US shellfisheries

- to ocean acidification. *Nat. Clim. Chang.*, **5**, 207-214.
- Elith J., Leathwick J. R., and Hastie T., 2008: A working guide to boosted regression trees. *J. Anim. Ecol.*, **77**, 802-813.
- Feely R. A., Alin S. R., Carter B., Bednarsek N., Hales B., Chan F., Hill T. M., Gaylord B., Sanford E., Byrne R. H., Sabine C. L., Greeley D., and Juranek L., 2016: Chemical and biological impacts of ocean acidification along the west coast of North America. *Estuar. Coast. Shelf Sci.*, **183**, 260-270.
- Feely R. A., Alin S. R., Newton J., Sabine C. L., Warner M., Devol A., Krembs C., and Maloy C., 2010: The combined effects of ocean acidification, mixing, and respiration on pH and carbonate saturation in an urbanized estuary. *Estuar. Coast. Shelf Sci.*, **88**, 442-449.
- Hales B., Suhrbier A., Waldbusser G. G., Feely R. A., and Newton J. A., 2017: The Carbonate Chemistry of the "Fattening Line," Willapa Bay, 2011-2014. *Estuar. Coast.*, **40**, 173-186.
- Hauri C., Gruber N., Vogt M., Doney S. C., Feely R. A., Lachkar Z., Leinweber A., McDonnell A. M. P., Munnich M., and Plattner G. K., 2013: Spatiotemporal variability and long-term trends of ocean acidification in the California Current System. *Biogeosciences*, **10**, 193-216.
- Hendriks I. E., Olsen Y. S., Ramajo L., Basso L., Steckbauer A., Moore T. S., Howard J., and Duarte C. M., 2014: Photosynthetic activity buffers ocean acidification in seagrass meadows. *Biogeosciences*, **11**, 333-346.
- Hettinger A., Sanford E., Hill T. M., Russell A. D., Sato K. N. S., Hoey J., Forsch M., Page H. N., and Gaylord B., 2012: Persistent carry-over effects of planktonic exposure to ocean acidification in the Olympia oyster. *Ecology*, **93**, 2758-2768.
- Hickey B. M. and Banas N. S., 2003: Oceanography of the US Pacific Northwest Coastal Ocean and estuaries with application to coastal ecology. *Estuaries*, **26**, 1010-1031.
- Kirby M. X., 2004: Fishing down the coast: Historical expansion and collapse of oyster fisheries along continental margins. *Proc. Natl. Acad. Sci. U.S.A.*, **101**, 13096-13099.
- McDevitt-Irwin J. M., Iacarella J. C., and Baum J. K., 2016: Reassessing the nursery role of seagrass habitats from temperate to tropical regions: a meta-analysis. *Mar. Ecol. Prog. Ser.*, **557**, 133-143.
- Mizuta D. D. and Vlachopoulou E. I., 2017: Satoumi concept illustrated by sustainable bottom-up initiatives of Japanese Fisheries Cooperative Associations. *Mar. Policy*, **78**, 143-149.
- NMFS, 2017: WA eelgrass and shellfish aquaculture workshop report (ed. by Hoberecht L.), National Marine Fisheries Service Western Region, Seattle, 64pp.
- Norkko J., Norkko A., Thrush S. F., Valanko S., and Suurkuukka H., 2010: Conditional responses to increasing scales of disturbance, and potential implications for threshold dynamics in soft-sediment communities. *Mar. Ecol. Prog. Ser.*, **413**, 253-266.
- Pacella S. R., Brown C. A., Waldbusser G. G., Labiosa R. G., and Hales B., 2018: Seagrass habitat metabolism increases short term extremes and long-term offset of CO₂ under future ocean acidification. *Proc. Natl. Acad. Sci. U.S.A.*, **115**, 3870-3875.
- Pan T. C. F., Applebaum S. L., and Manahan D. T., 2015: Experimental ocean acidification alters the allocation of metabolic energy. *Proc. Natl. Acad. Sci. U.S.A.*, **112**, 4696-4701.
- Polson M. P. and Zacherl D. C., 2009: Geographic distribution and intertidal population status for the Olympia oyster, *Ostrea lurida* Carpenter 1864, from Alaska to Baja. *J. Shellfish Res.*, **28**, 69-77.
- R Development Core Team, 2015: R: A language and environment for statistical computing, R Foundation for Statistical Computing, Vienna.
- Ruesink J. L., Hacker S. D., Dumbauld B. R., and Harbell S., 2009: Scale-dependent and indirect effects of filter feeders on eelgrass: Understanding complex ecological interactions to improve environmental impacts of aquaculture, in "Final Report to the Western Regional Aquaculture Center, 1-25", Dept. of Biology, University of Washington, Seattle.
- Ruesink J. L., Hong J. S., Wisheart L., Hacker S. D., Dumbauld B. R., Hessing-Lewis M., and Trimble A. C., 2010: Congener comparison of native (*Zostera marina*) and introduced (*Z. japonica*) eelgrass at multiple scales within a Pacific

- Northwest estuary. *Biol. Invasions*, **12**, 1773-1789.
- Ruesink J. L., Yang S., and Trimble A. C., 2015: Variability in Carbon Availability and Eelgrass (*Zostera marina*) Biometrics Along an Estuarine Gradient in Willapa Bay, WA, USA. *Estuar. Coast.*, **38**, 1908-1917.
- Ruesink J. L., Sarich A., and Trimble A. C., 2018a: Similar oyster reproduction across estuarine regions differing in carbonate chemistry. *ICES J. Mar. Sci.*, **75**, 340-350.
- Ruesink J. L., Stachowicz J. J., Reynolds P. L., Bostrom C., Cusson M., Douglass J., Eklof J., Engelen A. H., Hori M., Hovel K., Iken K., Moksnes P. O., Nakaoka M., O'Connor M. I., Olsen J. L., Sotka E. E., Whalen M. A., and Duffy J. E., 2018b: Form-function relationships in a marine foundation species depend on scale: a shoot to global perspective from a distributed ecological experiment. *Oikos*, **127**, 364-374.
- Rumrill S. S. and Poulton V. K., 2004: Ecological role and potential impacts of molluscan shellfish culture in the estuarine environment of Humboldt Bay, Ca, in "Final Annual Report to the Western Regional Aquaculture Center, 22", OR: Oregon Dept. State Lands, South Slough Natl. Estuarine Res. Reserve, Charleston.
- Smith S. R., 2016: Seagrasses as potential chemical refugia for acidification-sensitive bivalves (MS thesis), Oregon State University, Corvallis, 66pp.
- Steele E. N., 1964: The immigrant oyster (*Ostrea gigas*) now known as the Pacific oyster, Warren's Quick Print, Olympia.
- Tallis H. M., Ruesink J. L., Dumbauld B. R., Hacker, S. D., and Wisheart L. M., 2009: Oysters and aquaculture practices affect eelgrass density and productivity in a Pacific Northwest estuary. *J. Shellfish Res.*, **28**, 251-261.
- WADNR, 2017: Can eelgrass improve shellfish growth and pH in a halo around the meadow? Washington State Department of Natural Resources. https://www.dnr.wa.gov/publications/aqr_aamt_halo2_eelgrass.pdf
- Wagner E. L., Dumbauld B. R., Hacker S. D., Wisheart L. M., and Ruesink J. L., 2012: Density-dependent effects of an introduced oyster, *Crassostrea gigas*, on a native intertidal seagrass, *Zostera marina*. *Mar. Ecol. Prog. Ser.*, **468**, 149-160.
- Waldbusser G. G., Hales B., Langdon C. J., Haley B. A., Schrader P., Brunner E. L., Gray M. W., Miller C. A., Gimenez I., and Hutchinson G., 2015: Ocean acidification has multiple modes of action on bivalve larvae. *PLoS One*, **10**.
- Waldbusser G. G. and Salisbury J. E., 2014: Ocean acidification in the coastal zone from an organism's perspective: Multiple system parameters, frequency domains, and habitats. *Ann. Rev. Mar. Sci.*, **6**, 221-247.
- Washington State Blue Ribbon Panel on Ocean Acidification, 2012: Ocean Acidification: From Knowledge to Action, Washington State's Strategic Response (ed. by Adelman H. and Bender L. W.), Washington State Dept. Ecology, Olympia, 100pp.
- Waycott M., Duarte C. M., Carruthers T. J. B., Orth R. J., Dennison W. C., Olyarnik S., Calladine A., Fourqurean J. W., Heck Jr. K. L., Hughes A. R., Kendrick G. A., Kenworthy J. W., Short F. T., and Williams S. L., 2009: Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proc. Natl. Acad. Sci. U.S.A.*, **106**, 12377-12381.
- Wheat E. and Ruesink J. L., 2013: Commercially-cultured oysters (*Crassostrea gigas*) exert top-down control on intertidal pelagic resources in Willapa Bay, Washington, USA. *J. Sea Res.*, **81**, 33-39.
- Wisheart L. M., Dumbauld B. R., Ruesink J. L., and Hacker S. D., 2007: Importance of eelgrass early life history stages in response to oyster aquaculture disturbance. *Mar. Ecol. Prog. Ser.*, **344**, 71-80.
- Yang S., Wheat E. E., Horwith M. J., and Ruesink J. L., 2013: Relative Impacts of Natural Stressors on Life History Traits Underlying Resilience of Intertidal Eelgrass (*Zostera marina* L.). *Estuar. Coast.*, **36**, 1006-1013.
- Zu Ermgassen P. S. E., Spalding M. D., Blake B., Coen L.D., Dumbauld B., Geiger S., Grabowski, J. H., Grizzle, R., Luckenbach M., McGraw K., Rodney W., Ruesink J. L., Powers S. P., and Brumbaugh R., 2012: Historical ecology with real numbers: past and present extent and biomass of an imperilled estuarine habitat. *Proc. R. Soc. B: Biol. Sci.*, **279**, 3393-3400.

Annotated bibliography

(1) Barton A., Waldbusser G. G., Feely R. A., Weisberg S. B., Newton J. A., Hales B., Cudd S., Eudeline B., Langdon C. J., Jefferds I., King T., Suhrbier A., and McLaughlin K., 2015: Impacts of coastal acidification on the Pacific Northwest shellfish industry and adaptation strategies implemented in response. *Oceanography*, **28**, 146-159.

This is the most recent review of the history and science underpinning the effects of changing seawater chemistry on bivalve shellfish larvae and the impacts that have already taken place to the commercial shellfish aquaculture industry on the US West Coast. Multiple authors contributed to this review which addresses a broad audience but covers the leading research on direct effects to bivalve larvae as well as monitoring seawater conditions and adapting to these changes.

(2) Dumbauld B. R. and McCoy L. M., 2015: The effect of oyster aquaculture on seagrass (*Zostera marina*) at the estuarine landscape scale in Willapa Bay, Washington (USA). *Aquac. Environ. Interact.*, **7**, 29-47.

The authors groundtruthed and analyzed aerial photographs taken in three separate years to build spatial layers for seagrass cover in Willapa Bay, Washington, USA. They created spatial layers for shellfish aquaculture and several other factors such as distance to the estuary mouth and intertidal bathymetry that could influence eelgrass and then built a model to evaluate eelgrass cover in areas outside of shellfish aquaculture beds. This model was used to predict expected values within aquaculture beds and compare this with actual values to estimate the effect of aquaculture. The approach is unique in that it examined effects at the estuary scale and over several years and the authors have submitted a second manuscript that uses a similar approach to assess sea level rise.

(3) Dumbauld B. R., Ruesink J. L., and Rumrill S. S., 2009: The ecological role of bivalve shellfish aquaculture in the estuarine environment: A review with application to oyster and clam culture in West Coast (USA) estuaries. *Aquaculture*, **290**, 196-223.

The authors review the role of shellfish aquaculture in US West Coast estuaries. While subsequent studies have clarified this role and the interaction between shellfish culture and other estuarine habitats like seagrass, general conclusions remain the same and suggest that most forms of shellfish culture as currently practiced have only short term impacts in West coast US estuaries and habitats like eelgrass are generally resilient to these changes.

(4) Hales B., Suhrbier A., Waldbusser G. G., Feely R. A., and Newton J. A., 2017: The carbonate chemistry of the "Fattening Line," Willapa Bay, 2011-2014. *Estuar. Coast.*, **40**, 173-186.

The authors present detailed data on seawater chemistry (especially pCO₂ and aragonite saturation state) for Willapa Bay, Washington where Pacific oysters have been the mainstay of the oyster aquaculture industry for almost 100 years and there is a long term record of spawning and setting. They reconstruct this record for a longer historical period and their data suggest that recent conditions provide a smaller window of optimal conditions (low aragonite saturation state and warm enough temperatures for oyster spawning) than occurred historically. While they did not sample larvae (see Ruesink *et al.*, 2018a below) and therefore can't confirm effects, they substantiate the complexity of measuring these effects and attributing them to a single cause in a variable estuary.

(5) Ruesink J. L., Sarich A., and Trimble A. C., 2018a: Similar oyster reproduction across estuarine regions differing in carbonate chemistry. *ICES J. Mar. Sci.*, **75**, 340-350.

These authors measured seawater chemistry in Willapa Bay, Washington, but unlike Hales *et al.* (2017), they also present simultaneously collected data on four cohorts of Pacific oyster larvae that were collected over three summers. The southern end of Willapa Bay has two arms which create distinctly different characteristics because one is much more affected by riverine conditions that cause reduced aragonite saturation relative to the other. Oyster settlement differed greatly between cohorts, but they did not find differences they could attribute to this different water chemistry and instead found thermal

conditions were perhaps more important.

(6) Ruesink J.L., Yang S., and Trimble A. C., 2015: Variability in carbon availability and eelgrass (*Zostera marina*) biometrics along an estuarine gradient in Willapa Bay, WA, USA. *Estuar. Coast.*, **38**, 1908-1917.

These authors collected data on eelgrass (*Z. marina*) and seawater chemistry along an estuarine gradient

in Willapa Bay, Washington. They demonstrated that while eelgrass responded to carbonate chemistry (increased tissue carbon up estuary where $p\text{CO}_2$ increased due to freshwater input), eelgrass production was unchanged and instead responded more to a gradient with more organic rich sediments at this end.