Discussion

To date, no studies have incorporated the effects of other bivalve filter feeders and true environmental conditions on the filtration functions of Olympia oyster (*Ostrea lurida*) habitat. My results indicate that the habitat clearance rates (HCR) of *Crassostrea gigas* aquaculture and restored *O. lurida* habitat may be similar when measured in the field, but that HCRs are highly variable within and among sites. These findings suggest that previously measured differences in clearance rates between *O. lurida* and *C. gigas* (Gray & Langdon 2018) may not accurately reflect ecosystem filtration functions of *O. lurida* restoration and *C. gigas* aquaculture, possibly because they do not take into account that *O. lurida* is a foundation species that filters alongside other bivalves in dynamic environmental conditions.

Estimates of filtration functions of restored *O. lurida* habitats are currently made with single-species models (Ermgassen et al. 2013a, 2016, Gray et al. 2019). *O. lurida* are smaller and less robust filter feeders per unit biomass than *C. gigas* (Ermgassen et al. 2013a, Gray & Langdon 2018) and have larger gill ostea thought to be less effective at capturing smaller diameter particles (Elsey 1935, Gray 2016). Maximum clearance rates of *C. gigas* are almost twice that of *O. lurida* under laboratory conditions (Gray & Langdon 2018). These physiological differences have called into question the filtration functions that restored *O. lurida* habitat can provide to Pacific coast bays and estuaries (Ermgassen et al. 2013a). Based on single-species clearance rate studies, one would expect *C. gigas* aquaculture to outperform *O. lurida* restoration in filtration functions. I found evidence that *in situ* HCRs between native oyster restoration and introduced oyster aquaculture are likely more similar than estimated by previous studies (Figure **??**). Although my study only includes a single *C. gigas* aquaculture site, the use of three *O. lurida* restoration sites in two bays north and south of Morro Bay set up a comparison with fairly robust inferential strength, albeit limited to the particular contexts of the selected sites. While my evidence is generated from limited data, my findings indicate that at least this particular *C. gigas* aquaculture setup does not "stand out" from *O. lurida* restoration. Furthermore, *O. lurida*'s filtration functions on a bay-wide spatial scale may dramatically increase when spatially-explicitly hydrodynamics are accounted for (Gray et al. 2019).

Clearance rates are typically expressed as a function of dry tissue weight (DTW), consequently a direct comparison between Gray & Langdon (2018)'s results and my measured HCRs is only possible at the two sites (Deanza and San Rafael) where I can estimate clearance rates as a function of estimated biomass (DTW). Gray & Langdon (2018) measured *O. lurida* clearance rates that averaged 0.78 L hr^{-1}g^{-1} in the dry season and 0.19 L hr^{-1}g^{-1} in the wet season in Yaquina Bay, Oregon. *C. gigas* averaged 0.95 L hr^{-1}g^{-1} in the dry season and 1.06 L hr^{-1}g^{-1} in the wet season in the same location, whereas Wheat & Ruesink (2013) found that *C. gigas* grown on long-lines in Willipa Bay, Washington cleared 0.73 L hr^{-1}g^{-1} (0.24 SE). According to Gray &

Langdon's (2018) all-season model and the biomass of *O. lurida* at Deanza (1.36 g DTW m^{-2}), Deanza's HCR should be 1.13 L hr^{-1}m^{-2} using mean OC and temperature from my Deanza trials. In my study, the mean HCR at Deanza was 105 L hr^{-1}m^{-2}, two orders of magnitude higher than the single-species estimate made by Gray & Langdon (2018)'s all-season model. Two important points emerge from the difference between these estimates: 1) Filtration function estimates need to incorporate the contributions of other bivalve filter feeders, otherwise habitat-level estimates of filtration functions may be largely underestimated; 2) Using a model derived from Yaquina Bay, Oregon oysters and field conditions may not represent environmental conditions in California bays, which underscores the need for local measurements in order to accurately estimate filtration functions.

Bivalve Filter Feeding Community

The filtration contributions of non-oyster bivalves is best contextualized by biomass (g DTW m^{-2}). Biomass is an important metric that is proportional to shell length which is in turn proportional to gill size and thus bivalve pumping rate (Cranford et al. 2011). Thus, bivalve species biomass represents the proportional contribution that a species makes to the overall HCR. However, biomass is time consuming to measure directly and requires bivalve collection, sacrifice, removing tissue from the shell, oven drying, and weighing. Many restoration practitioners may not wish to sacrifice bivalves from a restored habitat or do not have the resources to process samples to measure biomass. This leaves a substantial knowledge gap for better understanding the effects of bivalve community composition on restored *O. lurida* habitat filtration functions, and making direct comparisons to previous research findings. Future studies will benefit from a suite of models that predict species-specific bivalve biomass from shell length measurements, allowing monitoring groups to measure bivalve shell length without disturbing the habitat to estimate filter feeders biomass. Here, I presented a highly predictive allometric model to estimate *O. lurida* biomass from shell length based on data from Newport Bay, CA (Figure **??**) that can be used in future southern California studies. Allometric relationships may vary regionally (Ross & Luckenbach 2006), necessitating more studies from other locations.

Environmental Conditions

Gray & Langdon's (2018) *O. lurida in situ* clearance rate model was conducted in a flow-through chamber and may not be directly applicable to estimating oyster habitat filtration functions without incorporating hydrodynamics (Gray et al. 2019). The *in situ* upstream-downstream method employed in my study inherently included natural hydrodynamic conditions formed by the interaction between the physical characteristics of oyster habitat and water flow dynamics, dictating food availability and quality to filter feeders. Hydrody-

namics interact with aquatic ecosystems from large bay-wide scales to small-scale plankton interactions, and are not easy to simulate (Sanford 1997). Bivalves living in restored *O. lurida* habitat create a rough surface that produces drag and breaks up the water flow momentum (Van Duren et al. 2006, Dame 2012). This basic interaction dissipates upward creating a velocity gradient from the bottom (lower velocity) into the water column (higher velocity) known as the boundary layer (Dame 2012). The boundary layer is important to bivalve filter feeders because this is where they access water column seston for feeding (Muschenheim 1987), and this motivated my decision to positioned my instruments at approximately the height of the oyster habitat (Grizzle et al. 2006). The height of the boundary layer can be affected by the arrangement of bivalves and flow speed (Lim et al. 2020), and mostly consists of turbulent flow in natural, rough environments like bivalve beds (Dame 2012, Styles 2015). Turbulent flow within the boundary layer increases interaction and mixing with the larger water current, thus influencing seston flux (Muschenheim 1987), and is generally characteristic of natural water bodies even in low velocity scenarios (Sanford 1997).

In this study, I detected the resuspension of photosynthetic material across all oyster habitats and mudflat controls; represented by negative HCRs (Table 1). Negative values are not surprising and do not necessarily suggest a lack of filter feeding activity, but instead that the filter feeding signal was clouded by the net sediment transport across the habitat (Grizzle et al. 2008, Wheat & Ruesink 2013, Milbrandt et al. 2015). Sediments can be resuspended by high water velocity (> 15 cm/s; Dame et al. 1985, > 20 - 25 cm/s in high density mussel beds; Widdows et al. 1998) but may depend on the local sediment profile and consolidation (see Ruesink et al. 2019, Wheat & Ruesink 2013, Guizien et al. 2014). My water velocity measurements ranged from 2-20 cm/s (Table 1), but velocities 15 cm/s and higher did not correlate with negative HCR values. Negative HCRs may also result because smaller, lighter, organic materials are re-suspended at lower water velocities than inorganic sediments (see Muschenheim 1987, Wheat & Ruesink 2013), and detected by Chl α sensors. Mudflat controls likely contain a number of infaunal filter feeders that contribute their own filtration functions, although I did not collect this data. My statistical comparison between oyster habitat HCR and mudflat controls HCR was not significantly different, but was also limited by my small sample size. Despite non-significant differences between oyster habitat (*O. lurida* restoration and *C. gigas* aquaculture) HCR and mudflat HCR, I found a very large effect size between the two. This suggests that *O. lurida* restoration and *C. gigas* aquaculture may provide greater HCR than their adjacent mudflat habitat and this prediction can be more robustly tested with more trials, particularly of the mudflats.

My HCR measurements are snapshots of filtration functions and sediment transport at four different oyster habitats. Measurements within Morro Bay, Shellmaker, and Deanza represent repeated measures of similar tidal and hydrodynamic conditions. San Rafael was the only site where filtration trials were conducted on both ebb and flood tides (Table 1). Water depth and hydrodynamics may partial explain the

similar HCRs between Morro Bay *C. gigas* aquaculture and restored *O. lurida* habitat. Morro Bay consisted of floating lines of grow bags that rose from the sediment surface with increasing water depth. This floating action may have created a 'moving target' for the water quality sondes. The water quality sensors were positioned at the height of the bivalves, but at Morro Bay this height gradually increased with the flood tide, and sensors may have partly missed the filtration signal, creating a lower HCR than expected for *C. gigas* aquaculture. In addition, Morro Bay and San Rafael were not continuous habitat like Deanza and Shellmaker, and contained intermixed mudflat and bivalve habitat. This patchy habitat may have caused eddies, where water is retained longer than the average water flow, physically removing seston (i.e. Chl α) from the main water flow measured by the downstream instrument. Chl α retention in eddies could be conflated as bivalve filtration, but is nonetheless capturing Chl α from the water column. This is especially possible at San Rafael, where the *O. lurida* habitat consisted of an array of 2 m x 2 m shell bag reefs each with a 1 m relief above the sediment. Considering the extremely low *O. lurida* biomass at San Rafael compared to Deanza (**??**), one would not expect San Rafael to have a similar filtration services (Figure **??**). Rather, seston removal at patchy and high relief habitats, like San Rafael, may have a substantial physical seston removal mechanism.

Given that trials within each site were conducted in similar tidal conditions, thus hydrodynamics, my results still show highly variable HCRs within each site (Figure **??**). My HCRs across all sites ranged from -2485 to 845 L hr^{-1}m^{-2} (Table 1), which encompasses the HCR range of previous studies. Milbrandt et al. (2015) used similar upstream-downstream *in situ* methods on restored bivalve beds in Florida and reported a range of habitat clearance rates from -26 to 157 L hr^{-1}m^{-2}. Approximately 38% of my HCR estimates exceed their largest positive value (Table 1). Jones et al. (2011) found the HCRs of infaunal cockles in New Zealand to be between 20 and 420 L hr^{-1}m^{-2}, where 10% of my HCR values exceed their largest positive value (Table 1). High variability is well documented in field filtration measurements even in short periods of time (Grizzle et al. 2008, reviewed by Cranford et al. 2011), and in bivalves feeding on natural seston over short and long periods of time (reviewed by Cranford et al. 2011). In addition, HCR variation could be the result of measuring hundreds to thousands of bivalves (Figure **??**). Individual feeding behavior can be highly variable in short time periods (Newell et al. 2005), and even under favorable conditions, a substantial portion of individual bivalves may not actively feed or may feed at a reduced capacity (Dolmer 2000, Saurel et al. 2007)

I found that temperature was the most important variable (23.1%) in predicting HCRs with my random forest model ($R^2 = 0.64$), aligning with previous bivalve feeding studies. Temperature affects bivalve physiology and water viscosity (reviewed in Cranford et al. 2011, Bayne 2017) and is found to be a highly predictive variable in bivalve feeding models (Ermgassen et al. 2013b, Gray & Langdon 2018, Moody & Kreeger 2020,

reviewed in Cranford et al. 2011). After temperature, variables relating to seston quantity and quality were reasonably important in predicting HCRs (turbidity 20.6%, TPM 16.8%, and OC 16.8%), also aligning with previous research (Gray & Langdon 2018, Moody & Kreeger 2020, reviewed in Cranford et al. 2011)

Conclusions

My results provide the first snapshot of habitat clearance rates of oyster habitats in California, and show that restored *O. lurida* habitat and *C. gigas* long-line aquaculture in California may clear similar amounts of water per unit area when compared in realistic biological and environmental conditions. Gray et al. (2019) also found that the filtration functions of *O. lurida* may be greater than previously thought when complex environmental conditions were accounted for. Furthermore, overall filtration functions of *O. lurida* habitat may continue to be underestimated, unless a whole-habitat perspective is taken; future filtration function measurements should incorporate the filtration contributions of other filter feeders residing on foundation oyster habitat. *O. lurida* restoration efforts on the North American Pacific coast aim to increase abundances of this foundation species and its purported filtration functions that may result from biological or physical removal mechanisms. My research represents the first direct measurements of restored *O. lurida* habitat filtration functions, and although highly variable, they show that restored *O. lurida* habitat is a valuable contributor to filtration functions within California bays, comparable with *C. gigas* aquaculture.

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