

IN SITU CLEARANCE RATES OF OLYMPIA OYSTER
(*OSTREA LURIDA*) HABITAT AND PACIFIC OYSTER
(*CRASSOSTREA GIGAS*) AQUACULTURE IN
CALIFORNIA

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Abstract

The Olympia oyster, *Ostrea lurida*, is the focus of many restoration projects along estuaries in the North American Pacific coast, whereas the non-indigenous Pacific oyster, *Crassostrea gigas*, makes up the vast majority of oyster aquaculture in the region. Both *O. lurida* habitat and *C. gigas* aquaculture provide filtration functions as filter feeders, my project investigated the contributions of both in three California bays using a whole-habitat, *in situ* approach. I collected upstream-downstream measurements of chlorophyll α , temperature, salinity, and turbidity to estimate habitat clearance rates (HCR, $L \text{ hr}^{-1} \text{ m}^{-2}$). In parallel, I estimated seston total particulate matter (TPM), and organic content (OC), and examined existing data on bivalve density and biomass. Twenty-two experimental trials and four control mudflat trials were conducted from February 2018 to June 2019. Mean HCR at *O. lurida* restoration sites were $166 \text{ L hr}^{-1} \text{ m}^{-2}$ ($SD = 255$) at San Rafael, $-464 \text{ L hr}^{-1} \text{ m}^{-2}$ ($SD = 1420$) at Shellmaker, and $105 \text{ L hr}^{-1} \text{ m}^{-2}$ ($SD = 251$) at Deanza, while the *C. gigas* aquaculture site at Morro Bay was $10.3 \text{ L hr}^{-1} \text{ m}^{-2}$ ($SD = 257$). HCRs were highly variable within and among sites, and not significantly different. Using random forest regression analysis, I found that temperature (29.4%) was relatively most important to HCR, followed by turbidity (16.8%), TPM (15.7%), OC (14.1%), site (12.2%), and salinity (11.9%). The contributions of all bivalve filter feeders and natural hydrodynamics are inherently included in whole-habitat *in situ* measurements in this study. My research indicates that the field filtration performance of *O. lurida* habitat and *C. gigas* aquaculture are similar in California bays.

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Introduction

Oyster Filtration Functions

In estuaries along the North American Pacific coast (NAPC), the Olympia oyster, *Ostrea lurida*, is a foundation species that autogenously creates complex three-dimensional habitat (Dayton 1972). The shells of living and dead oysters provide habitat for a variety of invertebrates (Kimbrough & Grosholz 2006, Rodney & Paynter 2006, Ramsey 2012, Boyer et al. 2017), nursery, refuge, and foraging habitat for fishes (Peterson et al. 2003, Coen et al. 2007, Stunz et al. 2010), and foraging habitat for birds (Galtsoff 1929, Boyer et al. 2017). *O. lurida* and other bivalves that recruit to oyster habitat are suspension feeders that remove particulate matter (seston) from the water column and deposit mucus-bound feces and pseudofeces (i.e. biodeposits) on the sediment surface (Elsey 1935, Baird & Ulanowicz 1989, Dame 1999, Kellogg et al. 2013). This feeding behavior contributes to three critical ecosystem functions including nutrient sequestration, trophic energy transfer, and water clarification. Most of the seston particulate organic matter (POM) is ingested by bivalves for growth and maintenance. Nutrients incorporated into bivalve shells can be sequestered long-term (Kellogg et al. 2013) when buried in sediments (Hu et al. 2011), and likely serve as a sink for anthropologically produced nutrients (Martinetto et al. 2006, Carmichael et al. 2012). Bivalve feeding is an important biochemical pathway, linking the water column to the benthos, that transfers energy to higher trophic levels (Kautsky & Evans 1987, Rodney & Paynter 2006) and supplies nutrients to benthic seagrasses (Peterson & Heck 1999). Bivalve biodeposits can have higher organic and nitrogen content than particles settling out of the water column (Kautsky & Evans 1987, Muschenheim 1987), providing high quality food for deposit feeders and subsequently feeding omnivores and carnivores including fish (Rodney & Paynter 2006). Lastly, seston removal via bivalve filter feeding increases water clarity (Newell & Koch 2004, Grizzel et al. 2008, 2018) and, thus, the amount of photosynthetically available radiation reaching benthic primary producers, such as seagrasses (Newell & Koch 2004) and microalgae (Newell et al. 2002).

At a regional scale, the capacity of *O. lurida*'s filtration functions was diminished when *O. lurida* populations were decimated in the late 1800s and early 1900s by destructive fishing practices (Kirby 2004), introduction of non-native species (Bonnot 1935), pollution, and excessive sedimentation (Nelson 1909, Gilbert 1917, Lotze et al. 2006). Currently, *O. lurida* populations are less than 10% of historical abundance in parts of the Pacific Northwest, and less than 1% in the rest of its geographic range (Beck et al. 2011, Ermgassen et al. 2012). The extreme reduction of native *O. lurida* abundances and, therefore, the important estuarine habitat *O. lurida* creates, is likely coupled

with the loss of water filtration functions. Restoring filtration functions is one motivation behind native *O. lurida* restoration and living shoreline projects efforts along the West Coast, along with restoring other habitat functions such as habitat provision and sediment stabilization (Dinnel et al. 2009, Henderson et al. 2015, Latta & Boyer 2015, Wasson et al. 2015, Zacherl et al. 2015). Restoring the filtration functions of *O. lurida* habitat is relative to the mudflats where restorations are often located, which have their own filtration functions driven by infaunal bivalves.

Dwindling *O. lurida* harvests led to the cultivation of the Japanese oyster, *Crassostrea gigas*, (Beattie et al. 1982) in the Salish Sea in the early 1920s (Quayle 1988), and in California in 1928 (Conte & Dupuy 1982). *C. gigas* now accounts for the overwhelming majority of commercial oyster harvest on the NAPC (Beattie et al. 1982, Pauley et al. 1988), and has established feral populations outside of aquaculture operations in the Salish Sea (Quayle 1988), Willipa Bay, Washington (Kincaid 1968), and southern California (Polson & Zacherl 2009, Crooks et al. 2015, Tronske et al. 2018). *C. gigas* is a large, fast growing oyster with higher filtration rates than *O. lurida* per unit dry tissue weight (DTW) (Bougrier et al. 1995, Ermgassen et al. 2013a, Gray & Langdon 2018, 2019), and it can exert top-down control of seston at aquaculture densities (Wheat & Ruesink 2013). Furthermore, *C. gigas* has a higher particle capture efficiency presumably because it has smaller gill ostrea than *O. lurida* (Elsey 1935, Gray 2016, Gray & Langdon 2018). Beyond differences in species physiology, many aquaculture operations cultivate oyster in off-bottom structures that are fundamentally different than natural oyster reefs and may alter how commercially grown *C. gigas* delivers pelagic seston resources to benthic communities. Therefore, ecosystem filtration functions (e.g. nutrient sequestration, sediment enrichment, and water clarification) and habitat quality in NAPC estuaries may differ between native *O. lurida* habitat and cultivated *C. gigas* aquaculture (Ruesink et al. 2006, reviewed by 2005).

Single-species Research

Estimating the filtration capacity of *O. lurida* habitat and *C. gigas* aquaculture currently relies on a handful of single-species studies (Ermgassen et al. 2013a, 2016, Gray & Langdon 2018, Gray et al. 2019) and a single field aquaculture study (Wheat & Ruesink 2013). Gray & Langdon (2018) estimated the clearance rates of *O. lurida* and *C. gigas* under a range of laboratory and seasonal *in situ* conditions using the biodeposition method (Hawkins et al. 1996). These models provide important insights into the feeding responses of individual *O. lurida* and *C. gigas* to specific conditions (temperature, salinity, turbidity, chlorophyll α , total particulate matter (TPM), and

organic content (OC)), but may not be appropriate for estimating whole-habitat clearance rates in the field (Cranford et al. 2011, Grizzle et al. 2018) because they do not incorporate local habitat or hydrodynamics conditions. For example, non-oyster filter feeders living in *O. lurida* habitat, contribute to the overall filtration capacity of the habitat (Grizzle et al. 2008, 2018, Byers et al. 2014, Gedan et al. 2014). These non-oyster filter feeders that occupy oyster habitat have species-specific feeding behavior (Møhlenberg & Riisgård 1979, Riisgård 1988, Riisgård & Larsen 2001, Cranford et al. 2011, Gedan et al. 2014, Gray 2016). The regional composition of this filter feeding guild is likely to change along the NAPC, consequently creating unique filtration signatures for different *O. lurida* habitat. In addition, clearance rates calculated based on biomass are not particularly useful in assessing whether restored *O. lurida* habitat is also restoring filtration functions unless species-specific allometric relationships are known and applied to estimate biomass, as restoration practitioners are hesitant to sacrifice bivalves to measure biomass directly.

Whole-Habitat Measurements

The complex biological and physical characteristics of oyster habitat highlight the need for *in situ*, whole-habitat filtration measurements (Grizzle et al. 2008, 2018, Byers et al. 2014, Gedan et al. 2014) specific to the habitat. Whole-habitat *in situ* filtration measurements have several distinct advantages over single-species measurements. First, *in situ* measurements include the contributions of the entire filter feeding guild. Next, individual bivalve feeding variation is aggregated with a higher precision in *in situ* measurements than filtration rates derived from individual bivalve feeding trials (Iglesias et al. 1998, Cranford et al. 2011, Jones et al. 2011). Filtration studies often exclude individuals that are not filtering (closed valves), and artificially inflate filtration models and overestimate filtration when extrapolated to the population level (Harsh & Luckenbach 1999, Cranford et al. 2011); this may partly explain why many field studies find lower filtration rates than laboratory studies (Newell et al. 2005, Grizzle et al. 2008, Cranford et al. 2011). Lastly, bivalve feeding responses to natural water flow dynamics along with spatial and seasonal changes in seston composition are inherently included in whole-habitat *in situ* measurements.

Water flow dynamics in the field are highly variable (Wilson-Ormond et al. 1997) due to the interaction of tidal prisms and the physical characteristics of bays and estuaries (Dame 2012). Whereas the direct effects of water velocity on bivalve filter feeding is unclear (Grizzle et al. 1992, Cranford et al. 1998, also see review in Judge et al. 1992), water velocity and depth affect water column mixing and sediment re-suspension (Widdows et al. 1998), and thus, food availability for

benthic filter feeders. The quantity, particle size, and organic content (OC) of seston available can affect filter feeders' feeding behavior (Cranford & Hill 1999, Newell et al. 2005, Velasco & Navarro 2005, Gray & Langdon 2018, 2019, Moody & Kreeger 2020a b). Natural seston is composed of phytoplankton (Navarro & Thompson 1995), zooplankton (Lehane & Davenport 2006, Trottet et al. 2008), macroalgae detritus (Kwak & Zedler 1997, Page 1997, Gilbane 2006), bacteria (Newell et al. 1989), and inorganic sediments (Wilson-Ormond et al. 1997, Gray & Langdon 2018). Although Gray & Langdon (2018) used ambient sea water from Yaquina Bay, Oregon in their *in situ* experiments across seasons; seston also changes spatially and temporally due to tides, wind, bathometry, and proximity to benthic organisms (Muschenheim 1987, Ashley & Grizzle 1988, Navarro & Thompson 1995, Moody & Kreeger 2020a), limiting their findings to bays with similar seston profiles.

Cranford et al. (2011) conducted a meta-analysis of 133 bivalve clearance rate studies and found highly variable short-term fluctuations in clearance rates, as well as intermittent feeding cessation when bivalves were fed with natural seston. This illustrates bivalves' highly variable feeding responses to natural conditions, further making the case that whole-habitat *in situ* measurements are needed for ecologically and environmentally realistic filtration estimates of *O. lurida* habitat and *C. gigas* aquaculture.

Research Questions

Here, I assessed the contributions of restored *O. lurida* habitat and *C. gigas* aquaculture to estuary filtration functions in California, as a function of natural water quality conditions and filter feeder communities, which are expected to vary among locations. My research questions were: 1) Do oyster habitat clearance rates (HCR) differ from adjacent mudflat habitat HCR? 2) How do the HCRs of restored *O. lurida* habitat compare to *C. gigas* aquaculture? 3) What biotic and abiotic factors are important in estimating HCR? 4) Is there a predictable allometric relationship between *O. lurida* shell length and dry tissue weight, allowing for accurate estimates of DTW without sacrificing restored oysters?

Methods

Study Sites

I selected four sites along the California coast to measure *in situ* filtration clearance rates that represent filtration function. The sites represent a range of constructed oyster habitats including shell bag reef, shell bed, and floating aquaculture long-lines. The San Francisco Living Shorelines Project is located in northern San Francisco Bay, California (latitude, longitude: 37.964179, -122.487217; henceforth, San Rafael), and contains *Ostrea lurida* reefs constructed from July to August 2012 by The Coastal Conservancy and collaborators (Environmental Science Associates 2014, Latta & Boyer 2015). San Rafael consists of a shell bag reef matrix with a 32 m x 10 m footprint with three rows of eight shell bag reefs constructed as *O. lurida* habitat (Environmental Science Associates 2014). Each reef unit measured 2 m x 2 m x 1 m and was composed of four shell bag elements measuring 1 m x 1 m x 1 m. A shell bag was made of plastic mesh filled with clean, commercially-grown *Crassostrea gigas* shell. The matrix was positioned approximately 200 m from shore on a mudflat at -0.3 m MLLW (Mean Low Lower Water) tidal elevation (Environmental Science Associates 2014).

The Upper Newport Bay Living Shorelines Project is located in Newport Bay, California and contains restored *O. lurida* beds. It was constructed in May 2017 by Orange County Coast Keeper, and collaborators at CSU Fullerton and CSU Long Beach (Wood 2018). My research included two sites: Shellmaker (33.622097, -117.892399) and Deanza (33.620291, -117.897692) that are about 550 m apart. The oyster beds measure 20 m x 1 m x 0.25 m and were constructed with coconut coir bags filled with clean, commercially-grown *C. gigas* and *Mytilus galloprovincialis* mussel shell. The beds were positioned approximately 30 m from shore on a mudflat at approximately -0.15 m MLLW (Wood 2018).

Morro Bay Oyster Company (MBOC) is a commercial aquaculture operation in Morro Bay, California (35.334707, -120.844000; henceforth, Morro Bay). MBOC grows *C. gigas* in plastic mesh bags measuring about (80 cm x 55 cm) attached to floating lines that stretch across an area about 75 m x 75 m. The oysters grown in the bags are approximately five to eight cm in length. The bags of oysters rest on the underlying mudflat at around 0 m MLLW, and float to the surface as the tide rises.

Experimental Setup

In situ filtration methods were adapted from Grizzle et al.'s (2006, 2008) upstream-downstream measurements of bivalve beds on the North American Atlantic coast. Two identical water quality sondes (Yellow Springs Instruments 6600EDS) measured the change in chlorophyll α (Chl α , fluorometer), temperature, salinity (automatically calculated from conductivity/temperature sensor), and turbidity (optical sensor) from positions upstream and downstream of the oyster habitat. The sondes were hung inside of freestanding PVC (polyvinyl chloride) housings with water flow slats (Figure 1) and were set at a height to align the sensors with the approximate height of the oyster beds, reefs, or floating bags.

Prior to each filtration trial, water tracing dye (Rhodamine WT) released upstream of the habitat provided a visual indicator of water flow direction and interfering currents or eddies and was recorded by a drone about 25 feet above the water. Trials were conducted close to low tide on either the ebb or flood tide depending on how the water flow direction transected the oyster habitat. The sonde housings were positioned to measure an uninterrupted linear water flow across the oyster habitat based on the dye. Linear water flow assumes that the upstream sonde is measuring the same water as the downstream sonde. An electromagnetic meter (Marsh-McBirney Flo-Mate 2000) measured water velocity at the depth of the sensors at the beginning, middle, and end of each trial. Water velocity measurements were taken at the downstream sonde position and in the middle of the transect, velocity was averaged across positions and time. Mean depth was determined by markings on the PVC sonde housings at the beginning and end of the trial, and distance between sondes was determined post-trial with a transect tape. The sondes recorded measurements every one second, and trials lasted as long as water flow direction was consistent; ranging from six and 40 minutes.

I took the mean of temperature, salinity, turbidity of the upstream sonde during the filtration trial for analyses, and the mean of Chl α at both upstream and downstream sondes for analyses. To compare the clearance rates of surrounding mudflat habitat to restored *O. lurida* and *C. gigas* aquaculture, I conducted a mudflat control trial at each site. Control trials used the same experimental set up, except the instruments were positioned over the mudflat adjacent to the oyster habitat. Data corresponding with field disturbances was cut from the time series. Field work was conducted from February 2018 to June 2019 and measured 22 oyster habitat filtration trials and four control mudflat trials.

Chlorophyll α Corrections

Chl α is a photosynthetic pigment whose concentration is a proxy for phytoplankton and macroalgal detritus consumed by filter-feeding bivalves, and is commonly used to measure filtration (Harsh & Luckenbach 1999, Grizzle et al. 2006, 2008, Wasson et al. 2015, Milbrandt et al. 2015). I compared Chl α sensors readings by conducting two side-by-side trials before and after filtration and control trials. In the side-by-side trials, I placed the sondes adjacent to one another to compare the sensors' Chl α concentration readings in the same mass of water for approximately 10 minutes. All data, in filtration, control, and side-by-side trials, was reviewed for extreme Chl α and turbidity spikes indicating disturbances to the trial. If extreme Chl α and turbidity values were corroborated by field notes, the time period was removed from the trial. Next, I corrected mean Chl α values in the filtration and control trials with the mean Chl α difference from the corresponding side-by-side trials. The mean difference between sondes in combined side-by-side trials was divided in half to produce a correction term. The sonde with higher mean Chl α in the side-by-side trials was corrected in the filtration and control trials by subtracting the correction term from mean Chl α measurements, and the lower sonde was corrected by adding the correction term.



Figure 1: Two identical YSI 6600EDS water quality sondes were used to measure chlorophyll α , temperature, salinity, and turbidity. The sondes were hung inside PVC housings to adjust the sensor depth in the water column. Water velocity measurements were taken with an Marsh-McBirney Flo-Mate 2000. Photo taken at Deanza, Newport Bay, California.

Seston Content

I determined seston total particulate matter (TPM), particulate inorganic matter (PIM), particulate organic matter (POM), and organic content (OC) gravimetrically. I collected water samples immediately adjacent to the experimental area during the filtration or control trials, and filtered the

water through a borosilicate glass microfiber filter (Whatman 9907-047 pre-wash and pre-weighed) in the field. The filters were stored on ice until they could be moved to a freezer. Thawed filters were rinsed with a 0.5 M ammonium formate solution to remove salt. Typically this step immediately precedes filtering (Gray & Langdon 2018), but this was not possible to do in the field. Filters were then dried in an oven at 60°C for 48 hours, and weighed to determine TPM (Equation 1). Next, the dried filters were ashed at 450°C for ≥ 4 hours and weighed to determine PIM (Equation 2) and POM (Equation 3). Seston OC is simply the ratio of POM to TPM. Gray & Langdon (2018) used washed and ashed filters; however, the filters I used that were only washed. The mean weight difference between ashed filters and washed only filters was 0.5%, which I used to correct the filter pre-weights in Equations 1 & 2. In addition, control filters, filtered with distilled water, were stored and processed with every sampling batch. The TPM and PIM of control filters represented processing contamination within each sample batch, and I used these values to correct sample TPM and PIM within each batch.

$$TPM(mg/L) = \frac{[FilterDryWeight(g) - FilterPreWeight(g)] \times \frac{100mg}{L}}{Watersamplevolume(mL) \times \frac{1L}{1000mL}} \quad (1)$$

$$PIM(mg/L) = \frac{[FilterAshWeight(g) - FilterPreWeight(g)] \times \frac{100mg}{L}}{Watersamplevolume(ml) \times \frac{1L}{1000mL}} \quad (2)$$

$$POM(mg/L) = TPM(mg/L) - PIM(mg/L) \quad (3)$$

Filtration Calculations

I paired upstream and downstream Chl α measurements in the experiment and control trials to determine how Chl α concentrations changed across the habitat. I used mean water velocity and sonde distance to estimate the time it took a parcel of water to travel from the upstream sonde to the downstream sonde. The travel time was subtracted from the time-stamps of each downstream Chl α measurement to pair with upstream Chl α measurements; unpaired measurements were discarded. Next, I calculated percent Chl α removal (Chl_{rmd} , Equation 4; Grizzle et al. 2008) and habitat clearance rate (HCR, Equation 5; Milbrandt et al. 2015) using average Chl α concentrations and habitat dimensions instead of biomass.

$$Chl_{rnd} = \frac{Chl_{up} - Chl_{down}}{Chl_{up}} \times 100 \quad (4)$$

$$HCR(Lhr^{-1}m^2) = \frac{A_{Xsec} \times V \times 1000}{A_{habitat}} \times \frac{Chl_{up} - Chl_{down}}{Chl_{up}} \quad (5)$$

A_{Xsec} is the cross-sectional area of the water column (mean water depth \times assumed 1 m width), V is the mean water velocity (m/hr), $A_{habitat}$ is the area being measured (distance between the instruments \times assumed 1 m width), Chl_{up} is the mean upstream Chl α concentration, and Chl_{down} is the mean downstream Chl α concentration.

Analysis

All data wrangling and analysis was conducted R 3.6.3 (R Core Team 2020, tidyverse R package; Wickham et al. 2019) and plotted using the ggplot2 package (Wickham 2016); the code is available in Github repository “Oyster-Insitu-Filtration”. Two field days (Morro Bay 2019-05-18 and Deanza 2018-10-25; Table 1) from my data set were missing TPM and OC values. I used a semi-parametric imputation to estimate the missing values (missForest R package; Stekhoven & Bühlmann 2012). Differences in temperature, salinity, turbidity, and Chl α among sites was investigated using a one-way ANOVA and post-hoc Tukey honestly significant difference (HSD) on significantly results. Percent Chl removal among sites was examined using a Kruskal-Wallis one-way analysis of variance.

To determine if there was a difference between mudflat control and oyster habitat filtration trial HCRs, I first used a two-sample, single-tail, t-test. To account for the effects of water quality (i.e. temperature, salinity, turbidity, TPM, OC) and site variables, I fit a random forest regression (including all filtration and control trials) to HCR with temperature, salinity, turbidity, TPM, OC, and site as predictor variables (randomForest R package Liaw & Wiener 2002). Control and filtration HCR were adjusted by the residuals of the random forest regression to control for the effects of water quality and site and were compared by a second two-sample, single-tail, t-test. The effect of site on filtration trial HCR was examined using a Kruskal-Wallis analysis. Another Kruskal-Wallis analysis examined the top 0.5 quantile of filtration trial data at each site to determine if the top HCR performance differed among sites. A quantile analysis ($\tau = 0.5, 0.9$) was used to see if water quality variables had differential relationships with HCR.

To examine the effect of water quality variables and site on HCR, I fit a second random forest regression that only included filtration trials (randomForest R package; Liaw & Wiener 2002).

The random forest model I fit is an ensemble of 2,000 individual decision trees. Each tree fits a random subset of the data and is prone to over-fitting. The final output (forest) is the average of the 2,000 individual trees, which corrects for the individual trees' weaknesses (i.e. ensemble learning, Sagi & Rokach 2018). I chose to use a random forest regression for several reasons. First, random forest regressions are non-parametric models that learn non-linearity relationships without explicitly modeling them (Grömping 2009). This works well for my data as previous research suggests that temperature, salinity, and TPM have non-linear relationships with *O. lurida* and *C. gigas* clearance rates (Gray & Langdon 2018). Second, random forest regressions work with missing data (Stekhoven & Bühlmann 2012), and I had two trials with missing TPM and OC values because of a processing error. Third, I had a large number of variables relative to observations; random forests regressions work well with this 'wide' data structure (Grömping 2009).

The relationship between TPM and OC was estimated using a linear model, as well as the relationship between *O. lurida* shell length at Deanza and DTW. Data corrections and statistical analyses were conducted in consultation with Dr. Kevin Nichols (CSUF Statistical Consulting Unit).

Results

Twenty-five experimental trials, across the four study sites, were included in the analyses; 21 filtration trials and four control trials. A single filtration trial at Deanza (2019-4-17; Table 1) was removed from the analysis because the mean upstream Chl α ($M = 0.1$, $SD = 0.54$) was within the detection limit of the sensor ($\pm 0.1 \mu\text{g/L}$). Filtration trials across sites were not distributed equally (Table 1), Deanza had more than twice the amount filtration trials ($N = 9$) as San Rafael ($N = 4$), Morro Bay ($N = 4$), and Shellmaker ($N = 4$), while each site had a single control.

Ambient water quality during filtration trials varied within and among sites (Figure 2). Salinity was significantly different among sites as determined by a one-way ANOVA at a $p < 0.05$ ($F(3, 17) = 24.7$, $p < 0.001$), along with turbidity ($F(3, 17) = 66.74$, $p < 0.001$), and TPM ($F(3, 15) = 20.06$, $p = < 0.001$) (Figure 2).

Temperature ($F(3, 17) = 2.43$, $p = 0.10$), and Chl α ($F(3, 17) = 2.17$, $p = 0.13$) were not different among sites (Figure 2). OC was significant among sites ($F(3, 15) = 3.92$, $p = 0.03$), but the post-hoc Tukey HSD did not reveal significant differences among sites. Therefore, I use a less conservative post-hoc analysis, the Newman-Keuls method, and found that OC was significantly different between Shellmaker and Deanza ($p = 0.01$).

Percent Chlorophyll α Removal

The mean percent Chl α removal at the San Rafael site was 1.2% ($N = 4$, $SD = 4.36$) (Figure 3) and was -1.3% in the single control trial (Table 1). Filtration trials at Morro Bay had a mean Chl α removal of 0.5% ($N = 4$, $SD = 15.1$) and -0.7% during the control trial. At Deanza, mean Chl α removal was 1.9% ($N = 9$, $SD = 7.5$) and -1% Chl α removal during the control trial. Mean Shellmaker Chl α removal was -11.2 % ($N = 4$, $SD = 34.3$) (Figure 3), and its control trial was -203.8 % (Table 1). Chl α removal in filtration trials did not differ significantly between sites (one-way Kruskal-Wallis, $p = 0.98$).

Oyster Habitat vs. Control

Habitat clearance rates (HCR) in filtration trials ($N = 21$) were not significantly different than in control trials ($N = 4$) (two-sample, one-tail $t(23) = 1.04$, $p = 0.19$). A statistical power analysis determined that the effect size between filtration and control trial HCR was very large ($ES = 1.36$), per the criteria in Sawilowsky (2009), but there was little power (0.78) to detect a statistical signal. A random forest model including all filtration and control trials HCR ($R^2 = 0.65$) indicated that

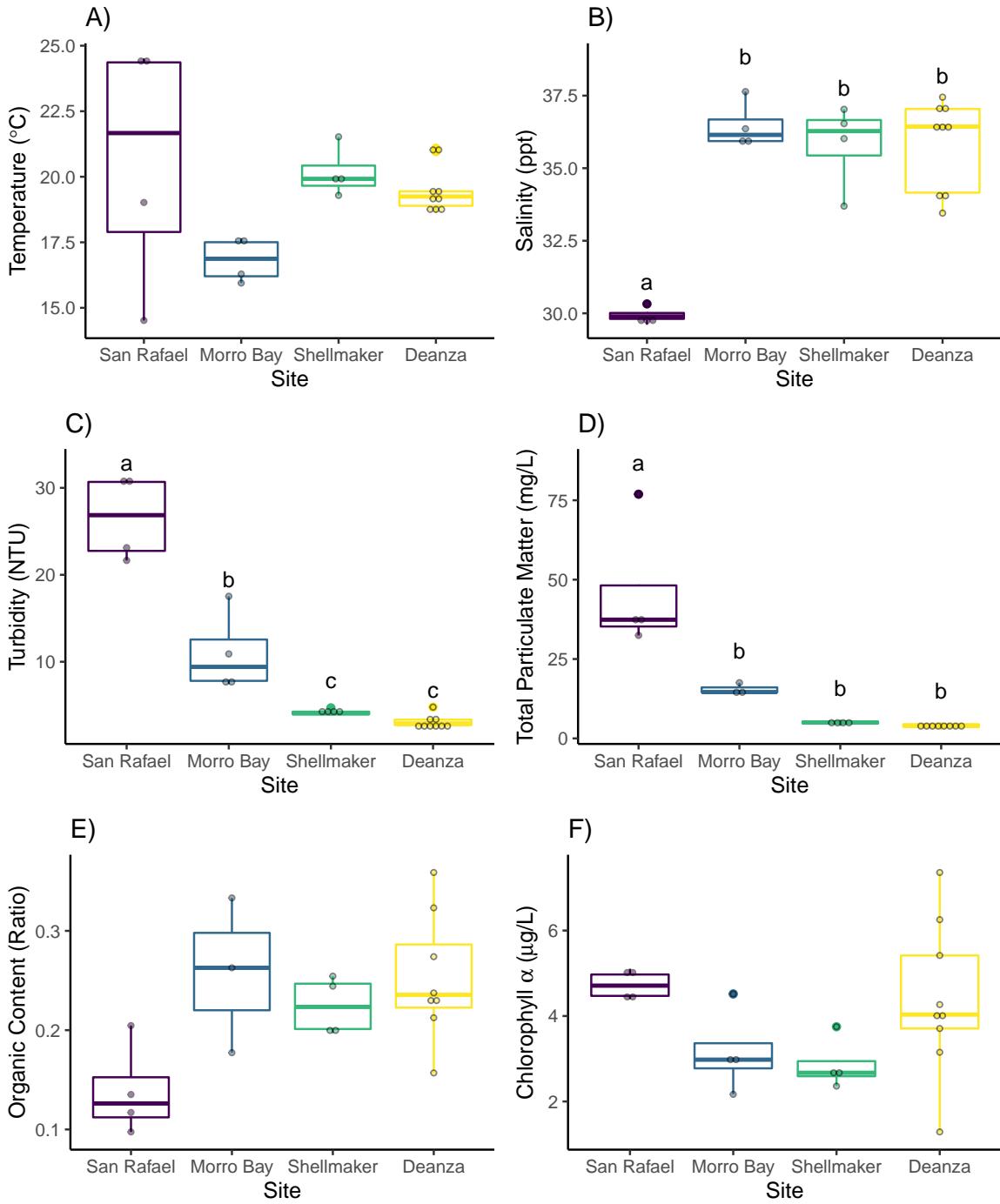


Figure 2: Box plots of ambient (upstream) A) temperature, B) salinity, C) turbidity, D) total particulate matter, E) organic content, and F) chlorophyll α from filtration trials. One-way ANOVAs compared the difference between water quality variables and site. Significantly different results were grouped by a post-hoc Tukey's HSD; significantly different sites do not share a common letter, and non-significant differences share letters. Site effects on OC were significant, and a Newman-Keuls post-hoc analysis determined a significant difference between San Rafael and Deanza undetected by Tukey's HSD. Trials were conducted from February 2018 to June 2019 at San Rafael, CA (restored reefs); Morro Bay, CA (Morro Bay Oyster Company, aquaculture); and Newport Bay, CA (Shellmaker and Deanza, restored beds).

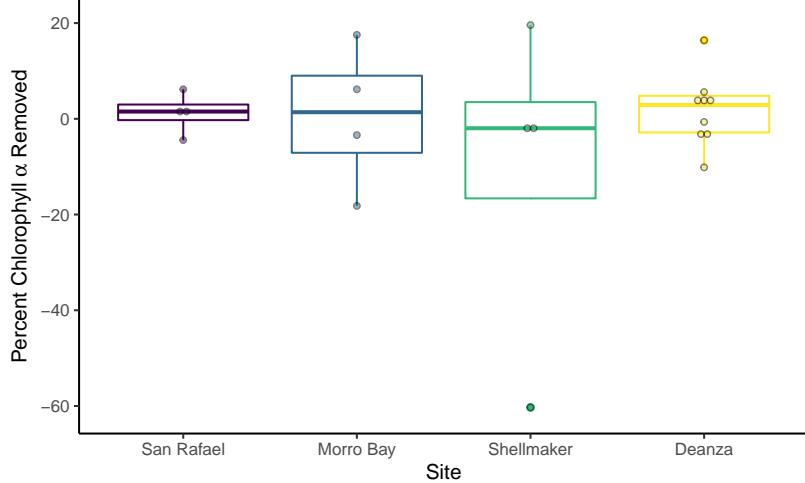


Figure 3: Box plots of percent chlorophyll α removal ($\text{Chl}_{\text{up}} - \text{Chl}_{\text{down}} / \text{Chl}_{\text{up}} * 100$) during filtration trials, control trials are listed in Table 1. Each data point is the mean of a single filtration trial. Filtration trials were conducted between February 2018 to June 2019 at San Rafael, CA (restored reefs); Morro Bay, CA (Morro Bay Oyster Company aquaculture); and Newport Bay, CA (Shellmaker and Deanza, restored beds).

temperature had the highest relative importance to the model (33.1%), followed by OC (29.1%), turbidity (18.4%), TPM (12.1%), salinity (5.9%), and site (1.4%). The residuals of this random forest regression adjusted the HCR values to account for variance caused by water quality variables and site. I then compared these adjusted HCRs between filtration and control trials; they were not significantly different (two-sample, one-tail $t(23) = 1.25, p = 0.149$). A statistical power analysis determined that the effect size of adjusted HCRs between filtration and control trials was still very large ($ES = 1.48$) (Sawilowsky 2009), and with only slightly improved power (0.84) than the unadjusted HCR t-test. Despite non-significant results between control and filtration trials, statistical power analysis indicated that my limited sample size is inhibiting statistical inference of a very large effect size between oyster habitat HCRs relative to mudflat control HCRs.

Habitat Clearance Rates

Mean HCR at San Rafael was $166.3 \text{ L hr}^{-1} \text{ m}^{-2}$ ($N = 4, SD = 254.7$), $10.3 \text{ L hr}^{-1} \text{ m}^{-2}$ ($N = 4, SD = 257.1$) at Morro Bay, $-463.9 \text{ L hr}^{-1} \text{ m}^{-2}$ ($N = 4, SD = 1420.2$) at Shellmaker, and $104.6 \text{ L hr}^{-1} \text{ m}^{-2}$ ($N = 9, SD = 250.9$) at Deanza (Figure 4). Control trials measured $-98.7, -19.4, -8844$, and $-210.3 \text{ L hr}^{-1} \text{ m}^{-2}$ at San Rafael, Morro Bay, Shellmaker, and Deanza respectively. HCR for filtration trials did not differ significantly among sites, see Figure 4 (one-way Kruskal-Wallis, $p = 0.83$). The upper 0.5 quantile of HCR at each site, representing the top filtration performance within each site, also did not differ among sites (one-way Kruskal-Wallis, $p = 0.86$). Individual water quality variables

did not significantly relate with HCR at 0.5 and 0.9 quantiles: temperature ($\tau = 0.5$, $\beta \pm SE = 56.81$, $p = 0.57$; $\tau = 0.9$, $\beta \pm SE = 66.84$, $p = 0.91$), salinity ($\tau = 0.5$, $\beta \pm SE = 41.99$, $p = 0.6$; $\tau = 0.9$, $\beta \pm SE = 38.51$, $p = 0.84$), turbidity ($\tau = 0.5$, $\beta \pm SE = 11.5$, $p = 0.56$; $\tau = 0.9$, $\beta \pm SE = 14.58$, $p = 0.91$), TPM ($\tau = 0.5$, $\beta \pm SE = 7.15$, $p = 0.88$; $\tau = 0.9$, $\beta \pm SE = 11.37$, $p = 0.88$), OC ($\tau = 0.5$, $\beta \pm SE = 1525.41$, $p = 0.9$; $\tau = 0.9$, $\beta \pm SE = 2072.31$, $p = 0.92$) (Figure 5).

Table 1: Details of Whole-habitat *In Situ* Filtration and Control Trials Across Four California Sites. All Values are Means from the Entire Trial. The Trial Separated at the Bottom is within the Chlorophyll α Sensor's Error and was Removed from the Analysis. Dashes Denote Missing Values.

Site	Date	Trial	Tide	HCR (Lhr ⁻¹ m ⁻²)	Chl _{rmnd} (%)	Chl _{up} (μ g/L)	Temp ($^{\circ}$ C)	Salinity (ppt)	Turb (NTU)	TPM (mg/L)	OC (ratio)	Depth (m)	Distance (m)	Velocity (m/s)
SR	2018-07-17	Fltr	Flood	-166	-4.5	4.4	24.51	29.6	30.6	76.91	0.12	0.72	21.0	0.03
SR	2018-07-18	Fltr	Flood	302	1.1	4.5	24.32	29.9	21.7	38.59	0.20	0.79	21.0	0.20
SR	2018-09-10	Fltr	Flood	112	1.9	4.9	19.02	30.3	23.1	36.19	0.10	0.89	25.3	0.05
SR	2018-11-07	Control	Ebb	-99	-1.3	6.9	16.45	29.9	25.5	30.04	0.17	0.40	11.6	0.06
SR	2018-11-08	Fltr	Ebb	417	6.2	5.1	14.52	29.9	30.9	32.45	0.14	0.69	12.3	0.03
MB	2018-07-27	Fltr	Flood	346	17.5	4.5	17.66	35.9	7.9	17.53	0.26	0.48	26.0	0.03
MB	2018-07-28	Fltr	Flood	65	6.2	3.0	17.45	35.9	74	14.60	0.33	0.30	27.0	0.03
MB	2019-05-18	Fltr	Flood	-128	-3.4	3.0	16.29	37.6	17.5	-	-	0.42	30.5	0.08
MB	2019-05-19	Fltr	Flood	-242	-18.2	2.2	15.94	36.4	10.9	14.45	0.18	0.45	30.5	0.02
MB	2019-06-06	Control	Flood	-19	-0.7	2.1	17.28	38.1	11.9	12.80	0.22	0.32	20.5	0.05
NPSM	2019-05-10	Fltr	Flood	-120	-1.9	3.7	19.78	37.0	4.1	5.90	0.24	0.38	13.0	0.06
NPSM	2019-05-11	Fltr	Flood	845	19.6	2.4	21.52	36.5	4.7	5.14	0.25	0.32	12.2	0.04
NPSM	2019-05-22	Fltr	Flood	-2485	-60.3	2.7	19.29	33.7	3.8	4.92	0.20	0.26	8.6	0.04
NPSM	2019-06-08	Fltr	Flood	-97	-2.1	2.7	20.06	36.0	4.0	3.95	0.20	0.26	8.6	0.04
NPSM	2019-06-09	Control	Flood	-8844	-203.8	1.1	22.40	36.0	5.9	4.02	0.18	0.30	11.2	0.04
NPD	2018-10-25	Fltr	Ebb	-216	-10.1	3.2	21.09	33.5	4.8	-	-	0.18	19.2	0.06
NPD	2018-10-26	Fltr	Ebb	467	16.4	4.0	20.96	36.4	2.4	4.39	0.36	0.19	19.2	0.08
NPD	2019-04-15	Fltr	Ebb	-22	-0.7	1.3	19.43	36.4	3.4	4.73	0.32	0.23	16.4	0.07
NPD	2019-05-09	Fltr	Ebb	242	4.6	5.4	19.44	37.0	2.3	2.67	0.21	0.32	15.0	0.07
NPD	2019-05-10	Fltr	Ebb	383	5.6	4.0	19.25	37.4	2.9	5.10	0.16	0.31	14.8	0.09
NPD	2019-05-11	Fltr	Ebb	248	2.9	3.7	18.85	36.5	2.9	4.00	0.24	0.35	15.0	0.10
NPD	2019-05-21	Fltr	Ebb	-153	-3.5	6.3	18.89	34.2	3.3	3.57	0.23	0.24	16.0	0.08
NPD	2019-05-22	Fltr	Ebb	149	4.8	7.4	18.62	33.9	2.8	3.83	0.23	0.22	15.7	0.06
NPD	2019-06-08	Fltr	Ebb	-156	-2.8	4.3	19.07	37.1	2.7	3.65	0.27	0.26	15.7	0.09
NPD	2019-06-09	Control	Ebb	-210	-1.3	3.0	19.29	37.0	1.7	2.80	0.21	0.48	12.8	0.12
NPD	2019-04-17	Fltr	Ebb	-4867	-108.9	0.1	19.41	37.4	4.9	4.03	0.23	0.18	16.4	0.11

San Rafael (SR); Morro Bay (MB); Shellmaker (NPSM); Deanza (NPD); Filtration (Fltr); habitat clearance rate (HCR); chlorophyll α removed (Chl_{rmnd}); chlorophyll α upstream (Chl_{up}); temperature (Temp); turbidity (Turb); total particulate matter (TPM); seston organic content (OC).

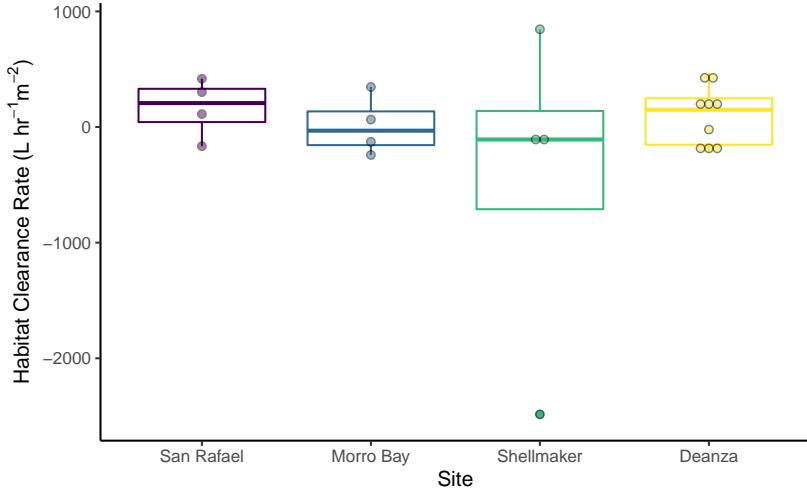


Figure 4: Box plots of habitat clearance rates (HCR) during filtration trials; control trials are listed in Table 1. Each data point is the mean of a single filtration trial. HCR was not statistically different among sites (one-way Kruskal-Wallis). Filtration trials were conducted between February 2018 to June 2019 at San Rafael, CA (restored *O. lurida* reefs); Morro Bay, CA (Morro Bay Oyster Company *C. gigas* aquaculture); and Newport Bay, CA (Shellmaker and Deanza, restored beds).

A random forest regression containing only filtration trials ($R^2 = 0.59$) indicated that temperature (25.9%) had the highest relative importance to the model, followed by turbidity (23.5%), TPM (16.5%), OC (12.3%), site (11.3%), and salinity (10.5%).

Seston Quantity and Quality

Total Particulate Matter (TPM) was significantly related to seston OC when sites were combined (Figure 6). This model includes all field days (filtration and controls) because water samples used to determine TPM and OC were collected the same way regardless of the trial. Northern San Francisco Bay (San Rafael) TPM averaged 42.84 mg/L ($N = 5$, $SD = 19.33$), and Morro Bay TPM averaged 14.85 mg/L ($N = 4$, $SD = 1.97$) (Figure 6). Newport Bay (Deanza and Shellmaker) TPM averaged 4.18 mg/L ($N = 15$, $SD = 0.87$). Northern San Francisco Bay (San Rafael) OC averaged 0.15 ($N = 5$, $SD = 0.04$), and Morro Bay OC averaged 0.25 ($N = 4$, $SD = 0$). Newport Bay (Deanza and Shellmaker) OC averaged 0.237 ($N = 15$, $SD = 0.05$) (Figure 6).

Filter Feeding Community

In November 2017 the estimated bivalve density at San Rafael was 420 individuals/m², all of which were *Ostrea lurida* (Figure 7). Other bivalves were noted, but were rare, and were not detected in sample bags (C. Zabin, unpublished data). Morro Bay had an estimated 409 *Crassostrea gigas* individuals/m² in the summer of 2018 (Morro Bay Oyster Company); personal field observa-

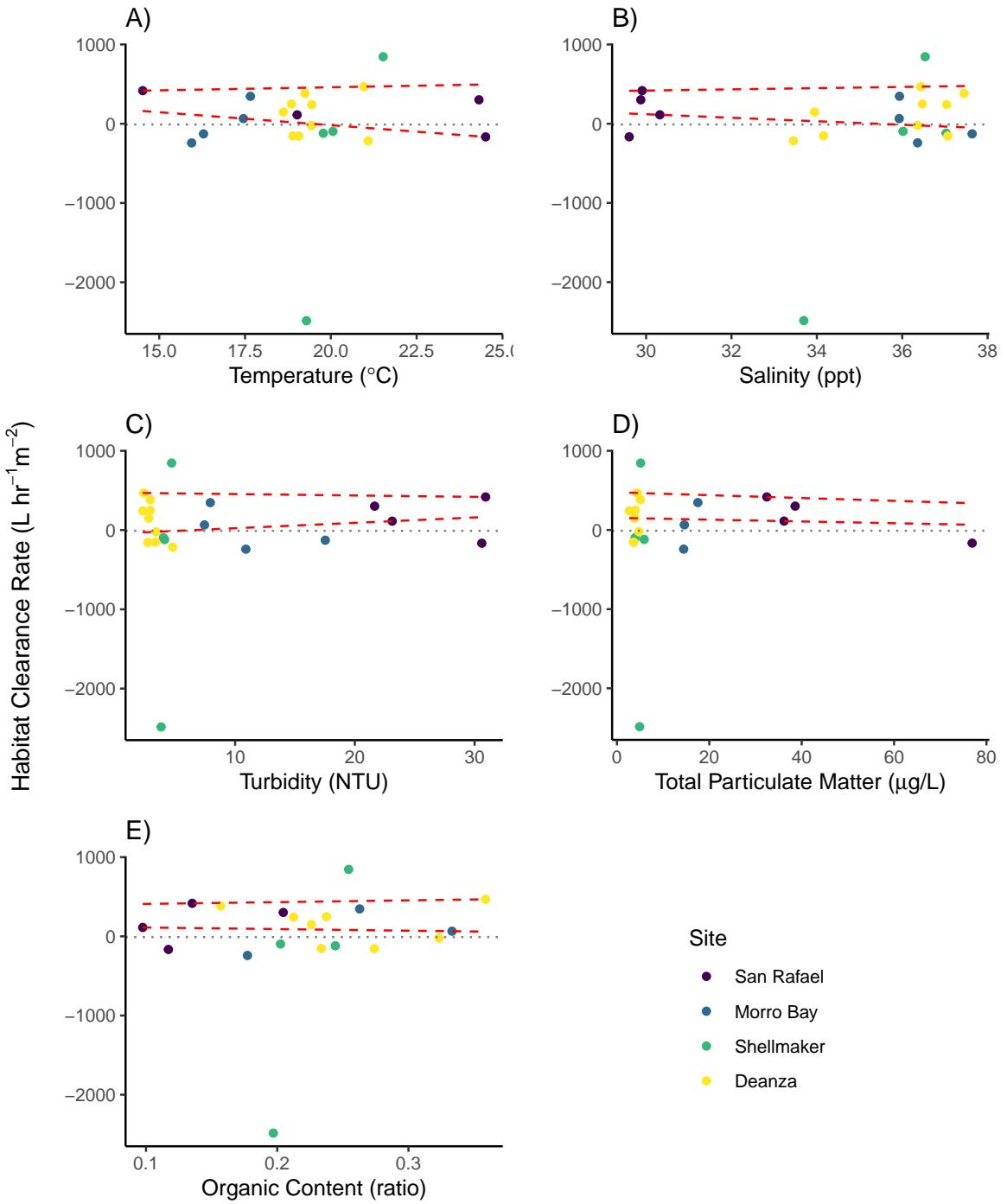


Figure 5: The relationship between water quality variables and habitat clearance rate (HCR). For all oyster habitat filtration trials, quantile regression with $\tau = 0.5$ and $\tau = 0.9$ was used to test whether HCR changed with A) temperature, B) salinity, C) turbidity, D) total particulate matter, or E) organic content; slopes that are not significantly different from zero are indicated by red dashed lines. Dotted gray lines are the mean value of HCR.

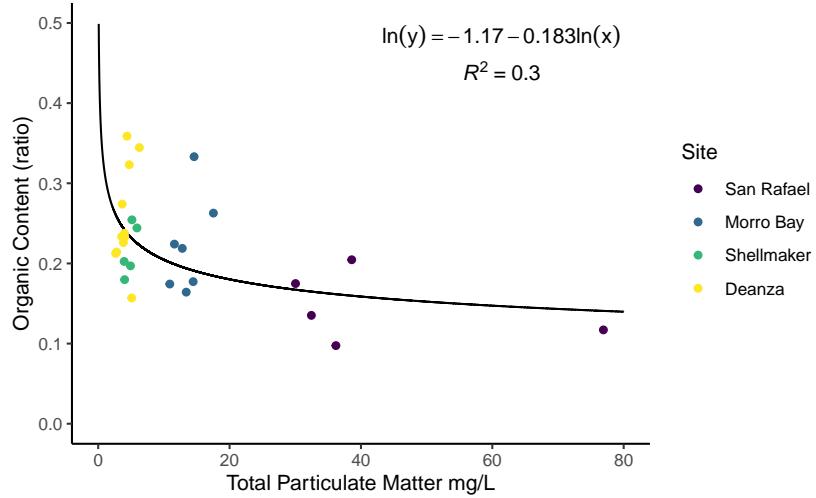


Figure 6: The relationship between seston total particulate matter (TPM) and seston organic content (OC) across sites and all trials. Two trials are not included because of missing TPM data.

tions confirm the lack of bivalve fouling on the aquaculture lines. In May 2018, Shellmaker had an estimated 1283.2 individuals/m², composed of *Adula diegensis* (545.6 individuals/m²), *Musculista senhousia* (438.4 individuals/m²), *O. lurida* (238.4 individuals/m²), *Mytilus galloprovincialis* (51.2 individuals/m²), *Geukensia demissa* (8 individuals/m²), and *Argopecten ventricosa* (1.6 individuals/m²) (Figure 7). Deanza had an estimated 2588.8 individuals/m² in May 2018, and was composed of *M. senhousia* (1979.2 individuals/m²), *A. diegensis* (296 individuals/m²), *O. lurida* (233.6 individuals/m²), *M. galloprovincialis* (80 individuals/m²) (Figure 7).

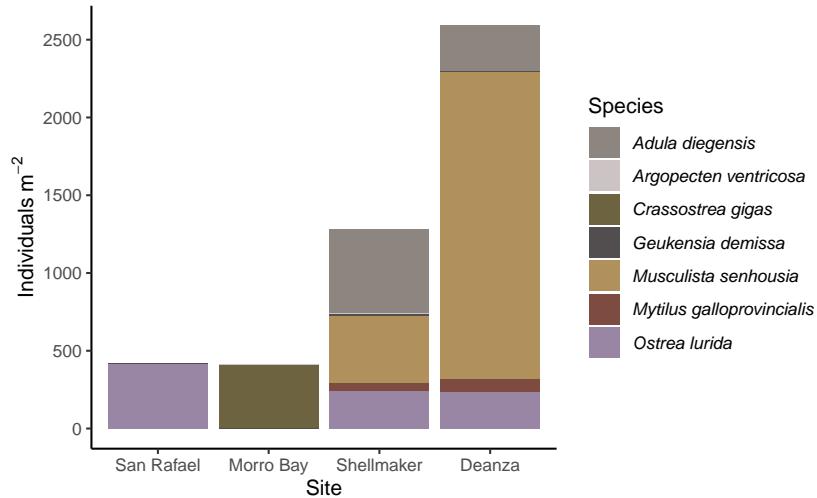


Figure 7: Bivalve community density and composition for each study site. San Rafael data were collected November 2017 by the Zabin lab at SERC, Morro Bay was estimated by Morro Bay Oyster Company in 2018, and Shellmaker and Deanza were surveyed in May 2018 by the Zacherl lab at CSUF.

Direct biomass data were only available for Deanza, which estimated 3.26 g/m^2 of bivalve dry tissue weight (DTW) (Figure 8). *O. lurida* had the highest DTW with 1.36 g/m^2 , followed by *M. galloprovincialis* (1 g/m^2), an unknown *Modiolus* sp. (0.44 g/m^2), *A. diegensis* (0.37 g/m^2), and *M. senhousia* (0.28 g/m^2) (Figure 8). San Rafael surveys did not directly measure biomass, but did include *O. lurida* shell length measurements which I used to estimate DTW (Figure 8) with a model describing the relationship between *O. lurida* shell length and DTW at Deanza ($\ln(y) = -10.8 + 2.38\ln(x)$, $R^2 = 0.73$, $p < 0.0001$) (Figure 9). I estimated San Rafael had 0.22 g/m^2 of *O. lurida* (Figure 8). A direct comparison between site biomass to HCR was not possible with my limited biomass and shell length data.

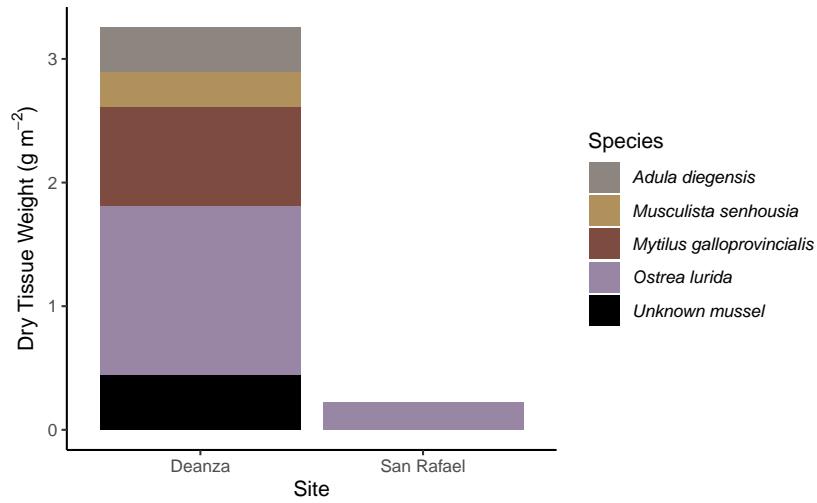


Figure 8: Estimated biomass of *O. lurida* habitat at Deanza and San Rafael sites. Data for Deanza was collected by the Zacherl lab (CSUF) in May 2018, the relationship between *O. lurida* shell length and dry tissue weight (DTW) from the survey was used to estimate DTW at San Rafael with shell length data collected by the Zabin lab (SERC) in November 2017.

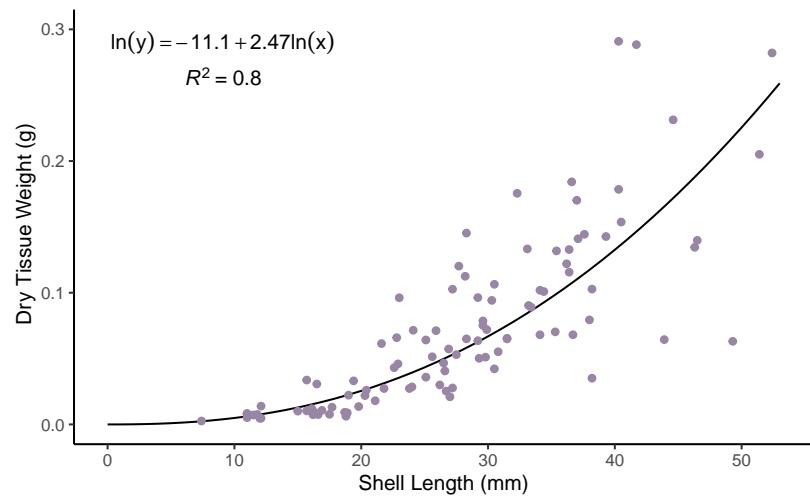


Figure 9: The relationship between *O. lurida* shell length and dry tissue weight (DTW) at the Deanza restoration site in Newport Bay, California.

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 ostrea 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 4). 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-explicit 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 $0.78 \text{ L hr}^{-1}\text{g}^{-1}$ in the dry season and $0.19 \text{ L hr}^{-1}\text{g}^{-1}$ in the wet season in Yaquina Bay,

Oregon. *C. gigas* averaged $0.95 \text{ L hr}^{-1}\text{g}^{-1}$ in the dry season and $1.06 \text{ L hr}^{-1}\text{g}^{-1}$ 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 $0.73 \text{ L hr}^{-1}\text{g}^{-1}$ (0.24 SE). According to Gray & Langdon's (2018) all-season model and the biomass of *O. lurida* at Deanza ($1.36 \text{ g DTW m}^{-2}$), Deanza's HCR should be $1.13 \text{ L hr}^{-1}\text{m}^{-2}$ using mean OC and temperature from my Deanza trials. In my study, the mean HCR at Deanza was $105 \text{ L hr}^{-1}\text{m}^{-2}$, 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 9) 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. Hydrodynamics 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 partially 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 (8), one would not expect San Rafael to have a similar filtration services (Figure 4). 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 4). 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⁻¹m⁻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 7). 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 2020a, 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 2020a, 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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