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 (± 0.1 μg/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 1). 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 1).

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 1). 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 2) 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 2), 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 ($R^2 = 0.61$) indicated that temperature had the highest relative importance to the model (46.8%), followed by OC (25.6%), turbidity (11.0%), TPM (8.5%), salinity (6.8%), and site

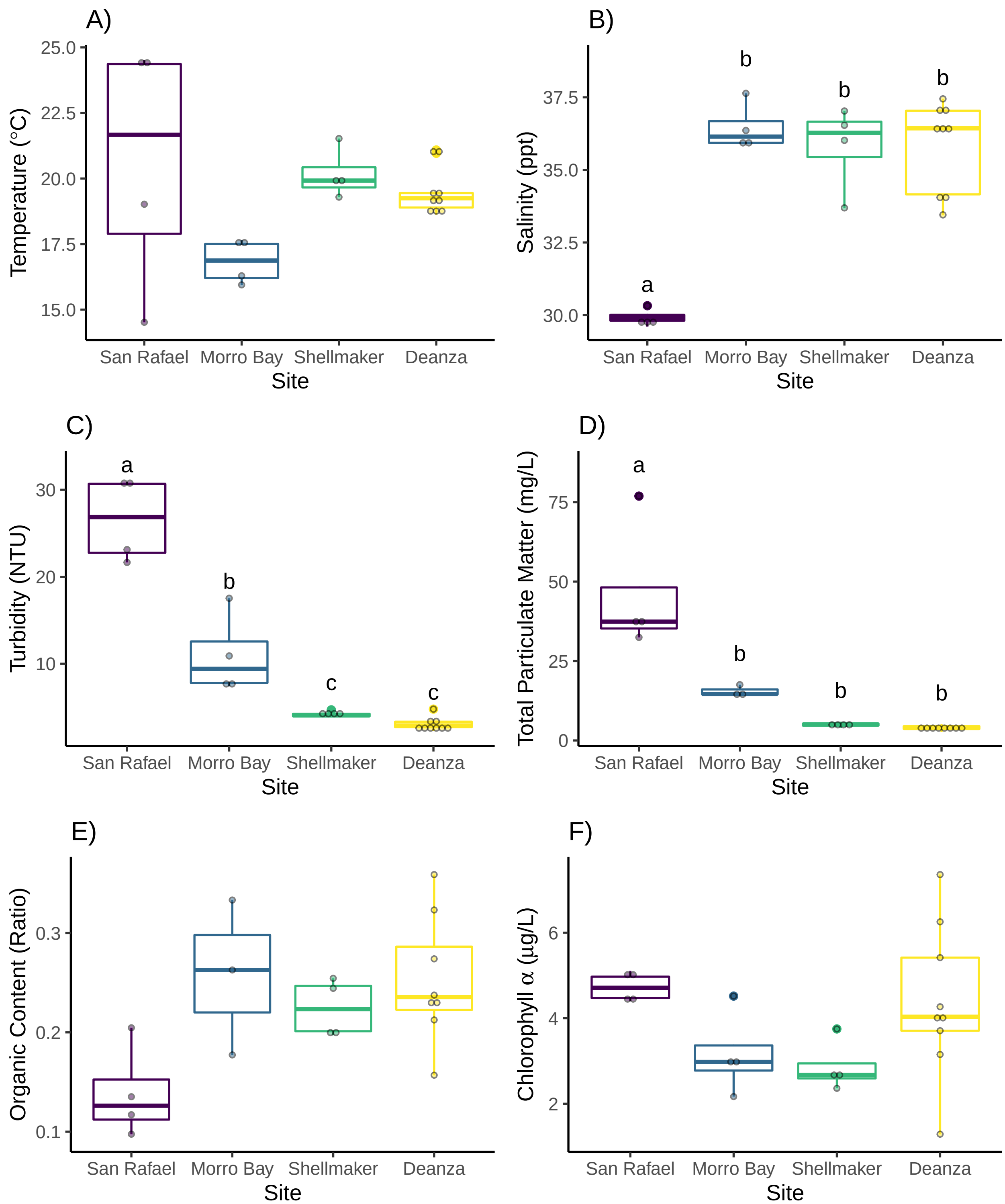

Figure 1: Box plots of ambient (upstream) A) temperature, B) salinity, C) turbidity, D) total particulate matter, E) organic content, and F) chlorophyll α from filtration trials. One-way ANOVAs compared the difference between water quality variables and site. Significantly different results were grouped 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).

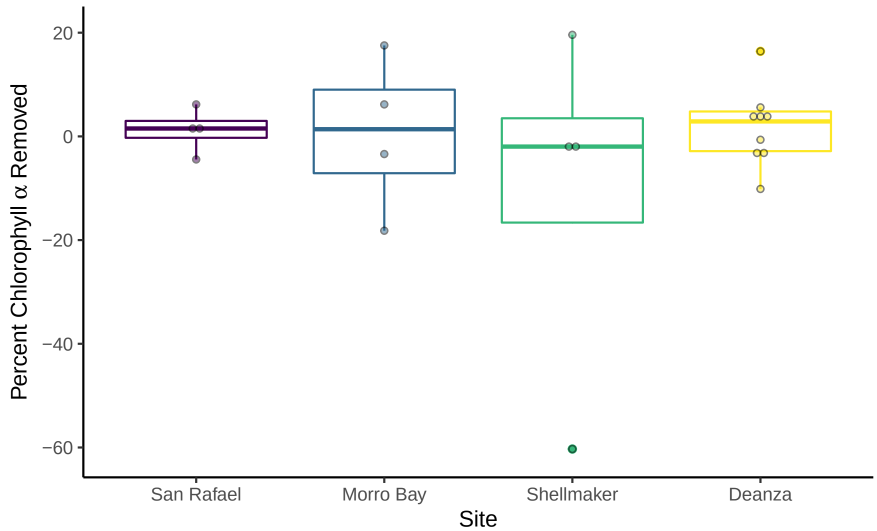

Figure 2: Box plots of percent chlorophyll α removal (Chl_{up} - Chl_{down} / Chl_{up} * 100) during filtration trials, control trials are listed in Table 1. Each data point is the mean of a single filtration trial. Filtration trials were conducted between February 2018 to June 2019 at San Rafael, CA (restored reefs); Morro Bay, CA (Morro Bay Oyster Company aquaculture); and Newport Bay, CA (Shellmaker and Deanza, restored beds).

(1.3%). 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 $t(23) = 1.25$, $p = 0.15$). A statistical power analysis determined that the effect size of adjusted HCRs between filtration and control trials was still very large ($ES = 1.47$) (Sawilowsky 2009), and with only slightly improved power (0.83) 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 L hr^{-1} m^{-2} ($N = 4$, $SD = 254.7$), 10.3 L hr^{-1} m^{-2} ($N =$ to 4, $SD =$ 257.1) at Morro Bay, -463.9 L hr^{-1} m^{-2} ($N = 4$, $SD = 1420.2$) at Shellmaker, and 104.6 L hr^{-1} m^{-2} ($N = 9$, $SD = 250.9$) at Deanza (Figure 3). Control trials measured -98.7, -19.4, -8844, and -210.3 L hr^{-1} m^{2} at San Rafael, Morro Bay, Shellmaker, and Deanza respectively. HCR for filtration trials did not differ significantly among sites, see Figure 3 (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 ($\tau = 0.5$, $\beta \pm SE = 57.01$, $p = 0.57$; $\tau = 0.9$, $\beta \pm SE = 66.93$, $p = 0.91$), salinity

($\tau = 0.5$, $\beta \pm SE = 41.4$, $p = 0.6$; $\tau = 0.9$, $\beta \pm SE = 40.24$, $p = 0.85$), turbidity ($\tau = 0.5$, $\beta \pm SE = 11.13$, $p = 0.55$; $\tau = 0.9$, $\beta \pm SE = 13.19$, $p = 0.9$), TPM ($\tau = 0.5$, $\beta \pm SE = 7.83$, $p = 0.89$; $\tau = 0.9$, $\beta \pm SE = 8.87$, $p = 0.84$), OC ($\tau = 0.5$, $\beta \pm SE = 1562.5$, $p = 0.9$; $\tau = 0.9$, $\beta \pm SE = 2141.16$, $p = 0.92$) (Figure 4).

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_{rmd} (%)	Chl_{up} ($\mu g/L$)	Temp (°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	7.4	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_{rmd}); chlorophyll α upstream (Chl_{up}); temperature (Temp); turbidity (Turb); total particulate matter (TPM); seston organic content (OC).

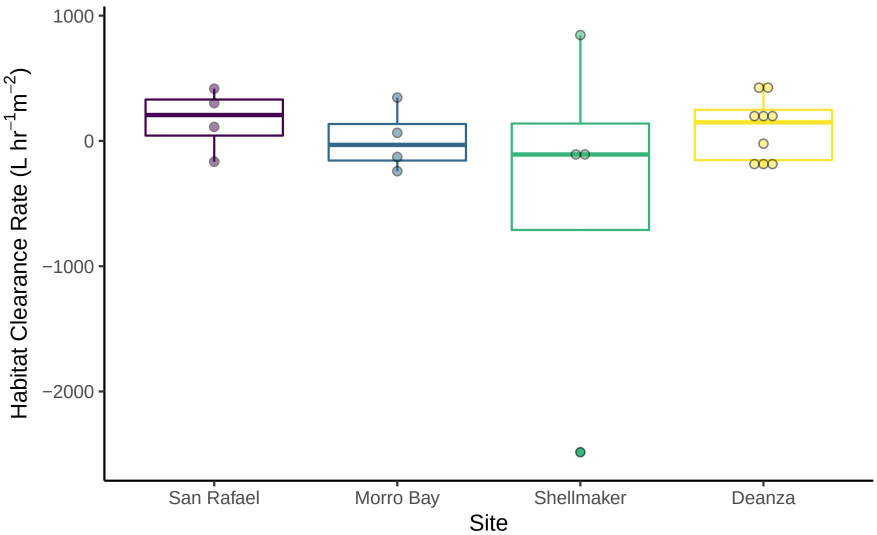

Figure 3: Box plots of habitat clearance rates (HCR) during filtration trials; control trials are listed in Table 1. Each data point is the mean of a single filtration trial. HCR was not statistically different among sites (one-way Kruskal-Wallis). Filtration trials were conducted between February 2018 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 (27.1%) had the highest relative importance to the model, followed by turbidity (18.6%), TPM (17.2%), OC (16.7%), site (14.4%), and salinity (6%).

Seston Quantity and Quality

Total Particulate Matter (TPM) was significantly related to seston OC when sites were combined (Figure 5). 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 5). 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 5).

Filter Feeding Community

In November 2017 the estimated bivalve density at San Rafael was 420 individuals/m^2, all of which were *Ostrea lurida* (Figure 6). Other bivalves were noted, but were rare, and were not detected in sample bags (C. Zabin, unpublished data). Morro Bay had an estimated 600 *Crassostrea gigas* individuals/m^2 in the

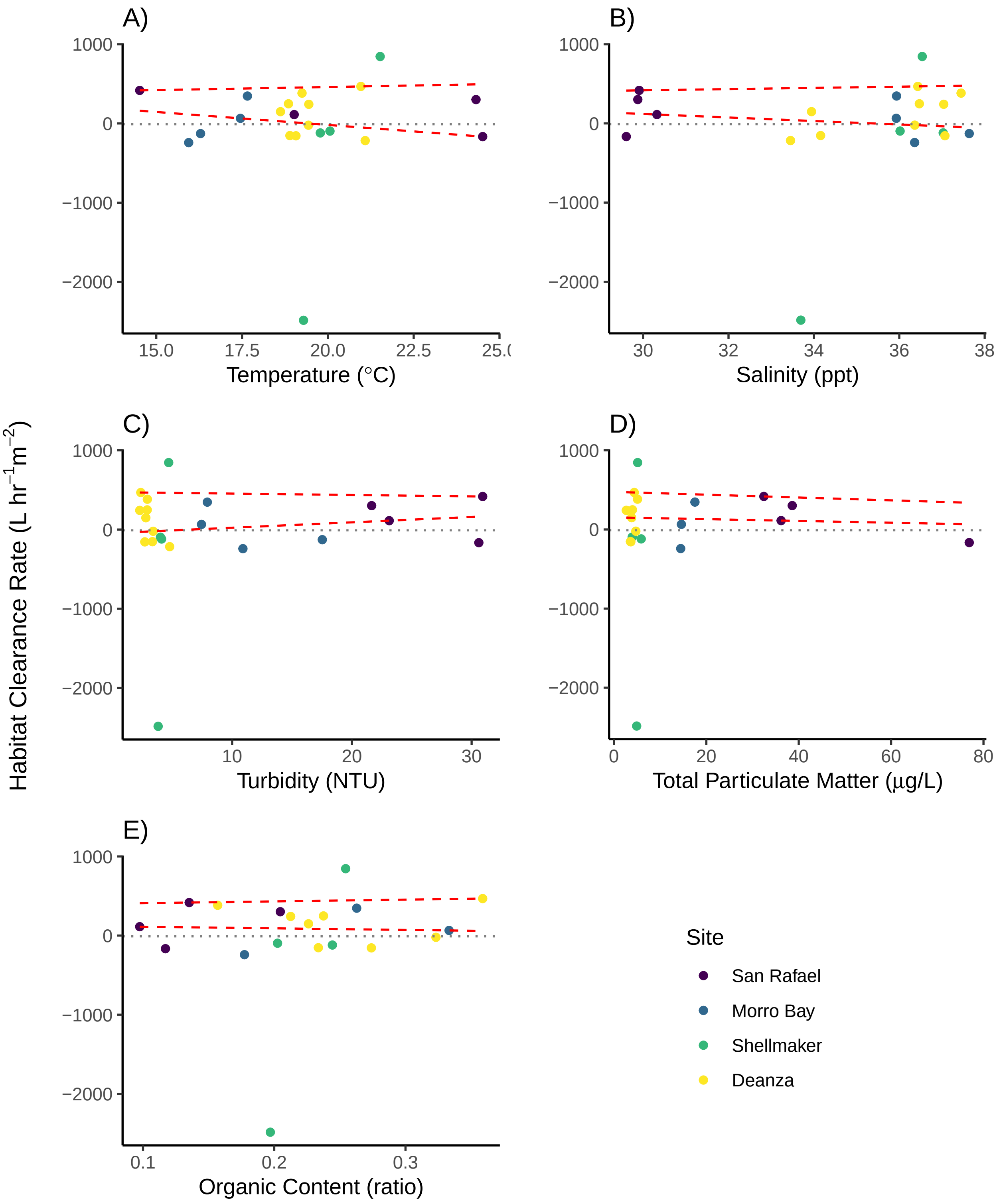

Figure 4: The relationship between water quality variables and habitat clearance rate (HCR). For all oyster habitat filtration trials, quantile regression with $\tau = 0.5$ and $\tau = 0.9$ was used to test wheather HCR changed with A) temperature, B) salinity, C) turbidity, D) total particulate matter, 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.

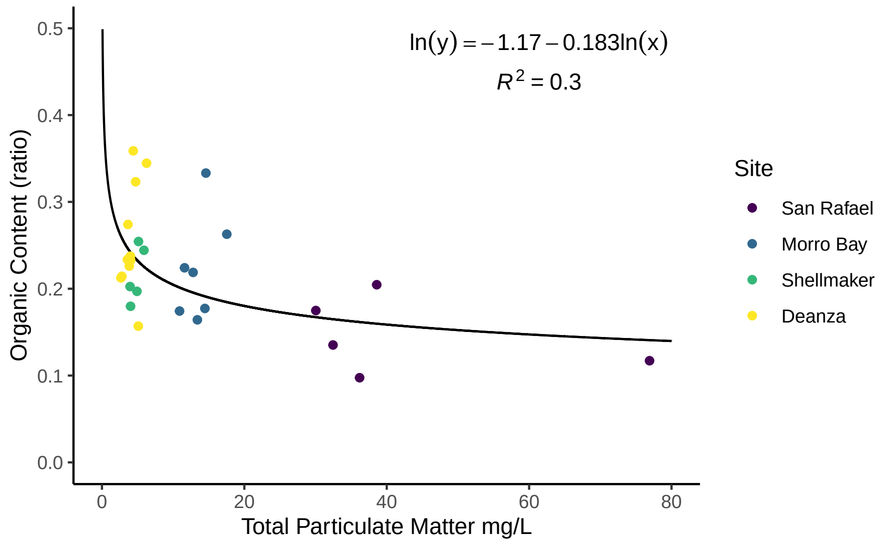

Figure 5: The relationship between seston total particulate matter (TPM) and seston organic content (OC) across sites and all trials. Two trials are not included because of missing TPM data.

summer of 2018 (Morro Bay Oyster Company); personal field observations confirm the lack of bivalve fouling on the aquaculture lines. In May 2018, Shellmaker had an estimated 1283.2 individuals/m^2, composed of *Adula diegensis* (545.6 individuals/m^2), *Musculista senhousia* (438.4 individuals/m^2), *O. lurida* (238.4 individuals/m^2), *Mytilus galloprovincialis* (51.2 individuals/m^2), *Geukensia demissa* (8 individuals/m^2), and *Argopecten ventricosa* (1.6 individuals/m^2) (Figure 6). Deanza had an estimated 2588.8 individuals/m^2 in May 2018, and was composed of *M. senhousia* (1979.2 individuals/m^2), *A. diegensis* (296 individuals/m^2), *O. lurida* (233.6 individuals/m^2), *M. galloprovincialis* (80 individuals/m^2) (Figure 6).

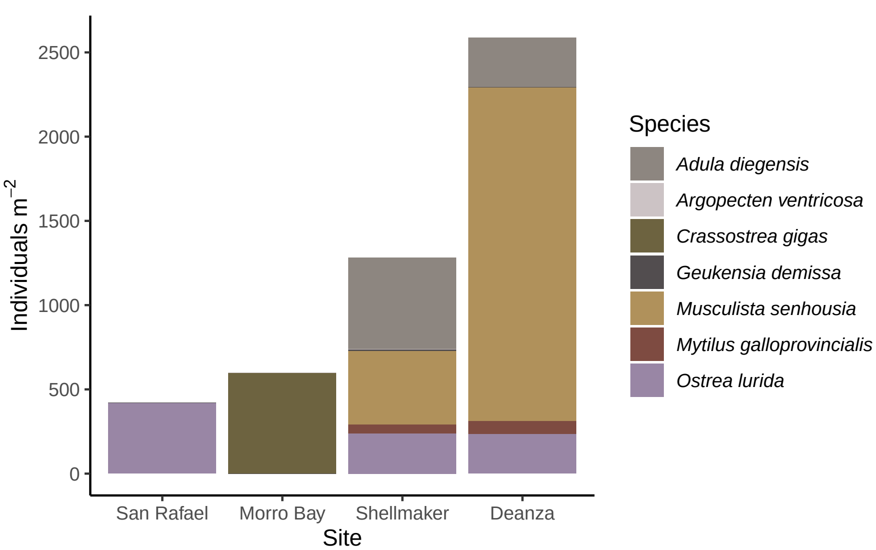

Figure 6: Bivalve community density and composition for each study site. San Rafael data were collected November 2017 by the Zabin lab at SERC, Morro Bay was estimated by Morro Bay Oyster Company in 2018, and Shellmaker and Deanza were surveyed in May 2018 by the Zacherl lab at CSUF.

Direct biomass data were only available for Deanza, which estimated 3.26 g/m^2 of bivalve dry tissue weight (DTW) (Figure 7). *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 7). San Rafael surveys did not directly measure biomass, but did include *O. lurida* shell length measurements which I used to estimate DTW (Figure 7) 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 8). I estimated San Rafael had 0.22 g/m^2 of *O. lurida* (Figure 7). A direct comparison between site biomass to HCR was not possible with my limited biomass and shell length data.

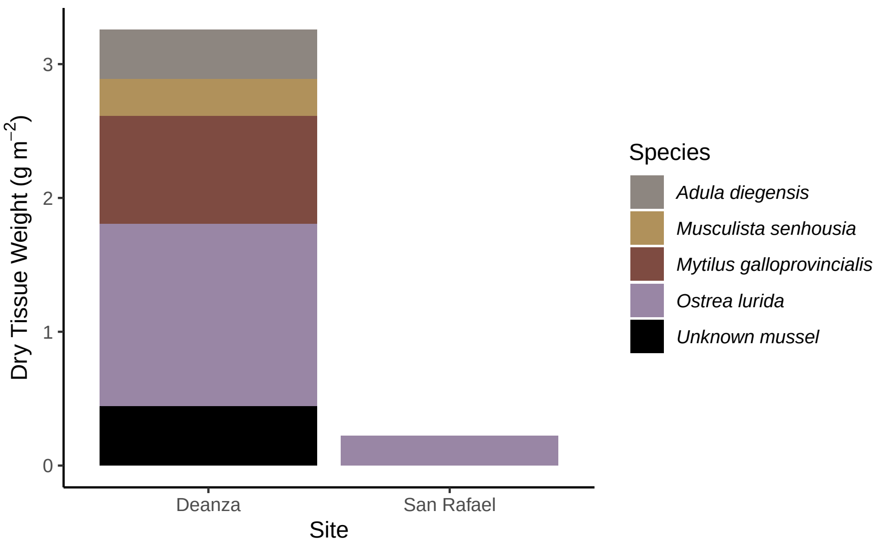

Figure 7: Estimated biomass of *O. lurida* habitat at Deanza and San Rafael sites. Data for Deanza was collected by the Zacherl lab (CSUF) in May 2018, the relationship between *O. lurida* shell length and dry tissue weight (DTW) from the survey was used to estimate DTW at San Rafael with shell length data collected by the Zabin lab (SERC) in November 2017.

Sawilowsky SS (2009) Very large and huge effect sizes. Journal of Modern Applied Statistical Methods 8:597–599.

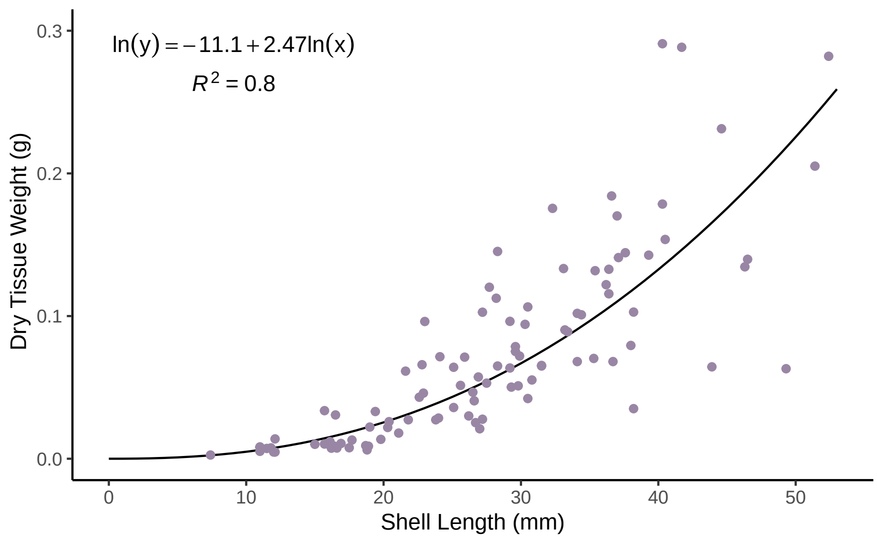

Figure 8: The relationship between *O. lurida* shell length and dry tissue weight (DTW) at the Deanza restoration site in Newport Bay, California.