EFFECTS OF INTERTIDAL OYSTER REEFS ON WATER QUALITY IN A TIDAL CREEK ECOSYSTEM

Kimberly A. Cressman

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Approved by

Advisory Committee

Lynn A. Leonard

Troy Alphin

Michael A. Mallin

Lawrence Cahoon

Martin H. Posey
Chair

Accepted by

Robert Roer
Dean, Graduate School

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ABSTRACT

The importance of oyster filtering in moderating aspects of water quality has received increased attention over the past several years. With population growth and increasing development in coastal watersheds come increased runoff and pollution of tidal creeks. It has been suggested that bivalves may play an important role in controlling phytoplankton levels in shallow coastal areas, with several laboratory studies and models estimating the potential filtration effects of these organisms. However, few field studies have been undertaken to quantify these effects. This study examined the influence of intertidal oyster reefs on chlorophyll *a*, fecal coliform bacteria and total suspended solid concentrations under field conditions in a tidal creek estuary. Oyster reefs of varying live oyster density were sampled during summer 2002, winter 2003 and spring 2003. Water samples were taken upstream and downstream of each reef as well as over a mudflat control area on an ebb tide and analyzed for concentrations of these water column constituents. Summer data showed consistent and statistically significant decreases in chlorophyll *a* concentrations as water moved over the reef, usually by 10-25%. Fecal coliform counts were frequently lower downstream, by up to 45%, but were much more variable and not statistically different in most cases. Data taken in winter, when temperatures and oyster feeding rates are lower, show less consistency in upstream vs. downstream patterns. In spring, chlorophyll *a* decreases were less frequent than in summer, but significant fecal coliform decreases were more frequent. Data from this study indicate that feeding by oysters and changes in water flow caused by the presence of reefs may both play a role in reducing particulate loads in the water column.

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INTRODUCTION

Increasing coastal populations and watershed development have led to concerns over water quality for both shellfishing and human contact waters. Among the water quality concerns in coastal areas are water-borne pathogens, eutrophication, increased turbidity and sediment loads. Most water pollution in coastal areas is from non-point, anthropogenic sources. Nutrients, sediments and pathogens enter natural water bodies through runoff and can have both human health and ecosystem-level impacts.

Microbial pathogens, particularly those from human and animal feces, can pose concerns for human health (Grimes 1991). Fecal coliform bacteria are used as indicators of pathogens associated with human and animal wastes, and their water column concentrations can be used to classify water bodies. Fecal coliform concentrations are strongly correlated with human population density, development, and especially with percent impervious surface coverage in a watershed (Young and Thackston 1999; Mallin et al. 2000). They have also been shown to be positively correlated with nitrate and orthophosphate concentrations (Mallin et al. 2000) and turbidity (Pommepuy et al. 1992; Mallin et al. 2000), and inversely correlated with salinity (Goyal et al. 1977; Mallin et al. 1999; Mallin et al. 2000). Suspended solids and turbidity can contribute to survival and even growth of fecal coliform bacteria by providing protection from light, an organic substrate, and a mechanism for transport downstream (Gerba and McLeod 1976; Pommepuy et al. 1992; Sayler et al. 1975). Additionally, rainfall events can be correlated with increases in fecal coliform concentrations (Goyal et al. 1977; Struck 1988; Howell et al. 1995) due to runoff inputs.

Increasing sedimentation and turbidity are concerns not only for their role in the survival of fecal coliforms, but also because of their effects on water column irradiance. Suspended solids and turbidity can prevent light from penetrating the water column and negatively impact the growth of primary producers such as rooted aquatic macrophytes, benthic microalgae, and phytoplankton (Cordone and Kelley 1961). Additionally, benthic community structure, including shellfish beds, can be affected by burial by sediments and interference with feeding (Loosanoff and Tommers 1948; Posey 1990; Shumway 1996). Major contributors to increased sedimentation are construction and increased runoff due to impervious surfaces and certain agricultural practices.

Nixon (1995) defines eutrophication as "an increase in the rate of supply of organic matter to an ecosystem." Direct effects of eutrophication include changes in chlorophyll, primary production, and phytoplankton communities (Cloern 2001). Dominance in the phytoplankton community with eutrophication can switch from diatoms to flagellates and cyanobacteria, and nuisance or toxic algal blooms can occur. Extreme phytoplankton biomass can result in hypoxia or anoxia when the algae die (Bricker et al. 1999). Indirect effects include changes in water transparency, nutrient cycling, benthic communities, and food web structure (Cloern 2001; Posey et al. 2002). These effects are moderated by system attributes; some areas are more sensitive to nutrient loading than others (Cloern 2001). The main cause of eutrophication is nutrient loading, which can come from fertilizers, human and animal wastes, and fossil fuel combustion (Nixon 1995, Bricker et al. 1999).

Eutrophication, sediment loading, and pathogen problems are all serious water quality issues to which watershed development contributes. Increasing populations lead

to increased demands on land and water, and proper management practices must be implemented as preventative measures. For example, vegetated buffer zones help filter water naturally and reduce sediment, nutrient and pollutant loads before runoff enters natural waterways. Other natural measures are being studied as possible remediation techniques. Some recent studies have centered on the role of bivalves, such as the eastern oyster, *Crassostrea virginica*, in regulating suspended particulate loads in estuarine systems.

Models based on laboratory studies of bivalve filtration rates predict that bivalves, when sufficiently abundant in shallow waters, can control phytoplankton biomass (Cloern 1982; Officer et al. 1982; Gerritsen et al. 1994). In the shallow freshwater and oligohaline portions of Chesapeake Bay, bivalves may consume more than 50% of annual primary production (Gerritsen et al. 1994). These models, however, are often based on high estimates of feeding rates from laboratory trials and fail to take into account variability in bivalve feeding rates under field conditions or bivalves' release of nutrients, which could actually stimulate phytoplankton growth. Oyster feeding rates can be affected by temperature, salinity, suspended solid concentrations, and other factors (Shumway 1996). Filter feeding is not the only possible mechanism for removal of particulate matter. It may also be caused by physical effects of oyster reefs on water flow (Dame 1987). The presence of reefs can cause eddies and turbulence, which lead to the settling of fine particles.

Field studies regarding removal of particulate matter by oyster reefs are somewhat limited. Dame et al. (1984, 1985, 1989) and Dame and Dankers (1988) used a plexiglass tunnel to measure the change in several water column constituents as water traveled over

the oyster reef. They found significant decreases in total organic carbon, particulate organic carbon, total suspended solids, nitrite+nitrate, and chlorophyll *a* (Dame et al. 1984; Dame et al. 1985; Dame and Dankers 1988). Ammonium concentrations increased downstream of oyster reefs, suggesting a role for oyster reefs in nutrient cycling (Dame et al. 1984; Dame et al. 1985; Dame et al. 1989; Dame and Dankers 1988, Nelson et al. 2003). Tidal creeks with oysters did not show significantly lower chlorophyll *a* levels than creeks without oysters, suggesting that oyster grazing may not limit phytoplankton growth at this scale (Dame and Libes 1993).

The eastern oyster is a filter feeder that is widely believed to reduce the amount of particulate matter in the water column. Field evidence to support this idea, however, is limited, and no field tests of fecal coliform reductions over oyster reefs have been published. This research assessed the impacts of intertidal oyster reefs on suspended solids, chlorophyll *a*, and fecal coliform bacteria in a human-impacted tidal creek, and examined whether live oyster density over natural ranges influenced rates of seston removal.

METHODS

Study Site

Six natural, intertidal oyster reefs were chosen for study in Hewletts Creek, southeastern North Carolina. Hewletts Creek is an anthropogenically impacted tidal creek with a watershed that is approximately 70% developed, with 18% impervious surface coverage (Mallin et al. 2000). The reefs used in this study were bar reefs approximately 10 m wide and were selected to provide a gradient of ambient live oyster density from "low" (79 live oysters m^{-2}) to "high" (167 live oysters m^{-2}; Table 1) based

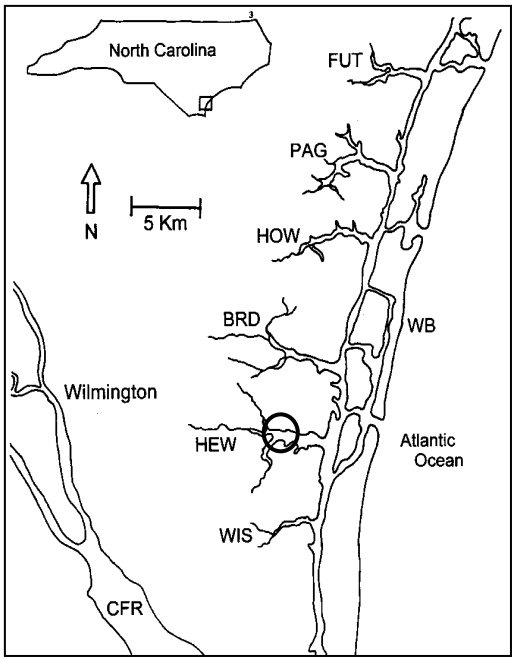
Table 1. Physical characteristics of oyster reefs used in the study. Live oyster densities (m^{-2}) were measured in Summer 2002 and Spring 2003. Also indicated is % shell cover, which is indicative of the amount of dead shell covering the reef. Width is the distance water traveled over the reef between upstream and downstream sampling locations; height is the vertical difference between the crest and base of the reef.

Reef #	Summer density	Spring density	% Shell cover	Length (m)	Width (m)	Height (m)	Vertical complexity
1	79	132	100	14.5	13.5	0.29	0.68
2	113	129	100	10.0	15.0	0.15	0.64
3	114	150	60	13.0	8.0	0.40	0.68
4	116	163	80	13.0	9.5	0.50	0.75
5	129	176	100	13.0	8.0	0.30	0.70
6	167	183	100	17.7	5.5	0.65	0.73

on live densities available in the study area. Because the amount of shell hash covering oyster reefs also may contribute to physical effects on water flow, reefs with different amounts of shell cover were used. Two of the reefs had low dead shell cover (approximately 60-80% of the reef consisted of live oysters, and the rest of the substrate was mud); the others were completely covered by live and dead shell. All reefs were located in the middle reaches of the creek (Fig. 1). They were located near a channel in the creek to ensure sufficient flow and were at least 5 m distant from other reefs. They were not immediately adjacent to marsh, thus reducing potential effects of sedimentation associated with marshes. A mudflat area immediately upstream of the selected reefs was used as a no-oyster control (Fig. 1). The vertical height and vertical complexity of each reef were measured, as they may impact physical effects such as flow velocity (Lenihan 1999; Table 1). Reef height was measured while water covered the crest of the reef by recording the depth of water over the crest and subtracting this from the depth of water covering the edges of the reef. Vertical complexity was calculated by allowing a 1 m long chain to conform to the vertical contours of the reef and measuring the actual horizontal distance covered by the chain. Complexity was measured as a ratio of straight distance after conforming to the contours divided by 1 m. Values for complexity range from 0-1, with smaller values indicative of higher complexity.

Flow Studies

To ensure that the same water mass was sampled as it flowed over a reef, a series of dye studies was conducted on ebbing tides with tidal ranges consistent with those used for sampling. A pellet of Formulabs fluorescent yellow/green tablets was dissolved in a



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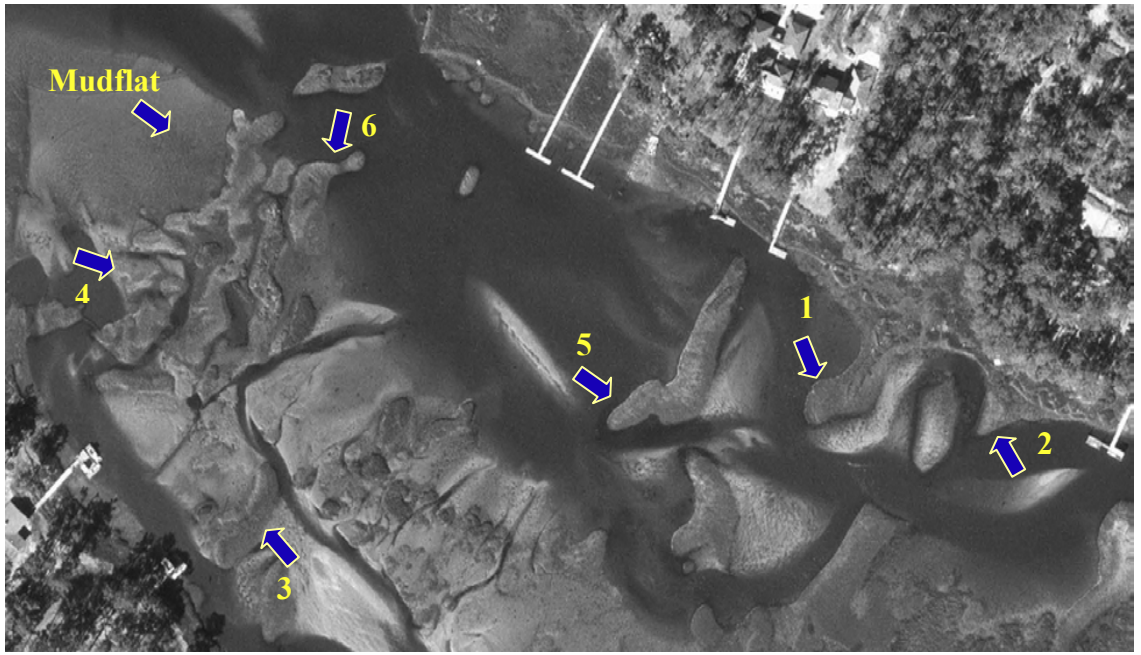


b.

Figure 1. The study site: a)location b) relative positions of oyster reefs used in the study. Aerial photograph from New Hanover County GIS, 1998.

bucket of creek water. A syringe was used to inject this colored water into the current at approximately mid-depth just upstream of the reef, and the direction of flow as well as the point of departure downstream of the reef were recorded.

Because flow speed can affect bivalve growth and filtration (Lenihan et al. 1996) as well as sediment deposition, it was important to characterize the flow regime of each reef in this study. Flow measurements were taken with a Marsh McBirney, Inc. Flo-mate Model 2000 hand-held current meter once in the summer and during sample collection in winter and spring. A SonTek Handheld ADV FlowTracker was used to take three-dimensional current measurements upstream, downstream and over the crest of each reef on a characteristic ebb tide in March 2003.

Sampling

Fecal coliform and chlorophyll *a* concentrations in tidal creeks have been shown to be highest at approximately mid-to-low tide (Mallin et al. 1999). Additionally, significant decreases in chlorophyll *a* concentrations downstream of a created oyster reef in the study area were observed 3 hours after high tide (Nelson et al. 2003). To increase the likelihood of detecting effects, water samples were taken as close as possible to mid-ebb tide (generally about 2 hours after high tide). Samples were taken from a canoe to avoid disturbing sediment. All sampling was conducted on ebb tides with a predicted range of 0.9 – 1.1 m after a high tide of approximately 1 m. Water depth was less than 35 cm on the upstream and downstream sides of the reef at the time of sampling and only a few cm of water were present over the crest, thereby maximizing the amount of water that came into contact with the oysters.

Samples were taken at two locations upstream and two locations downstream of each reef. The two upstream samples were approximately 1 m apart from each other, as were the downstream samples. Upstream samples were taken at mid-depth in the water column. The flow studies showed that water from mid-depth flowed up over the crest of the reef and stayed near the surface, so downstream samples were taken just under the surface of the water. Because sampling could resuspend solids in the water column, downstream samples were taken before upstream samples. This practice avoided collection of sediments that had been stirred up by prior sampling. For the same reason, the first reef sampled in a day was downstream of the second reef.

Sampling of the six reefs, as well as a mud-bottom control area, was accomplished over a period of three days during each sampling period, with two reefs sampled per day. Sampling was conducted twice per season during summer 2002 (once in July and once in August) and spring 2003 (twice in May, approximately two weeks apart). Due to low concentrations of water column constituents as well as weather limitations, only one sampling period was conducted in winter 2003 (February). Sampling within 24 hours of rain was avoided due water column composition that could potentially be altered by stormwater runoff. In winter, however, there were such low concentrations of the water column constituents of interest that it was necessary to sample after a rain event, in addition to the scheduled sampling period, to have sufficiently high chlorophyll *a* and fecal coliform concentrations to allow detection of potential effects. The two highest live-oyster density reefs and the mudflat control area were all sampled the day after a rainfall of approximately 3 cm in February 2003.

Chlorophyll *a* samples were taken in triplicate into 125 mL opaque plastic bottles. A fourth bottle was used to ensure collection of enough water for total suspended solids (TSS) analysis. Fecal coliform samples were collected using autoclaved 500 mL glass bottles. All samples were kept on ice until they were filtered. Water remaining after filtration of fecal coliforms and chlorophyll *a* was combined and stored at 4^{o} C until it could be used in analysis of TSS. Originally, this project was intended to focus on changes in turbidity rather than total suspended solids. However, initial attempts to measure turbidity met with methodological difficulties, and TSS analysis was added to the study in the second summer sampling period.

Sample Processing

Fecal coliform and chlorophyll *a* samples were filtered upon return to the lab and within 6 hours of collection. Fecal coliform bacteria concentrations were determined according to the Membrane Filter Procedure, using mFC medium (APHA 1995). Chlorophyll *a* samples were filtered through Gelman A/E glass fiber filters with 1.0 μm pore size. The filters were wrapped individually in aluminum foil and frozen in a sealed container with desiccant. Concentrations were determined flourometrically (Welschmeyer 1994) within three weeks. TSS were analyzed gravimetrically (APHA 1995) using 500 mL of water from each sampling location. TSS were filtered through pre-dried, Gelman A/E 47 mm diameter glass fiber filters with 1.0 μm pore size.

Sediment Analysis

Oyster reefs may cause settling of fine particles, and it was desirable to determine whether sediment composition was different upstream versus downstream of the reefs in this study. Two sediment samples were taken from each side of the reef (upstream and downstream), at approximate water column sampling locations, on a low tide in June 2003. Samples were refrigerated overnight at 4^{o} C. They were then passed through a 1.7 mm sieve and grain size fractions were determined using a Beckman LS Coulter Counter. Due to the counter configuration, which did not place a division at the particle size of 62.5 μm (the standard delineation between fine sediment and sand), the cutoff between fine and course sediment was chosen to be 63.41 μm.

Statistical Analysis

The parameters of chlorophyll *a* and fecal coliform concentrations were tested for normality and non-heterogeneity of variances. Though variances upstream and downstream of reefs were non-heterogeneous for both parameters, neither showed a normal distribution, leading to the use of non-parametric tests. Kruskal-Wallis tests were used (Sokal and Rohlf 1995) to test upstream versus downstream concentrations of the sampled variables and to determine whether they were significantly different across each individual reef for each sampling period. In all other analyses, which involved concentration changes of variables and not the non-normally distributed concentrations themselves, parametric methods were used. Multiple regression was used to determine whether the concentration changes of the studied variables were related to live oyster density, mean upstream flow speed, tidal range and the amount of time between high tide

and sampling. Time after the high tide was included in the regressions because, although similar predicted tides were used for sampling, weather phenomena caused differences in the timing of the correct water level. Because flow was not measured concurrently with sampling in summer, it was not included in the summer multiple regression model. In winter, samples were only taken once for each reef (as opposed to twice in summer and spring); this led to reduced degrees of freedom so interactions could not be included in the model. An ANOVA was used to test for differences between the high-shell and low-shell reefs of the same live oyster density. A t-test was used to test for overall reef effects within a season (i.e. did the reefs show consistently decreased concentrations downstream?). All analyses utilized SAS (SAS Institute, Inc. 1989). For all tests, $p<0.05$ was considered significant.

RESULTS

Summer

Mean chlorophyll *a* concentrations ranged from 2.3-10.6 μg L^{-1} over the reefs and mudflat during the summer sampling periods. Mean fecal coliform concentrations ranged from 1.3-54.8 colony forming units (CFU) 100 mL^{-1}. Total suspended solid concentrations ranged from 10-27 mg L^{-1}. Temperature was approximately 25-27^{o} C and salinity ranged from 30-36 ppt at the study site during these sampling periods.

Chlorophyll *a* was significantly lower downstream of reefs than upstream in summer for 9 of 12 comparisons, two comparisons for each of the six reefs (Table 2). This overall reef effect was significant for all reefs combined ($p=0.002$), for high-shell cover reefs ($p=0.023$) and for low-shell cover reefs ($p=0.053$). Each reef demonstrated a

Table 2. Results of Kruskal-Wallis Tests on upstream vs. downstream concentrations of chlorophyll *a* (chl) and fecal coliform bacteria (fc) concentrations. Significant differences are in bold. All significant changes were reductions (lower downstream) except for one, designated with a $^{+}$. Each reef was sampled twice in Summer, 2002 and Spring, 2003 and once in Winter, 2003. The mudflat was only sampled once in Summer, and Reef 6 was sampled twice in Winter.

Reef	Season	Parameter	df	chi-square	K-W p-value
	Summer 1	chl	10	5.8099	**0.0159**
	Summer 2	chl	10	0.8186	0.3656
	Winter	chl	5	3.6667	0.0555
	Spring 1	chl	10	0.8499	0.3566
1	Spring 2	chl	10	9.0000	**0.0027**
	Summer 1	fc	9	3.4268	0.0641
	Summer 2	fc	10	0.3152	0.5745
	Winter	fc	10	4.0460	**0.0443**
	Spring 1	fc	8	0.0994	0.7526
	Spring 2	fc	10	0.6595	0.4167
	Summer 1	chl	9	0.1377	0.7106
	Summer 2	chl	10	8.7675	**0.0031**
	Winter	chl	10	1.0000	0.3173
	Spring 1	chl	10	1.1692	0.2796
2	Spring 2	chl	10	4.3734	**0.0365**
	Summer 1	fc	10	6.3218	**0.0119**
	Summer 2	fc	10	1.6643	0.1970
	Winter	fc	9	0.2222	0.6374
	Spring 1	fc	10	0.5229	0.4696
	Spring 2	fc	10	0.2409	0.6236
	Summer 1	chl	10	8.3662	**0.0038**
	Summer 2	chl	7	5.4915	**0.0191**
	Winter	chl	10	4.0833	**0.0433**
	Spring 1	chl	10	8.3662	**0.0038**
3	Spring 2	chl	9	5.3065	**0.0212**
	Summer 1	fc	10	0.0068	0.9341
	Summer 2	fc	8	0.7024	0.4020
	Winter	fc	10	2.8978	0.0887
	Spring 1	fc	10	6.6572	**0.0099**
	Spring 2	fc	10	3.7183	**0.0538**

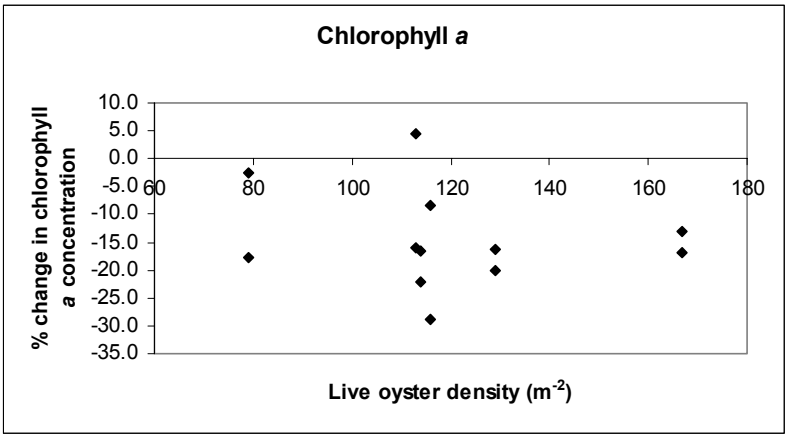
Table 2 continued.

Reef	Season	Parameter	df	chi-square	K-W p-value
	Summer 1	chl	10	8.4255	**0.0037**
	Summer 2	chl	10	4.7903	**0.0286**
	Winter	chl	10	5.9783	**0.0145**
	Spring 1	chl	10	4.3333	**0.0374**
4	Spring 2	chl	10	4.8889	**0.0270**$^{+}$
	Summer 1	fc	10	0.0581	0.8095
	Summer 2	fc	9	0.5333	0.4652
	Winter	fc	10	0.9462	0.3307
	Spring 1	fc	10	0.4103	0.5218
	Spring 2	fc	10	0.2349	0.6279
	Summer 1	chl	10	8.3958	**0.0038**
	Summer 2	chl	10	8.6400	**0.0033**
	Winter	chl	10	0.0000	1.0000
	Spring 1	chl	10	1.3309	0.2487
5	Spring 2	chl	10	5.8428	**0.0156**
	Summer 1	fc	10	2.8569	0.0910
	Summer 2	fc	10	0.1026	0.7488
	Winter	fc	10	0.2435	0.6217
	Spring 1	fc	8	2.4545	0.1172
	Spring 2	fc	10	0.0262	0.8714
	Summer 1	chl	10	2.9293	0.0870
	Summer 2	chl	10	5.8099	**0.0159**
	Winter 1	chl	10	3.0083	0.0828
	Winter 2	chl	10	1.6369	0.2008
6	Spring 1	chl	10	0.2316	0.6304
	Spring 2	chl	10	0.1637	0.6858
	Summer 1	fc	9	1.6559	0.1982
	Summer 2	fc	9	7.5688	**0.0059**
	Winter 1	fc	10	5.5065	**0.0189**
	Winter 2	fc	10	0.0072	0.9326
	Spring 1	fc	10	6.5641	**0.0104**
	Spring 2	fc	10	1.7129	0.1906
	Summer	chl	10	6.6103	**0.0101**
	Winter	chl	10	3.2083	0.0733
	Spring 1	chl	10	0.0579	0.8099
Mudflat	Spring 2	chl	10	3.2743	0.0704
	Summer 2	fc	9	0.3070	0.5795
	Winter	fc	10	6.5871	**0.0103**
	Spring 1	fc	10	5.0433	**0.0247**
	Spring 2	fc	10	0.0000	1.0000

significant decrease in chlorophyll *a* at least one of the two times it was sampled over the summer. There was no significant difference in percent removal of chlorophyll *a* between the high shell cover and low shell cover reefs of the same live oyster density ($p=0.516$). The mudflat was only sampled once during summer, and at that time chlorophyll *a* was significantly lower downstream than upstream ($p=0.010$). Changes in chlorophyll *a* concentrations were not significantly related to live oyster density (Fig. 2a, Table 3) or tidal range.

Fecal coliform concentrations were most often lower downstream of reefs than upstream (8 out of 12 comparisons), although only two differences were statistically significant and there was not a significant overall reef effect ($p=0.221$). Fecal coliform concentrations were higher downstream on the mudflat than upstream, but this difference was not significant. Changes in fecal coliform concentrations were not significantly related to live oyster density (Fig. 2b, Table 4) or tidal range. There was no significant difference in percent fecal coliform removal between the high shell and low shell reefs of the same live oyster density ($p=0.859$).

Because of difficulties encountered when measuring turbidity, total suspended solid concentrations were added to sampling during the second summer sampling period. Three of the six reefs showed large (24-38%) decreases in TSS concentrations downstream, while two showed large increases (25 and 43%) and one showed only a very small increase (2%). There was no significant overall reef effect on TSS concentrations ($p=0.444$). The mudflat showed no change in TSS concentration. Due to a lack of replication (only two samples upstream and two downstream), no statistical test could be run on the differences across each reef or the mudflat. Changes in TSS concentrations



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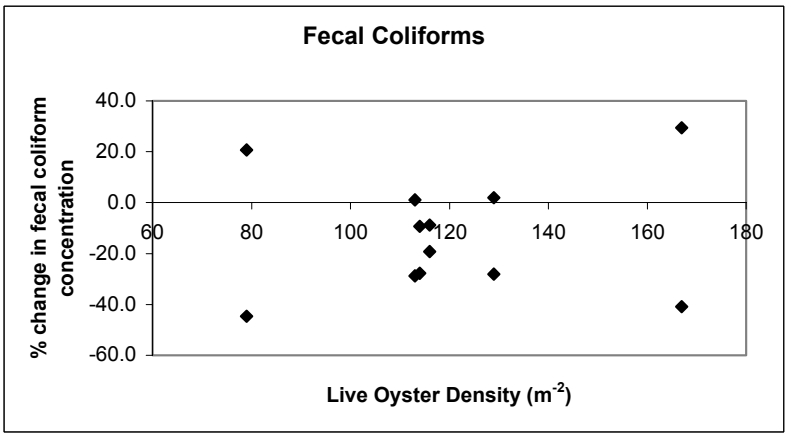

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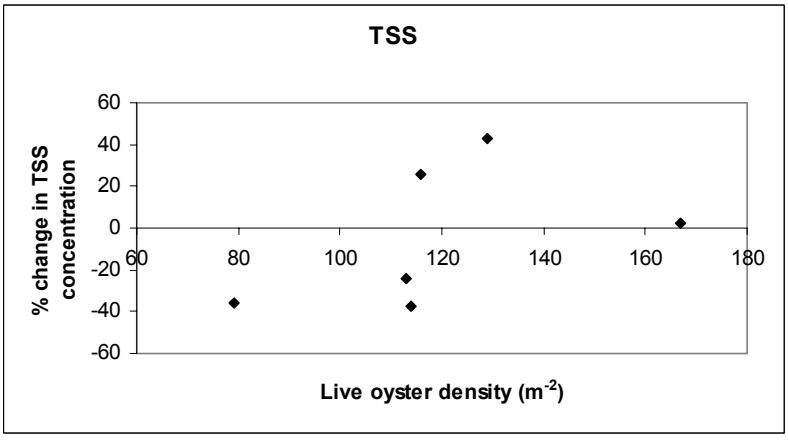


c.

Figure 2. Water column constituents as related to live oyster density, Summer, 2002: Percent changes in a) chlorophyll *a*; b) fecal coliforms; and c) TSS. Negative numbers represent a lower concentration downstream of the reef than upstream.

Table 3. Multiple regression statistics for changes in chlorophyll *a*.
Tide = predicted difference between high and low tides; Dens = live oyster density; mnflow = mean flow speed upstream of the reef; mnturb = mean turbidity upstream of the reef; time = amount of time after high tide that samples were taken.

Parameter	slope	t-value	p
Summer 2002			
Tide	-1.454	0.59	0.5691
Dens	-0.058	0.94	0.3770
Tide*Dens	0.016	0.82	0.4358
Winter 2003			
Tide	-2.020	0.28	0.8254
mnflow	0.004	0.24	0.8521
Dens	-0.006	0.39	0.7638
Spring 2003			
Tide	-4.484	0.12	0.9141
time	21.275	1.01	0.4193
mnflow	-0.453	0.36	0.7523
Dens	-0.188	0.30	0.7918
mnflow*Dens	0.005	0.54	0.6426
Tide*Dens	0.015	0.07	0.9472
time*Dens	-0.152	1.04	0.4067

Table 4. Multiple regression statistics for changes in fecal coliform concentrations.

Parameter	slope	t-value	p
Summer 2002			
Tide	-9.585	0.45	0.6679
Dens	-0.593	1.08	0.3110
Tide*Dens	0.167	1.00	0.3448
Winter 2003			
Tide	73.920	0.49	0.7075
mnflow	-0.176	0.45	0.7305
Dens	0.130	0.44	0.7387
Spring 2003			
Tide	224.173	0.62	0.5964
time	-47.481	0.23	0.8391
mnflow	0.075	0.01	0.9956
Dens	7.283	1.19	0.3551
mnflow*Dens	-0.002	0.02	0.9827
Tide*Dens	-1.492	0.74	0.5360
time*Dens	0.418	0.29	0.7974

were not significantly related to live oyster density (Fig. 2c, Table 5) or tidal range, and percent change was not significantly different between the high shell and low shell reefs of the same live oyster density ($p=0.800$).

Winter

Mean chlorophyll *a* concentrations ranged from 0.3-1.5 μg L^{-1} over the reefs and mudflat during the winter sampling period. Mean fecal coliform concentrations ranged from 0.2-8.0 CFU 100 mL^{-1} over the reefs and 22.5-36.7 CFU 100 mL^{-1} over the mudflat. Temperature was approximately 4^{o} C and salinity ranged from 17-35 ppt at the study site during this sampling period. Turbidity was very low, ranging from 1.5-5.0 NTU, and TSS concentrations were between 1.8-7.5 mg L^{-1}.

Because concentrations of the studied water column constituents were so low, the two highest live oyster density reefs (both with high dead shell cover) and the mudflat were sampled after approximately 3 cm of rain, when the creek water level was higher than normal. After this rain event, mean chlorophyll *a* concentrations ranged from 1.8-2.6 μg L^{-1} and mean fecal coliform concentrations were approximately 146-516 CFU 100 mL^{-1}. Temperature was 4^{o} C and salinity ranged from 15-29 ppt among sites on the same day. Water flow speed was higher than normal after the rain event. This was due partly to a larger tidal range than was normally sampled (1.5 m; usually a range of 0.9-1.1 m) as well as flow effects from stormwater runoff. Turbidity was comparable to warmer water turbidity, ranging from 7.8-12.5 NTU. TSS concentrations were 9.0-15.4 mg L^{-1}.

During the regular winter sampling period, there were 2 significant decreases ($p<0.05$) in chlorophyll *a* concentrations over the reefs (Table 2). A t-test did not show a

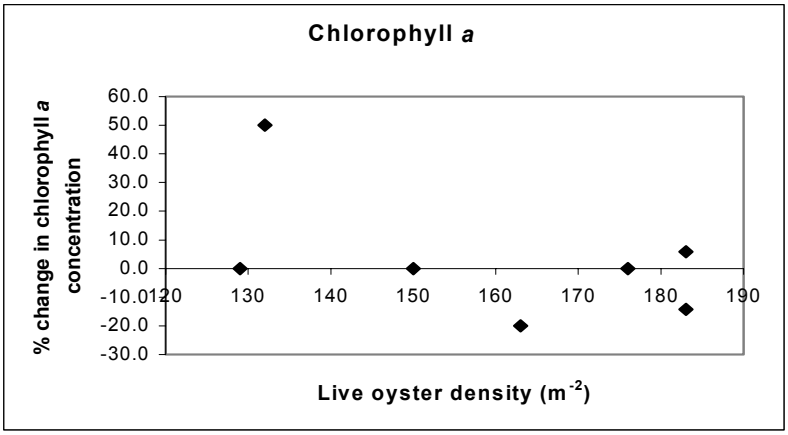
Table 5. Multiple regression statistics for changes in total suspended solids.

Parameter	slope	t-value	p
Summer 2002			
Tide	-8.228	0.32	0.7818
Dens	-0.262	0.38	0.7378
Tide*Dens	0.152	0.70	0.557
Winter 2003			
Tide	-49.594	2.04	0.2903
mnflow	0.077	1.20	0.4412
Dens	-0.103	2.13	0.2794
Spring 2003			
Tide	-106.113	2.04	0.1785
time	48.663	1.63	0.2447
mnflow	-1.551	0.88	0.4737
Dens	-1.860	2.10	0.1701
mnflow*Dens	0.013	1.01	0.4204
Tide*Dens	0.566	1.94	0.1923
time*Dens	-0.339	1.64	0.2434

significant overall reef effect on this variable for all reefs combined (p=0.691), for high-shell cover reefs (p=0.582), or for low-shell cover reefs (p=0.323). The observed decreases occurred over the two intermediate live oyster density, low dead shell cover reefs. There was not a significant difference between these reefs and the high shell cover reef of the same density (p=0.564). Over the mudflat, there was no significant change in chlorophyll *a*. Changes in chlorophyll *a* in winter were not significantly related to live oyster density (Fig. 3a), mean flow speed upstream of the reefs, or change in flow speed (Table 3). After the rain event, both reefs and the mudflat showed slight, non-significant increases in chlorophyll *a*.

In the normal winter sampling period, fecal coliforms were lower downstream than upstream 5 times (out of 7 comparisons; the highest density reef was sampled twice in winter), but this overall reef effect was not significant for all reefs combined (p=0.259), for high-shell cover reefs (p=0.224) or for low-shell cover reefs (p=0.856). Two of the fecal coliform decreases were significant and these occurred over the highest density reef (p=0.019) and the lowest density reef (p=0.044; Table 2). Fecal coliform concentrations significantly decreased over the mudflat (p=0.010) during this sampling period. Changes in fecal coliform concentrations were not correlated with live oyster density (Fig. 3b), upstream flow speeds, or changes in flow (Table 4). There was no significant difference between percent change in fecal coliform concentrations between the high shell and low shell reefs of the same live oyster density (p=0.667).

After the rain event, fecal coliform concentrations were elevated above non-rain conditions. Due to crowding of the petri dishes, the counts could not be considered reliable enough for statistical analysis. However, it was apparent that fecal coliform



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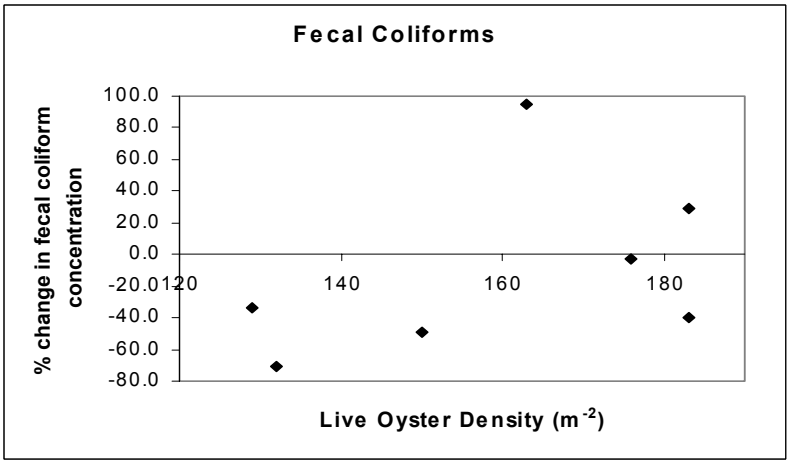

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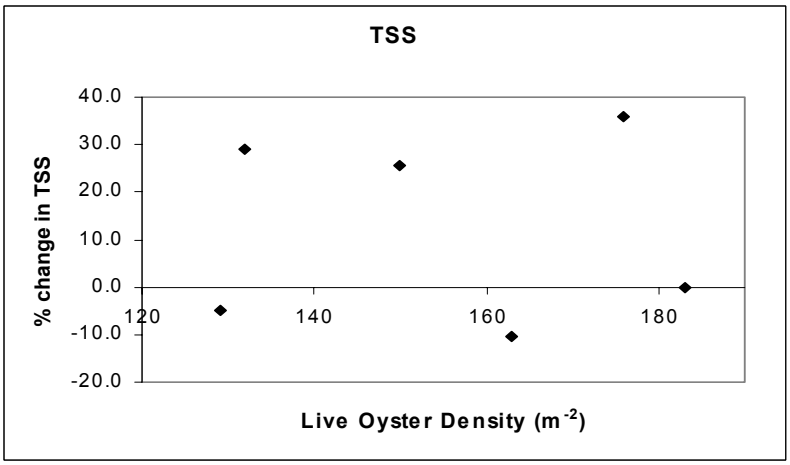


c.

Figure 3. Water column constituents as related to live oyster density, Winter, 2003: Percent changes in a) chlorophyll *a*; b) fecal coliforms; and c) TSS. Negative numbers represent a lower concentration downstream of the reef than upstream.

concentrations were highest over the mudflat (approximately 400 CFU 100 mL^{-1}), lower over the highest density reef, which was slightly downstream of and adjacent to the mudflat (Reef 6 in Fig. 1; approximately 360 CFU 100 mL^{-1}), and lowest over the most downstream reef (Reef 5 in Fig. 1; approximately 180 CFU 100 mL^{-1}).

During the normal winter sampling period, TSS concentrations were higher (25-36%) downstream of reefs as compared to upstream three times. They were moderately lower (10%) once, and twice were only slighly (<5%) lower downstream. Given the low TSS concentrations during this sampling period, however, an increase of <1 mg L^{-1} could translate to a 30% change. There was no significant overall reef effect in concentration changes (p=0.252). Upstream to downstream changes in TSS concentrations were not significantly related to live oyster density (Fig. 3c), flow speed of water upstream of the reefs, or changes in flow speed during the winter sampling period (Table 5). There was no significant difference in TSS change between high shell and low shell reefs of the same live oyster density (p=0.744). TSS concentrations were 0.7% higher downstream than upstream over the highest density reef after the rain event, but were 30% higher over the second-highest density reef. Over the mudflat, TSS concentrations were approximately 11% lower downstream.

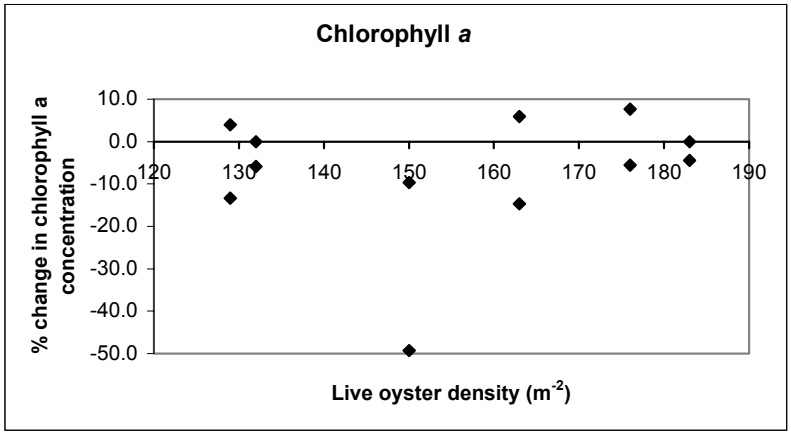
Spring

Mean chlorophyll *a* concentrations ranged from 1.3-7.1 μg L^{-1} over the reefs and 2.0-12.2 μg L^{-1} over the mudflat during the spring sampling period. Mean fecal coliform concentrations ranged from 8-330 CFU 100 mL^{-1} over the reefs and mudflat. Fecal coliform counts were higher during the first spring sampling period due to a long rainy

period preceding sampling. Samples were not taken within 24 hours of rain, but the earlier rain did affect the water column. Temperature was approximately 24^{o} C and salinity ranged from 19-25 ppt during the first spring sampling and 30-34 ppt during the second spring sampling period. Turbidity ranged from 5.8-9.8 NTU over both spring sampling periods.

In spring, there were 6 significant decreases and one significant increase in chlorophyll *a* concentrations across the reefs (Table 2). Changes in chlorophyll *a* concentrations did not show an overall reef effect for all reefs combined ($p=0.180$), for high-shell cover reefs ($p=0.189$) or for low-shell cover reefs ($p=0.276$). Chlorophyll *a* changes also were not significantly related to live oyster density (Fig. 4a), flow speed upstream of the reefs, change in flow speed, or how long after the high tide samples were taken (Table 3). There was no significant difference in percent removal of chlorophyll *a* between high and low shell cover reefs of similar live oyster density ($p=0.448$).

Ten of 12 comparisons showed fecal coliform concentrations that were lower downstream than upstream in spring. Three of these decreases were significant (Table 2), as was the overall reef effect ($p=0.009$). The mudflat showed a significant ($p=0.025$) downstream decrease in fecal coliforms during one of the two spring sampling periods. Changes in fecal coliform concentrations were not correlated with live oyster density (Fig. 4b), flow speed upstream of reefs, or changes in flow (Table 4). A t-test did show significantly decreased fecal coliform concentrations downstream of oyster reefs in spring for all reefs combined ($p=0.0086$). High-shell cover reefs did not show this overall effect ($p=0.101$); it was driven by the low-shell cover reefs ($p=0.012$). However,



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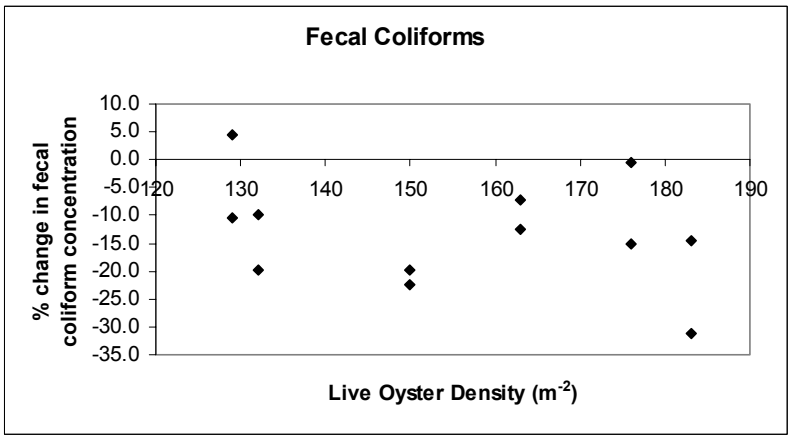

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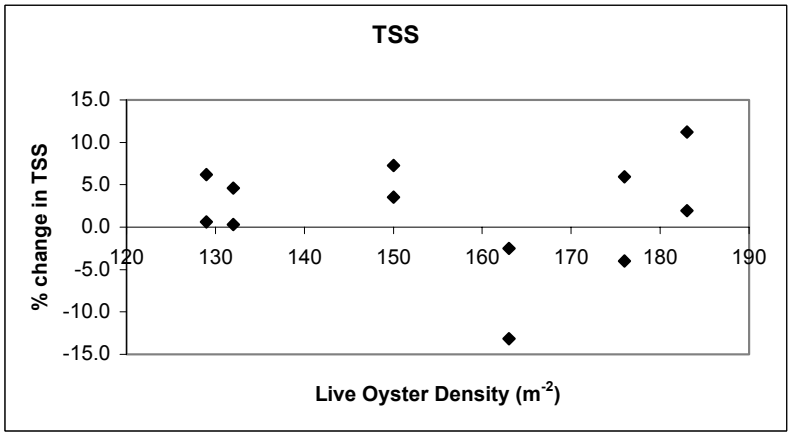


c.

Figure 4. Water column constituents as related to live oyster density, Spring, 2003: Percent changes in a) chlorophyll *a*; b) fecal coliforms; and c) TSS. Negative numbers represent a lower concentration downstream of the reef than upstream.

high-shell and low-shell cover reefs of similar live oyster density did not show significantly different patterns of fecal coliform removal in spring (p=0.155).

TSS did not exhibit a significant pattern with respect to the variables examined in spring. Out of 12 comparisons, downstream TSS concentrations were higher 7 times, lower 3 times, and unchanged twice. There was not a significant overall reef effect on TSS concentration changes (p=0.291). TSS concentrations were higher downstream once over the mudflat, and remained unchanged during the other spring sampling period. The observed changes in TSS concentrations were not correlated with live oyster density (Fig. 4c), water flow speed upstream of the reefs or changes in flow (Table 5). Percent removal of TSS was not significantly different between high shell and low shell cover reefs of the same live oyster density (p=0.540).

Overall

During the warm seasons of summer and spring, chlorophyll *a* was significantly lower downstream of reefs than upstream a total of 13 times (out of 24 observations). Only once was it significantly higher. In summer, chlorophyll *a* concentrations were significantly lower downstream of oyster reefs than upstream (p=0.002) overall. In spring, however, there was no significant reef effect. Fecal coliforms were reduced the majority of the time during the warm seasons (18 of 24 comparisons), but only 4 of these decreases were statistically significant. In summer, this overall reef effect was not statistically significant, but it was significant in spring (p=0.009).

Chlorophyll *a* concentrations were significantly and inversely related to TSS concentrations in spring and across all seasons. In winter, there was no significant

relationship between the two (Fig. 5). In spring, as well as across all seasons, chlorophyll *a* showed a significant positive relationship with turbidity (Fig. 6). Fecal coliform counts showed a significant negative relationship to TSS in both spring and winter, but across all seasons, there was a weak but significant positive relationship (Fig. 7). In summer, fecal coliform concentrations were significantly and positively related to turbidity and in spring there was a weak but significant positive relationship (Fig. 8). For all seasons combined, there was not a significant relationship (Fig. 8). Concentrations of all water column constituents were higher during the first spring sampling period than the second, perhaps due to the effects of rain in the days preceding sampling.

Water flow varied somewhat from reef to reef. The lowest observed flow over the parts of the reef from which samples were taken was 6 cm s^{-1}. Flow velocity reached 22 cm s^{-1} over the other reefs. The three-dimensional current study showed increases in flow speed over the crest of three of the reefs, and decreases over the other three. However, differences in flow speeds between reefs were not correlated with changes in the water column constituents. Vertical complexity was approximately equal over the reefs (Table 1). Over five of the six reefs, downstream sediments showed a larger amount of coarse sediment than upstream (by 8-12%; Table 6). The mudflat did not exhibit the same distribution of sediment texture.

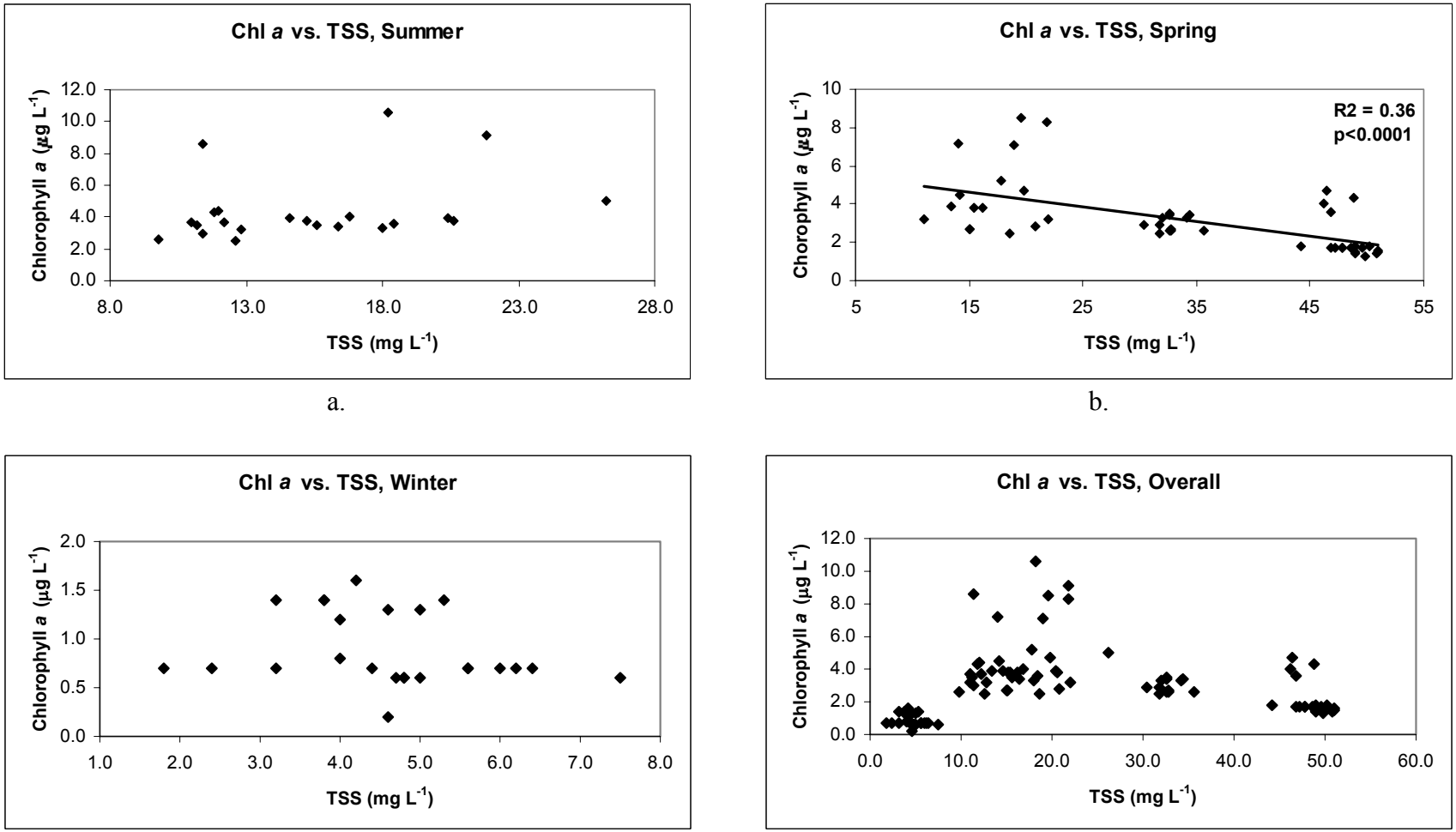
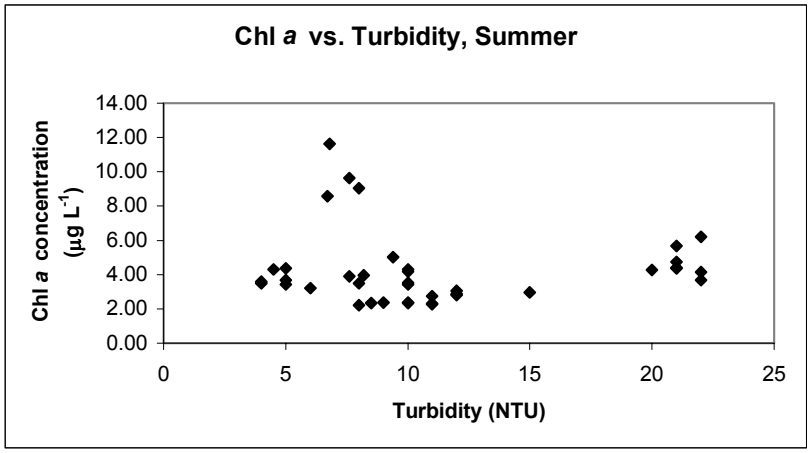


Figure 5. Chlorophyll *a* concentrations as related to TSS concentrations during: a) Summer; b) Spring; c) Winter; and d) All seasons combined.



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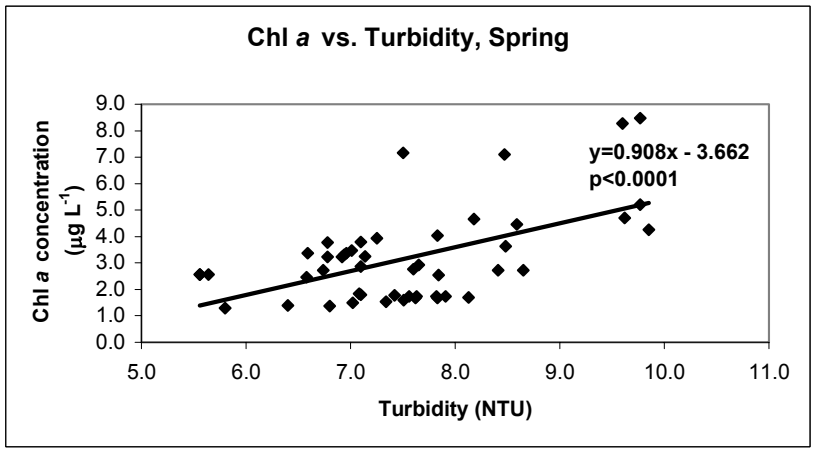

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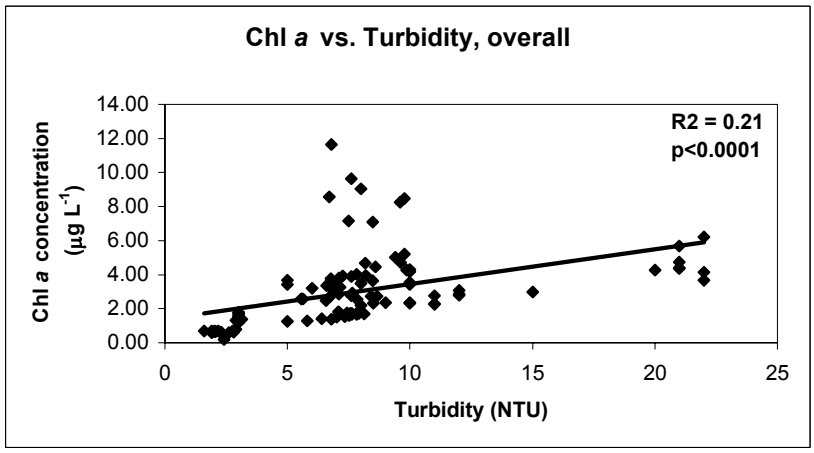

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Figure 6. Chlorophyll *a* as related to turbidity during: a) Summer; b) Spring; and c) All seasons combined.

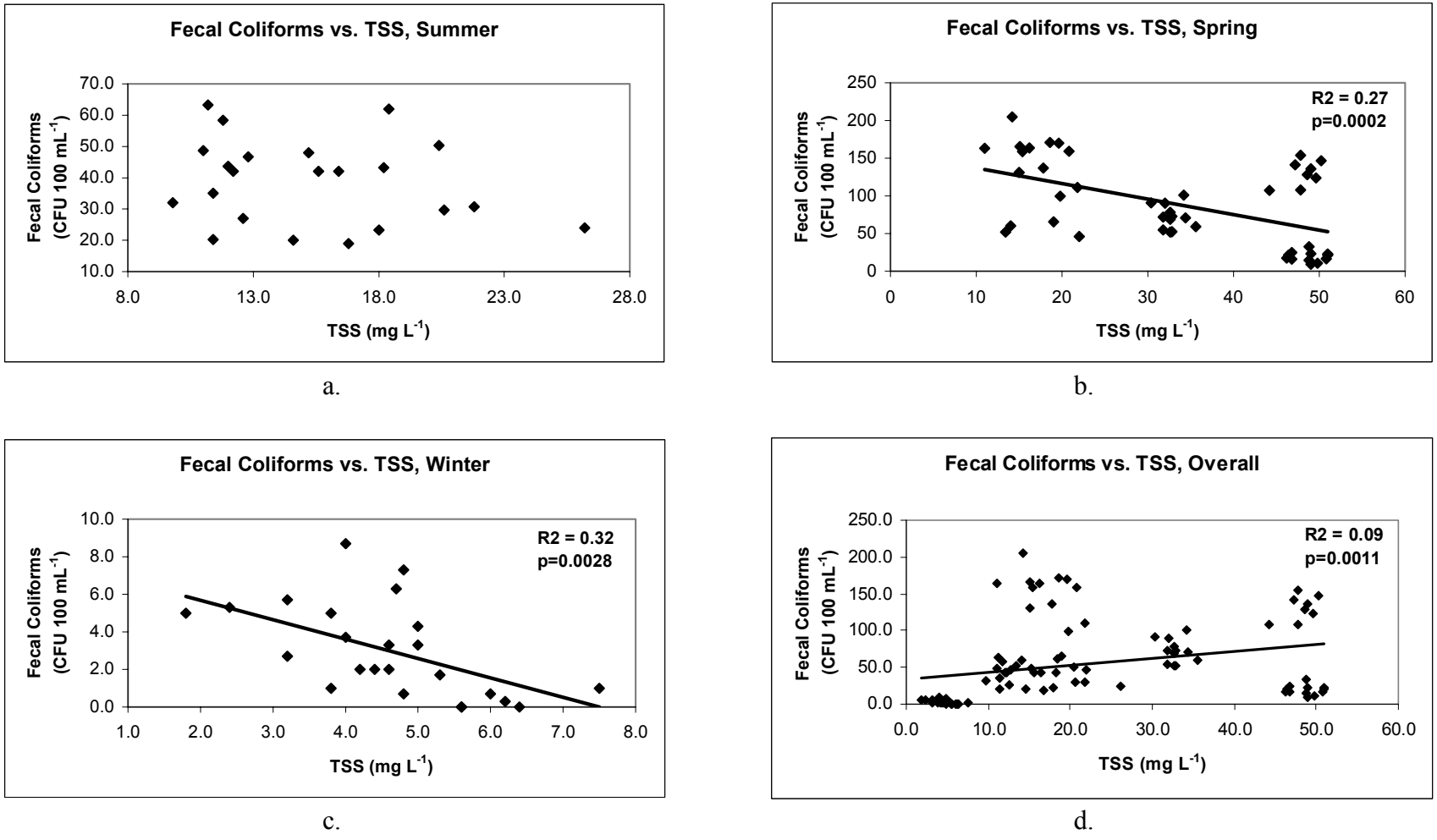
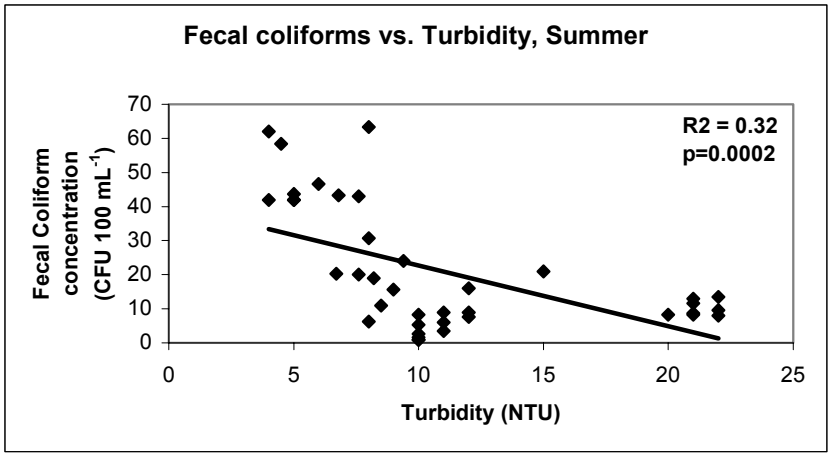


Figure 7. Fecal coliform concentrations as related to TSS concentrations during: a) Summer; b) Spring; c) Winter; and d) All seasons combined.



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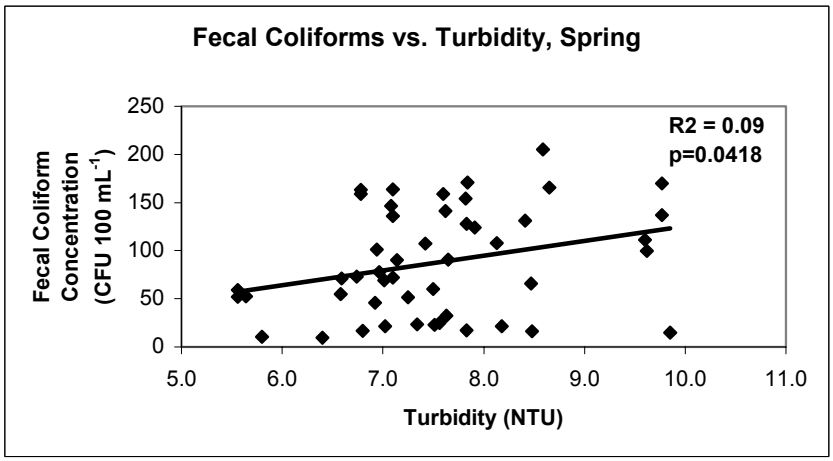

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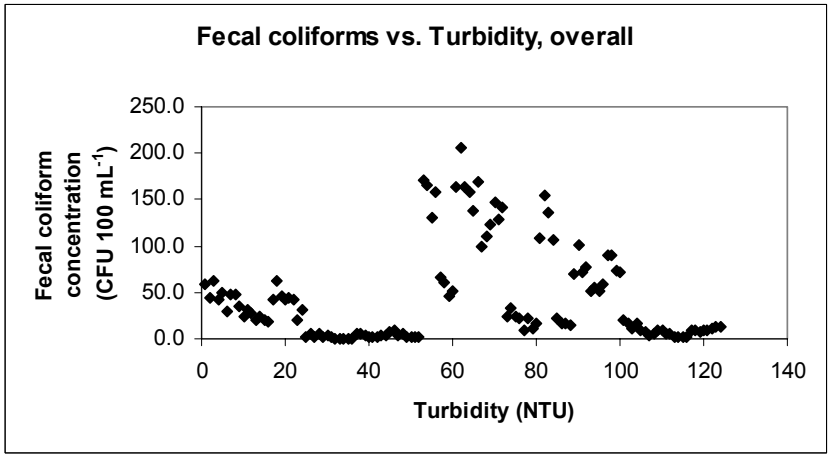

c.

Figure 8. Fecal coliform concentrations as related to turbidity during: a) Summer; b) Spring; and c) All seasons combined.

Table 6. Sediment composition, as % fine sediment (defined as less than 63.41 μm diameter), upstream and downstream of the oyster reefs.

Reef	% fine upstream	% fine downstream
1	40	32
2	38	21
3	72	70
4	85	78
5	41	30
6	64	51
Mudflat	40	41

DISCUSSION

In summer, oyster reefs caused significant reductions in chlorophyll *a* concentrations in Hewletts Creek. In spring, these effects were not as strong. However, the effect of reef presence on of fecal coliform counts was stronger in spring than summer. TSS did not show any clear effects.

Haven and Morales-Alamo (1970) found that, by doubling the number of oysters in an experimental tank, removal rates of particulate matter approximately doubled. Changes in suspended particulate concentrations, then, should be significantly related to live oyster density if oyster feeding is the main factor in particulate removal. In this study, such a relationship was not observed. One possible explanation for this observation is a threshold effect, some critical density of live oysters at which a measurable effect can be detected. Alternatively, the relationship between changes in seston and live oyster densities could exist on a larger scale. The oyster reefs used in this study provided only a small range of live oyster densities, especially after a large spatfall in summer 2002 (Posey and Alphin, unpublished data). Thus, the examined range of live oyster densities may have been too narrow for a density relationship to be detected. Further, because the changes in concentrations of the studied water column constituents were not significantly related to flow speeds or changes in flow speed across the reefs, it is unlikely that the observed changes were due solely to flow speed.

Live oyster lengths near the study site averaged 65 mm (Harwell, Posey and Alphin, unpublished data). Using the methods of Dame (1972), the mean dry weight for these oysters was calculated to be 1.33 g. Newell's (1988) estimate of oyster clearance rates of 5 L hr^{-1} g^{-1} were used to calculate the potential volume of water that could be

cleared by each oyster reef in this study. In summer, flow velocities upstream of the oyster reefs ranged from 6-21 cm s^{-1}, and the reefs could only clear 5-15% of the water moving over them. Many of the observed chlorophyll *a* differences in summer were greater than the potential filtration capacity of the oysters on the reefs based on these estimates (up to 30% removal), suggesting that either oyster feeding rates are higher than Newell's (1988) estimate or that factors other than oyster feeding (i.e. other filter feeders or physical effects) are important in particulate removal.

Calculations of approximate clearance rates, assuming 100% efficiency of particle removal, were made using the observed summer decreases in chlorophyll *a* concentrations. These rates ranged from 3-18 L hr^{-1} g^{-1} across the reefs. The mean was 10 L hr^{-1} g^{-1}, which is consistent with Jordan's (1987) laboratory estimate. Oysters do not remove all particles from water with 100% efficiency, however, so this estimate may be conservative. Efficiency of particle removal increases with increasing particle size (Haven and Morales-Alamo 1970; Riisgard 1988), and feeding effects are further complicated by oyster selectivity. Oysters are able to feed preferentially on high-quality food particles (Loosanoff 1949; Newell and Jordan 1983; Wetz et al. 2002).

Other filter feeders, such as mussels, were not abundant on these oyster reefs and therefore cannot account for the larger than expected effects. Even though flow velocities did not decrease downstream of the reefs, particle trapping within the reef crest may have occurred in shadow zones between oyster culms. This explanation is consistent with chlorophyll *a* and fecal coliform data in that the reefs that consistently showed significant decreases in chlorophyll *a* and fecal coliform concentrations were the reefs with low shell cover (i.e. low areas floored by mud). These were also the reefs with the

lowest flow velocities (approximately 8 cm s^{-1}). Dame et al. (1985) and Dame (1987) found that most material uptake over an oyster reef in North Inlet occurred when flow was less than 15 cm s^{-1} and attributed this to a combination of biofiltration and sedimentation. Above this velocity, resuspension occurred. Lower flow speeds could contribute to removal of particles by increasing the time water is in contact with the oysters and thus increasing their ability to filter particulates; it could also be that particles settled out of the water at these lower speeds.

Oyster reefs have been shown to play a role in nutrient cycling in tidal creeks by releasing NH_4^+ (Dame et al. 1984; Dame et al. 1985; Dame et al. 1989; Dame and Dankers 1988; Nelson 2003). As such, it could be argued that chlorophyll *a* concentrations should actually be higher downstream of reefs than upstream. Ammonium released by bivalves can be taken up by phytoplankton and lead to increased phytoplankton biomass. Asmus and Asmus (1991) made this argument for systems impacted by a mussel bed, though their field study showed significant decreases in phytoplankton biomass across the bed. Increased phytoplankton production due to nutrient release is also a possibility for oyster reefs. However, there is a lag time of a few hours before the ammonium shows up as primary production in the water column, and any increased production may be appearing further downstream of the reefs than the location of sample collection for this study. In terms of the parameters examined by this study, the only change that would be immediate enough to detect as water flows over the oyster reefs is particle removal.

Fecal coliform concentrations were often lower downstream of reefs than upstream, but the differences were rarely significant. The overall reef effect of decreased

fecal coliform concentrations was significant in spring but not summer, the opposite of the effect for chlorophyll *a*. Fecal coliform counts are extremely variable, necessitating large changes before a significant effect can be detected. In spring, tests were slightly more powerful (with a power of 0.56 rather than 0.24, where 0.80 is desirable), most likely due to larger concentrations of fecal coliforms. Counts were higher in spring than in summer, possibly because runoff in summer was limited due to a severe drought.

C. virginica filters unattached bacteria with an efficiency of only 5% (Langdon and Newell 1990). However, fecal coliforms have been associated with turbidity and suspended sediments in the water column (Sayler et al. 1975; Pommepuy et al. 1992; Mallin et al. 2000) and may be removed with suspended particulate matter through either filtration or settling. In this study, fecal coliform counts did not have consistent relationships with either turbidity or TSS. However, this project was not designed to test these relationships and these were ancillary data comparisons. As such, the range of concentrations may not have been large enough to accurately indicate a relationship (or lack thereof) between fecal coliforms and either turbidity or TSS. This may also be the reason changes in fecal coliform concentrations were different from changes in TSS concentrations. Changes in fecal coliform concentrations were not significantly related to live oyster density, flow speeds or changes in flow speed across the reefs. None of these factors is readily apparent as the most influential one, and changes in fecal coliform concentrations are likely due to a combination of factors.

Changes in TSS concentrations did not exhibit any significant patterns relative to the variables examined in this study. Due to a lack of replication, statistical tests could not be used to determine whether changes across a reef were significant. However, tests

could be run to detect an overall reef effect within a season, and none of these were significant for TSS. Changes in TSS were not consistently positive or negative in any season.

Water temperature in winter was 4° C, lower than the minimum temperature (5° C) at which oysters typically feed (Galtsoff 1928; Loosanoff 1953, 1958, 1965; in Shumway 1996). Chlorophyll *a* and fecal coliforms were consistently decreased in the warm seasons of summer and spring, but neither showed a consistent effect in winter. Feeding effects are suggested by a lack of consistent change in water column constituents during winter, even when concentrations were high enough to detect a difference (after the rain event).

Flow conditions may also have contributed to changes in water column constituents; particles may have settled over the crest of the reefs (also suggested by Dame 1987). Sediments were finer on the side of the reefs that were upstream during ebb tide. Flow could be faster on ebb tide than on flood tide, leading to more deposition of fine particles during flood tide than ebb (Dame 1987). Under these conditions, the particles would be deposited downstream during flood tide, which is the upstream side of the reef during ebb tide. This study did not examine effects of oyster reefs during flood tides chlorophyll *a* and fecal coliform concentrations are highest during ebb tides (Mallin et al. 1999).

While there was never a significant difference in changes of chlorophyll *a*, fecal coliform, or TSS concentrations between high-shell cover and low-shell cover reefs, the reefs themselves showed different patterns of significance. The reefs with low-shell cover were also the reefs with lowest flow velocities and showed consistent removal of

fecal coliforms in spring, whereas the other reefs did not. Vertical complexity was approximately equal between all reefs, and complexity may be a more important component in flow effects than the presence of shell itself.

Multiple factors could be responsible for the observed effects on chlorophyll *a,* fecal coliform and TSS concentrations. Filtration by oysters and flow patterns over oyster reefs could both contribute to particle removal in tidal creek ecosystems.

CONCLUSIONS

Significant changes in concentrations of chlorophyll *a* and fecal coliform bacteria were detected during warm seasons, even when effects on total suspended solid concentrations were not observed. None of the examined variables were significantly related to live oyster density, flow speed, or change in flow speed across reefs, suggesting possible threshold effects. Oyster reefs do have detectable effects on chlorophyll *a* and fecal coliform concentrations under field conditions, though effects vary temporally. The degree of removal suggests physical mechanisms for removal in addition to filtration effects.

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Appendix: Flow velocity, turbidity, and mean concentrations of chlorophyll *a*, fecal coliforms, and TSS at upstream and downstream locations on oyster reefs. Two upstream and two downstream locations showed for each sampling period (two sampling periods in summer and spring, one in winter).

Reef	Dens	Loc	flow cm s^{-1}	turb NTU	chl_a $\mu g\ ml^{-1}$	FC CFU 100 ml^{-1}	TSS mg l^{-1}
		up	.	.	3.9	50.3	20.4
		up	.	.	3.8	29.7	20.6
		down	.	.	3.8	48.0	15.2
1	79	down	.		3.7	48.7	11.0
	Summer	up	.	12	2.9	9.0	.
		up	.	12	2.8	7.7	.
		down	.	11	2.3	3.5	.
		down	.	10	2.4	5.3	.
		up	.	.	3.0	35.0	11.4
		up	.	.	3.3	23.3	18.0
		down	.	.	2.6	32.0	9.8
2	113	down	.	.	2.5	27.0	12.6
	Summer	up	.	11	2.3	9.0	.
		up	.	10	2.3	8.3	.
		down	.	8	2.2	6.3	.
		down	.	11	2.8	6.0	.
		up	.	8.3	.	20.0	24.1
		up	.	9.4	5.0	24.0	26.2
		down	.	7.6	3.9	20.0	14.6
3	114	down	.	8.2	4.0	19.0	16.8
	Summer	up	.	10	4.2	1.0	.
		up	.	10	4.3	2.7	.
		down	.	10	3.5	1.0	.
		down	.	10	3.4	1.7	.
		up	.	5	3.7	42.0	12.2
		up	.	8	3.5	63.3	11.2
		down	.	6	3.2	46.7	12.9
4	116	down	.	5	3.4	42.0	16.4
	Summer	up	.	21	5.7	8.3	.
		up	.	22	6.2	9.7	.
		down	.	22	4.1	8.0	.
		down	.	20	4.3	8.3	.
		up	.	4.5	4.3	58.3	11.8
		up	.	5	4.4	43.7	12.0
		down	.	4	3.6	62.0	18.4
5	129	down	.	4	3.5	42.0	15.6
	Summer	up	.	15	3.0	21.0	.
		up	.	12	3.1	16.0	.
		down	.	8.5	2.3	11.0	.
		down	.	9	2.4	15.7	.

Appendix continued.

Reef	Dens	Loc	flow cm s^{-1}	turb NTU	chl_a $\mu g\ ml^{-1}$	FC CFU 100 ml^{-1}	TSS mg l^{-1}
		up	.	6.8	11.6	43.3	16.6
		up	.	7.6	9.6	43.0	19.8
		down	.	6.7	8.6	20.3	11.4
6	167	down	.	8	9.0	30.7	26.0
	Summer	up	.	21	4.7	8.7	.
		up	.	21	4.4	11.7	.
		down	.	21	4.4	13.0	.
		down	.	22	3.7	13.5	.
		up	3	2.4	0.2	2.0	4.6
1	132	up	8	1.9	0.6	3.3	5.0
	Winter	down	7	2.6	0.6	1.0	7.5
		down	5	2.3	0.6	0.7	4.8
		up	20	2.76	0.7	0.0	6.4
2	129	up	28	2.04	0.7	0.7	6.0
	Winter	down	20	1.59	0.7	0.3	6.2
		down	7	2.04	0.7	0.0	5.6
		up	.	3	1.4	5.7	3.2
3	150	up	16	3	1.4	5.0	3.8
	Winter	down	8	2.9	1.3	4.3	5.0
		down	2	3.13	1.4	1.0	3.8
		up	8	3	1.4	1.7	5.3
4	163	up	4	3	1.6	2.0	4.2
	Winter	down	11	3	1.2	3.7	4.0
		down	7	5	1.3	3.3	4.6
		up	15	1.95	0.7	2.7	3.2
5	176	up	11	2.17	0.7	5.0	1.8
	Winter	down	14	2.06	0.7	2.0	4.4
		down	8	1.91	0.7	5.3	2.4
		up	15	2.8	0.6	7.3	4.8
		up	12	2.9	0.8	8.7	4.0
		down	11	2.25	0.6	3.3	4.0
6	183	down	6	2.3	0.6	6.3	4.7
	Winter	up	.	3	1.8	1.0	5.3
		up	.	3	1.6	2.3	4.3
		down	20	3	1.8	1.7	4.4
		down	.	3	1.7	2.7	5.2
		up	26	7.56	1.7	24.7	46.8
		up	.	7.63	1.7	32.7	48.8
		down	6	7.34	1.5	23.3	49.0
1	132	down	18	7.51	1.6	22.7	51.0
	Spring	up	16	7.01	3.5	69.0	32.6
		up	17	6.94	3.3	101.0	34.2
		down	20	6.59	3.4	71.0	34.4
		down	19	6.96	3.4	78.0	32.6

Appendix continued.

Reef	Dens	Loc	flow cm s^{-1}	turb NTU	chl_a $\mu g\ ml^{-1}$	FC CFU 100 ml^{-1}	TSS mg l^{-1}
		up	12	6.40	1.4	9.3	49.0
		up	14	7.02	1.5	21.3	51.0
		down	16	5.80	1.3	10.7	49.8
2	129	down	17	6.80	1.4	16.7	50.8
	Spring	up	10	5.56	2.6	52.0	32.6
		up	15	6.58	2.5	54.7	31.8
		down	15	5.64	2.6	52.3	32.8
		down	16	5.56	2.6	59.0	35.6
		up	8	8.47	7.1	65.7	19.0
		up	9	7.50	7.2	60.3	14.0
		down	13	6.92	3.2	46.0	22.0
3	150	down	.	7.25	3.9	51.7	13.4
	Spring	up	13	7.14	3.3	90.3	32.0
		up	14	7.65	2.9	90.7	30.4
		down	18	6.74	2.7	73.0	32.8
		down	15	7.10	2.9	72.0	31.8
		up	12	7.10	3.8	163.7	16.2
		up	.	8.59	4.5	205.0	14.2
		down	11	6.78	3.2	163.3	11.0
4	163	down	.	6.78	3.8	158.7	15.4
	Spring	up	23	8.13	1.7	108.0	47.8
		up	.	7.82	1.7	154.0	47.8
		down	28	7.10	1.8	136.0	49.0
		down	24	7.42	1.8	107.3	44.2
		up	16	7.84	2.5	171.0	18.6
		up	.	8.65	2.7	165.3	15.1
		down	11	8.41	2.7	131.3	15.0
5	176	down	.	7.60	2.8	159.0	20.8
	Spring	up	22	7.91	1.7	124.0	49.6
		up	.	7.08	1.8	146.7	50.2
		down	22	7.83	1.7	128.0	48.6
		down	19	7.62	1.7	141.3	47.2
		up	6	9.77	5.2	137.0	17.8
		up	21	9.77	8.5	169.7	19.6
		down	14	9.62	4.7	99.7	19.8
6	183	down	20	9.60	8.3	111.0	21.8
	Spring	up	12	8.18	4.7	21.3	46.4
		up	.	8.48	3.6	16.0	46.8
		down	16	7.83	4.0	17.3	46.2
		down	15	9.85	4.3	14.7	48.8