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Impacts of Oyster Reef Restoration on Primary Productivity and Nutrient Dynamics in Tidal Creeks of the North Central Gulf of Mexico

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Abstract The ability of oysters to remove large quantities of particulates from the water column, thereby potentially improving water quality, has been cited as one of the reasons for oyster reef restoration. However, this ability has not yet been effectively demonstrated in the field. As part of the Alabama Oyster Reef Restoration Project, this study was designed to assess impacts of restored eastern oyster (*Crassostrea virginica*) reefs on primary production, nutrient dynamics, and water quality in shallow tidal creeks. Using a Before–After-Control–Impact (BACI) design, we monitored tidal creeks around Dauphin Island, AL, for changes induced by the introduction of oyster reefs. Reef placement resulted in increased ammonium (NH_4^+) in two of the three experimental creeks. Interestingly, oyster reefs did not seem to reduce water column particulates or have an impact on phytoplankton or microphytobenthic biomass or productivity. We do not believe that our data discount the importance and/or usefulness of oysters in modifying the water column. Rather, we acknowledge that it is difficult to detect these impacts/environmental services in this type of system (i.e., a tidal creek system), because they seem to be very localized and short-lived (i.e., not ecologically relevant on a creek-wide scale). This study highlights the need to consider location and habitat in planning oyster restoration projects. Also, it demonstrates that the types, magnitudes, and spatial extent of changes in ecosystem services that should be expected after reef restoration might need to be re-evaluated.

Keywords *Crassostrea virginica* · Restoration · Water quality · Ecosystem services · Filter feeders · Oyster reef

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Introduction

The eastern oyster (*Crassostrea virginica*) inhabits estuaries from the St. Lawrence River to the Atlantic coast of Argentina and is of great socioeconomic importance throughout its range. In recent years, however, overharvesting (Newell 1988; Dame 1993; Jackson et al. 2001), disease (Andrews 1988, 1996), predation (Soniat et al. 2004), habitat loss, competition with exotic species, (Cohen and Carlton 1998), and environmental degradation (Encomio and Chu 2000) have substantially reduced the occurrence of oyster reefs and their productivity along the Atlantic and Gulf coasts of the USA.

As one of the few hard substrata found in the northern Gulf of Mexico, oyster reefs play an important role in many estuaries. Arguably, their ecological role could be more

important than their economical role (Soniat et al. 2004). Oyster reefs are extremely important marine habitats (Jackson et al. 2001) and have been referred to as "keystone species" (Paine 1966) and "ecosystem engineers" (Jones et al. 1994); oysters can influence the tropic structure, alter species composition, and determine ecosystem structure.

Oysters are natural filters, capable of clearing gallons of water per day per animal, helping to improve water quality by reducing total suspended solid and chlorophyll *a* concentrations by up to 75% (Dame et al. 1984; Nelson et al. 2004). Oyster reefs act as sedimentation traps, increasing particle settlement by up to seven times (Dame 1999), thereby stabilizing sediments and reducing erosion (Meyer et al. 1997).

Estuaries, oyster habitat, are among the most damaged ecosystems in the world largely due to anthropogenic activities. More than 70% of the human population resides in watersheds draining to the coast, and this number is rising, increasing pressure on coastal ecosystems (Vitousek et al. 1997; Peierls et al. 1991) primarily through eutrophication and chemical pollutant loading. Eutrophication can stimulate harmful algal blooms, sometimes resulting in shellfish poisonings and serious ecological damage (Wynne et al. 2005). Accumulation of phytoplankton blooms in sediments will cause anoxia and hypoxia due to the oxygen demand of decomposition (Paerl et al. 2003). In addition to the effects of dissolved oxygen, blooms can dramatically shade benthic producers, such as microphytobenthic or seagrass communities (Sand-Jensen and Borum 1991; Duarte 1995). However, some organisms that inhabit estuarine systems (e.g., oysters and other filter feeders) may mitigate such effects. Reef-creating eastern oysters, as suspension feeders, can also play a major role in nutrient recycling in estuaries. Oyster reefs remove seston from the water column, reducing suspended sediment, detritus, and particulate nutrients (Dame et al. 1984; Gerritsen et al. 1994; Brumbaugh et al. 2000; Mann 2000). Even at modest levels (25 g dry tissue weight per square meter; Newell and Koch 2004), oyster reefs have been shown to greatly reduce phytoplankton abundance (Cloern 1982; Cohen et al. 1984).

The drastic declines in oyster populations and the realization of their ecological importance have prompted attempts to restore reefs in areas where they were once abundant. While first large-scale efforts toward oyster restoration were made in Chesapeake Bay, present efforts are being made to restore reef habitat along the North Central Gulf Coast. Historically, restoration studies have focused on the success of fish associated with oyster reefs and improvement of water quality, but more recent studies have focused on the ecological aspects of the newly created habitat such as primary productivity and nutrient dynamics (e.g., Coen and Luckenbach 2000).

Tidal creeks are prominent in coastal ecosystems and play an important role in mediating the exchange of materials between terrestrial and marine environments (Valiela et al. 2000; Tobias et al. 2003). As an integral part of the Alabama Oyster Reef Restoration Project, the goal of this study was to investigate impacts on water quality, microphytobenthic and phytoplankton productivity, and nutrient flow in tidal creeks associated with artificial *C. virginica* reefs.

Materials and Methods

Oyster reefs were placed in tidal creeks around Dauphin Island, Alabama (Fig. 1). The tidal creeks are moderately sized, ranging from 147 to 2,116 m^2, and shallow, with mean depth ranging from 0.27 to 0.54 (±0.02) m. These creeks were sparsely populated with natural oysters, ranging between 0.59 and 5.58 individuals per square meter. Furthermore, these creeks are characterized by sandy, muddy sediments, and delineated by *Juncus romerianus* (black needlerush) marsh. The tide is generally diurnal, with a mean annual amplitude of 0.38±0.02 m, recorded with a tidal gauge located at the Dauphin Island Sea Lab.

Creeks were paired based on proximity. Each experimental creek (cultch + oysters) was paired with a Control creek (no cultch or oysters). Oyster reefs were established in the experimental creeks (I-1, I-2, and I-3) in March 2005, with target densities of 150 adults per square meter (i.e., the estimated mean natural density for oyster reefs in the northern Gulf of Mexico; May 1971). Although the number of oysters declined over the two-year study period, densities remained consistently higher than the target density (~150–250 adults m^{-2}). Tidal creek area and depth at high tide were used to determine the number of oysters needed to filter the entire volume of the creek every 12 h, assuming a filtration rate of 0.0045 m^3 $oyster^{-1}$ h^{-1} (Newell 1988). Adults are defined as >60 mm shell height (SH). Each reef was rectangular in shape and situated close to the mouth of the creek; structures were approximately 0.5 m in height and covered 10% of the total creek area.

To ensure that impact treatments maintained the desired oyster density of 150 oysters per square meter, biannual sampling on the restored reefs began immediately following reef construction. Reefs were sampled by haphazardly tossing a 0.25-m^2 quadrat on the reef surface and removing all shell from within the quadrat. Approximately 20% of the reef was sampled, and the removed shell was counted, measured, and placed into four categories: juvenile oysters (less than 3-cm shell height), adult oysters (greater than 3-cm SH), dead oysters, and mussels.

Five sampling stations were established along a central transect at +2, +0.5, −0.5, −2, and 4 m relative to the reef/

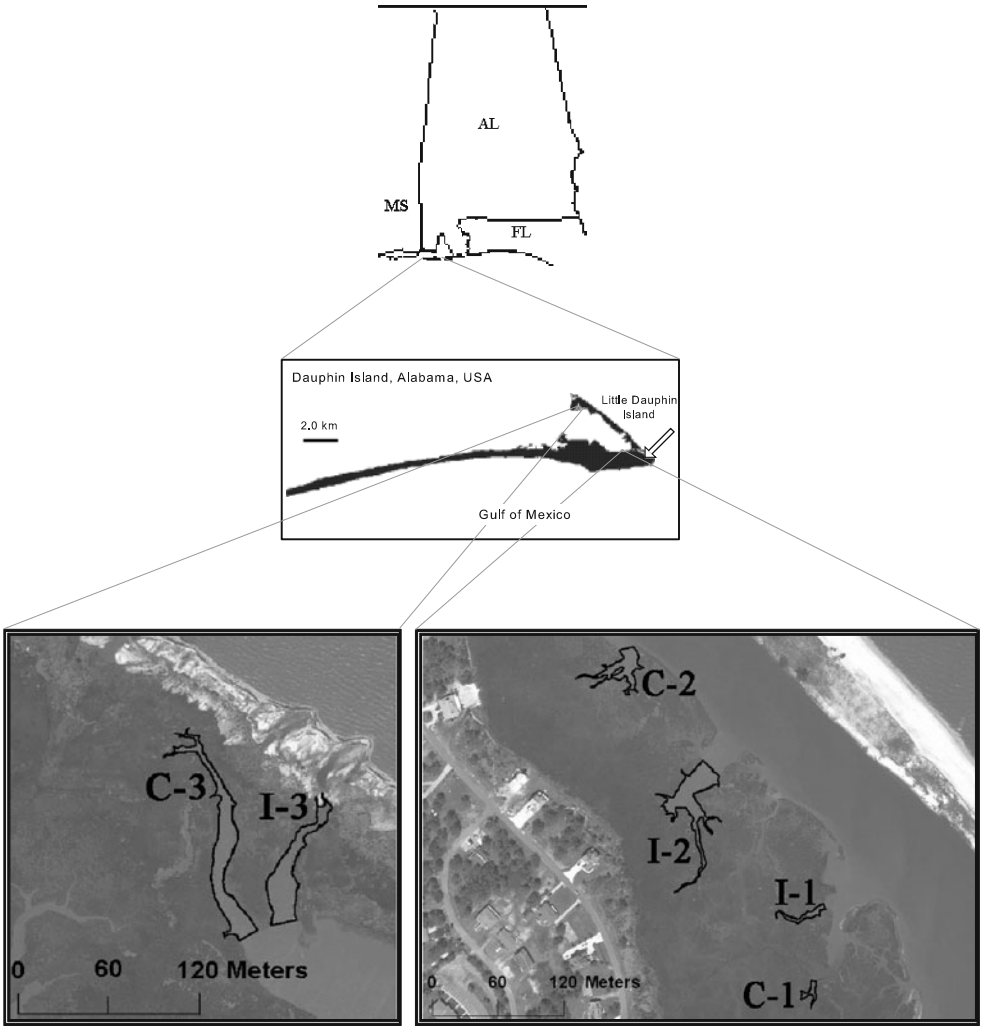

Fig. 1 Aerial view of study location on Dauphin Island, Alabama

control position (positive and negative numbers refer to downstream and upstream from the reef, respectively). Monthly sampling began in June 2004 and continued through summer 2006, except a few months of unfavorable meteorological conditions, and all creeks were sampled at roughly the same point in the tidal cycle. Pre-treatment sampling was conducted from June 2004 through February 2005 to establish a baseline reference. After the establishment of reefs/controls in March 2005, sampling continued through August 2006. This design allowed for a Before–After-Control–Impact (BACI) analytical treatment, including comparisons of response variables between pre-oyster reef and post-oyster reef conditions and between paired sites after reef construction. Our use of the BACI design made it likely that any detected changes resulted from the addition of oyster reefs and not from other sources of spatial and temporal variability (Underwood 1992).

We examined four metabolic response variables in both the sediment and water column (i.e., net community production, community respiration, gross community production, and chlorophyll *a* (Chl-*a*) concentration) as indicators of primary producer abundance (see Pinckney 1999). Monthly metabolism measurements were made using light/dark incubations (i.e., the oxygen evolution method). At each station, one pair (one clear + one dark) of 300-mL biological oxygen demand (BOD) bottles was deployed at the water surface with buoys, and a second pair was anchored to the creek bottom with PVC poles. Each bottle was filled with ambient water and retrieved following a 3-h incubation period. Initial and final oxygen concentrations were measured using a WTW® oxy-197*i* dissolved oxygen meter.

In addition to BOD bottles, a pair of benthic chambers was deployed at each station. Each chamber had a base diameter of 18.42 cm, a total volume of approximately 3 L, and was positioned approximately 2 cm into the sediment. Initial oxygen concentrations in the chambers were assumed to be similar to those in bottles positioned at the same station. After 3 h, water was extracted with a syringe and carefully injected into a 60-mL BOD bottle to avoid introduction of air bubbles. For each station, sediment metabolism was determined as the difference between

chamber measurements (which include the sediment and overlying water column) and measurements of the corresponding BOD bottle (i.e., a proxy for the overlying water column enclosed in the chamber). Metabolic rates were calculated as follows:

$$\mathrm{WNP} = C_{\mathrm{NP}}(F_{\mathrm{CB}} - I_{\mathrm{CB}})/t \quad (1)$$

$$\mathrm{WR} = C_{\mathrm{R}}(F_{\mathrm{DB}} - I_{\mathrm{DB}})/t \quad (2)$$

$$\mathrm{SNP} = VC_{\mathrm{NP}}((F_{\mathrm{CC}} - I_{\mathrm{CC}}) - (F_{\mathrm{CB}} - I_{\mathrm{CB}}))/(tA) \quad (3)$$

$$\mathrm{SR} = VC_{\mathrm{R}}((F_{\mathrm{DC}} - I_{\mathrm{DC}}) - (F_{\mathrm{DB}} - I_{\mathrm{DB}}))/(tA) \quad (4)$$

where WNP, WR, SNP, and SR are water column net production, water column respiration, sediment net production, and sediment respiration; F_{CB}, F_{DB}, F_{CC}, and F_{DC} are the final oxygen concentrations in clear bottles, dark bottles, clear chambers, and dark chambers (milligrams O_2 per liter); I_{CB}, I_{DB}, I_{CC}, and I_{DC} are the initial oxygen concentrations in clear bottles, dark bottles, clear chambers, and dark chambers (milligram O_2 per liter); t is incubation time (hour); C_{NP} (0.313 mg C mg O_2^{-1}) and C_{R} (0.375 mg C mg O_2^{-1}) represent the conversion factors from oxygen to carbon assuming photosynthetic and respiratory quotients of 1.2 and 1 (Strickland and Parsons 1972); V is the volume of water enclosed in the chamber (liter); and A is the area of the incubation chamber (square meter). Finally, we derived water column and sediment gross community production values for each station from the sum of net community production and the absolute value of community respiration.

In addition to metabolic response variables, water column and sediment Chl-*a* and water column nutrient concentrations were measured at each station. Chl-*a* concentrations were measured monthly, while nutrient concentrations were measured biweekly. One-liter water samples were collected at approximately mid-water column, put on ice, and taken to the laboratory, where 100 mL from each 1-L sample was filtered onto a Pall® 47-mm glass microfiber filter (GF/F). Filters were frozen at −80°C until analysis. Additionally, sediment cores (2.5 cm in diameter) were sampled, and the top 1 cm of sediment was collected for Chl-*a* determination.

Chl-*a* was extracted from filters and sediment samples using approximately 10 and 25 mL of a 2:3 mixture of dimethyl sulfoxide and 90% acetone, respectively (Shoaf and Lium 1976). Chl-*a* concentration (microgram per liter or milligram Chl-*a* per square meter) was determined fluorometrically (Turner Designs® TD-700) using the method by Welschmeyer (1994), which is designed to be minimally sensitive to chlorophyll *b* and chlorophyll degradation products.

To explore short-term variability of Chl-*a*, we deployed Yellow Springs Instruments 6600 automated sensors. The YSI instruments were deployed at the −0.5 m station in pair 2 from April 30, 2006 to May 19, 2006 and in pair 3 from June 26, 2006 to July 26, 2006; Chl-*a* concentrations were continually monitored every 15 min throughout the period of deployment.

Water column particulate organic matter (POM), dissolved nutrient (NO_3^-, NO_2^-, NH_4^+, DON, and PO_4^{3-}), particulate organic nitrogen and carbon (PON and POC), and dissolved organic carbon (DOC) concentrations were measured from the 1-L water samples collected at each station. Using a Pall® 47-mm pre-muffled glass microfiber filter (GF/F), 400 mL of each 1-L water sample was filtered. Filters were stored in a drying oven at approximately 60°C and POM (grams per liter) calculated by loss on ignition. Ten milliliters of filtered water served as samples for DOC analysis, using the Shimadzu TOC-500 as described by Pennock and Cowan (2001). An additional 60 mL of filtered water was used for analyses of dissolved inorganic and organic nitrogen (DIN and DON), using a Skalar Autoanalyzer as described by Pennock and Cowan (2001). From the same 1-L sample, 100 mL was filtered onto a Whatman® 25-mm pre-muffled glass microfiber filter (A/E) for the determination of PON and POC using a CarloErba CNS as described by Pennock and Cowan (2001).

Additionally, in situ measurements of water temperature (degrees Celsius), salinity (parts per thousand), dissolved oxygen (milligram per liter), surface irradiance (micromole photons per square meter per second), and light attenuation levels (per meter) were measured at stations 2 and −2. Lastly, Heck et al. (submitted) obtained continuous irradiance measurements, integrated over 15-min intervals, at the −0.5 station using a LICOR (4π) spherical sensor and datalogger.

Statistical Analyses

Initially, separate two-way analysis of variance (ANOVA) analyses were performed on Control and Impact creek data to determine if there were differences according to station (i.e., distance from the reef). We subsequently analyzed creek-integrated Control–Impact (C-I) values for each pair of creeks. For each dependent variable, all C-I values (i.e., average for all stations in the Control creek minus the average for all stations in the Impact creek for any given sampling date) before reef deployment were compared with all C-I values after reef deployment for each pair of creeks using a one-way ANOVA. Data were analyzed using Minitab 15 statisti-

cal software. The threshold of statistical significance for this study was α=0.05.

Results

Two-way ANOVAs revealed very few significant differences with station, and those few differences were inconsistent. A creek-integrated approach was taken for all subsequent analyses. Although creeks were paired according to "similarities," creek pairs were different from one another regarding size, position, and environmental characteristics. Taking this into consideration, creek pairs were not treated as replicates; they were independently analyzed. Thus, variability due to location was removed from statistical analyses, making any changes due to oyster reef placement easily identifiable.

To identify trends, we examined the C-I values (i.e., to determine whether they became more positive or negative upon addition of the reefs). When measured values increased in the Impact creek, C-I values became more negative. When measured values decreased, C-I values for the pair became more positive. Creek pairs are referenced as pair 1 (C-1 and I-1), pair 2 (C-2 and I-2), and pair 3 (C-3 and I-3). Here, we focus on variables that exhibited a significant change in at least one creek pair.

Metabolism and Chlorophyll *a*

Mean C-I values for water column Chl-*a* before and after oyster introduction were 2.07 and 0.91 μg L^{-1}, respectively, and mean C-I values for sediment Chl-*a* before and after were 0.01 and −0.27 μg cm^{-2}, respectively. Mean C-I values for water column net community production before and after oyster introduction were 0.007 and 0.004 mg C cm^{-2} h^{-1}, respectively, and sediment net community production means before and after were −4.89 and 2.49 mg C cm^{-2} h^{-1}, respectively. Mean values (±SE) of metabolism and Chl-*a* for Control and Impact creeks before and after oyster deployment are summarized in Table 1.

In general, the intrinsic differences between Control and Impact creeks with reference to water column Chl-*a*, net community production, and community respiration did not change with the deployment of oyster reefs in any of the three creek pairs (Table 2, Fig. 2). There was one statistically significant increase in water column Chl-*a* noted in pair 3 (p=0.036). For benthic Chl-*a*, only pair 1 (p=0.025) exhibited a significant effect, where sediment chlorophyll values for the Impact creek were lower when compared to those of the control. For benthic metabolism, we found a significant increase in community respiration in pair 3 (p=0.019), leading to a significant decrease in net community production (p=0.016) upon reef introduction (Table 2, Fig. 3).

Table 1 Mean values (±SE) of metabolism and Chl-*a* for Control and Impact creeks before and after oyster deployment

	Control Before	Control After	Impact Before	Impact After
W-C Chl-*a* (μg L^{-1})	10.5±1.04	8.725±0.393	8.423±0.751	7.818±0.318
WR (mg C L^{-1} h^{-1})	−0.015±0.003	−0.018±0.003	−0.01±0.003	−0.01±0.003
WNP (mg C L^{-1} h^{-1})	0.041±0.004	0.056±0.004	0.048±0.004	0.06±0.004
NH_4^+ (μM)	5.045±0.834	3.706±0.125	4.462±1.045	4.124±0.13
PO_4^{3-} (μM)	0.41±0.036	0.245±0.006	0.356±0.034	0.269±0.007
PON (mg L^{-1})	0.218±0.033	0.268±0.008	0.142±0.014	0.24±0.006
POC (mg L^{-1})	2.099±0.374	1.969±0.074	1.275±0.152	1.696±0.052
Sed Chl-*a* (μg cm^{-2})	17.334±0.706	14.34±0.385	17.32±0.67	14.61±0.339
SR (mg C cm^{-2} h^{-1})	−11.98±1.133	12.67±0.719	−12.44±0.949	−13.54±0.728
SNP (mg C cm^{-2} h^{-1})	6.894±1.489	1.685±0.951	11.79±1.869	−0.081±1.008
Pore NO_2 + NO_3 (μM)	ND	2.014±0.145	ND	2.018±0.143
Pore NH_4^+ (μM)	ND	57.21±3.024	ND	55.62±2.307
Pore PO_4^{3-} (μM)	ND	3.021±0.33	ND	2.529±0.243
Depth (m)	0.408±0.03	0.538±0.022	0.413±0.027	0.562±0.02
Bottom irradiance (μmol m^{-2} s^{-1})	956.5±66.06	1,118±41.79	1,034±6,053	1,064±46.76
O_2 (mg L^{-1})	6.638±0.357	14.75±3.499	6.79±0.366	18.87±8.845
Temperature (°C)	24.74±0.933	25.76±0.0.596	24.27±0.965	25.5±0.596
Salinity	17.27±0.917	17.38±0.709	17.23±0.955	17.3±0.728

Table 2 ANOVA results for water column and sediment biological variables

	Pair 1	Pair 2	Pair 3
W-C Chl-*a*	p=0.985	p=0.393	p=0.036[a]
W-C NP	p=0.182	p=0.174	0.939
W-C R	p=0.248	p=0.156	p=0.37
Sed Chl-*a*	p=0.025[a]	p=0.145	p=0.08
Sed NP	p=0.376	p=0.629	p=0.016[a]
Sed R	p=0.806	p=0.647	p=0.019[a]

[a] Statistically significant difference

Nutrients

Mean C-I values for PON before and after oyster introduction were 0.076 and 0.028 mg L^{-1}, respectively, and POC C-I values before and after were 0.824 and 0.273 mg L^{-1}, respectively. Mean C-I values for water-column ammonium (NH_4^+) before and after oyster introduction were 0.583 and −0.0418, respectively. Mean C-I values for phosphate (PO_4^{3-}) before and after oyster introduction were 0.054 and −0.024, respectively.

Water column ammonium (NH_4^+) was the only variable that exhibited change in more than one creek. There were significant increases in ammonium in the Impact creeks of pairs 1 and 2 (p=0.001 and p=0.029, respectively). We also noted a difference in water column phosphate (PO_4^{3-}) between creeks of pair 1 (p<0.001), where the Impact creek showed increased concentrations compared to those of the Control creek upon oyster reef introduction. Significant changes were observed for water column PON (p=0.007) and POC (p=0.022) in pair 2, where the Impact creek showed increased PON and POC concentrations compared to those of the Control creek upon oyster reef introduction (Table 3, Fig. 4a, b).

Discussion

Oysters are known for their high filtration rates and, consequently, the rapid removal of particulates from overlying water. However, filtration rates are temperature-dependent. At temperatures ranging from 16°C to 28°C, when other factors are held constant, filtration rates of oysters remain constant but can considerably increase at temperatures above 28°C (Korringa 1952). Over the course of our study, water temperatures were nearly always above 28°C from May through September each year, indicating that filtration rates were likely high during these months.

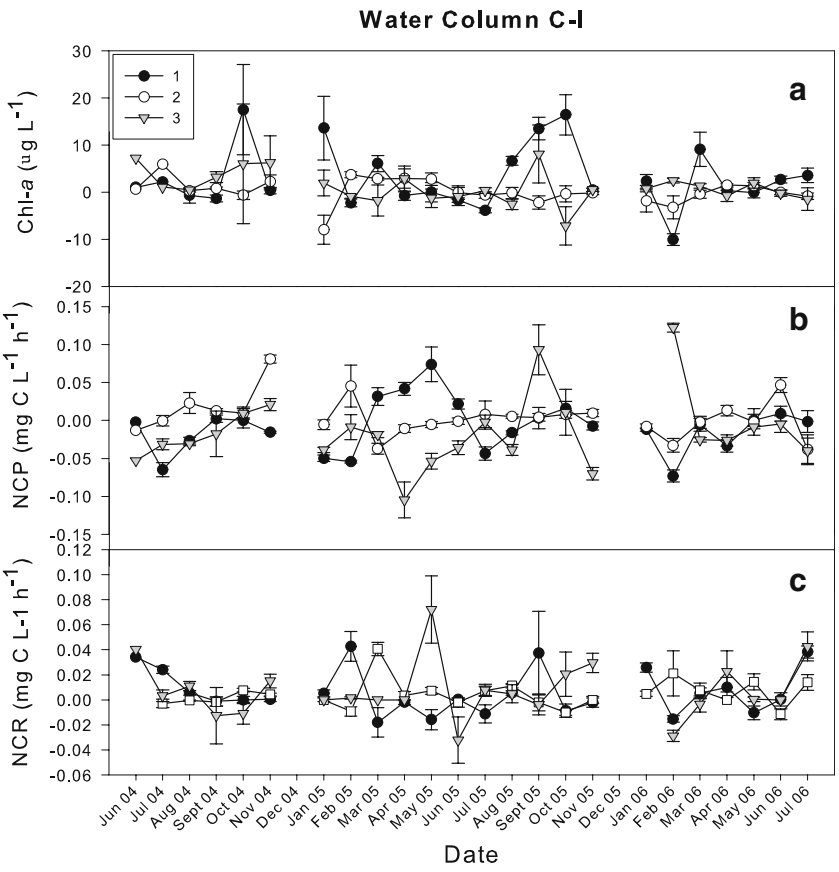

Fig. 2 Graph of intrinsic differences between Control and Impact creeks with reference to water column Chl-*a*, net community production, and community respiration with the deployment of oyster reefs in the three creek pairs

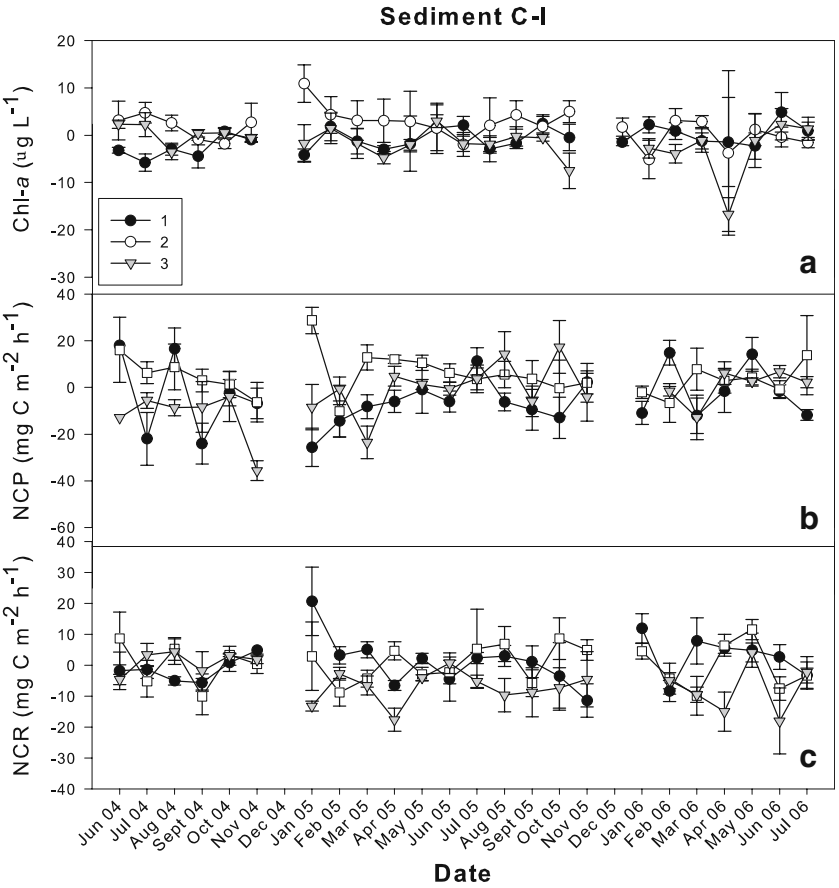

Fig. 3 Graph of intrinsic differences between Control and Impact creeks with reference to sediment Chl-*a*, net community production, and community respiration with the deployment of oyster reefs in the three creek pairs

Despite the expectation that the addition of oysters at such high densities as those used in this study would have a substantial impact on the water column around the reef, this did not appear to be the case. Although we noted that the presence of oysters influenced sediment Chl-*a* and metabolism, as well as water column nutrient concentrations, impacts were inconsistent and did not support a clear cause–effect relationship attributable to newly deployed reefs. The lack of consistent differences between Control and Impact creeks also applied to monthly and continuous measurements of photosynthetically active radiation (Heck et al. submitted).

The lack of consistent "oyster effects" in this study was likely due, in part, to spatial scale. For example, a significant difference in water column Chl-*a* may have been detected, if sampling had been conducted at a finer scale (i.e., over a few centimeters), as opposed to the meter-scale employed here. Small oyster reefs placed in tidal creeks have been shown to have a significant impact on water column Chl-*a* concentrations and total suspended solids at a distance of 5 cm from the reef (Nelson et al. 2004). It is possible that the closest measurements in this study (i.e., 50 cm from the reef) were beyond the "zone of impact" and outside the range over which oysters have a significant impact on water quality. Indeed, samples taken directly above the reef, or at the same relative position in Control creeks, showed lower water column Chl-*a* concentrations in Impact than Control creeks, indicating that the effect of oysters on phytoplankton biomass was spatially restricted to the area immediately above the reefs (Heck et al. submitted; Fig. 5). This seems to support the view of Pomeroy et al. (2006) that oysters have a limited ability to improve water quality on a large scale but see Newell et al. (2007) and Coen et al. (2007).

Since reefs were only built to a height of 0.5 m, it is possible that the oysters never had access to a portion of the water column due to stratification, particularly in the summer when south winds resulted in water levels that were elevated above those predicted. Our initial assumption

Table 3 ANOVA results for water column nutrients exhibiting at least one significant impact

	Pair 1	Pair 2	Pair 3
PON	$p=0.286$	$p=0.007$[a]	$p=0.667$
POC	$p=0.229$	$p=0.002$[a]	$p=0.630$
NH_4^+	$p=0.001$[a]	$p=0.029$[a]	$p=0.251$
PO_4^{3+}	$p<0.001$[a]	$p=0.119$	$p=0.104$

[a] Statistically significant difference

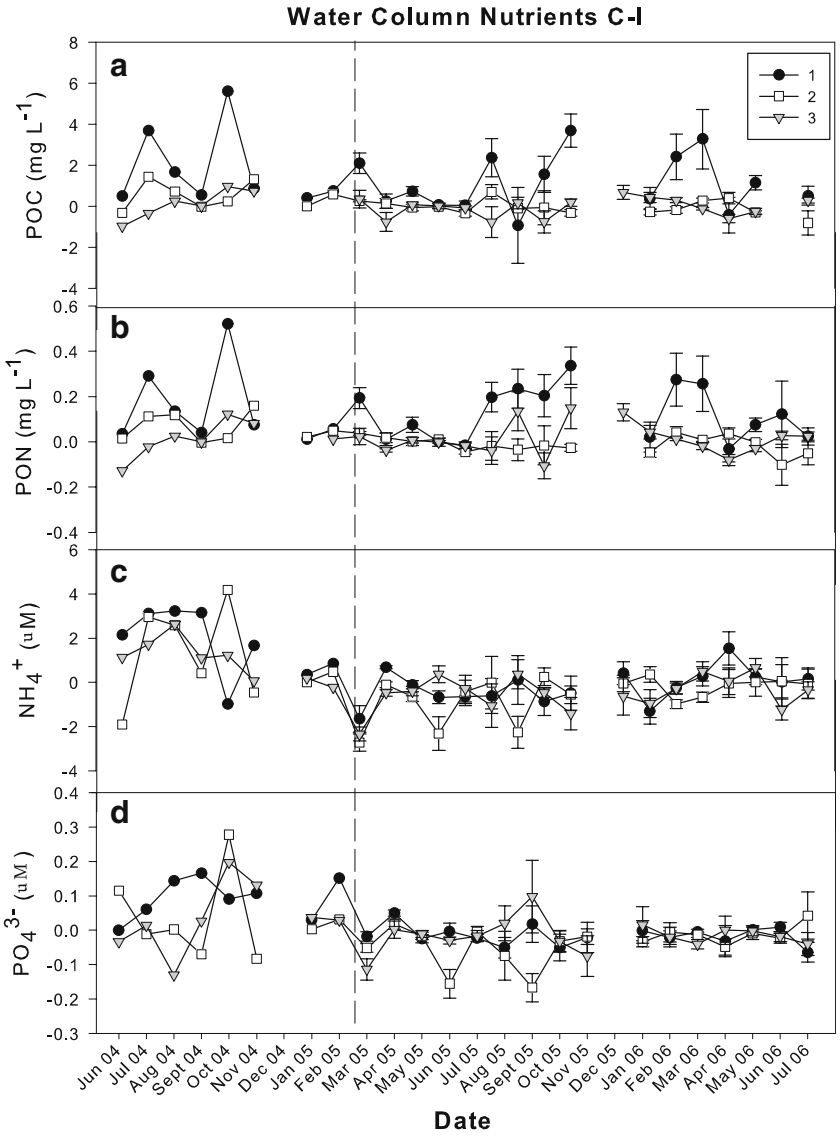

Fig. 4 Graph of intrinsic differences between Control and Impact creeks with reference to water column PON, POC, ammonium, and phosphate

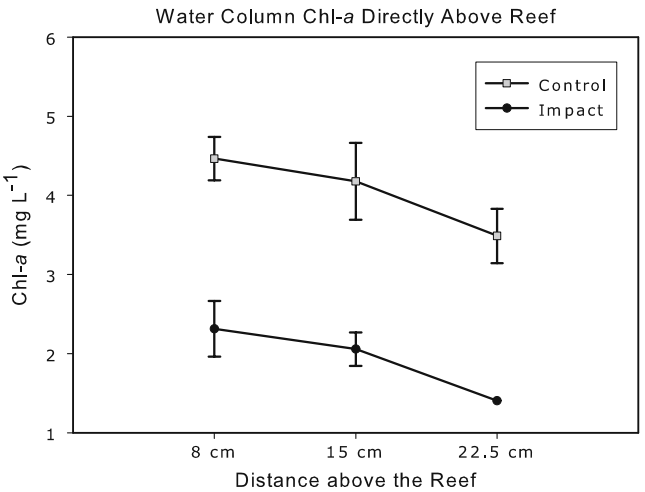

Fig. 5 Samples taken directly above the reef, and at the same relative position in Control creeks, showed lower water column Chl-*a* concentrations in Impact than Control creeks

was that the shallowness of the water column (mean depth <1 m) would ensure complete mixing. However, Riisgard et al. (2007) reported that similarly shallow water in Denmark remained stratified unless winds blew consistently at velocities greater than 8 m s^{-1}. Filter feeders in the shallow fjord system often did not come in contact with much of the water column, and filtration ability was in practice much lower than those previously published (Riisgard et al. 2007). Only when wind velocities were above the 8 m s^{-1} threshold did mixing occur and substantial depletion of the water column took place. Since wind velocities are usually low in the north-central Gulf of Mexico (monthly means always <8 m s^{-1}, Zhao and Chen 2008), it is quite possible that only a small portion of the lower water column regularly came in contact with the oysters on the reef.

Several other factors might have contributed to the lack of consistent impacts of created oyster reefs on microalgal

abundance and productivity, metabolism, and nutrient dynamics in tidal creeks, including location. The tidal creeks examined in this study are surrounded by *Juncus roemerianus* (black needlerush) marshes. Large quantities of particulate and dissolved organic matter can flow from the marshes into the creeks, particularly during heavy rain events or during summer when marshes are regularly flooded by high tides (Mallin et al. 2002). Hence, significant input from surrounding marshes might have played a role in masking impacts of the oyster reefs on water quality. Also, high frequency data from the deployed YSI instruments showed large temporal oscillations in the concentration of Chl-*a* in the water column for both control and oyster-seeded creeks. Oscillations in Chl-*a* likely represent another confounding factor, contributing to the overall lack of significant effect of oyster reefs in this tidal creek system. Spectral analysis of this data indicated that there were multiple significant frequencies, pointing to several underlying causes for Chl-*a* oscillations. However, the dominant frequency for all creeks was approximately 24 h. This suggests that despite a weak tidal signal, tidal forcing was primarily responsible for these oscillations.

Although 10% of the creek bottom area was covered by reef and oyster density within the reef was high, water may not have been in contact with oysters long enough to result in a detectable oyster effect. Creeks 1–4 are located along a channel with heavy boat traffic, which increases flushing rates and could reduce contact time between inflowing water and oysters. Moreover, coincident with fast flow and short residence time, wind-driven sediment re-suspension could significantly elevate dissolved and particulate organics in the water column.

It is also possible that the reefs are part of a feedback loop, where phytoplankton-derived particulate nitrogen is ingested by oysters, rapidly re-mineralized, and released as ammonium to support phytoplankton growth. Such a loop might have had a role in obscuring any noticeable impact of oyster filtration on water quality.

Finally, the five tropical storms that made landfall within 110 nautical miles of our sites during the 2-year study period (Hurricane Ivan, Sept. 16, 2004; Tropical Storm Arlene, June 11, 2005; Hurricane Cindy, July 6, 2005; Hurricane Dennis, July 10, 2005; Hurricane Katrina, Aug. 29, 2005) could have masked the impact of outplanted oysters on primary productivity, metabolism, and nutrient dynamics of the creeks studied. Indeed, Cebrian et al. (2008) showed that Hurricane Ivan did not affect water-column Chl-*a* concentration and primary productivity but caused a considerable decrease in sediment Chl-*a* and primary productivity for several months afterward. The storms could have masked the effect of the oysters on sediment Chl-*a*, but not on productivity, metabolism, or nutrient cycling (Cebrian et al. 2008).

Conclusions

Despite our inability to reject the null hypothesis for most variables measured (i.e., the establishment of oyster reefs had no effect), oyster reefs are likely capable of significantly altering productivity and water quality in a different location or with a different design (e.g., a model that optimizes residence time and contact between oysters and overlying water). The reef design employed in this study was not necessarily intended to imitate the structure of natural oyster reefs. Rather, the design was chosen to simplify sampling (i.e., logistics) and maintain a degree of standardization from creek to creek. While this design, in this location, seemed to work well enough to foster oyster growth and survival, it did not yield measurable benefits such as increased water clarity or benthic primary productivity in the creeks—benefits that might be taken for granted in habitat restoration planning. Improvements in water clarity and increased benthic production might be more likely through a reef design which maximizes the volume of water in contact with the reef surface. Also, the types, magnitudes, and spatial extent of changes in ecosystem services that should be expected after reef restoration might need to be re-evaluated.

The results reported here suggest that specific goals must be well defined to properly evaluate the success of oyster reef restoration. As structure does not always confer function in ecological restoration, our study confirms that oyster arrangement, reef size and shape, and system characteristics that could be complicating factors should be taken into consideration when attempting to expressly address issues of water quality and overall community productivity.

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References

Andrews, J.D. 1988. Epizootiology of the disease caused by the oyster pathogen *Perkinsus marinus* and its effects on the oyster industry. *American Fisheries Society Special Publication* 18: 47–63.

Andrews, J.D. 1996. History of *Perkinsus marinus*, a pathogen of oysters in Chesapeake Bay 1950–1984. *Journal of Shellfish Research* 15: 13–16.

Brumbaugh, R.D., L.A. Sorabella, C.O. Garcia, W.J. Goldsborough, and J.A. Wesson. 2000. Making a case for community-based oyster restoration: An example from Hampton Roads, Virginia, USA. *Journal of Shellfish Research* 19: 397–400.

Cebrian, J., C.D. Foster, R. Plutchak, K. Sheehan, A. Anton, M. Miller, K. Major, K. Heck, and S.P. Powers. 2008. The impact of Hurricane Ivan on the primary productivity and metabolism of marsh tidal creeks in the North Central Gulf of Mexico. *Aquatic Ecology* 42: 391–404.

Cloern, J.E. 1982. Does the benthos control phytoplankton biomass in south San Francisco Bay? *Marine Ecological Progress Series* 9: 191–202.

Coen, L.D., and M.W. Luckenbach. 2000. Developing success criteria and goals for evaluating oyster reef restoration: Ecological function or resource exploitation? *Ecological Engineering* 15: 323–343.

Coen, L.D., R.D. Brumbaugh, D. Bushek, R. Grizzle, M.W. Luckenbach, M.H. Posey, S.P. Powers, and S.G. Tolley. 2007. Ecosystem services related to oyster restoration. *Marine Ecology Progress Series* 341: 303–307.

Cohen, R.R.H., and J.T. Carlton. 1998. Accelerating invasion rate in a highly invaded estuary. *Science* 279: 555–558.

Cohen, R.R.H., P.V. Dresler, E.J.P. Philips, and R.L. Cory. 1984. The effect of the Asiatic clam, *Corbicula fluminea*, on phytoplankton of the Potomac River, Maryland. *Limnology and Oceanography* 29: 170–180.

Dame, R.F. 1993. The role of bivalve filter feeder material fluxes in estuarine ecosystems. In *Bivalve filter feeders in estuarine and coastal ecosystem processes*, ed. R.F. Dame, 245–269. Heidelberg: Springer.

Dame, R.F. 1999. Oyster reefs as components in estuarine nutrient cycling: incidental or controlling? In *Oyster reef habitat restoration: A synopsis and synthesis of approaches*, ed. M.W. Luckenbach, R. Mann, and J.A. Wesson, 267–280. Williamsburg, VA: Virginia Institute of Marine Science.

Dame, R.F., R.G. Zingmark, and E. Haskin. 1984. Oyster reefs as processors of estuarine material. *Journal of Experimental Marine Biology and Ecology* 83: 239–247.

Duarte, C.M. 1995. Submerged aquatic vegetation in relation to different nutrient regimes. *Ophelia* 41: 87–112.

Encomio, V., and F.L.E. Chu. 2000. The effect of PCBs on glycogen reserves in the eastern oyster *Crassostrea virginica*. *Marine Environmental Research* 50: 45–49.

Gerritsen, J., A.F. Holland, and D.E. Irvine. 1994. Suspension-feeding bivalves and the fate of primary production: An estuarine model applied to Chesapeake. *Estuaries* 17: 403–416.

Jackson, J., M.X. Kirby, W.H. Berger, K.A. Bjorndal, L.W. Botsford, B.J. Bourque, R.H. Bradbury, R. Cooke, J. Erlandson, J.A. Estes, T.P. Hughes, S. Kidwell, C.B. Lange, H.S. Lenihan, J.M. Pandolfi, C.H. Peterson, R.S. Steneck, M.J. Tegner, and R.R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293: 629–647.

Jones, C.G., J.H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos* 69: 373–386.

Korringa, P. 1952. Recent advances in oyster biology. *Quarterly Review of Biology* 27(3): 266–308.

Mallin, M.A., S.H. Ensign, T.L. Wheeler, and D.B. Mayes. 2002. Pollutant removal efficacy of three wet detention ponds. *Journal of Environmental Quality* 31(2): 654–660.

Mann, R. 2000. Restoring the oyster reef communities in the Chesapeake Bay: A commentary. *Journal of Shellfish Research* 19: 335–339.

May, E.B. 1971. A survey of the oyster and oyster shell resources of Alabama. Alabama Department of Conservation, Dauphin Island, Alabama. *Alabama Marine Resources Bulletin* 4: 1–52.

Meyer, D.L., E.C. Townsend, and G.W. Thayer. 1997. Stabilization and erosion control value of oyster cultch for intertidal marsh. *Restoration Ecology* 5: 93–99.

Nelson, K.A., L.A. Leonard, M.H. Posey, T.D. Alphin, and M.A. Mallin. 2004. Using transplanted oyster (*Crassostrea virginica*) beds to improve water quality in small tidal creeks: A pilot study. *Journal of Experimental Marine Biology and Ecology* 298: 347–368.

Newell, R.I.E. 1988. Ecological changes in the Chesapeake Bay: Are they the result of overharvesting the American oyster, *Crassostrea virginica*? In *Understanding the estuary: Advances in Chesapeake Bay research*, ed. M.P. Lynch and E.C. Krome, 536–546. Baltimore, Maryland: Chesapeake Bay Research Consortium, Publication 129.

Newell, R.I.E., and E.W. Koch. 2004. Modeling seagrass density and distribution in response to changes to turbidity stemming from bivalve filtration and seagrass sediment stabilization. *Estuaries* 27(5): 793–806.

Newell, R.I.E., W.M. Kemp, J.D. Hagy III, C.A. Cerco, J.M. Testa, and W.R. Boynton. 2007. Top-down control of phytoplankton by oysters in Chesapeake Bay, USA: Comment on Pomeroy et al. (2006). *Marine Ecology Progress Series* 341: 293–298.

Paerl, H.W., J. Dyble, P.H. Moisander, R.T. Noble, M.F. Piehler, J.L. Pinckney, T.F. Steppe, L. Twomey, and L.M. Valdes. 2003. Microbial indicators of aquatic ecosystem change: current applications to eutrophication studies. *FEMS Microbial Ecology* 46: 233–246.

Paine, R.T. 1966. Food web complexity and species diversity. *The American Naturalist* 100: 65–75.

Peierls, B.L., N.F. Caraco, M.L. Pace, and J.J. Cole. 1991. Human influence on river nitrogen. *Nature* 350: 386–387.

Pennock, J.R., and J.L.W. Cowan. 2001. Analytical instrumentation methods manual. Marine environmental sciences consortium. *Technical Report* 98–003: 69.

Pinckney, J.I. 1999. Responses of the phytoplankton community growth rate to nutrient pulses in variable estuarine environments. *Journal of Phycology* 35: 1455–1463.

Pomeroy, L.R., C.F. D'Elia, and L.C. Schaffner. 2006. Limits to top-down control of phytoplankton by oysters in Chesapeake Bay. *Marine Ecology Progress Series* 325: 301–309.

Riisgard, H.U., J. Lassen, M. Kortegaard, L.F. Moller, M. Friedrichs, M.H. Fensen, and P.S. Larsen. 2007. Interplay between filter-feeding zoobenthos and hydrodynamics in the shallow Odense Fjord (Denmark)—earlier and recent studies, perspectives and modeling. *Estuarine, Coastal and Shelf Science* 75: 281–295.

Sand-Jensen, K., and J. Borum. 1991. Interactions among phytoplankton, periphyton, and macrophytes in temperate freshwater and estuaries. *Aquatic Botany* 41: 137–175.

Shoaf, W.T., and B.W. Lium. 1976. Improved extraction of chlorophyll *a* and *b* from algae using dimethyl sulfoxide. *Limnology and Oceanography* 21: 926–928.

Soniat, T.M., C.M. Finelli, and J.T. Ruiz. 2004. Vertical structure and predator refuge mediate oyster reef development and community dynamics. *Journal of Experimental Marine Biology and Ecology* 340: 163–182.

Strickland, J.D.H., and T.R. Parsons. 1972. A practical handbook of seawater analysis. *Bulletin of the Fisheries Research Board of Canada* 167: 1–310.

Tobias, C.R., M. Cieri, B.J. Peterson, L.A. Deegan, J. Vallino, and J. Hughes. 2003. Processing watershed-derived nitrogen in a well-flushed New England estuary. *Limnology and Oceanography* 48 (5):1766–1778.

Underwood, A.J. 1992. Beyond BACI: The detection of environmental impacts on populations in the real, but variable, world. *Journal of Experimental Marine Biology and Ecology* 161(2):145–178.

Valiela, I., M. Geist, J. McClelland, and G. Tomasky. 2000. Nitrogen loading from watersheds to estuaries: Verification of the Waquiot Bay nitrogen loading model. *Biogeochemistry* 41 (3):277–293.

Vitousek, P.M., H.A. Mooney, J. Lubchenco, and J.M. Mellilo. 1997. Human domination of Earth's ecosystem. *Science* 277: 494–499.

Welschmeyer, N.A. 1994. Fluorometric analysis of chlorophyll *a* in the presence of chlorophyll *b* and pheopigments. *Limnology and Oceanography* 39(8): 1985–1992.

Wynne, T.T., R.P. Stumpf, M.C. Tomlinson, V. Ransibrahmanakul, and T.A. Villareal. 2005. Detecting *Karenia brevis* blooms and algal resuspension in the western Gulf of Mexico with satellite ocean color imagery. *Harmful Algae* 4: 992–1003.

Zhao, H., and Q. Chen. 2008. Characteristics of extreme meteorological forcing and water level in Mobile Bay, Alabama. *Estuaries and Coasts* 31: 704–718.