CHAPTER 20

Ecosystem Services Provided by Shoreline Reefs in the Gulf of Mexico
An Experimental Assessment Using Live Oysters

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CONTENTS

20.1 Introduction ................................................................. 402
20.2 Methods ......................................................................... 403
  20.2.1 Study Sites ................................................................. 403
  20.2.2 Oyster Reef Restoration ............................................... 403
  20.2.3 Monitoring ................................................................. 404
    20.2.3.1 Microalgae .............................................................. 406
    20.2.3.2 Infauna ................................................................. 407
    20.2.3.3 Fish and Mobile Invertebrates ................................. 407
20.3 Statistical Analyses ......................................................... 407
  20.3.1 Microalgae ................................................................. 407
  20.3.2 Infauna ................................................................. 408
  20.3.3 Fish and Mobile Invertebrates .................................... 408
20.4 Results ......................................................................... 408
  20.4.1 Study Site Characteristics ........................................... 408
  20.4.2 Algal Biomass ............................................................. 409
  20.4.3 Infauna ................................................................. 411
  20.4.4 Fish and Mobile Macroinvertebrates ............................ 413
    20.4.4.1 Seine Results ......................................................... 413
    20.4.4.2 Gillnet Results ....................................................... 413
20.5 Discussion .................................................................. 414
  20.5.1 Lack of Effects on Algal Biomass and Infaunal Abundance .... 415
  20.5.2 Small Effects on Fish and Mobile Macroinvertebrates ........ 416
20.6 Conclusions ................................................................. 417
Acknowledgments ................................................................. 418
References ........................................................................ 418
20.1 INTRODUCTION

In addition to playing their traditional role as producers of a valuable shellfish resource (Breitburg 1999; Coen and Luckenbach 2000; Coen et al. 1999), oyster reefs are increasingly recognized for the many valuable ecosystem services they provide. As discussed by Lenihan and Peterson (1998) and Dame et al. (2000), some of the most important services provided by oyster reefs are shoreline protection, the provision of three-dimensional structures that shelter diverse assemblages of invertebrates and small fishes (Bahr and Lanier 1981; Breitburg 1999; Coen et al. 1999; Harding and Mann 1999; Lehner and Allen 2002; Lenihan et al. 2001; Zimmerman et al. 1989), and the filtration of large amounts of particulate material from the water column, with potential large-scale effects on phytoplankton assemblages, nutrient dynamics, and sediment biogeochemistry (Dame 1993, 1996; Newell 1988). Nearly 30 years ago, Newell (1988) suggested that intense oyster harvesting in Chesapeake Bay could have increased the Bay’s susceptibility to the harmful effects of eutrophication because of the reduction in the abundance of suspension feeders. The formulation of this hypothesis was preceded by evidence that large populations of clams could greatly reduce phytoplankton abundance and thereby increase water clarity in San Francisco Bay (Cloern 1982; Officer et al. 1982) and the Potomac River (Cohen et al. 1984). If similar reductions in algal abundance occurred when oyster densities were restored to former levels, improved water clarity in estuarine systems could lead to enhanced productivity by benthic plants and a system-wide shift in the balance from pelagic to benthic productivity (Baird and Ulanowicz 1989; Newell 1988; Newell et al. 2002).

Despite the increasing recognition of the ecological benefits of oyster reefs, only a few empirical studies quantifying these benefits have been conducted and published. Several investigators have used models (Grabowski and Peterson 2007; Pomeroy et al. 2006; Ulanowicz and Tuttle 1992 [but see responses by Cerco and Noel 2007; Coen et al. 2007; Newell et al. 2007]) or extrapolations from localized, short-term studies (Dame et al. 1984; Porter et al. 2004) to predict the potential effects of oyster removal or enhancement on coastal ecosystems. To date, however, we are aware of only two experimental field tests of the effects of oyster removal or addition on the structure and function of coastal ecosystems. The first was a removal experiment carried out in intertidal reefs in South Carolina marsh complexes (Allen et al. 2007; Dame et al. 2000, 2002). There, the removal of oysters was not clearly related to either changes in water clarity or use of the creek by mobile invertebrates and fishes (Allen et al. 2007; Dame et al. 2000, 2002). The second was an addition experiment carried out in intertidal reefs in North Carolina salt marshes (Cressman et al. 2003; Nelson et al. 2004), where although there were some significant increases in water clarity at the oyster addition study sites in North Carolina, as shown by reduced amounts of suspended solids and chl-a, those differences were inconsistent and not of the magnitude expected.

Although South and North Carolina marshes are representative of the southeastern Atlantic Coast, they are markedly different from other locations where oyster reefs also thrive, such as the microtidal northern Gulf of Mexico. Thus, additional experiments in which the effects of oyster additions or removals are compared with unaltered controls are needed in other locations to assess the many ecosystem services that shoreline oyster reefs are believed to provide. Such studies will be useful in developing the predictive ability necessary to justify the high cost of many shoreline oyster reef restoration programs.

Toward this end, we quantified the most important ecosystem services believed to be provided by nearshore oyster reefs. The central hypothesis of our study was that there would be measurable increases in water clarity, benthic algae, infaunal abundance, and the abundance of juvenile fishes and invertebrates in areas where healthy oyster reefs were restored to pre-harvest levels. To test this hypothesis and quantify the spatial scale at which these effects could be detected, we experimentally introduced oyster reefs to a number of oyster-poor marsh creeks and compared critical ecosystem processes between those creeks and control creeks without oyster additions. We also quantified the effects of oyster reef addition on the dynamics of nutrients and organic matter...
within the water-column and sediments, including nutrient export from the creeks, and carried out a detailed examination of the effects of oyster reef additions on fish community structure. Some of these results have been previously reported in detail elsewhere (Geraldi et al. 2009; Plutchak 2008; Plutchak et al. 2010) and here we only summarize them. However, they are important in allowing us to present a comprehensive overview of the entire suite of variables measured in our investigation of the ecosystem-level changes that occurred after construction of the reefs.

20.2 METHODS

20.2.1 Study Sites

In the northern Gulf of Mexico, owing to the small tidal range, most large oyster reefs are subtidal (Kilgen and Dugas 1989). In shallow water, oysters often occur as islands or peninsulas that are exposed at extremely low tides. These oyster formations may be oriented either parallel or perpendicular to current flow and often occur near or just seaward of the mouths of marsh creeks. The summary of northern Gulf reefs by Kilgen and Dugas (1989) contains a thorough description of reef development in the microtidal northern Gulf, with diagrams of the different types of subtidal and intertidal reefs and where they are typically found.

To quantify the ecosystem services provided by shallow intertidal oyster reefs in coastal Alabama, we employed a relatively simple replicated Before–After, Control–Impact, Paired (BACIP) design (cf. Osenberg and Schmitt 1996; Underwood 1997). Based on maps, geo-referenced aerial photography (provided by the Mobile Bay National Estuary Program), and a field survey, six small tidal creeks were chosen as study locations along Dauphin Island Bay (Alabama, USA [N 30.255; W 88.109]; Figure 20.1). Tidal creeks were paired, based on physical similarities (i.e., size, depth, orientation, proximity, shoreline vegetation, and natural oyster density), with one paired creek receiving the treatment (oyster reef added) and the other serving as the control (no oyster reef added). Tidal creek surface area, length, and mouth width were determined from the geo-referenced aerial photos using ArcGIS at a scale of 1:2000, which is the smallest scale at which features in the photos were discernible.

Sparse populations of natural oysters were present in all creeks, and to ensure that these natural populations were similar among pairs, surveys of 10% of each creek were conducted in the fall of 2004. Using Hawth’s Analysis Tools extension for ESRI ArcGIS 9 (Beyer 2004), random dots were generated with latitude and longitude coordinates so that 10% of the creek would be sampled if each dot represented 1 m². During the field survey, the position of each dot was found using a handheld GPS and a 1-m² quadrat was then placed on the sediment surface so that the position of the dot would be centered within the quadrat. If quadrats happened to overlap, they were moved until the quadrats were adjacent to each other and new coordinates were recorded. All live oysters visible to the naked eye were then enumerated and returned to their original location, and the total abundances in paired creeks were compared with a two-tailed, paired t test.

20.2.2 Oyster Reef Restoration

One tidal creek from each pair was randomly chosen for oyster reef restoration (DIF 2, DIF 3 and LDI 1; Figure 20.1). All creeks contained scattered clumps of oysters and were judged to be suitable sites for the emplacement of living oyster reefs. Tidal creek area, maximum depth at high tide, and literature values for oyster filtration rates were used to determine the reef area required for the oysters in restored reefs to filter a volume of water equal to the entire volume of water within the creek every 12 h (Table 20.1). We used a 12-h period because we reasoned that the creeks would fill in roughly 12 h and empty roughly 12 h later in accord with the diurnal tidal regime in the study area. Adult oysters were assumed to filter 0.0045 m³ of water per individual per hour (Newell 1988).
Figure 20.1  Aerial photographs of the six tidal creeks around the east end of Dauphin Island, Alabama (top right inset) that were studied. The upper photo shows the two paired sites on Little Dauphin Island and the lower photo shows the four tidal creeks on Dauphin Island. The sites were paired based on similarity in physical parameters (LDI 1 and 2, DIF 1 and 2, and DIF 3 and 4) and are shown within the white lines. Treatment creeks were randomly chosen and the reef areas are indicated by black polygons. The lower right inset shows one of the reefs.

A target density of 150 adult oysters m$^{-2}$ was used, which is the estimated mean historical density for oyster reefs in the harvested areas of Mobile Bay (cf. May 1971), and should represent an appropriate density for measuring the effects attributed to healthy oyster reefs. From initial calculations, it was determined that approximately 10% of the creek area should receive oysters (Figure 20.1; Table 20.1). Reef sizes were calculated to be 43 m$^{2}$ for DIF 2, 207 m$^{2}$ for DIF 3, and 161 m$^{2}$ for LDI 1. Reefs were placed at and across the mouth of the tidal creek and consisted of an oyster shell pad of approximately 10 cm in height that was covered with live oysters and associated organisms such as polychaetes, mud crabs, barnacles, and mussels. Shell pads were put in place by a contractor (J & W Marine Inc., Bayou la Batre, Alabama) on February 21–24, 2005. Live oysters and associated fauna were tonged by local oystermen from Little Dauphin Island Bay and placed on top of the shell pad on February 28, 2005 to March 9, 2005.

### 20.2.3 Monitoring

Within each tidal creek, sampling stations were established along a transect perpendicular to the reef, originating 2 m in front of (i.e., toward the mouth of the creek) and extending 4 m behind the
### Table 20.1  The Physical Parameters of the Six Tidal Creeks

<table>
<thead>
<tr>
<th>Site</th>
<th>Treatment</th>
<th>Interpolated Creek Area (m²)</th>
<th>Creek Mouth Width (m)</th>
<th>Depth at Low Tide (m)</th>
<th>Depth at High Tide (m)</th>
<th>Estimated Maximum Volume of Creek (m³)</th>
<th>Estimated Velocity (cm/s)</th>
<th>Calculated Area of Reef (m²)</th>
<th>Live Oysters Added</th>
</tr>
</thead>
<tbody>
<tr>
<td>DIF 1</td>
<td>Control</td>
<td>147</td>
<td>9.14</td>
<td>0.6</td>
<td>1.1</td>
<td>88.18</td>
<td>0.06</td>
<td>20</td>
<td>8187</td>
</tr>
<tr>
<td>DIF 2</td>
<td>Treatment</td>
<td>368</td>
<td>8.77</td>
<td>0.65</td>
<td>1.2</td>
<td>239.48</td>
<td>0.31</td>
<td>43</td>
<td>207</td>
</tr>
<tr>
<td>DIF 3</td>
<td>Treatment</td>
<td>1752</td>
<td>19.69</td>
<td>0.5</td>
<td>1.05</td>
<td>876.41</td>
<td>0.31</td>
<td>207</td>
<td>34,082</td>
</tr>
<tr>
<td>DIF 4</td>
<td>Control</td>
<td>844</td>
<td>11.82</td>
<td>0.4</td>
<td>0.85</td>
<td>337.61</td>
<td>0.25</td>
<td>86</td>
<td>86</td>
</tr>
<tr>
<td>LDI 1</td>
<td>Treatment</td>
<td>1585</td>
<td>27.99</td>
<td>0.6</td>
<td>1.2</td>
<td>951.28</td>
<td>0.20</td>
<td>161</td>
<td>35,232</td>
</tr>
<tr>
<td>LDI 2</td>
<td>Control</td>
<td>2116</td>
<td>15.79</td>
<td>0.6</td>
<td>1.2</td>
<td>1270</td>
<td>0.47</td>
<td>314</td>
<td></td>
</tr>
</tbody>
</table>

*Note:* Areas were calculated using aerial photographs in ArcGIS. Parameters were used to calculate the size of the reef and the number of oysters that were added to the treatment creeks assuming there were 150 oysters m⁻².
reef. Five sampling stations were established along each transect at +2 m, +0.5 m, −0.5 m, −2.0 m, and −4.0 m (+ indicates stations in front of [seaward] and − indicates stations behind [landward of] the reef). Thus, all monitoring of response variables (with the exception of fishes and large mobile macroinvertebrates reported on by Gerald et al. 2009) was made in the immediate vicinity of the reefs or the creek mouths (in the case of controls). At each station, the following response variables were measured: water column and sediment chl-a concentrations and density of infaunal invertebrates. Sampling for physical data (salinity, temperature, dissolved oxygen, and photosynthetically active radiation) was conducted within a meter of the reefs. Salinity, temperature, and dissolved oxygen were measured using a handheld YSI-85 dissolved oxygen and conductivity meter. Photosynthetically active radiation was measured with two spherical sensors connected to a LI-COR 1400 datalogger, which recorded the 5-s averaged value for each sensor. One sensor was placed on the water’s surface and the other was placed in 0.5-m increments starting just beneath the water’s surface until the sensor reached the sediment. We typically allowed 2 weeks before the LICOR data loggers were downloaded and the data retrieved.

To observe initial (i.e., pretreatment) environmental conditions, response variables were sampled monthly in all creeks for nearly 10 months before construction of experimental reefs. To investigate the effects that oyster reefs had on response variables, monthly sampling continued for 18 months after reef placement.

To ensure that the desired density of 150 live adult oysters m⁻² was maintained in treatment creeks, bimannual sampling on the restored reefs began immediately after construction. Reefs were sampled at low tide by haphazardly tossing a 0.25-m² quadrat on the reef surface and removing by hand all oysters and associated fauna above the shell pad from within the quadrat. Six quadrats were collected at DIF 2 and 24 at DIF 3 and LDI 1, for a total sampled area of approximately 3.5% of the reef at DIF 2, 2.9% at DIF 3, and 3.7% at LDI. The removed shell was counted, measured, and placed into four categories: juvenile oysters (less than 3 cm shell height [SH]), adult oysters (greater than 3 cm SH), dead oysters, and mussels. After being counted, all living oysters, shells, and mussels were returned to their original location.

To document how chl-a concentration was affected by oyster reefs on a small, localized scale (i.e., directly above each reef), we conducted a small-scale sampling on April 14, 2006. Samples were taken with a device consisting of four 100-cc syringes attached equidistantly along a wooden base. This sampling device, described by Judge et al. (1993), allowed four water samples to be taken simultaneously, thus avoiding any influences of short-term turbidity changes (e.g., the suspension of sediment that might have occurred while accessing the site). Duplicate water samples were taken at the surface of the oyster reef (0 cm) and at 8, 15, and 22.5 cm directly above the reef in each treatment creek, or in the same relative position in control creeks. Upon return to the laboratory 40 mL of water from each depth were filtered onto a Whatman 25-mm glass microfiber filter (GF/F) and frozen at −80°C until analysis. Chlorophyll a was extracted from the filters using approximately 10 mL of a 2:3 mixture of dimethyl sulfoxide:90% acetone (Shoaf and Lium 1976), respectively. The chl-a content (µg L⁻¹) was fluorometrically (Turner Designs TD-700) determined using the Welschmeyer method, which is designed to be minimally sensitive to chlorophyll b and chlorophyll degradation products (Welschmeyer 1994).

### 20.2.3.1 Microalgae

At each station within each creek, we examined sediment (microphytobenthos) and water-column (phytoplankton) chl-a concentrations monthly, as indicators of algal abundance. One liter of water was collected at approximately mid-water depth at each station and 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, samples from the top 1 cm of sediment were haphazardly collected for chl-a analysis where and when water samples were collected, using a modified plastic 60-mL
syringe (2.5 cm diameter). The total area of sediment collected by the syringe was approximately 4.9 cm². Data from these sampling efforts have been previously reported on by Plutchak et al. (2010) and here we only summarize them.

20.2.3.2 Infauna

The abundance of benthic macrofaunal invertebrates was estimated by a monthly core sample (7.6 cm ID) of infauna at all stations within each tidal creek. Macrofauna was retained on a 0.5-mm mesh and frozen until samples could be processed. Samples were stained with rose bengal and macrofauna sorted from any retained sediment or detritus and identified to the ordinal or class level. One percent of the entire sample set was checked by a second person for consistency in identification. Samples were considered accurate/consistent for both the sorting and identification when they were in 95% agreement, and all samples fell within this range. After identification, the ash-free dry weight (AFDW) of each taxon was determined using a muffle furnace. Densities of benthic macrofauna were expressed per unit area for ease of comparison with previous studies.

20.2.3.3 Fish and Mobile Invertebrates

Demersal fishes and crustaceans present in control and treatment creeks were sampled approximately once a month using seines and block nets. Sampling was conducted during the day, and time of collection was chosen haphazardly so that samples were taken at all tidal heights, except extreme low tides. Each creek was sampled both in front of, and behind, the reef. To maintain a balanced design, control creeks were also seined twice as if an oyster reef existed between the two areas sampled.

Data from both seining and gill net collections have been published by Gerald et al. (2009) and, as with data on algae, we only summarize their findings here.

20.3 STATISTICAL ANALYSES

20.3.1 Microalgae

Chlorophyll a measurements were initially analyzed by separate two-way analysis of variance (ANOVA) performed on each creek to determine if there were station differences (i.e., with distance from the reef) across dates (Plutchak et al. 2010). If station differences were not significant \((p < 0.05)\), values for all stations within a creek were averaged and used for a creek-integrated BACIP analysis.

BACIP values were calculated by subtracting the measured value of a parameter (e.g., water column chl-\(a\)) taken at a control creek (a creek without restored oyster reefs) from the value taken at its paired treatment creek (a creek with restored oyster reefs). To identify trends, we looked at whether the impact (= treatment) minus control \((I - C)\) values became more positive or negative after the addition of reefs. When values increased in treatment creeks, the \(I - C\) values became more positive. When values in the treatment creeks decreased, the \(I - C\) values for the pair became more negative. When \(I - C\) values after reef deployment were significantly different from those before reef placement, a significant reef effect was indicated.

Although creeks were paired according to physical similarities, the three creek pairs differed from one another in size, location, and some environmental characteristics. Therefore, creek pairs were not treated as replicates but were independently analyzed, effectively removing variability owing to location and making changes owing to oyster reef emplacement more easily identifiable. Creek pairs are referenced as pair 1 (DIF 1 and DIF 2), pair 2 (DIF 3 and DIF 4), and pair 3 (LDI 1
and LDI 2). Two-tailed t tests were conducted between I–C values before and after oyster deployment to determine if there were differences between the measurements obtained before and after reef construction. Data were analyzed using Minitab 15 statistical software, and the threshold of significance was set at \( p < 0.05 \).

### 20.3.2 Infauna

Infaunal abundance and biomass data were analyzed by calculating the BACIP values for each paired station (+2 m, +0.5 m, −0.5 m, −2.0 m, and −4.0 m) and each major taxonomic group, as well as for the total number of organisms collected.

To determine if there were significant differences before and after oyster reef restoration, two-tailed t tests were conducted on the calculated BACI values for each station in each of the three creek pairs. Each pair was independently analyzed (as above) and the threshold of significance was set at \( p < 0.05 \). Data were analyzed using SPSS 12.0 statistical software.

### 20.3.3 Fish and Mobile Invertebrates

Seine data were analyzed using a BACI intervention analysis (Hewitt et al. 2001) because sampling protocol was different compared to other response variables (cf. Geraldi et al. 2009). For each dependent variable, the difference between the treatment and control creek of each pair was calculated for each sampling date after the “in front” and “behind” reef seine data were averaged. A two-way general linear model (GLM) was run with date (random factor) nested in before–after the addition of the reef (fixed factor) as independent variables and the difference between the treatment and control creek for any given parameter as the dependent variable. GLMs were also run for the abundance and biomass of the five most abundant species.

Although gillnet samples were not taken before construction of the reefs, the effect of the addition of oyster reefs on large transient species caught in the gillnets was quantified using similar analyses. Two-way GLMs were run with date as a random factor and reef (presence/absence) as a fixed factor (cf. Geraldi et al. 2009).

### 20.4 RESULTS

#### 20.4.1 Study Site Characteristics

Tidal creeks were paired based on creek similarities and proximity, with volume ranging from 162 to 2540 m\(^3\) and depth ranging from 0.85 to 1.2 m (Table 20.1). Temperature ranged between 13.4°C and 35.9°C following a typical seasonal pattern with high temperatures recorded in late spring to early fall and low temperatures during winter months. Salinity ranged from 2.9 to 29 and was highly variable in these shallow creeks.

Surveys of the creeks before reef construction showed that the natural density of oysters within the entire creek area was low, only ranging between 0.59 and 5.58 individuals m\(^{-2}\). Paired t tests for each tidal creek pair revealed no significant difference between any of the tidal creek pairs (all \( p \) values \( >0.05 \)). Densities of oysters on the restored reefs were sampled three times—immediately after reef construction in April 2005, 6 months after reef construction in September 2005, and 1 year after reef construction in February 2006—to verify that the density remained above the target of 150 oysters m\(^{-2}\). Densities of adult oysters (>30 mm in length) were highest immediately after reef construction, ranging from 253 to 446 oysters m\(^{-2}\) (Figure 20.2); subsequent sampling indicated that adult oyster density declined at all sites, with ranges of 191 to 354 oysters m\(^{-2}\) in September 2005 and 176 to 205
ECOSYSTEM SERVICES PROVIDED BY SHORELINE REEFs IN THE GULF OF MEXICO

Figure 20.2  Mean number (±SE) of live oysters (spat and adults), dead oysters, and mussels determined from sampling 20% of the reef using 0.25-m² quadrats. The dashed horizontal line indicates the target density of 150 oysters m⁻², which theoretically would filter the entire creek every 12 h.

Oysters m⁻² in February 2006. Although the number of oysters at each of the restored reefs declined over time, the density remained above the target density of 150 oysters m⁻². In addition, spat settlement began soon after reef construction and continued throughout the study period (Figure 20.2).

Ten days before reef construction, average chl-α concentrations at the permanent monitoring stations were not significantly different between treatment and control creeks (cf. 4.14 ± 0.37 and 4.52 ± 0.38 μg L⁻¹, respectively). However, when measured during midday approximately 1 year after reef construction, the localized water column chl-α concentrations directly above the reef, or in similar areas in the control sites, were significantly different between treatment and control creeks (p value <0.0001), but varied at marginally significant levels (p = 0.053) with increasing distance above the reef (Figure 20.3). The mean chl-α concentration directly above the reef in treatment creeks was 2.46 ± 0.24 μg L⁻¹ compared to 7.62 ± 1.32 μg L⁻¹ in control creeks.

20.4.2 Algal Biomass

Phytoplankton chl-α concentration tended to be highest in spring and lowest during winter months (Figure 20.4). However, the single highest mean value for chl-α was measured in September 2005 (32.2 μg L⁻¹) after the landfall of Hurricane Katrina, while the lowest was recorded just 2 months later in November 2005 (1.5 μg L⁻¹). Trends in microphytobenthic chl-α were characterized by high values in spring, and low values in fall/early winter with the highest and lowest mean
Figure 20.3 Chlorophyll a concentration (μg L⁻¹) ± standard error estimated from water samples taken directly above the restored oyster reef or area where a reef would have been restored in the control creeks. (After Plutchak, R., K. Major, J. Cebrian, C. D. Foster, M.-E. C. Miller, A. Anton, K. L. Sheehan, K. L. Heck, Jr., and S. P. Powers. 2010. Impacts of oyster reef restoration on primary productivity and nutrient dynamics in tidal creeks of the north central Gulf of Mexico. *Estuaries and Coasts* 33: 1355–1364.)

chl-a concentrations obtained in August 2004 (28.5 µg cm⁻²) and September 2004 (4.5 µg cm⁻²), respectively, immediately before and after Hurricane Ivan (Figure 20.5).

There were no obvious trends in water column chl-a between any of the creek pairs (Figure 20.4). Similarly, sediment chl-a showed no overall pattern (Figure 20.5). However, a significant ($p = 0.027$) effect was identified for creek pair 1, where the treatment creek exhibited lower chl-a concentrations compared to that of the control after construction of the oyster reef.

### 20.4.3 Infauna

Infaunal assemblages were dominated by polychaetes, which made up nearly 96% of all individuals collected, although other invertebrate taxa such as amphipods, and some epifaunal species of isopods, gastropods, bivalves, small shrimp, and crabs were occasionally found. Polychaete abundances ranged from 227 to 21,136 individuals m⁻²; biomass ranged from 0.02 to 7.68 g m⁻² AFDW.

Although creeks were paired based on physical similarities (size, depth, area, etc.), there were large infaunal differences before reef construction between treatment and control creeks, with treatment creeks having greater numbers of organisms than control creeks. This is illustrated by the representative results for the −0.5-m station shown in Figure 20.6. These differences were reduced after a highly active 2004 hurricane season, which brought BACI values to near zero, indicating that the treatment and control creeks were similar. This trend was not observed the following year (2005), which was also a highly active hurricane season along the Northern Gulf Coast, and infaunal abundances varied substantially among pairs with no consistent pattern (Figure 20.6).
Figure 20.6 Monthly Treatment—Control values for polychaete (a) abundance and (b) biomass at the −0.5-m station for each creek pair separately. Dashed line indicates time of reef deployment. Pair 1 = DIF 1 and DIF 2, pair 2 = DIF 3 and DIF 4, and pair 3 = LDI 1 and LDI 2.
20.4.4 Fish and Mobile Macroinvertebrates

20.4.4.1 Seine Results

As reported by Geraldi et al. (2009), biomass in seine hauls was dominated by blue crab, grass shrimp, striped mullet, brown shrimp, spot, and pinfish, and abundance by grass shrimp, which made up of more than 48% of the individuals caught. Both biomass and abundance were highly variable, with biomass ranging from 0.01 to 38.40 g m\(^{-2}\) and abundance ranging from 0.08 to 115.19 individuals m\(^{-2}\).

Two-way GLMs of date and reef addition showed no significant effect of date on the biomass or abundance of fish, demersal fish, sciaenids, or crustaceans (Figure 20.7a). Reef presence was significant for demersal fish abundance (Figure 20.7b; \(p < 0.01\)), but not for the abundance or biomass of other faunal groups, although all groups were more abundant after reef addition.

20.4.4.2 Gillnet Results

Geraldi et al. (2009) found that biomass in gillnet collections ranged from 0 to 814 g m\(^{-2}\) and abundance ranged from 0 to 2.06 individuals m\(^{-2}\). Together, red drum (20%), blue crab (12%), hardhead catfish (12%), southern flounder (11%), silver perch (9%), and speckled trout (9%) made up 73% of the biomass, while silver perch (22%), blue crab (15%), croaker (12%), hardhead catfish (10%), and speckled trout (8%) were most abundant.

![Figure 20.7](image)

Figure 20.7 Mean differences (±1SE) in biomass (a) and abundance (b) of taxa collected by seine between treatment and control creeks, both before and after reef construction (* \(p > 0.05\)). (After Geraldi, N., S. P. Powers, K. L. Heck, Jr. and J. Cebrian. 2009. Can habitat restoration be redundant? Response of mobile fishes and crustaceans to oyster reef restoration in marsh tidal creeks. *Marine Ecology Progress Series* 389: 171–180.)
Figure 20.8 Mean differences (±1SE) in biomass (a) and abundance (b) of taxa collected by gillnet between treatment and control creeks (*p < 0.05). (After Gerald, N., S. P. Powers, K. L. Heck, Jr. and J. Cebrian. 2009. Can habitat restoration be redundant? Response of mobile fishes and crustaceans to oyster reef restoration in marsh tidal creeks. Marine Ecology Progress Series 389: 171–180.)

Two-way ANOVAs of fish, demersal fish, sciaenids, and crustaceans found significantly fewer sciaenids in reef than control creeks (Figure 20.8a). All other fish groups had, on average, less biomass and fewer individuals, although not significantly so, in reef than control creeks.

Two-way ANOVAs of biomass and abundance of the five most important species caught in gill nets (southern flounder, silver perch, blue crabs, croaker, and catfish) found only southern flounder to significantly increase in the presence of reefs, while creeks with reefs had significantly reduced biomass and abundance of silver perch.

20.5 DISCUSSION

Restoration of oyster reefs within the tidal creeks was successful: populations of adult oysters remained above the targeted 150 oysters m⁻² for 2 years post-construction; the abundance of
juvenile oysters increased; and the number of dead adults remained constant, and relatively low, as the study progressed. Despite the expectation that the addition of oysters at the densities used in this study would reduce phytoplankton biomass in the water column of the creeks with reefs, there was no significant impact on water column chl-a in any of the three creek pairs (Figure 20.4; Plutchak et al. 2010). Instead, the only observable effects of the reefs on algal biomass were at small distances directly above the reefs (Figure 20.3; Plutchak et al. 2010). Given that there were no large changes in water clarity that would enhance the abundance and production of microphytobenthos, and the fact that these primary producers did not substantially respond to reef emplacement, it was not surprising that benthic infaunal macroinvertebrates showed no large reef-associated responses (Figure 20.6). Somewhat more unexpectedly, Geraldi et al. (2009) reported few significant reef effects on the abundance or biomass of large, mobile macroinvertebrates or fish (Figures 20.7 and 20.8). Below, we discuss several potential reasons for the absence of consistent effects of reef construction on many of our response variables.

20.5.1 Lack of Effects on Algal Biomass and Infaunal Abundance

There are a number of non–mutually exclusive factors that may explain the noticeably absent “oyster reef impact” on water column and sediment chl-a, infaunal invertebrates, and fish and macrocrustaceans, and we consider them in turn. First, the creeks we studied were completely surrounded by Juncus roemarianus (black needle rush). Undoubtedly, runoff from marshes flooded by high tides (especially during summer or particularly heavy rain events) contributed nutrients and suspended solids to the creeks (cf. Mallin et al. 2002). Runoff may have stimulated algal production above that, which is possible at ambient nutrient levels, thereby partially overcoming the ability of oysters to reduce water column chl-a concentrations. Perhaps, although less likely, oyster fecal deposits containing plankton-derived particulate nitrogen could have been rapidly remineralized to produce ammonium that, in turn, led to increased phytoplankton growth. This type of feedback loop would obscure the impacts of filtration except when in proximity to the reef.

Depending on temperature, adult oysters can filter around 9.5–19.9 L of water per hour (0.0095–0.0199 m³ h⁻¹), and at temperatures above 28°C, filtration rate rapidly rises (Korringa 1952). During our study, water temperatures were predominantly above 28°C from May to September each year, indicating that filtration rates were likely very high during these months. While one can question our initial assumption that oysters filtered water at a rate of 0.0045 m³ h⁻¹, since this rate is based on results obtained at 25°C (Pomeroy et al. 2006), the average water temperature over the study duration was, according to records from the monitoring station at Dauphin Island, Alabama (http://www.mobilebaynep.com/mondata/mainmenu.cfm), approximately 23°C. Thus, it seems unlikely that the deviations in filtration as a result of temperature could have resulted in large errors in our a priori calculations.

Alternatively, since reefs were only built to a height of 0.5 m, they were not always in contact with the entire water column, particularly in the summer when south winds resulted in water levels that were elevated above those predicted. In addition, our reefs were located at the mouth of the tidal creeks and incoming and outgoing tidal waters interacted with the reef during a small portion of the tidal cycle. Although our measurements did show a significant reduction in chl-a at small distances above the reef, measurements made at distances only 0.50 m from the reef were beyond the “zone of impact” and outside the range at which oysters had a significant impact on water clarity.

We also believe that, for much of the time, oysters in treatment creeks may never have come in contact with substantial portions of the water column because of stratification. Our initial assumption was that the shallowness of the water column (mean depth <1 m) would ensure complete mixing; however, Riisgård et al. (2007) reported that similarly shallow water columns in Denmark remained stratified unless winds blew consistently at velocities greater than 8 m s⁻¹. Thus, filter feeders in the shallow fjord studied by Riisgård et al. (2007) often did not come in contact with
much of the water column and their effective filtration ability was lower when compared to other rates reported in the literature. Only when wind velocities were above the 8 m s⁻¹ threshold did mixing occur and substantial filtration of the water column take 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 was available for filtration by oysters on the reefs.

We also had the opportunity to examine the impact of tropical storms on the creeks. A dramatic decrease in sediment chl-a concentration was observed after the landfall of Hurricane Ivan on September 16, 2004 (Cebrian et al. 2007). This catastrophic storm resulted in atypically low chl-a concentrations during September 2004. During the following year, the Gulf Coast again experienced several tropical storms, which likely contributed to the unusually low chl-a concentrations observed throughout this study. Indeed, substantial drops in sediment chl-a concentration were observed after Tropical Storm Arlene (June 11, 2005), Hurricane Cindy (July 6, 2005), Hurricane Dennis (July 10, 2005), and Hurricane Katrina (August 29, 2005), all of which made landfall near our study sites. Frequent storms repeatedly scoured and disturbed the sediments, resulting in an entire summer of depressed algal biomass (Cebrian et al. 2007). Thus, storm events likely masked any impacts of oyster emplacements on the microphytobenthos. Similarly, storms could have homogenized the sediments, thereby reducing the overall impacts of the treatment reefs on infauna. For example, the infaunal differences that were evident before Hurricane Ivan subsequently disappeared after the storm (Figure 20.6).

Storms were also likely responsible for the high water column chl-a concentrations noted in post-storm sampling events, and these events were probably a result of large short-term contributions of suspended microphytobenthic chl-a to the water column. Moreover, storm impacts on the water column were short lived, as the creeks were flushed by tides and particulate matter settled from suspension.

Because of Hurricane Ivan, pre-reef data in 2004 were likely lower than they otherwise would have been, and it appeared that Ivan and subsequent storms of 2005 overwhelmed any effects of reef construction on chl-a concentrations. However, the central Gulf of Mexico has historically experienced substantial hurricane activity, and organisms in the Gulf have evolved with frequent tropical storm/natural disturbance. Thus, we might have expected to observe strong reef effects, if they exist, even during periods of elevated tropical storm activity. Furthermore, the summer of 2006 was free of tropical storm activity; thus, if a reef effect was present, we would expect to see it during this time of low disturbance.

As noted previously, the lack of obvious reef effects on macrofaunal invertebrates seems to follow directly from the paucity of significant effects on benthic algae. This is because the deposition of reef-associated fecal material or the improved water clarity attributed to oysters should have stimulated microphytobenthic algal production that would, in turn, lead to increased numbers of deposit-feeding invertebrates. Since the presence of reefs had little effect on benthic algae, there was similarly little effect on macroinvertebrates in treatment creeks.

### 20.5.2 Small Effects on Fish and Mobile Macroinvertebrates

Demersal fish were the only species that significantly increased in treatment creeks, even though their abundance was still greater in control creeks after the addition of reefs (Figure 20.7; Geraldi et al. 2009). For those groups that did not show significant effects, our conclusions are likely robust because of the BACI-type design (Peterson et al. 2003). Although we had only three paired sites, and our ability to detect significant impacts could have been increased with more replicates, this would not likely have affected the general nature of our conclusions, given the high p values obtained in a number of our tests.

The few significant increases in abundance of fishes after reef addition reported by Geraldi et al. (2009) is at odds with the current paradigm of fish enhancement by oyster reefs (Coen and
ECOSYSTEM SERVICES PROVIDED BY SHORELINE REEFS IN THE GULF OF MEXICO

Luckenbach 2000; Lehnert and Allen 2002; Lenihan et al. 2001; Peterson et al. 2003). Although there are no other investigations of the effect of the addition of oyster reefs in semi-enclosed systems such as ours, several other studies in open systems did not find that oyster reefs significantly increased the abundance of nonresident species (Allen et al. 2007; Dame et al. 2002; Grabowski et al. 2005; Harding and Mann 1999, 2001; Luckenbach et al. 2005).

Our findings also agree with Peterson et al. (2003), who reported that many of the species caught in this study were not augmented by the presence of oyster reefs. For example, the most abundant demersal species caught by seine—blue crab, brown shrimp, darter goby, pinfish, spot, and white shrimp—were not found by Peterson et al. (2003) to be enhanced by reef restoration. Four species caught by gillnet—Atlantic croaker, blue crab, red drum, and speckled trout—were also found by Peterson et al. (2003) to be unaffected by the presence of oyster reefs. However, southern flounder was enhanced by oyster reef in both our study and those reviewed by Peterson et al. (2003).

Grabowski et al. (2005) found increased juvenile fish on oyster reefs surrounded by mud flats. They did not, however, find similar enhancement on oyster reefs adjacent to salt marsh or seagrass, which they attributed to the functional redundancy of adjacent "nursery" habitats such as marshes and seagrass meadows. Others have noted the importance of the surrounding landscape and the synergistic effects that adjacent "nursery habitats" may have on fishes (Peterson and Lipcius 2003). We believe that functional redundancy of biogenic structure in the form of marsh plants likely caused our finding that oyster reefs did not significantly increase mobile fish and macrocrustaceans. That is, biogenic structure was not a limiting factor at our study sites because of the abundant salt marsh creek habitat that existed before reef construction (Geraldi et al. 2009).

20.6 CONCLUSIONS

While there were small-scale increases in water clarity, and scattered, inconsistent treatment effects, we found few persistent changes in our response variables between treatment and control creeks after the construction of oyster reefs. The absence of dramatic effects was likely caused by a combination of factors, including lack of vertical mixing, inputs of nutrients from adjacent marshes, suspension of microphytobenthos, abundance of adjacent "nursery" habitat, and intense tropical storm activity. It is also certainly possible that reef impacts might occur at times beyond the 18-month post-reef monitoring we carried out. Clearly, monitoring for longer periods, perhaps on the order of the generation time of the longest-lived organisms being studied (cf. Dayton and Tegner 1984), is desirable. However, the time encompassed by our study was sufficient to have detected large impacts of the reefs if they existed, since most of the study taxa (e.g., algae and infaunal invertebrates) have fast turnover rates and would have gone through several generations during our study period.

We find it noteworthy that our results are qualitatively similar to those of the other experimental studies that have investigated the ecosystem services provided by oyster reefs. For example, a study of intertidal reefs in North Carolina salt marshes (Cressman et al. 2003; Nelson et al. 2004) found some significant increases in water clarity, as shown by reduced amounts of suspended solids and chl-a, although the differences between sites with and without oyster additions were inconsistent and small. Similarly, the removal of oysters from marsh creeks in South Carolina was not clearly related to changes in water clarity or use of the creeks by mobile invertebrates and fishes (Allen et al. 2007; Dame et al. 2000, 2002).

Thus, there is little existing evidence of large ecosystem-wide effects of oyster enhancement or removal in studies done to date. Regardless of the reasons, we did not find substantial changes in water clarity and biological activity in the treatment creeks. In addition, our results suggest that if a major goal of oyster reef enhancement is to directly benefit mobile fishes and macroinvertebrates, surrounding landscapes can play a critical role. In closing, we emphasize that our results should
not be interpreted as to meaning that restoration of nearshore oyster reefs should not be carried out, especially since our reef restoration was successful, and because functional oyster reefs offer many benefits such as enhanced benthic–pelagic coupling (Baird and Ulanowicz 1989) and denitrification (Newell et al. 2002). They do mean, however, that the types, magnitudes, and spatial extent of changes in ecosystem services that should be expected after reef restoration need to be reevaluated.

ACKNOWLEDGMENTS

We thank Cissie Davis, Kevan Gregalis, Drew Foster, Lesley Baggett, Mairi Miller, Josh Goff, Andrea Anton, and Kate Sheehan for help in carrying out this project. Support was provided by NOAA via the University of South Alabama Oyster Reef Restoration Program and the Dauphin Island Sea Lab (DISL).

REFERENCES


