



Can habitat restoration be redundant? Response of mobile fishes and crustaceans to oyster reef restoration in marsh tidal creeks

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ABSTRACT: Expectations of ecological and fisheries benefits of habitat restoration are commonly used to justify its high financial cost; however, few empirical studies that rigorously test these expectations exist. Here, we describe the results of a study designed to quantify the effects of restoring oyster reefs in marsh tidal creeks on the mobile macrofauna. We used a before/after control/impact (BACI) design in which fishes and crustaceans within 6 tidal creeks were sampled 7× before and 14× after the addition of live oyster reefs to 3 of the tidal creeks. We detected no significant effects of the addition of oyster reefs on the overall fish or crustacean assemblages within the tidal creeks, and a weak positive effect on the abundance of demersal fishes. These results challenge current predictions that restoration of oyster reefs will result in an increase in mobile fauna. Our findings of no increase in mobile fauna may have resulted from the functional redundancy of a nearby biogenic habitat because reefs were placed in tidal creeks that were surrounded by dense salt marsh. We conclude that a positive correlation between mobile fauna and oyster habitat is not automatic, and that the role of the surrounding landscape is important in predicting the response of transient fish and crustaceans to oyster reef restoration.

KEY WORDS: Oyster reef · Ecosystem services · Landscape · Restoration · Fish habitat

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INTRODUCTION

Overharvest of many fishes, coupled with the loss and degradation of marine habitats, has resulted in major changes in coastal ecosystems (Pauly & Christensen 1995, Botsford et al. 1997, Vitousek 1997, Myers & Worm 2003). In many estuaries, dramatic loss of oyster reefs is now recognized to be a consequence of an overall decline in ecosystem health (Kirby 2004). The decline of oyster reefs has resulted primarily from a legacy of destructive harvest practices, introduction of diseases, and an overall reduction in water quality along the western Atlantic and the Gulf of Mexico (Rothschild et al. 1994). Reduction in oyster reefs does

not only negatively affect the fishery but also eliminates the complex reef structure that serves as a habitat for demersal fishes and crustaceans, many of which are economically important (Coen & Luckenbach 2000, Peterson & Lipcius 2003, Peterson et al. 2003a).

In an effort to reduce habitat loss and ultimately increase coastal fishery landings, resource managers have focused on the conservation and restoration of nursery habitats (Peterson et al. 2003b, Browman & Stergiou 2004). The potential of habitat restoration to mitigate losses due to anthropogenic impacts, including overfishing, is commonly used to justify the high costs of restoration. Unfortunately, a complete understanding of how restored biogenic habitats function to

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replace lost ecosystem services is lacking. In particular, few empirical studies have rigorously examined this assumption for oyster reefs.

Compared to other biogenic habitats such as salt marshes and seagrass meadows, studies of community and population dynamics of animals associated with oyster reefs are relatively rare. For example, Minello et al. (2003) included 2 oyster reef studies, compared to 15 for seagrasses and 22 for salt marshes, in their meta-analysis of nursery habitats. Although based on a limited number of studies, Heck et al. (2003) concluded that all 3 biogenic habitats provided refuge and greater surface area upon which food could grow. Thus, one could conclude that the creation of oyster reefs would yield many of the same benefits provided by seagrass or salt marsh restoration. Alternatively, if the quantity of habitat passes the threshold at which refuge or food are no longer limiting, then additional biogenic habitat may be redundant.

Previous studies have determined that resident species living within the shell matrix of oyster reefs increase in abundance with increased reef area (Breitburg 1999, Coen & Luckenbach 2000, Glancy et al. 2003, Grabowski et al. 2005, Luckenbach et al. 2005); however, evidence for enhancement of transient species has been equivocal (Harding & Mann 1999, 2001, Grabowski et al. 2005, Allen et al. 2007). As part of a larger project designed to measure the effects of oyster restoration on tidal creek ecosystems, we used a before/after control/impact (BACI) design experiment to test the null hypothesis that addition of oyster reefs have no effect on the species composition or abundance of transient fishes and crustaceans within tidal creeks.

MATERIALS AND METHODS

Study site. Based on aerial photos and field surveys, 6 tidal creeks (3 pairs of control and experimental creeks) on or near Dauphin Island (Alabama, USA) were chosen for study (Fig. 1): Little Dauphin Island (LDI) 1 and 2 and Dauphin Island Ferry (DIF) 1, 2, 3 and 4. Tidal creek surface area, length, and mouth width were determined from georeferenced aerial photos (provided by the Mobile Bay National Estuary Program) using ArcGIS. Tidal creeks had surface areas ranging from 146 to 2117 m², with relatively flat bottoms composed of soft silt/sand. Tides are diurnal with a mean range of 0.4 m. Water depth at mean low tide was ~0.4 m at the creek mouths. Fringing marsh (*Juncus roemerianus* and *Spartina alterniflora*) was flooded ~25% of the tidal cycle. Water temperature of the creeks varied from 14 to 33°C with a mean of 25°C, and salinity ranged from 4 to 28 with a mean of 16.5.

Tidal creeks were sparsely populated with natural oysters. The natural abundance of oysters within the creeks was quantified by randomly sampling 10% of the creek bottom using 1 m² quadrats. To test for differences in abundance of oysters within paired creeks prior to restoration, a 2-tailed, paired *t*-test was run (MINITAB). Each 1 m² quadrat was used as a replicate.

Oyster reef restoration and monitoring. Tidal creeks were paired (LDI 1 and LDI 2, DIF 1 and DIF 2, DIF 3 and DIF 4) based on size, depth, orientation, sediment type, and shoreline vegetation. After 10 mo of monitoring, oyster reefs were added near the mouths of 3 experimental creeks (LDI 1, DIF 2, and DIF 3) by a contracted company (J & W Marine, Bayou LaBatre, AL). 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 m³ oyster⁻¹ h⁻¹ (Newell 1988). Bottom reef area was then calculated using a density of 150 oysters m⁻², which is the estimated mean natural density for oyster reefs in the northern Gulf of Mexico (May 1971, K. L. Heck unpubl. data). In all creeks, the calculated bottom reef area turned out to be ~10% of the creek bottom (Fig. 1). Oyster shell was used as a base for the reefs, covering the area that was previously calculated to a height of 10 cm above the bottom. Live oysters with associated attached fauna (e.g. hooked mussels and barnacles) were tonged by local oystermen from Little Dauphin Island Bay, transported, and placed on top of the oyster shell at a density of 150 m⁻². Reefs were constructed at the upstream side of the creek mouth.

Oyster densities were quantified semi-annually in the restored reefs to ensure that treatments were maintained. The area sampled was scaled to the size of the reef, which resulted in 6 quadrat samples for the smaller DIF 2 and 24 quadrat samples for DIF 3 and LDI 1. Reefs were sampled using a 0.25 m² quadrat that was haphazardly placed on the reef. All removed shell was counted, measured, and placed under 4 categories: juvenile oysters <3 cm in shell height (SH); live oyster >3 cm in SH; dead oyster shell; and mussels. Shells were returned to their original location after being counted.

Fishes and crustaceans. Fishes and crustaceans were sampled once a month from May 2004 to August 2006 (n = 21) using seines and block nets. Sampling was conducted during the day and time of collection was chosen haphazardly. This ensured that samples were taken at all tidal heights, except extreme low tides. Tidal height was not controlled because the tides are microtidal, semidiurnal, and largely influenced by wind, which cannot be included into a sampling schedule. Before sampling, water temperature, salinity, and time were recorded. After the creeks were sampled 7 ×

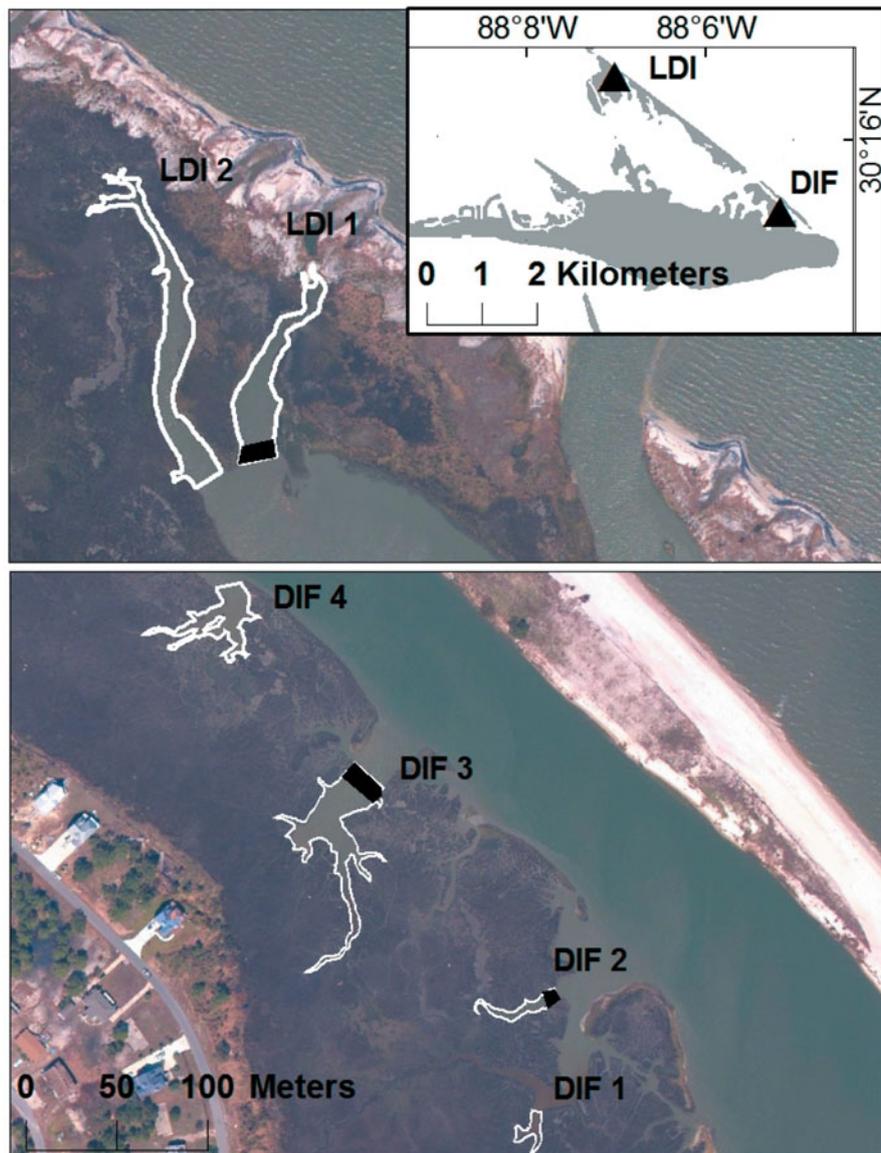


Fig. 1. Aerial photographs of the 6 tidal creeks around the east end of Dauphin Island, Alabama (top right insert). Upper photo: the 2 paired sites on Little Dauphin Island (LDI sites), lower photo: the 4 tidal creeks on Dauphin Island (DIF sites). The sites were paired based on similarity in physical parameters (LDI 1 and 2, DIF 1 and 2, and DIF 3 and 4) and are shown within the white lines. Experimental creeks were randomly chosen. Black polygons: reef areas

(May 2004 to February 2005) to generate baseline data, live oysters were added to the experimental creeks. Before the addition of the reefs, we sampled the creeks once in the delineated reef area on each sampling date, but sampled one time in front of the reef and a second time behind it after the reefs were added. To maintain a balanced design, control creeks were also seined twice as if an oyster reef existed.

The creeks were sampled using a 4 mm delta mesh bag (7.32 m long, 1.22 m high, 1.22 × 1.22 m center) seine. Although seines have lower catch efficiency than enclosure devices (Rozas & Minello 1997), a large

sample area was needed to ensure the capture of reef associated fishes ranging from 4 to 8 cm in length. Seined areas were first enclosed by block nets (1 m high × 10 m long, 4 mm delta mesh) before the seining was conducted to maximize collection efficiency. The reefs were created with defined edges, so block nets were set up <10 cm from the reef. Three block nets were quickly unrolled and erected in a U-shape. The area was seined starting at the open end of the block nets. Once the seine reached the closed end of the block net, the lead line was quickly raised against the block net. Small natural clumps of oyster were present

in both control and experimental creeks, but they were not large enough to reduce sampling efficiency. Seined areas were determined by measuring the length and width of the block nets.

The catch was sieved through a 4 mm wire mesh to remove dirt and debris. Large specimens (>10 cm) were identified to species, weighed, and measured (total length) before being returned to the water. Smaller specimens (<10 cm) were immediately put on ice and identified later in the laboratory. Twenty specimens of each species were measured (total length) for size frequencies, and the total abundance and weight were also recorded for each species.

To evaluate differences in larger transient fishes between the control and experimental creeks, gillnets were set 12 times, approximately once a month after the construction of the oyster reefs, from May 2005 to August 2006. Gillnets had a stretched mesh of 5 cm and were set at dusk and retrieved the next morning, thus soak times varied with seasonal changes in daylight. The nets were set directly over the reef or over the area where the reef would have been in the control creeks, and spanned ~75% of the creek mouth. Gillnet lengths were measured so that catches could be standardized. Fishes captured in gillnets were put on ice and brought to the laboratory where they were identified to species, weighed, and measured.

To determine if there was an overall change in community composition from the seine data as a result of the addition of oyster reefs, a 1-way ANOSIM (analysis of similarity, Clarke & Warwick 2001) was run on both the before and after data on fishes and crustaceans. Before and after data were evaluated separately to determine any pre-existing difference between control and experimental creeks, and any changes that might have occurred after the oyster reefs were added to experimental creeks. ANOSIM was performed on square root transformed biomass and abundance data (dependent variables), with site as the independent variable and each date as a replicate. Only species that made up >1% of either abundance or biomass were included. Small pelagic species (e.g. anchovy) were also removed from the analysis because they are not associated with biogenic structures (Peterson et al. 2003b).

To quantify the effect of oyster reef addition on groups of taxa or individual species, univariate statistical analyses were performed on seine and gillnet catch data. Seine data were analyzed using a BACI intervention analysis (Hewitt et al. 2001). This analysis simplifies the statistics by removing the control/impact comparison through the use of the difference between impact and control sites and the before/after factor tests the effect of the oyster addition. Thus, if the before/after factor was significant, then the oyster reef

had an effect on the dependent variable. For each dependent variable, the difference between the experimental and control creeks of each pair was calculated for each sampling date after the 'in front' and 'behind' the reef seine data were averaged, which resulted in 3 replicates for each sampling date. A constant was added to all the dependent variables so that the minimum value would be 1. The abundance and biomass data were square root transformed to satisfy the assumption of homogeneity of variance for General linear models (GLM), which was tested using Levene's test. A 2-way GLM was then run, with date (random factor) nested in before/after the addition of the reef (fixed factor) as independent variables, and the difference between the experimental and control creeks for a given parameter as the dependent variable. Biomass and abundance for 4 groups (total fishes, demersal fishes, sciaenids, and decapod crustaceans, see Table 1) were analyzed using MINITAB. GLMs with the same independent variables as the fauna groups were also run for the 5 species with the largest biomass and the highest abundance.

The effect of the addition of oyster reefs on larger transient species caught in gillnets were quantified using similar analyses. The abundance and biomass data from gillnets were square root transformed to satisfy the assumption of homogeneity of variance for GLMs. The effect of oyster reefs on groups of taxa as well as on the 5 most abundant species was analyzed using 2-way GLMs with date as a random factor and reef (presence/absence) as a fixed factor.

RESULTS

Oyster reef restoration and monitoring

There were no significant differences in natural oyster abundance between any of the paired creeks (*t*-test, $p > 0.05$) prior to oyster reef restoration. The mean density of natural oysters within the creeks was 2.9 m^{-2} ($\pm 0.35 \text{ SE}$). Densities of oysters on the created reefs were highest on the first sampling date after the addition of the reefs (April 2005) with all 3 reefs having >250 adult (>30 mm SH) oysters m^{-2} (Fig. 2). Although oyster density on the created reefs was lower for the September 2005 and February 2006 sampling dates, it still remained above the target density of 150 oysters m^{-2} for all 3 creeks. The density of juvenile oysters (<30 mm SH) was lowest in April 2005 with average values ranging from 3 to 8 oysters m^{-2} , and the range increasing to 53 to 94 m^{-2} in February 2006. The density of dead oysters changed little throughout the experiment, with the average density ranging from 23 to 102 m^{-2} .

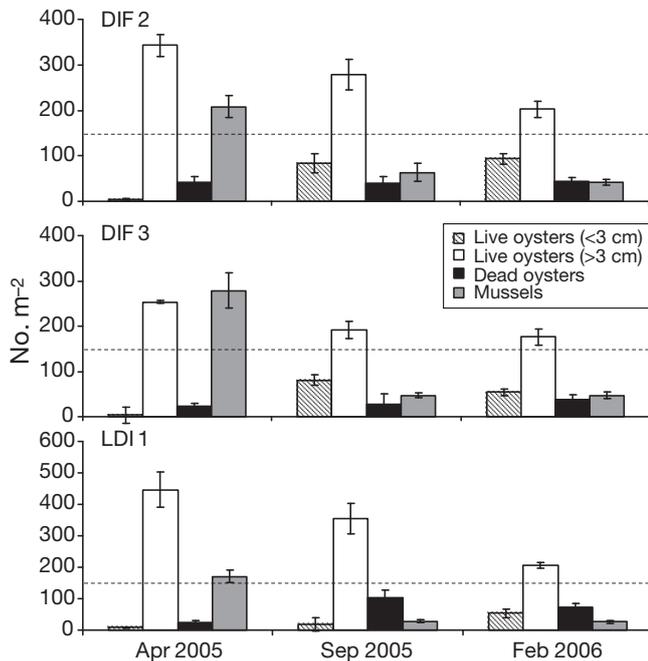


Fig. 2. Mean number (\pm SE) of live oyster, dead oyster, and mussels m^{-2} based on bi-annual sampling of the restored oyster reefs for experimental tidal creeks DIF 2, DIF 3, and LDI 1. Dashed horizontal line: target density of oysters, $150 m^{-2}$

Fishes and mobile crustaceans

Seine results

A total of 54 species was collected in all seines throughout the entire study, with 34 species constituting <1% of the biomass or abundance (Table 1). Based on biomass, the catch was dominated by *Callinectes sapidus*, *Palaemonetes* spp., *Mugil cephalus*, *Penaeus aztecus*, *Leiostomus xanthurus*, and *Lagodon rhomboides*, each of which made up >5% of the biomass and in combination comprised 62% of it. Based on abundance, the seine catch was dominated by *Palaemonetes* spp., which represented >48% of the individuals caught. *M. cephalus*, *Anchoa mitchilli*, *L. xanthurus*, and *Litopenaeus setiferus* in combination made up 32% of all the individuals caught. Both total biomass and abundance were highly variable through time: biomass ranged from 0.01 to $38.40 g m^{-2}$, while abundance ranged from 0.08 to $115.19 ind. m^{-2}$.

Prior to reef construction, the communities of fishes and crustaceans collected by seine, whether analyzed using species biomass or abundance, were not significantly different between any of the creeks (ANOSIM, $p > 0.05$). After restoration, the communities were significantly different among the creeks when species abundance data were used (ANOSIM, global $R =$

0.074; $p < 0.01$), and marginally significantly different with species biomass data (ANOSIM, global $R = 0.035$; $p = 0.062$). However, pairwise contrasts between control and experimental creeks after the addition of oyster reefs failed to detect significant differences between the pairs ($p > 0.05$).

BACI analysis of the seine data using 2-way GLMs detected no significant effect of date on the biomass or abundance of total fishes, demersal fishes, sciaenids or crustaceans (Table 2, Fig. 3). Before/after addition of the reef had a significant effect on the abundance of demersal fishes (Fig. 4, $p < 0.01$) and marginally significant effect on total fish biomass (Table 2, $p = 0.092$), but not on the abundance or biomass of the other faunal groups, although means for all groups were higher after reef addition.

Although there was some variation through time for all taxa, date was not significant for any individual species. Addition of the reefs did not have a significant effect on the biomass of *Callinectes sapidus*, *Leiostomus xanthurus*, *Penaeus aztecus*, *Lagodon rhomboides*, or *Arius felis* (Fig. 5A). It also did not have a significant effect on the abundance of *Palaemonetes* spp., *L. xanthurus*, *Litopenaeus setiferus*, *P. aztecus*, or *C. sapidus* (Fig. 5B).

Gillnet results

A total of 19 species was collected in the gillnet survey (Table 1). The total biomass caught ranged from 0 to $814 g m^{-2}$ and total abundance ranged from 0 to $2.1 ind. m^{-2}$. *Sciaenops ocellatus* (20%), *Callinectes sapidus* (12%), *Arius felis* (12%), *Paralichthys lethostigma* (11%), *Bairdiella chrysoura* (9%) and *Cynoscion nebulosus* (9%) made up 73% of the total biomass. Total abundance was dominated by *B. chrysoura* (22%), *C. sapidus* (15%), *Micropogonias undulatus* (12%), *A. felis* (10%), and *C. nebulosus* (8%).

Separate 2-way GLMs performed for total fishes, demersal fishes, sciaenids, and crustaceans caught in gillnets revealed no consistent effects of oyster reef addition. The only significant results found was for sciaenids, which were fewer in experimental than in control creeks (Fig. 6), and an effect of date on the abundance of crustaceans ($p < 0.05$). The mean values of biomass and abundance for all other groups caught in gillnets were lower in experimental than in control creeks, although not significantly so (Fig. 6).

In 2-way GLMs of the 5 most abundant demersal species, *Bairdiella chrysoura* and *Paralichthys lethostigma* did not pass Levene's test for homogeneity of variance after square root transformation. The heterogeneity of variance resulted from the fluctuation in catch over time, which is common when quantifying

Table 1. Total biomass (g) and abundance (no. of ind.) of species caught in the tidal creeks by seine and gillnet. Seine catch was from 209 seines covering 9958 m². Gillnet catch was from 2811 m of gillnet surveyed from 65 net sets

	Common name	Scientific name	Seine		Gillnet	
			Biomass	Abundance	Biomass	Abundance
Fish						
Pelagic	Atlantic bumper	<i>Chloroscombrus chrysurus</i>	17	18		
	Bay anchovy	<i>Anchoa mitchilli</i>	1238	4334		
	Gulf menhaden	<i>Brevoortia patronus</i>	284	854	3593	26
	Inland silverside	<i>Menidia beryllina</i>	2130	1303		
	Ladyfish	<i>Elops saurus</i>	182	4	8926	51
	Scaled sardine	<i>Harengula jaguana</i>	153	93		
	Skipjack herring	<i>Alosa chrysochloris</i>			519	4
	Striped anchovy	<i>Anchoa hepsetus</i>	1704	1228		
	Striped mullet	<i>Mugil cephalus</i>	5116	6329	5823	32
	Sciaenids	Atlantic croaker	<i>Micropogonias undulatus</i>	239	39	12714
Black drum		<i>Pogonias cromis</i>	149	6	1937	24
Freshwater drum		<i>Aplodinotus grunniens</i>	13	3		
Red drum		<i>Sciaenops ocellatus</i>	172	10	41687	46
Sand trout		<i>Cynoscion arenarius</i>	51	66	11226	60
Silver perch		<i>Bairdiella chrysoura</i>	716	262	19244	230
Southern kingfish		<i>Menticirrhus americanus</i>			3871	29
Spotted sea trout		<i>Cynoscion nebulosus</i>	669	257	18830	79
Spot		<i>Leiostomus xanthurus</i>	2972	4527	861	12
Other		Atlantic stingray	<i>Dasyatis sabina</i>	1579	2	
	Atlantic needlefish	<i>Strongylura marina</i>	65	7		
	Bay whiff	<i>Citharichthys spilopterus</i>	489	485		
	Bayou killifish	<i>Fundulus pulvereus</i>	30	66		
	Bighead searobin	<i>Prionotus tribulus</i>	7	24	347	5
	Blackcheek tongue fish	<i>Symphurus plagiusa</i>	125	139		
	Bluntnose jack	<i>Hemicaranx amblyrhynchus</i>	1	1		
	Code goby	<i>Gobiosoma robustum</i>	11	19		
	Darter goby	<i>Gobionellus boleosoma</i>	383	1421		
	Diamond killifish	<i>Adinia xenica</i>	8	10		
	Feather blenny	<i>Hypsoblennius hentz</i>	10	2		
	Gulf killifish	<i>Fundulus grandis</i>	1319	321		
	Gulf pipefish	<i>Syngnathus scovelli</i>	20	116		
	Hardhead catfish	<i>Arius felis</i>	2087	108	24633	101
	Highfin goby	<i>Gobionellus oceanicus</i>	103	10		
	Inshore lizardfish	<i>Synodus foetens</i>	221	54		
	Jack crevalle	<i>Caranx hippos</i>	5	1		
	Leatherjack	<i>Oligoplites saurus</i>	16	19		
	Lyer goby	<i>Evorthodus lyricus</i>	6	4		
	Grey snapper	<i>Lutjanus griseus</i>	17	17		
	Mosquitofish	<i>Gambusia affini</i>	4	5		
	Mojarra	<i>Eucinostomus</i> spp.	72	144		
	Naked goby	<i>Gobiosoma bosc</i>	7	23		
	Pigfish	<i>Orthopristis chrysoptera</i>	16	32		
	Pinfish	<i>Lagodon rhomboides</i>	2296	309	724	17
	Puffer fish	<i>Sphoeroides</i> spp.	1	2		
	Sheepshead	<i>Archosargus probatocephalus</i>	337	3	2	3
	Sheepshead minnow	<i>Cyprinodon variegatus</i>	122	217		
	Skilletfish	<i>Gobiesox strumosus</i>	1	3		
	Southern flounder	<i>Paralichthys lethostigma</i>	279	5	22936	41
	Southern stringray	<i>Dasyatis americana</i>			5132	8
	Spanish mackerel	<i>Scomberomorus maculatus</i>	46	6		
Tripletail	<i>Lobotes surinamensis</i>	0	2			
Crustaceans						
	Banded snapping shrimp	<i>Alpheus armillatus</i>	0	3		
	Blue crab	<i>Callinectes sapidus</i>	10801	1672	25050	153
	Brown shrimp	<i>Penaeus aztecus</i>	2670	1855		
	Flat mud crab	<i>Eurypanopeus depressus</i>	5	9		
	Grass shrimp	<i>Palaemonetes</i> spp.	4148	28081		
	White shrimp	<i>Litopenaeus setiferus</i>	2024	3702		

faunal abundance over multiple seasons. Although many have noted the robustness of GLMs even when variance is not homogeneous (Underwood 1981), caution should be exercised when interpreting the results for these 2 species. Presence of the oyster reef signifi-

cantly increased *P. lethostigma* (Fig. 7; $p < 0.05$) but significantly reduced *B. chrysoura* (Fig. 7B, $p < 0.05$). For the remaining species, mean values of abundance and biomass were lower in experimental than in control creeks, although not significantly so. Date had a significant effect on the biomass and abundance of *Callinectes sapidus* and *B. chrysoura* ($p < 0.05$).

Table 2. Generalised linear model (GLM) analysis of fish biomass m^{-2} . The 2 independent variables were date (random factor) nested in before/after the addition of the reef (fixed factor), while the dependent variable was the difference between the experimental and control creeks for the given parameter

Source	df	Adjusted MS	F	p
Before/After	1	1.3285	3.14	0.092
Date (Before/After)	19	0.4226	1.04	0.443
Error	42	0.4073		
Total	62			

DISCUSSION

Oyster reefs were successfully established in 3 tidal creeks as part of a BACI assessment of the effects of oyster reef restoration on fish and mobile crustaceans. Populations of adult oysters on the restored reefs remained above the targeted 150 oysters m^{-2} , the abundance of juvenile oysters increased, and the number of dead adults changed little as the study pro-

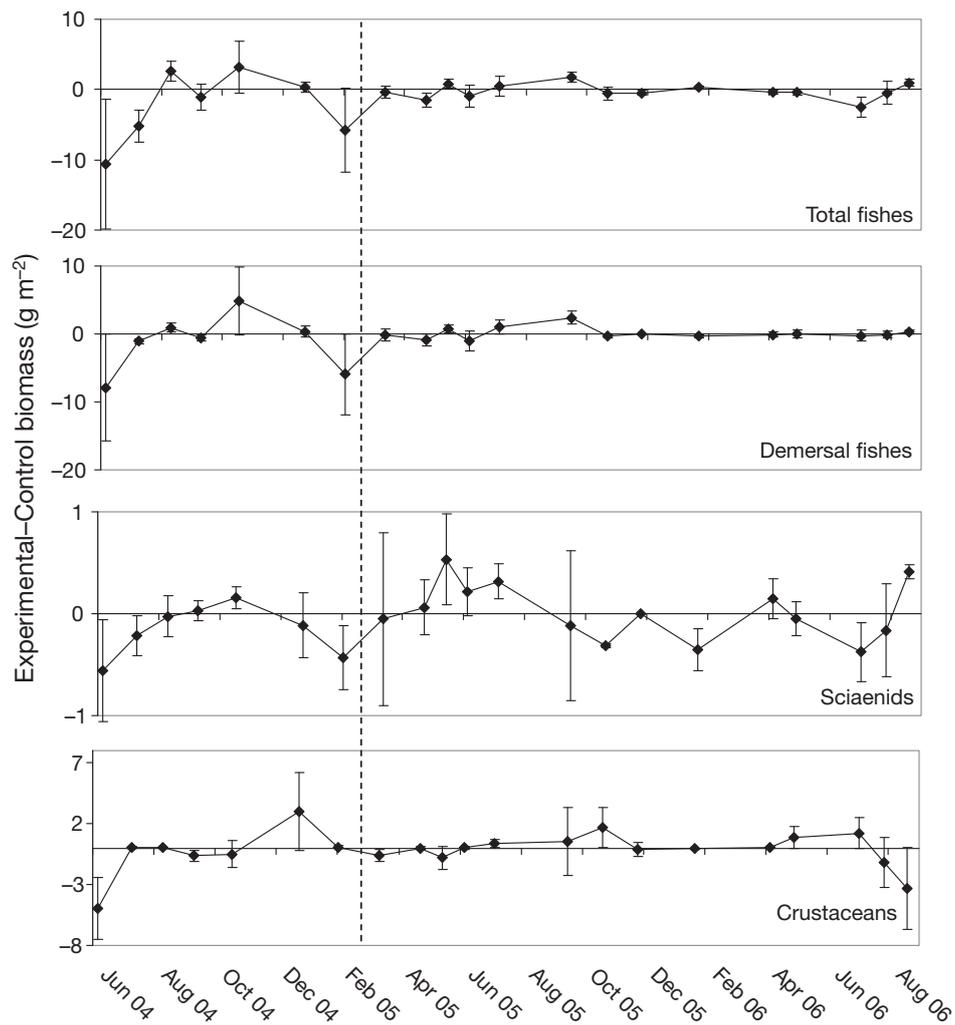


Fig. 3. Mean differences (± 1 SE) in biomass between paired tidal creeks for 4 groups of taxa over time. Data points >0 indicate greater biomass in the experimental creeks. Dashed lines: addition of oyster reefs to the experimental tidal creeks

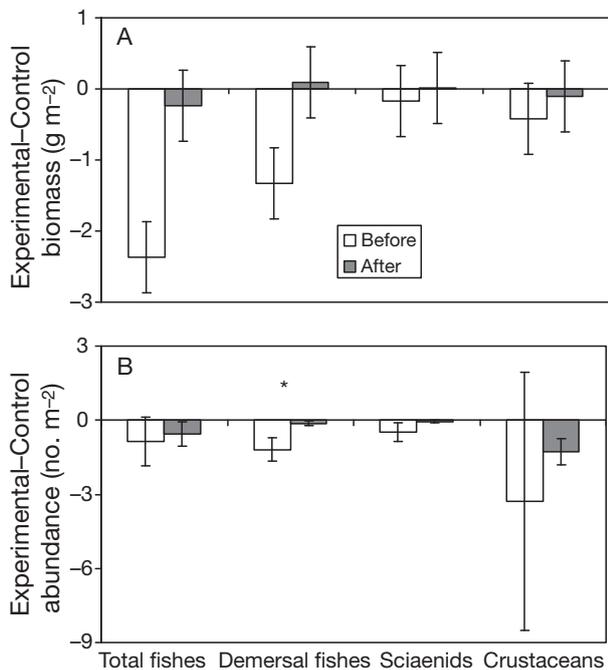


Fig. 4. Mean differences (±1 SE) in the (A) biomass (g m⁻²) and (B) abundance (no. m⁻²) of groups of taxa between experimental and control creeks resulting from the addition of oyster reefs. Significance was tested using 2-way generalised linear models (GLMs) on square root transformed data. *p < 0.05

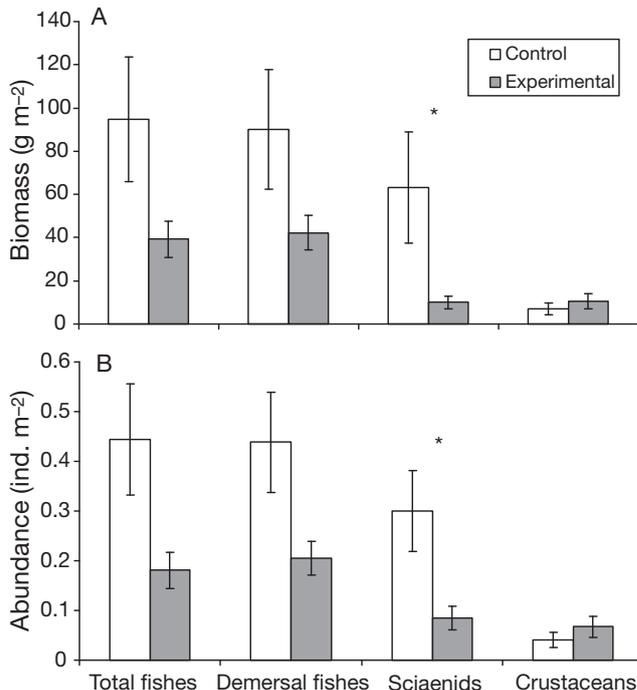


Fig. 6. (A) Biomass (g m⁻²) and (B) abundance (no. m⁻²) (±1 SE) of fish caught in gillnets in experimental and control creeks. Generalised linear models (GLMs) were performed on square root transformed data for each faunal group to test for significant differences between experimental and control creeks. *p < 0.05

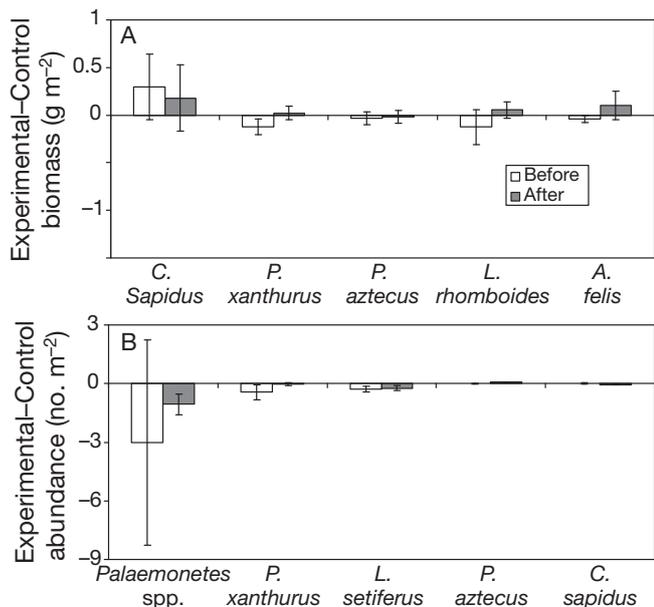


Fig. 5. Mean differences (±1 SE) in the (A) biomass (g m⁻²) and (B) abundance (no. m⁻²) of species between experimental and control creeks resulting from the addition of oyster reefs. Significance was tested using 2-way generalised linear models (GLMs) on square root transformed data; no significant differences were found (p > 0.05)

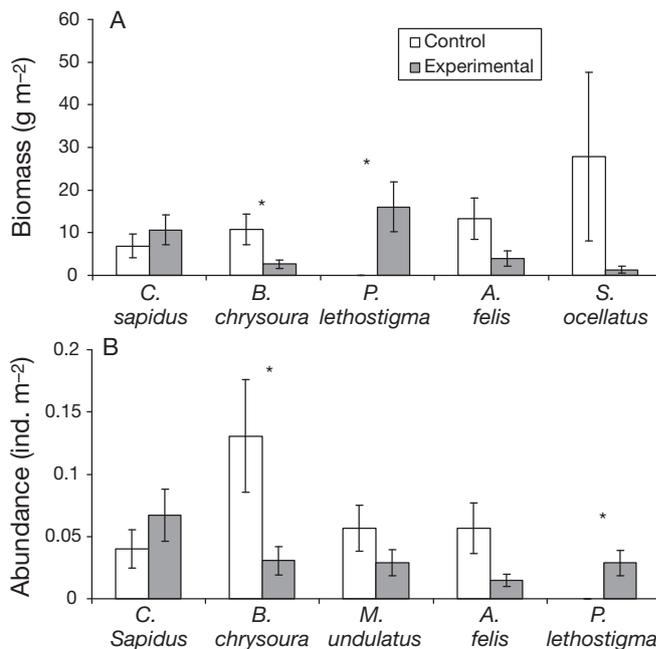


Fig. 7. (A) Biomass (g m⁻²) and (B) abundance (no. m⁻²) (±1 SE) of 5 taxa caught in gillnets in experimental and control creeks. Generalised linear models (GLMs) were performed on square root transformed data for each species to test for significant differences between experimental and control creeks. p < 0.05

gressed. Our use of the BACI design ensured that any detected changes resulted from the addition of oyster reefs and not from other sources of spatial and temporal variability (Underwood 1992). The use of BACI analysis to measure ecological expectations of habitat restoration has been advocated by many scientists (e.g. Peterson et al. 2003a); however, the lack of pre- or post-restoration sampling, adequate controls, and replication have limited the use of the analysis. Overall, our study found few creek-wide effects attributable to the addition of oyster reefs. Community level analyses of the fish and mobile invertebrate assemblages revealed no significant differences between tidal creeks with and without restored oyster reefs. Of all the groups of fishes and invertebrates analyzed, demersal fishes were the only group that significantly increased in abundance in experimental creeks after the addition of oyster reefs, although their abundance remained lower than in control creeks (Fig. 4B). The BACI design was key to detecting this effect. Had the 'before' data not been collected, no effect of oyster reef addition on the abundance of demersal fishes would have been detected.

The result that demersal fishes was the only group whose abundance increased significantly after the addition of oyster reefs contradicts the current paradigm of fish enhancement by oyster reefs (Coen & Luckenbach 2000, Lehnert & Allen 2002, Peterson et al. 2003b). There are no other investigations of the effects of oyster reefs in small tidal creeks such as the ones studied here, but studies in other systems have found that oyster reefs did not significantly increase nonresident fishes (Harding & Mann 1999, Harding & Mann 2001, Dame et al. 2002, Grabowski et al. 2005, Luckenbach et al. 2005, Allen et al. 2007). Many of these studies, however, still touted the potential of oyster reefs to increase nonresident fish abundance. In a review, Peterson et al. (2003b) estimated the enhancement of fish production attributable to oyster reef restoration. Out of the 10 species that are common to the Peterson et al. (2003b) review and our study, only 1 species (*Paralichthys lethostigma*) showed evidence of enhancement by oyster reefs in both studies. Despite these similarities in results, the overall conclusion of Peterson et al. (2003b) was that oyster reefs enhanced the production of fish and large mobile crustaceans. Thus, closer inspection of past studies revealed that the paradigm of increased secondary production by oyster reefs is not always true.

Increases in secondary production attributed to oyster reefs may be dependent on surrounding habitats. For instance, Grabowski et al. (2005) found that oyster reefs increased the abundance of juvenile fishes when the reefs were surrounded by mud flats, but this was not the case for oyster reefs adjacent to salt marsh or

seagrass beds. These authors attributed their findings to the functional redundancy of adjacent biogenic habitats. Others have noted the importance of the surrounding landscape and the synergistic effects that adjacent 'nursery habitats' may have on secondary production resulting from oyster reef addition (Peterson & Lipcius 2003). In our study, the functional redundancy of biogenic structure in the form of a saltmarsh nursery habitat (Minello et al. 2003) may have played an important role in our findings that oyster reef did not significantly increase the abundance or biomass of mobile fishes and crustaceans. In accordance with this possibility, many individuals caught in our study were juveniles. This also agrees with the findings of Heck et al. (2003), who concluded that oyster reefs, seagrass beds, or marshes have elevated and similar importance as nursery habitats for juvenile fish. Our results suggest that the oyster reefs added in the tidal creeks studied are redundant with the surrounding marsh, at least in terms of their provision of shelter and food for fish and decapod crustaceans. This is not to say that restoration of oyster reefs should not be carried out, especially since reefs can be successfully constructed and functional oyster reefs can likely provide other benefits that are not examined here, such as enhanced benthic-pelagic coupling and denitrification through deposition of feces onto sediments (Newell et al. 2002). Nevertheless, our findings indeed suggest that the surrounding landscape should be considered if the goal of oyster reef restoration is to enhance mobile fishes and decapod crustaceans.

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