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Oyster Reef Restoration: Impacts on Infaunal Communities in a Shallow Water Estuary

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ABSTRACT: Oyster reefs are important estuarine ecosystems that provide habitats to many species, including threatened and endangered wading birds and commercially important fishes and crabs. Infaunal organisms (i.e. aquatic, sediment-dwelling organisms) are also supported by oyster reef habitats. Infaunal organisms are critical to oyster-based food webs and are consumed by many important estuarine species. Due to their critical role in coastal food webs, infauna are hypothesized to be strong indicators of habitat productivity. With the dramatic global loss of intertidal oyster reefs, organisms that depend on oyster reef infauna are likely negatively impacted. Fortunately, oyster reef restoration is currently underway in many locations. We hypothesized it would be possible to document the transition from a dead oyster reef to a fully-functioning restored oyster reef by examining changes in infaunal communities before restoration and over time following restoration. Research was conducted in the Mosquito Lagoon of the northern Indian River Lagoon system. Three replicate samples were collected from 12 intertidal oyster reefs (four dead, four live, four restored). Samples were collected one-week pre-restoration and one month and six months post-restoration. Infaunal taxa abundance and composition were recorded. Reef infaunal abundance increased following restoration; restored reefs became more similar to live reefs over time. Live reefs consistently had high infaunal abundance and dead reefs consistently had low abundance, while restored reefs were intermediate. These data suggest restored reefs are more productive than their dead counterparts, with restoration showing a positive trajectory to support numerous infaunal species and their associated food webs.

KEYWORDS: infauna; infaunal communities; oyster reef; restoration; food web

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INTRODUCTION

The eastern oyster, *Crassostrea virginica*, provides an abundance of ecosystem services that benefit estuaries. Oysters filter out excess nutrients and phytoplankton in the water, improving local water quality (Coen et al. 2007, Grabowski and Peterson 2007); they are also known carbon sinks (Peterson and Lipcius 2003, Chambers et al. 2018) and act as wave breaks to mitigate erosion (Meyer et al. 1997). Acting as ecosystem engineers, oysters create reef habitats that are utilized by many commercially important fishes and crabs and threatened species of wading birds. Many estuarine animals utilize oyster reefs for foraging, and crabs and juvenile fish also use the reefs as refuge from predators.

Over the past century, however, 85% of shellfish reef habitats have been lost worldwide (Beck et al. 2011). The global loss of oyster reefs is attributed to over-harvesting, exploitation, and habitat loss and degradation from anthropogenic use. As ecosystem engineers, the loss of oyster reefs has detrimental affects on estuarine ecosystems through the loss of the ecosystem services provided by the reefs. Therefore, oyster reef restoration is crucial to restore the ecological function of oyster reef habitats (Coen and Luckenbach 2000).

Intertidal oyster reefs in Mosquito Lagoon, Florida have experienced large losses in acreage since 1943 (Garvis et al. 2015). The decrease of oyster reefs in this area is attributed to recreational boat wakes (Grizzle et al. 2002). Wave motion and sediment loading caused by boat wakes is correlated with an increase in oyster reef dead margins. (Wall et al. 2005; Garvis et al. 2015). Boat wakes create waves that dislodge live oyster clusters and wash them up on the reef above the water level. The oysters die, resulting in piles of bleached white shell.

Oyster reef restoration in Mosquito Lagoon helps restore dead reef margins to living reefs. Oyster mats, consisting of mesh mats zip-tied with disarticulated oyster shell, are laid out on flattened dead reef margins and held down with cement weights (Garvis et al. 2015). Oyster larvae recruit on the disarticulated shell and a new reef is able to establish. This method of restoration prevents oyster clusters from being dislodged by boat wakes and has proven to be very effective. Three and a half years following restoration, restored reefs had equal live oyster densities as natural reefs in Mosquito Lagoon (Birch and Walters 2012).

Oyster reefs provide habitat to infaunal organisms that hold significant positions in the estuarine food web (Meyer and Townsend, 2000). Infaunal organisms are small, marine organisms that burrow in the sediment (e.g. worms, clams). Many threatened and endangered wading birds and commercially important fishes and crabs depend on infauna as a main food source. On intertidal oyster reefs in the North Inlet Estuary of South Carolina, a species of infaunal amphipods was found to make up 10% of wading birds' diets in the area (Grant 1981). The rest of the wading birds' diets consisted of infaunal polychaetes and bivalves. Juvenile fish in Alaskan estuaries were found to rely on polychaetes, bivalves, and decapods to make up 90% of their diet (Grabowski et al. 2002). On restored mudflat oyster reefs in North Carolina, increases in juvenile fish abundances were positively correlated with the abundance of infaunal food sources and oyster habitat structure (Grabowski et al. 2005). These studies suggest large infaunal communities are critical to supporting higher trophic level species in coastal estuaries.

Oyster reefs function as foraging grounds for many important species, and restoration has been shown to increase the complexity of food webs in estuaries. A literature review on shorebird diets in the Western Hemisphere suggests that management efforts to improve food sources for shorebirds should focus on the restoration and management of ecosystem processes. Management and restoration increased the populations of naturally-occurring invertebrate and infaunal organisms, therefore providing an important food source for shorebirds in the Western Hemisphere (Skagen and Oman 1996). In the Chesapeake Bay, three-to five-year-old restored oyster reefs increased the energy transfer to higher trophic levels in the reef community (Paynter and Rodney 2006). Restoration increased the biomass of prey species that are a primary food source for commercially and recreationally important fish in the area. These observations demonstrate that mature, restored reefs have the ability to support more complex trophic structures than degraded, non-restored reefs.

Infaunal organisms are strong indicators of oyster reef productivity not only because of their important role in the food web, but because they are typically the first organisms to recolonize a habitat after a disturbance. A study done in Tampa Bay, Florida on short-term faunal recolonization demonstrated that infaunal habitats were recolonized within hours after removal of these organisms (Bell and Devlin 1983). Within 25 hours, the

infaunal species abundance had returned to the level it was before the removal occurred. If infaunal species are the first macro-organisms to recolonize an oyster reef after the disturbance of restoration, it is likely that these early successional species may facilitate other organisms colonizing the reef soon thereafter.

Several studies have examined the impact of restoration on faunal abundance, but few have assessed the impact of habitat restoration on infaunal abundance (Meyer and Townsend 2000, Hadley et al. 2010). To our knowledge, no studies have been conducted in Mosquito Lagoon to understand how infaunal organisms are impacted by oyster reef restoration. We predict that if restoring dead oyster reefs allows them to function as natural, live reefs and live reefs maintain a high abundance of infauna, then infaunal abundance and composition will increase over time after restoration.

METHODS

Infaunal organisms were collected from 12 intertidal oyster reefs in Mosquito Lagoon: four dead, four live, and four restored reefs, spanning a distance of about three km (Figure 1).

All 12 sites were part of a large, multi-investigator study of the effects of restoration on infauna, sessile invertebrates, mobile invertebrates, fishes, and wading birds in Mosquito Lagoon. Infaunal samples were collected one week pre-restoration (June 2017), and one month (July 2017) and six months (January 2018) post-restoration. Three samples were collected per site from the mid-intertidal reef level on each sampling date. The mid-intertidal reef level was chosen as the sampling area because it is expected that many infaunal predators use this part of the reef throughout the tidal cycle. A quadrat was used to maintain an area of 15 cm x 15 cm on the surface of the reef. Sediment was collected to 15 cm deep, obtaining a sediment volume of 15 cm x 15 cm x 15 cm. The samples were pre-sieved using a bucket with mesh (2 cm diameter) in place of the bottom. This mesh removed all larger shell material from each sample. The remaining sediment was then sieved through a 2000-micron sieve and a 500-micron sieve. All sediment and organisms retained in the 500-micron sieves were kept. Any larger infaunal organisms found in the 2000-micron sieve were also kept. The samples were stored in containers with 200 mL of seawater; 50 mL of a formaldehyde (preservative) and a rose bengal (vital stain) mixture was added to the seawater to obtain a seawater to formaldehyde ratio of

4:1. After one week, the samples were sieved a second time through the 500-micron sieve to reduce the amount of sediment retained. The samples were then transferred to 75% ethanol for long-term storage.

Infaunal organisms, already preserved in ethanol, were sorted from the sediment samples using a dissecting microscope (magnification: 20X). Organisms were counted to assess infaunal abundance per sample and sorted into one of the six taxonomic categories: polychaete, amphipod, isopod, bivalve, gastropod, or decapod. Infaunal organisms that did not fit into one of these categories were rare and were not included in the subsequent analyses. Sorted infaunal organisms were stored in glass scintillation vials with 75% ethanol.

A two-way ANOVA with interaction (Reef Type x Time) was used to compare the reef type and time for the total abundance of infauna. Data did not violate the assumptions of the ANOVA. This test was run in the statistical program R with a significance level of $p = 0.05$.

RESULTS

The mean (\pm S.E.) total number of infauna is shown for the three reef types in Figure 2. These values were compared across the three collection periods: pre-restore, one-month post-restoration, and six months post-restoration. Infaunal abundance increased on restored oyster reefs following restoration; from pre-restore to one-month post-restoration, restored reefs show an average increase in infauna of 231 organisms (Figure 2). A two-way ANOVA with interaction (Reef Type x Time) tested the significance of these results. The interaction between reef type and time was found to be significant [$F(8, 96) = 9.83, p < 0.0001$], demonstrating that both reef type and collection time impacted abundance. Before restoration, dead reefs had an average of 520 fewer organisms than live reefs and restored reefs had an average of 450 less organisms than live reefs. Furthermore, before restoration dead and restored reefs had an average difference in abundance of only 70 organisms, indicating that before restoration, restored and dead reefs had similar infaunal abundance, while live reefs had a much higher abundance.

Figure 2 shows additional, preliminary patterns suggesting that infaunal abundance on restored reefs does increase following restoration and therefore suggests that restored reefs become more similar to live reefs over time. By one month after restoration, restored reefs increased

in infaunal abundance by about 230 organisms, which was a 90% increase in infauna. One-month restored reefs had an average of 290 fewer organisms than live reefs at the one-month collection time. By six months post-restoration, restored reefs had only an average of 31 less organisms than live reefs. The difference in abundance between dead and restored reefs became greater over time. At one month after restoration, restored reefs had an average of 228 more organisms than dead reefs, and by six months restored reefs had an average of 358 more organisms than dead reefs. Restored reefs were most similar to live reefs at six months after restoration, but this result may be associated with a seasonal temporal decline in infaunal abundances across all reef types at this colder January collection time. The results of these comparisons support the hypothesis that following restoration, infaunal abundance on restored reefs increased and started to become more similar to infaunal abundance on live reefs.

Polychaetes were the most abundant type of infaunal organism found on all reefs (Figure 3). Polychaetes consisted of many species within this taxon. Some of the common polychaetes identified to the family level included Nereididae, Opheliidae, Hesionidae, Syllidae, and Spionidae (Table 1). These infaunal polychaetes were typically less than two centimeters in length. Polychaetes in the family Eunicidae were much larger at five to eight centimeters in length. Eunicidae was not very abundant on oyster reefs, with typically only three to five of this taxa found in a sample. However, these polychaetes were larger than the other infaunal organisms and thus worth noting. Eunicidae were found on live oysters reefs and on some restored reefs following restoration.

There was an average increase in amphipod abundance by about 100 organisms on restored reefs one month after restoration and slight increases in isopod, bivalve, and decapod abundances (Figure 4). Gammaridae and Ampithoidae were common infaunal amphipod families identified on oyster reefs (Table 1). A few Corophiidae and Caprellidae amphipods were also identified. The most common isopod species found were *Harrieta faxoni* (family: Sphaeromatidae) and *Amakusanthura magnifica* (family: Anthuridae). There were a few different species of bivalves, but bivalves mainly consisted of species in the Tellinidae family. The main gastropod species found were mostly likely of the Vitrinellidae family. Only two species of decapods were found and identified – the porcelain crab *Petrolisthes armatus* (family: Porcellanidae) and the Atlantic mud crab *Panopeus herbstii* (family:

Panopeidae). Both crabs were most common on live reefs and restored reefs following restoration.

DISCUSSION

With the global loss of oyster reef habitats, oyster reef restoration is vital to restoring ecosystem services, preventing economic losses, and providing habitat to important estuarine species (Beck et al. 2011). Infaunal organisms are a key food source in this ecosystem for many commercial, recreational, and endangered species (Meyer and Townsend, 2000). Based on the importance of infaunal organisms in the food web, infauna may also play an important role in habitat recovery after restoration and may be strong indicators of habitat productivity (Bell and Devlin 1983; Paynter and Rodney 2006). Even so, few studies have examined the direct impacts of oyster reef restoration on infaunal communities. This study focuses on the impact of oyster reef restoration on infaunal abundance and composition and documents the change to infaunal communities on restored oyster reefs in Mosquito Lagoon, Florida.

Infaunal abundance increased following restoration on restored oyster reefs, even with seasonal temporal changes taken into consideration. This study supports the expectation that live reefs have high infaunal abundance; this expectation was made based on other studies of infaunal communities (Grabowski et al. 2005). Following restoration, restored oyster reefs increased in infaunal abundance by about 230 organisms, a 90% increase in infauna. One month after restoration, restored reefs became more similar to live reefs in terms of infaunal abundance. These data support the hypothesis that restoration increases infaunal abundance and allows restored reefs to function more similarly to live reefs.

A large primary food source is important to support larger species and a more complex trophic structure (Paynter and Rodney 2006). With an increase in infaunal abundance, it is likely that restored reefs will be better able to support other estuarine species. Many species of wading birds are known to depend on infauna as part of their diet, including the white ibis, sandpipers, plovers, gulls, and American oystercatchers (Kushlan and Kushlan 1975; Goss-Custard et al. 1977; Skagen and Oman 1996). Increased infaunal abundance would give wading birds a larger food source and could allow restored oyster reefs to support more birds.

Many of the infaunal families found on oyster reefs in

Mosquito Lagoon are cited as important food sources for wading birds, such as the polychaete families: Nereididae, Spionidae, and Eunicidae (Figure 5); amphipod families: Gammaridae and Corophiidae; and bivalve family: Tellinidae (Goss-Custard et al. 1977; Goss-Custard et al. 1991; Skagen and Oman 1996). These studies focus on birds in the Charadriiform order, including plovers, terns, oystercatchers, and sandpipers. All of the listed infaunal families were found on restored reefs following restoration. Nereididae and Gammaridae were some of the more common infaunal organisms on restored reefs and are most likely to contribute the most to wading bird diets on these reefs.

A recent study on avian community structure and behavior in Mosquito Lagoon confirms the importance of restored oyster reef habitats in bird's foraging behaviors. Shaffer et al. (2019) found that wading bird's foraging behavior was greatest on live and restored oyster reefs, with little foraging behavior observed on dead reefs. This study suggests that restored oyster reefs, at least two years after restoration, are able to provide similar food sources and foraging opportunities as live reefs in Mosquito Lagoon. It is likely that the demonstrated increase in infaunal abundance on restored reefs has a direct impact on the proportion of birds observed foraging on restored reefs. This observation directly demonstrates that restoration allows restored reefs to provide necessary food sources and foraging grounds to wading birds in Mosquito Lagoon.

The largest increase in infaunal abundance on restored reefs occurred one month after restoration. This increase in abundance is not wholly surprising as infaunal species are typically the first organisms to colonize oyster reefs after a disturbance like restoration (Bell and Devlin 1983). This increase in abundance was expected to continue, yet, at the six-month collection period, there was a decrease in infaunal abundance across all reef types. Based on other studies of infaunal communities, this decrease is most likely due to seasonal changes in infaunal communities. The six-month samples were collected in January and other studies note a decrease in infaunal abundance corresponding with winter months (Zajac and Witlatch 1982). Restored reefs had the smallest decrease in abundance at the six-month time period, only decreasing by an average of 50 organisms, although it is unclear if this has any correlation to the restoration efforts.

This study covers infaunal abundance up to six months

after restoration. This is a short time period compared to other food web studies of oyster reef restoration projects (Meyer and Townsend 2000; Paynter and Rodney 2006). In this short time, however, there were positive impacts on infaunal communities on restored oyster reefs following restoration. Six months after restoration, restored reefs were more productive with higher infaunal abundance than their non-restored, dead reef counterparts. Given more time, restored reef infaunal communities may become increasingly similar to live reef communities. Restoration has also allowed restored oyster reefs to function as a foraging ground for important species of wading birds by providing a habitat to infaunal organisms that make up a large part of the birds' diets. At six months after restoration, oyster reef restoration has increased numerous infaunal species and shows a positive trajectory to support their associated food webs.

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APPENDIX A

Figure 1: Map of the 12 oyster reef sites (spanning about three km) where infauna samples were collected in Mosquito Lagoon on the east coast of Florida.

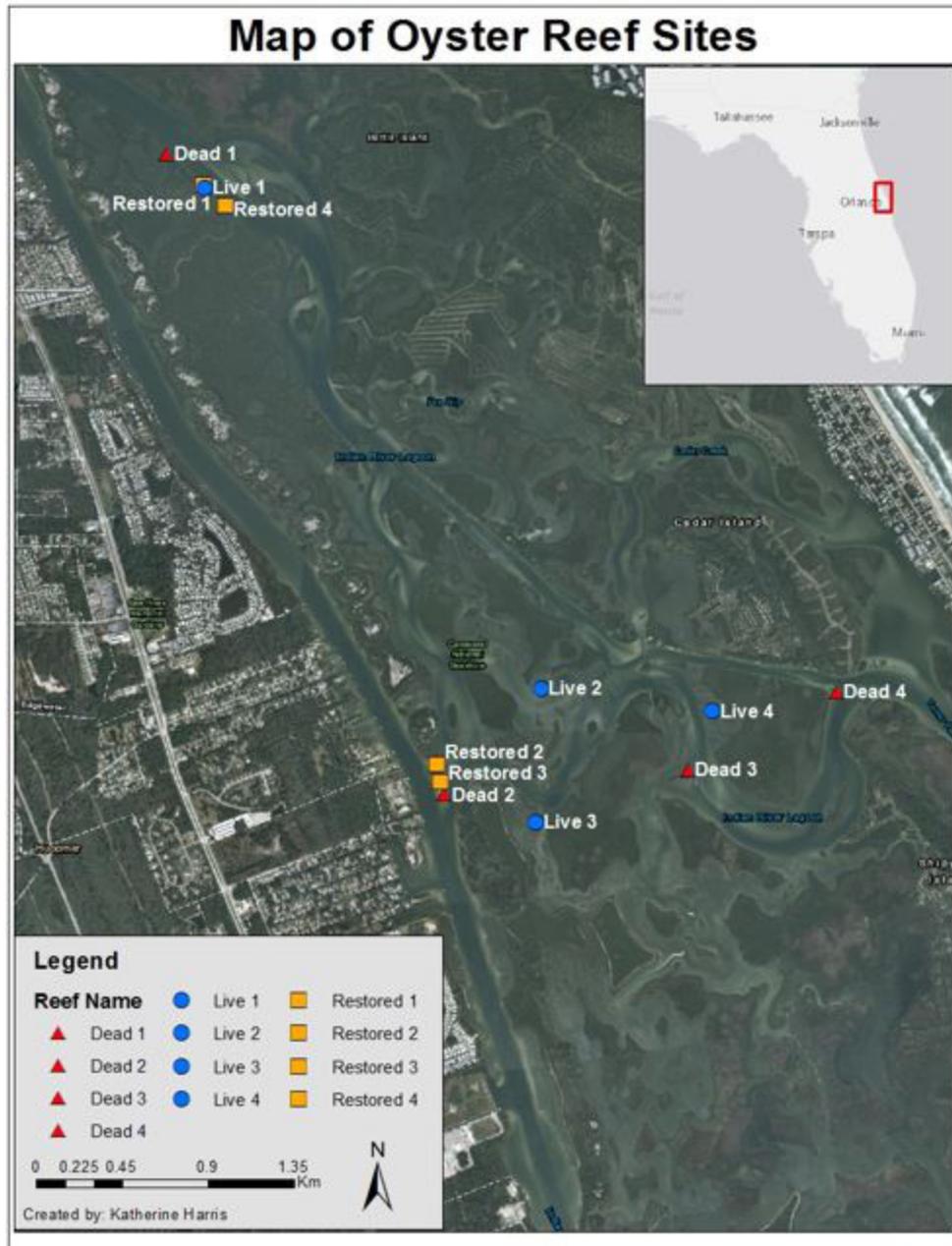


Figure 2: Mean (\pm S.E.) of total infaunal abundance from pre-restoration, one-month and six-month post restoration. N = 108 cores (15cm x 15cm x 15cm of sediment collected per sample), [F (8, 96) = 9.83, p < 0.0001].

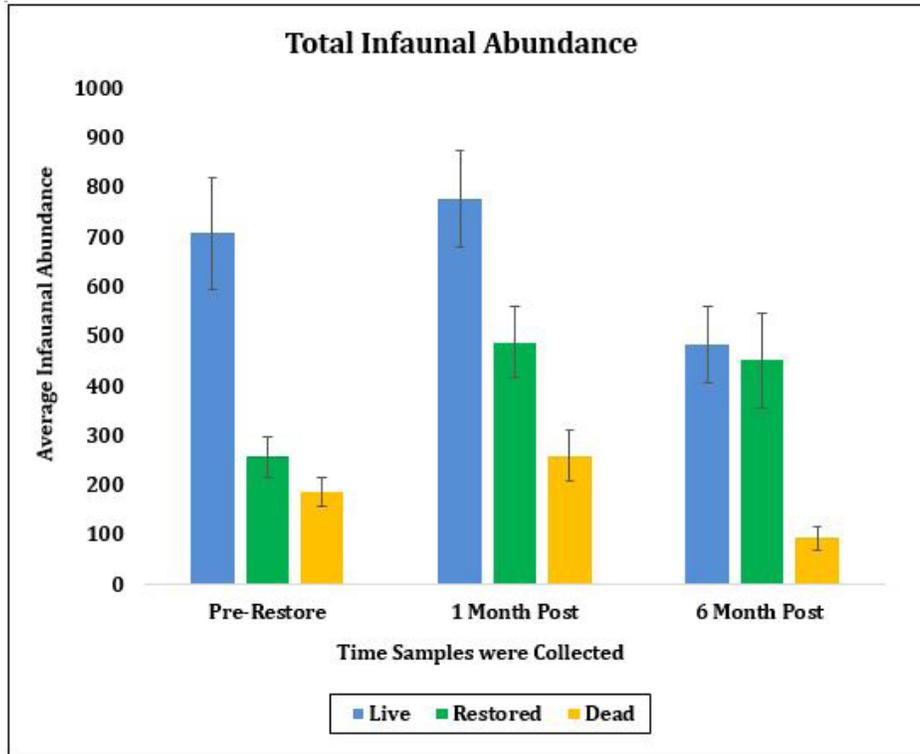


Figure 3: Mean (\pm S.E.) for infaunal composition and abundance on oyster reefs pre-restoration, one-month and six-months post restoration. N = 108 cores (15cm x 15cm x 15cm of sediment collected per core).

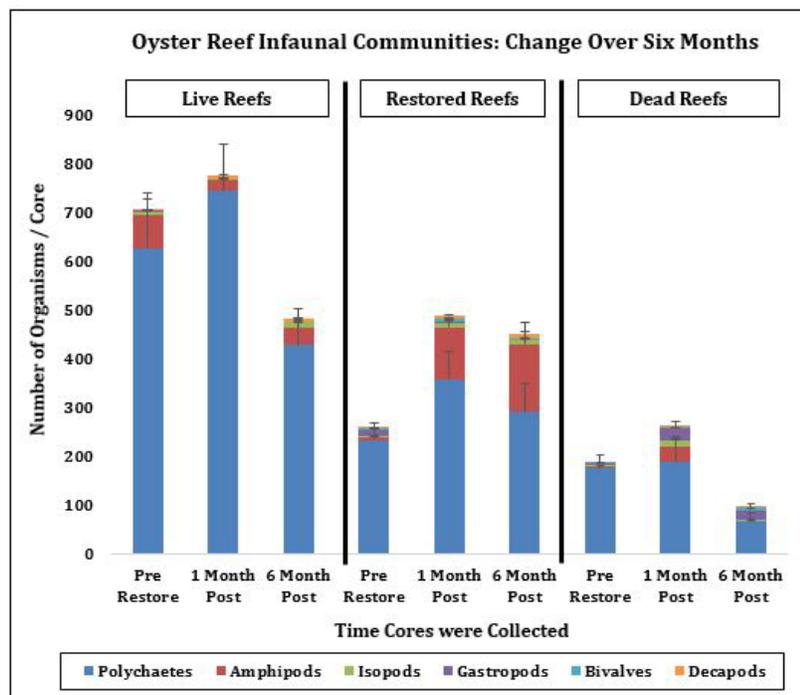


Figure 4: Mean (+ S.E.) for infaunal composition and abundance excluding polychaete taxa. N = 108 cores (15 cm x 15 cm x 15 cm of sediment collected per core).

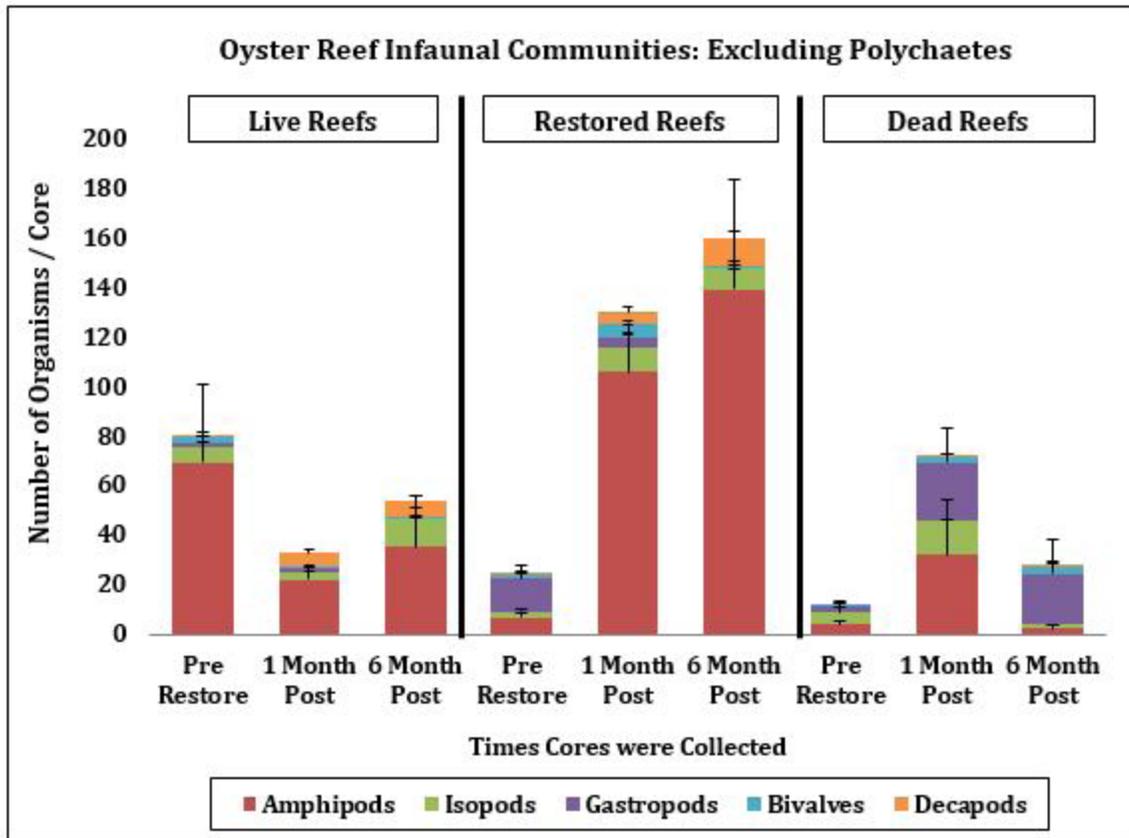


Figure 5: Polychaete families Nereididae, Spionidae, and Eunicidae (respectively) are important food sources for wading birds.



APPENDIX B

Table 1: Mean number of infauna per core on restored oyster reefs with the list of identified infaunal families and species found on restored reefs following restoration.

Polychaetes	Amphipods	Isopods	Gastropods	Bivalves	Decapods
325/core	123/core	9/core	2/core	4/core	7/core
Nereididae	Gammaridae	Sphaeromatidae (<i>Harrieta faxoni</i>)	Vitrinellidae	Tellinidae	Porcellanidae (<i>Petrolisthes armatus</i>)
Opheliidae	Ampithoidae	Anthuridae (<i>Amakusanthura magnifica</i>)		Nuculidae (<i>Nucula proxima</i>)	Panopeidae (<i>Panopeus herbstii</i>)
Hesionidae	Corophiidae				
Syllidae	Caprellidae				
Spionidae					
Eunicidae					

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