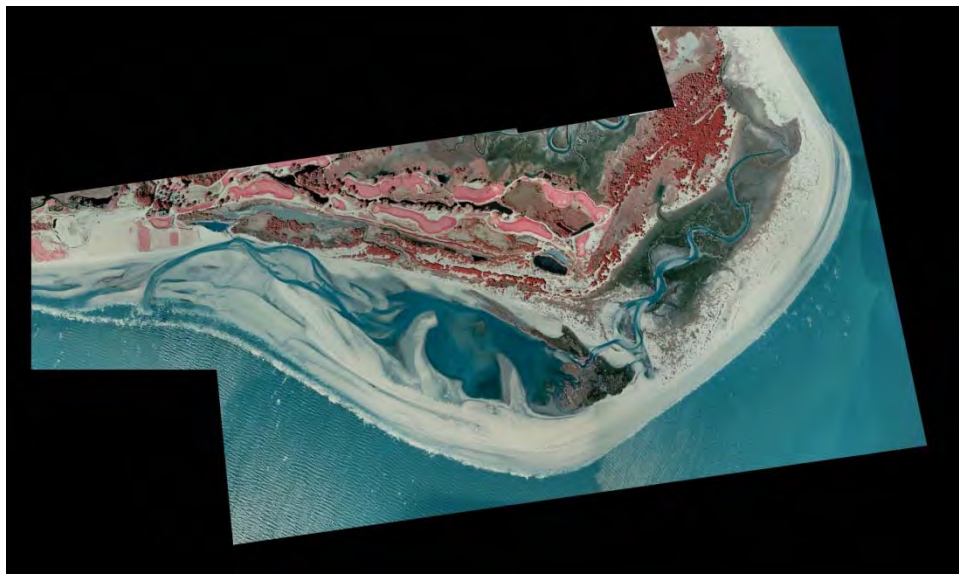


**KIAWAH ISLAND EAST END EROSION AND BEACH
RESTORATION PROJECT:**

**SURVEY OF CHANGES IN POTENTIAL MACROINVERTEBRATE
PREY COMMUNITIES IN PIPING PLOVER (*Charadrius melodus*)
FORAGING HABITATS**



FINAL REPORT



DNR

Submitted to:
Town of Kiawah

Prepared by:
Marine Resources Research Institute
Marine Resources Division
South Carolina Department of Natural Resources



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Final Report

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2011

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EXECUTIVE SUMMARY

Modification of ocean shorelines can significantly impact the quality of shorebird habitat and may pose a serious threat for threatened and endangered shorebirds that use these areas for migratory stopover and overwintering habitat. In 2006, a lagoon supporting an overwintering population of piping plovers (*Charadrius melodus*) was modified as part of a tidal inlet relocation and beach restoration project on Kiawah Island, SC, USA. As part of a larger monitoring project, the macroinvertebrate communities within the project area and a second nearby island were monitored in order to address two objectives: 1) assess changes in the macroinvertebrate community in piping plover foraging sites around the Kiawah Island lagoon, 2) determine changes in the macroinvertebrate community associated with piping plover foraging site abandonment within the lagoon.

Between April 2006 and April 2011, specific piping plover foraging areas in the lagoon system on Kiawah Island and on Bird Key, a nearby undeveloped island also used as piping plover overwintering habitat, were monitored during April/May (“Spring”) and August/September (“Fall”) each year. At least two sites of active foraging by piping plovers (occupied sites) were identified through bird surveys. A transect passing through each site was sampled every season until it was abandoned, at which point it was sampled one more time. Macroinvertebrates were surveyed by collecting ten randomly-placed push cores along each transect, sieving the core contents and identifying all invertebrates under a microscope. Differences in total infaunal, polychaete, amphipod, and mollusk densities in occupied foraging sites were examined using analysis of variance with island (Kiawah Island vs. Bird Key), season (Spring vs. Fall) and year as main factors. Changes in these same measures between a site being occupied and subsequently abandoned were examined using the same procedure. The same analyses were also performed using only a subset of macroinvertebrate taxa found in piping plover fecal samples. Differences in finer-scale taxonomic composition were examined using multivariate statistics.

Due to a late start in the monitoring efforts and unexpected modification of the intended control island (Bird Key), the necessary controls for a Before-After-Control-Impact study design were not attainable, and it was not possible to detect impacts to the

macroinvertebrate communities of piping plover foraging areas due to Kiawah Island East End Erosion and Beach Restoration Project. The data were sufficient to address study objectives as well as provide substantial information on the kinds of changes that may influence overwintering/migratory piping plovers in this area. Rates of site abandonment were similar on both islands and were fairly consistent through time. Early in the study, most occupied foraging sites were in protected lagoon or back beach habitats while later in the study, foraging sites were often in exposed active beach and inlet edge habitats. Overall, there was little evidence the macroinvertebrate communities differed between islands or sampling seasons or that they changed differently through time at the two islands. Because both the project area and the intended control area were anthropogenically modified, this only indicates that no differences were observed between two human-disturbed systems. The most apparent pattern was a significant shift from relatively high polychaete densities and low amphipod densities early in the study to low polychaete densities and high amphipod densities later in the study. As many of the taxa found in piping plover fecal samples were among those that changed during this period, the temporal shift in community composition likely affected the diet of migratory and overwintering piping plovers in this system. The cause of this change is not clear, but may be partially explained by a change in foraging habitat from more protected to more exposed habitats. The decreasing trend in polychaete density was accompanied by a decrease in the number of overwintering piping plovers in the system, suggesting a link between the two. Abandoned foraging sites supported lower densities of practically all taxa regardless of island, season or year, and the changes that occurred in association with site abandonment were very similar to the changes that occurred at occupied feeding areas over the course of the study. Multivariate analyses showed that many of the taxa responsible for the temporal changes in community composition of occupied foraging sites were also responsible for the changes occurring with site abandonment. This reinforced the hypothesis that changes specific to taxa in the diets of migratory/overwintering piping plovers were occurring both within individual foraging sites leading to subsequent abandonment and within the larger Kiawah Island/Bird Key system, perhaps leading to declines in the overwintering population. The quantity and quality of prey are often critical during the energetically demanding process of foraging and migration. The data presented here suggests that larger, errant polychaetes such as

the families Nereididae, Glyceridae and Oeonidae may be particularly important to piping plover overwintering in this region. Consequently, habitat changes, whether natural or anthropogenic in origin, that affect polychaete densities may also affect overwintering populations of the piping plover.

INTRODUCTION

Coastal habitats experience a wide range of anthropogenic impacts stemming from the need to protect human infrastructure in areas facing chronic or storm-induced erosion. “Soft” engineering solutions such as inlet dredging and beach nourishment have become the preferred methods over “hard” solutions (seawalls, groins, revetments, etc.) for countering erosion as soft solutions are typically less expensive and considered lower-impact. Although substantial data have been advanced to support a relatively low impact of soft solutions (e.g. Wilber *et al.* 2003; NRC 1995), the assumption that these solutions are benign has come under increasing scrutiny (Peterson and Bishop 2005; Speybroeck *et al.* 2006; Defeo *et al.* 2007). In fact, a recent study found that physical habitat changes following one kind of soft solution, beach nourishment, may be associated with changes in infaunal macroinvertebrate distributions and subsequent reductions in shorebird utilization of the affected habitat (Peterson *et al.* 2006). The ubiquity of impacts of anthropogenic coastal modification to shorebirds is not currently known, but where beach systems support threatened and endangered shorebirds, physical and biological habitat impacts could prove a serious obstacle to species recovery.

Ocean shorelines of the southeastern U.S. form an important part of the overwintering range for the threatened/endangered shorebird, the piping plover (*Charadrius melodus*) (USFWS 2009). Piping plovers form three primary distinct breeding populations, Atlantic, Great Lakes, and Great Plains (USFWS 1985). While migrants from all three breeding populations will use habitats in the southeast, individuals from the Great Lakes and Great Plains populations comprise the greatest proportion of the birds overwintering in this region. In fact, coastal habitats in the southeastern US may host approximately 75% of the Great Lakes population, the smallest and most at-risk of the three populations and the only population to be listed as endangered on the breeding grounds (USFWS 1985; USFWS 2001; Gratto-Trevor *et al.* 2009). Consequently, of the entire piping plover wintering range, impacts to overwintering habitats in this region could have the severe effects on the persistence of this endangered population.

For migratory birds, conditions on overwintering habitats can be critically important for long-term survival and population growth and, for many, may be more important than conditions on their breeding grounds (Sherry and Holmes 1996; Marra *et al.* 1998; Webster *et al.* 2002; Norris *et al.* 2003). This is particularly true of piping plovers which spend up to ten months migrating and overwintering and spend up to eight of those months as overwintering residents (Haig and Oring 1985; Nicholls and Baldassarre 1990). While overwintering, piping plovers divide time between roosting and foraging, with a majority of that time spent foraging (Nichols and Baldassarre 1990; Maddock *et al.* 2009). Overwintering foraging activity occurs almost entirely in intertidal coastal habitats including tidal sand and sandy-mud flats, spits, overwash areas, lagoons, coastal ponds and inlet-associated shoals and sandbars (Harrington 2008; Nichols and Baldassarre 1990). The primary dietary prey include infaunal and epifaunal marine invertebrates such as polychaete worms, crustaceans and bivalve mollusks as well as occasional insects (Nichols 1989; Zonick and Ryan 1996). Because piping plovers display a strong site fidelity both within and between overwintering seasons (Drake *et al.* 2001; Stucker *et al.* 2010), disruption of the physical and biological characteristics of overwintering areas could have substantial long-lasting impacts on their remaining populations.

Disturbance, modification and loss of coastal habitats can negatively affect habitat use, survival, condition and reproductive success of migrant and overwintering shorebirds (Myers 1983; Sutherland 1996; Durell *et al.* 1997; West 2003; McLuskey *et al.* 1992; Foster *et al.* 2009; Convertino *et al.* 2011). In some cases, habitat losses and subsequent shorebird impacts have been associated with coincident losses in invertebrate biomass and density (McLuskey *et al.* 1992), but explicit linkages between these responses can be very hard to quantify using field data. However, numerous modeling studies have suggested that loss or reductions in the densities of specific prey items can adversely affect the survival of a wide range of foraging shorebirds (Goss-Custard 1995; Stillman *et al.* 2005; West *et al.* 2007). Of the few direct studies of relationships between piping plover habitat use and coastal land impacts, Lott (2009) found a strong negative correlation between beach nourishment projects and the presence of non-breeding piping plovers on the west coast of Florida. Also along the Florida Gulf coast, Convertino *et al.* (2011) found that habitats that had experienced renourishment were 3.1 times more likely

to not be used as overwintering habitat by piping plovers compared to habitats that had not been renourished. Very little direct evidence is available to determine the potential consequences of the loss or modification of overwintering habitat for piping plovers or the relationships between habitat modification, invertebrate prey communities and piping plover overwintering behavior.

Many beach-associated systems in South Carolina are either routinely or episodically modified via nourishment, inlet relocation, and groin construction to reduce or compensate for erosion. In 2006, ongoing shoreline erosion on the eastern end of Kiawah Island had removed close to 100m of dunes along the Oceans Golf Course and threatened existing infrastructure in the area. To protect infrastructure and benefit recreational and commercial use of these beaches, the Kiawah Island East End Erosion and Beach Restoration Project (for brevity, hereafter referred to as the Kiawah Erosion Project) was performed with the goal of preventing further erosion and reversing the erosion that had occurred (CSE 2007). Prior to the Kiawah Erosion Project, the east end of Kiawah Island hosted a large intertidal-subtidal lagoon that exchanged tidally with the Atlantic Ocean through a narrow channel on the lagoon's west end. The erosion had occurred in association with tidal flushing through this channel. The Kiawah Erosion Project filled the channel and constructed a series of dunes using ~550,000 cy of sand excavated from intertidal shoals along the seaward edge of the dunes separating the lagoon from the ocean. A new channel was then excavated at the east end of the lagoon near the Stono River tidal inlet. While the project was expected to benefit human use of the area, numerous concerns persisted regarding impacts to a large number of shorebirds that utilized the lagoon for roosting and foraging, including an overwintering population of the threatened/endangered piping plover.

The purpose of the effort reported here was to determine whether the macroinfaunal community in piping plover foraging habitat showed evidence of changing following the Kiawah Erosion Project. This study was conducted as one component of a larger series of studies that also included aerial photograph mosaics, habitat classification maps, and bird count surveys within and around the lagoon. The prey surveys sought to address two objectives: 1) assess changes in the macroinvertebrate community in piping plover foraging sites around the Kiawah Island lagoon, 2) determine changes in the macroinvertebrate community associated with piping plover foraging site abandonment

within the lagoon. The study addressed these objectives by examining the invertebrate communities in active and abandoned piping plover foraging sites both in the lagoon at Kiawah Island and on a reference area, Bird Key.

METHODS

Study Sites

The long axis of Kiawah Island is oriented roughly east-west at its east end and is bounded to the north by the Kiawah River, the northeast and east by the Stono River and the southeast and south by the Atlantic Ocean (Figure 1). The lagoon that forms the primary study area was formed by sand that migrated onshore from the south and east, attached to the shore and slowly formed an enclosing arc (CSE 2007). At the time of the present study, the lagoon consisted of a range of different habitat types including vegetated dunes, salt marsh (*Spartina alterniflora*), and both intertidal and subtidal sand flats and mudflats. The sand bar separating the lagoon from the ocean was largely supralittoral although parts of it were overwashed during spring high tides. Over the course of this study, the location and morphology of the tidal exchange channel between the lagoon and Atlantic Ocean changed substantially. During the summer 2006, the Kiawah Erosion Project moved the channel from the west end to the east end of the lagoon, but the channel did not remain at that location (Figure 2A,B). By the spring 2007, the new channel at the east end of the lagoon had largely closed and a new channel breached the overwash habitat between the lagoon and the ocean near the center of the lagoon (Figure 2C). This channel increased in sinuosity and slowly migrated west over the next four years, and a second channel breached the lagoon to the east of the first channel in 2010. The lagoon and surrounding environs proved a dynamic environment that changed in numerous ways during the study. Most notably, salt marsh encroached into previously unvegetated portions of the lagoon and a sand bar moved onshore at the eastern corner of the lagoon creating large intertidal sandflats along the Atlantic shoreline.

Nearby Bird Key is also known as an overwintering habitat for piping plovers. The Bird Key study area is the largest and most distal feature within the Skimmer Flats complex located between Folly Island and Kiawah Island and near the intersection of the

Folly and Stono Rivers (Figure 1). Although this area is commonly known as Bird Key, the island historically referred to as Bird Key was located further west and south (closer to Kiawah) and disappeared following the dredging of the Folly River in 1993. The “new” Bird Key consisted of many of the same habitat types as the Kiawah Island lagoon. The landward side of the island along the Folly River was dominated by intertidal and subtidal sand flats and mudflats. Early in the project, salt marsh was present on the landward side but was not particularly pervasive; by the end of the study, this part of the island had transitioned to primarily salt marsh habitat. The active beach



Figure 1. Map showing location of the lagoon on the east end of Kiawah Island and the reference island, Bird Key.

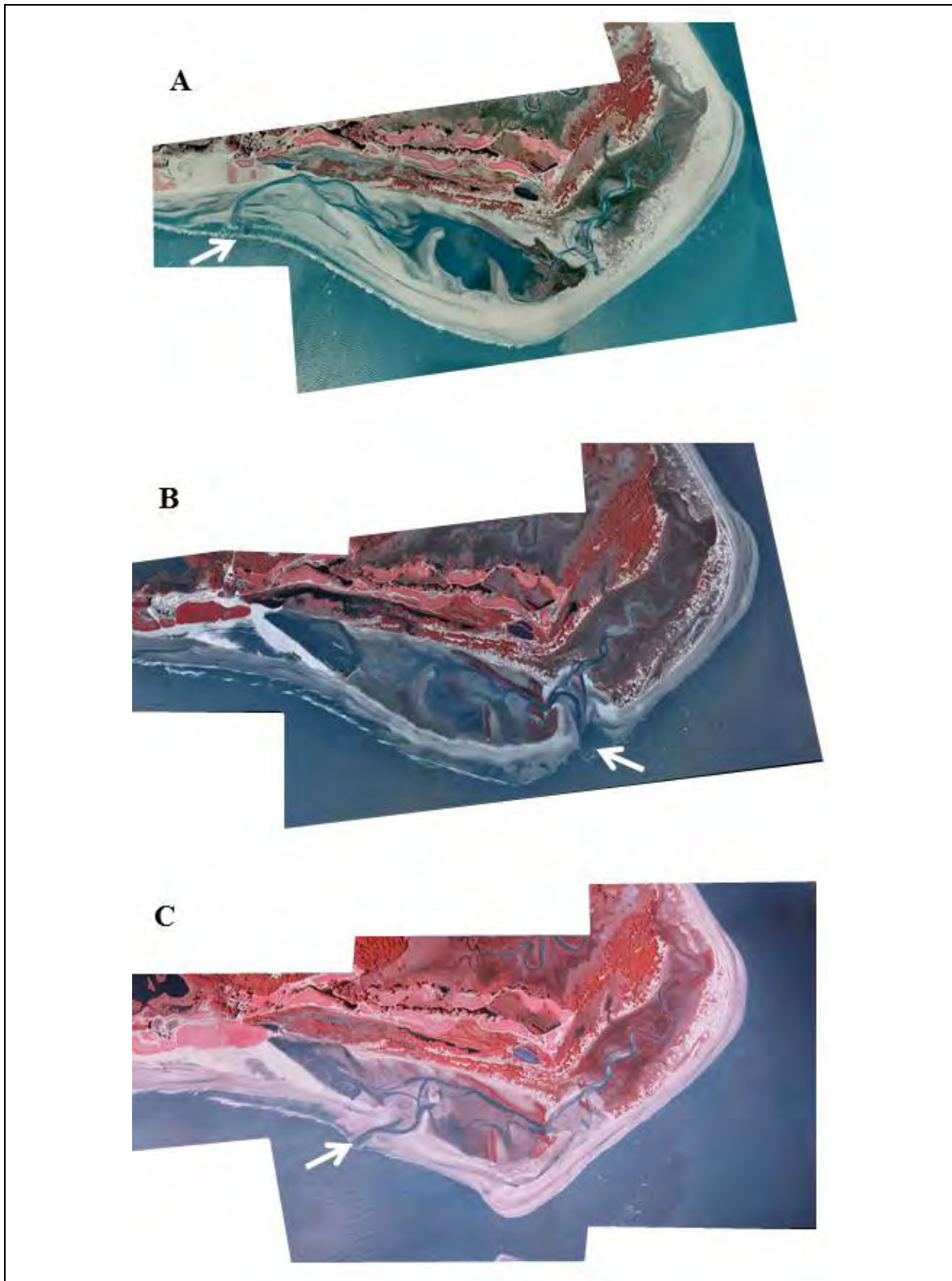


Figure 2. Maps showing major events in the evolution of the lagoon on Kiawah Island's east end A) prior to inlet relocation, B) immediately following inlet relocation, and C) one year following inlet relocation. The white arrow indicates the location of the primary lagoon inlet during each time.

habitats along the seaward and Stono River sides of the island also accumulated substantial volumes of sand and transitioned to extensive intertidal sand flats during the study period. Bird Key was intended to provide an undisturbed control site with which to compare any changes occurring at Kiawah Island. However, Bird Key was modified unexpectedly when the US Army Corps of Engineers placed sand onto Bird Key in 2006 as part of a beneficial re-use of dredge material to increase bird habitat in the area. This sand was placed on the Atlantic shoreface of Bird Key, but some overwashed into the small lagoon on the Folly River side of the island.

Study Design

Due to short notice, applicability of a Before-After Control-Impact (BACI) study design was limited. Both areas were sampled twice during each year: once during spring migration from the overwintering grounds to the nesting grounds (late-March/early-April, referred to here as the “spring” season), and once during the summer/fall migration from the nesting grounds to the overwintering grounds (late-August/early-September, referred to here as the “fall” season). Because project construction occurred during the summer of 2006 and the earliest monitoring could begin was spring 2006, pre-project sampling involved only a single event (spring 2006). No pre-project fall sampling was possible. Unexpected modification of the control area (Bird Key) further prevented even a more simplified comparison of the impacted area to a non-impacted control area. Consequently, the study areas will not be referred to as control and impact but simply as Bird Key and Kiawah Island, respectively. Because long-term changes may be expected as new erosion and accretion patterns become established, both study areas were sampled during the spring and fall seasons for five years post-project (2006-2011).

Field and Laboratory Methods

Based on observations by Town of Kiawah and USFWS biologists, the piping plovers in the study sites fed primarily at low tide and appeared to forage consistently in small, spatially-discreet areas at each site. Prior to the start of sampling for this study, foraging activity occurred on exposed yet saturated sand flats and along steeper emerged shores near the water’s edge (pers. comm., J. Jordan and M. Bimbi). The rather small

size of the foraging sites relative to the overall size of the lagoon on Kiawah suggested that a random sampling pattern within the entire lagoon habitat would require an unfeasibly large number of samples to adequately characterize and detect changes in those areas where the plovers foraged. To overcome this challenge, the decision was made to identify specific foraging sites using routine bird count surveys then sample those sites while being actively foraged by plovers (hereafter “occupied”) and until the first sampling season after the plovers ceased foraging at the site (hereafter “abandoned”). No study sites remained occupied for more than three consecutive seasons, and no abandoned sites were ever re-occupied. The result was that a study site was sampled at least twice (first season when occupied and first season when abandoned). This allowed the identification of potential changes or difference in the types of communities being foraged (comparison of occupied sites through time and between islands) and of potential changes in communities following abandonment of a previous foraging site.

In each season, specific foraging sites at each location were identified by monitoring studies performed by the Town of Kiawah and USFWS. On Kiawah Island, bird count surveys were performed weekly during the migratory period and monthly during the overwintering period as part of the larger monitoring program for the project. The Town of Kiawah biologists performing the surveys noted those areas being used most regularly for foraging and, in later study periods, whether those areas continued to be used by at least one piping plover. The former identified candidates for “occupied” foraging sites, and the latter identified whether previous foraging areas had become “abandoned”. Because the larger monitoring plan did not require bird count surveys be performed anywhere but on Kiawah Island, similar surveys were not performed on Bird Key. Independent surveys of Bird Key were further complicated by boat-only access to that area. Consequently, bird count surveys were only conducted twice during each sampling season on Bird Key: once in the week leading up to invertebrate sampling and once on the day invertebrate sampling occurred. These surveys were performed by SCDNR and/or USFWS personnel. The only exception was between 2007 and 2009 when USFWS had contracted monthly surveys of all plover overwintering grounds (Maddock *et al.* 2009). Regardless, identification of occupied and abandoned foraging sites on Bird Key were based on surveys with a lower temporal resolution.

During the first sampling period (spring 2006), two active foraging sites at each of Kiawah and Bird Key were sampled. In the fall 2006 sampling season, the same transects were sampled and identified as occupied or abandoned. For each site that had been abandoned, a new occupied site was identified and sampled. This pattern continued throughout the study, ensuring that at least two active foraging sites were sampled on each island during each sampling time (Table 1). Additionally up to two abandoned foraging sites were sampled on each island during each later sampling period. In a few instances, at the time sampling was performed, plovers were observed foraging at a site not noted during bird count surveys; this site was sometimes also sampled as it represented a site of active current foraging.

Each foraging site was sampled by walking a transect across the site and counting the number of paces required to cross it. A random number table was then used to choose ten random points along the transect based on the number of paces (Figure 3). At each random point, actual sample locations were determined by randomly walking between zero and five paces perpendicular to the transect (Figure 3). On sloped surfaces, transects were walked along the water’s edge and sample locations were walked upslope. On flat surfaces, transects crossed through the center of a feeding area and sample locations were placed on a single randomly-chosen side of the transect. At each of the ten sample locations, a 7.62 cm diameter PVC push core, referred to as the “benthic core”, was inserted to a depth of 20 cm to collect infaunal macroinvertebrates, and the contents were placed in a cloth bag for later processing. A second core (3.5 cm diameter), referred to as the “sediment” core, was inserted beside the larger core for potential later determination

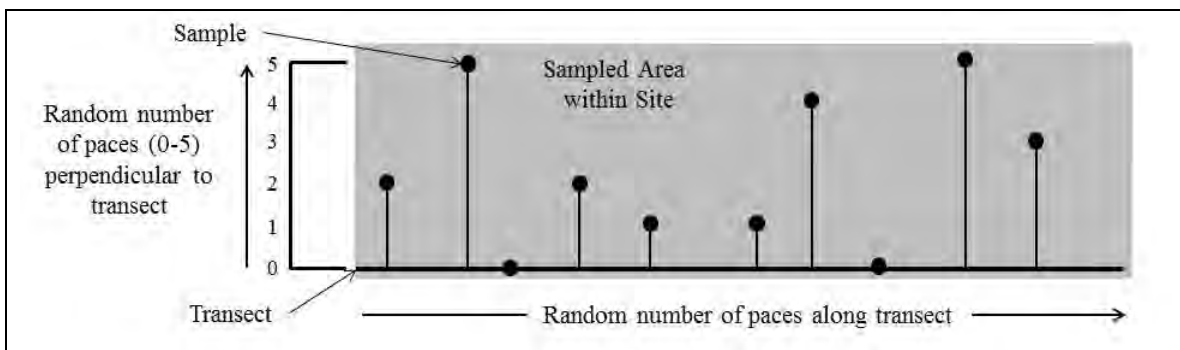


Figure 3. Layout of sampling positions along transects through foraging habitats. Note the scale perpendicular to the transect is enlarged for purposes of illustration.

Table 1. Status of foraging sites as occupied or abandoned on Kiawah Island and Bird Key during the study. Shaded "O" = occupied, "A" = abandoned. All sites and times enclosed by a box were sampled.

Island	Site	2006		2007		2008		2009		2010		2011	
		Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	
Kiawah	1	O	A										
	2	O	A	A									
	3	O	O	A									
	4		O	O	A								
	5			O	A								
	6				O	A							
	7				O	A							
	8					O	A	A					
	9					O	A						
	10						O	A					
	11						O	O	A				
	12							O	A				
	13								O	A			
	14								O	A			
	15									O	A		
	16									O	A		
	17										O	A	
	18										O	A	
	20												O
	Bird Key	1	O	A									
2		O	A										
3			O	O	A								
4			O	A									
5				O	A								
6					O	A							
7					O	A							
8						O	A						
9						O	O	O	A				
10							O	A					
11							O	O	O	A			
12								O	A				
13									O	O	A		
14										O	A		
15											O	A	
16											O	A	
17													O

of sediment characteristics. Determination of sediment characteristics was not part of the original scope of work for the project, but these samples were collected in case large changes in invertebrate community structure were detected and the opportunity arose to process the samples.

Benthic core samples were washed through a 0.5 mm sieve to retain all infaunal macroinvertebrates. Organisms and sediment retained on the sieve were preserved in a buffered solution of 10% formalin/seawater containing rose bengal stain. Benthic organisms were sorted from retained material under a magnifying lens, and each individual specimen was identified to the lowest possible taxonomic level under dissecting and compound microscopes. All subsequent analyses excluded meiofaunal species (such as nematodes and copepods that are not well quantified using a 0.5 mm sieve). Organisms which could not be identified to species level due to damage were merged with those that could be identified to species to avoid overestimating the total number of species (e.g. *Prionospio* sp. included *Prionospio* that could be identified to species) unless the damaged organism was clearly representing a unique taxon. A voucher collection of representative specimens of each taxon was created for the project and maintained by the Environmental Research Section at the SCDNR Marine Resources Research Institute (Charleston, SC).

Data Analysis

Total macroinvertebrate density, polychaete density, amphipod density, and mollusk density (the dominant faunal taxa) were calculated for each core and quantitatively compared amongst seasons, control and impact sites, and occupied and abandoned feeding areas. The data were subdivided into a series of data subsets and general linear models were used to make several specific comparisons.

Objective 1 of this study was to assess changes the macroinvertebrate community in occupied foraging habitats. To address this objective, the dataset was limited to only occupied sites on Kiawah Island and Bird Key and examined using Analysis of Variance (ANOVA) with Island (Bird Key vs. Kiawah), Season (Spring vs. Fall) and Year as the main factors. The interaction terms Island X Season and Island X Year were also included in order to determine whether the islands were changing differently through time. A nested analysis (site nested within Island) could not be performed using

individual sample data, because an abundance of zero values in individual samples (push cores) for most measures caused uncorrectable heteroscedasticity. Instead, densities in the ten individual samples collected along each transect were averaged and statistical comparisons were performed using those averages.

Objective 2 of this study was to determine whether macroinvertebrate communities changed between the time when foraging habitats were occupied and later abandoned by piping plovers. To examine this statistically, the sample average (average of ten cores along the transect) of the last occupied season for each site was subtracted from the subsequent sample average of the site once abandoned. This produced a difference value that would be negative if the measure decreased between being occupied and abandoned or positive if the measure increased between being occupied and abandoned. These differences were then analyzed using ANOVA with Island, Abandonment Season (whether the site went from occupied to abandoned during the fall to spring or spring to fall period), and Abandonment Year (the year in which the site was abandoned) as main factors. The interaction terms Island X Abandonment Season and Island X Abandonment Year were also included.

In a recent study, piping plover fecal samples were collected on Bird Key and Harbor Island (another overwintering area in South Carolina) and examined under a microscope for refractory materials that may indicate invertebrate taxa consumed by piping plovers in this area (USFWS, unpublished data). The dominant recognizable components in these samples were various polychaete parts (setae, acicula and jaws), primarily from the large, errant genera Nereididae, Glyceridae, and Oeonidae (formerly Arabellidae), which were found in eight of twelve fecal samples at Bird Key and five of six fecal samples from Harbor Island. The remaining recognizable marine invertebrate parts belonged to crustaceans (primarily exoskeletal parts of Haustoriid amphipods) and molluscan shell fragments (mostly of the small intertidal bivalve *Donax* spp. and one piece of a gastropod potentially belonging to the genus *Assimineia*). With the exception of the gastropod, all of these taxa were also found in the push cores collected in piping plover foraging areas on Kiawah Island and Bird Key. In order to focus on more probable food items, additional analyses were performed on groupings of the taxa found in fecal samples: 1) “consumed polychaetes”--the sum of the polychaetes belonging to the families Nereididae, Glyceridae, and Oeonidae, 2) “consumed amphipods”--sum of

amphipods in the family Haustoriidae, 3) “consumed molluscs”--sum of molluscs in the genus *Donax*, and 4) “total consumed fauna”--the sum of 1, 2 and 3 representing all primary marine macroinvertebrates found in the fecal samples. These four groups were analyzed following the same procedures described above.

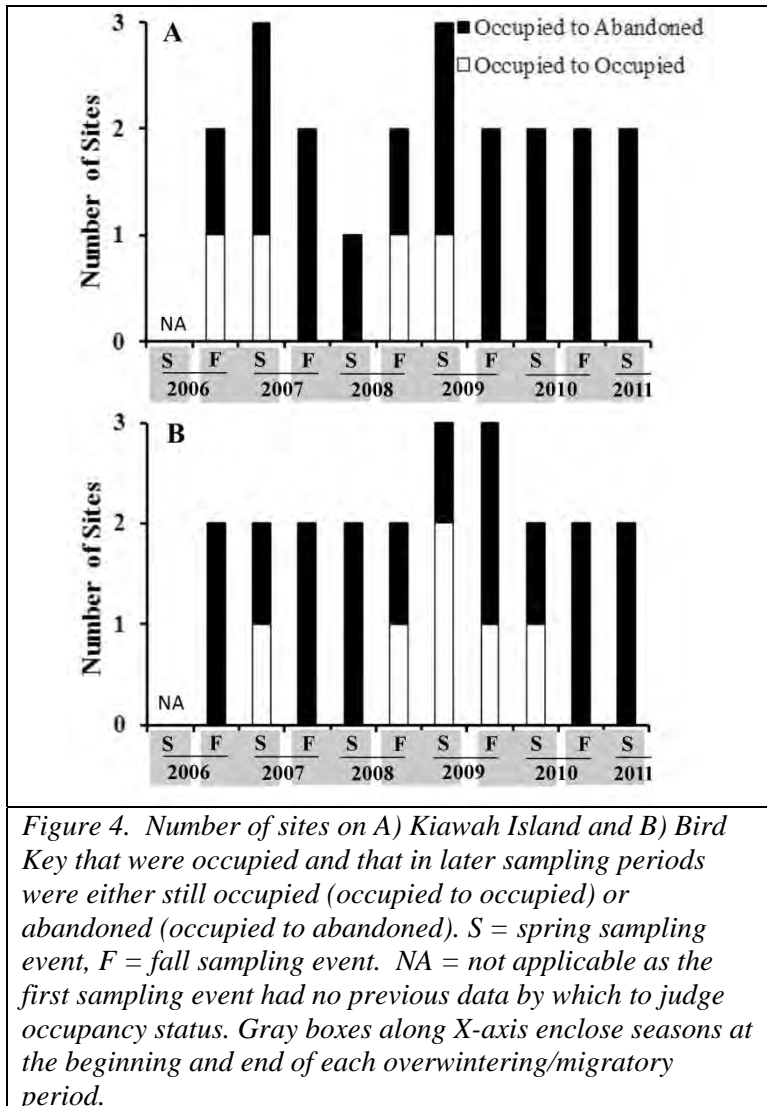
Multivariate analysis of the macroinvertebrate communities was performed using Primer v6.1.9 software (Clarke and Gorley 2006). The average density of each taxon was calculated for each transect during each sampling time period for a total of 46 occupied and 33 abandoned transects/sites. Bray-Curtis similarities were calculated among all pairs of sites following a fourth-root transformation of taxon densities to improve normality. Analysis of Similarities (ANOSIM) was used to determine if community composition varied significantly between occupied and abandoned foraging sites overall. Similarity Percentages (SIMPER) was used to determine the taxa most responsible for the dissimilarities between occupied and abandoned sites. The species matrix was then reduced to include only occupied sites. Because of the large number of factor levels relative to the overall sample size, hypothesis testing under a full model involving Island, Year, and Season was not possible, instead an exploratory analysis of the data structure was undertaken. First, hierarchical clustering was performed using the CLUSTER routine and the significance of different clusters were tested using similarity profile permutation tests (SIMPROF). The significant clusters were overlaid on an MDS ordination plot and SIMPER was used to identify which taxa were most responsible for the between-cluster dissimilarity.

RESULTS

Habitat Utilization

On both Kiawah Island and Bird Key, piping plovers tended to abandon foraging sites between sampling seasons (Figure 4). Piping plovers abandoned 81% and re-occupied only 19% of sampled foraging sites between seasons, while on Bird Key piping plovers abandoned 73% and re-occupied 27% of sites between seasons (Figure 4). Foraging site abandonment occurred throughout the study, and incidence of abandonment did not show a tendency to increase or decrease through time on either island (Figure 4). Piping plover foraging activity showed evidence of shifting from primarily sheltered

intertidal flats to exposed beach and inlet channel shores over the course of the study (Figure 5). On Kiawah Island, foraging occurred entirely within sheltered habitats between spring 2006 and spring 2008 after which it was divided between sheltered and exposed habitats (Figure 5). On Bird Key, foraging occurred in both sheltered and exposed habitats throughout much of the study, then occurred entirely in exposed habitats during the 2010-2011 overwintering season (Figure 5).



Macroinvertebrate Community

The macroinvertebrate community composition as measured using major taxonomic groups, indicated that the foraging areas being actively used by piping plovers (occupied sites) were significantly different among years but not between islands or seasons (Table 2). Although not significant, total faunal and polychaete densities tended to be higher at Bird Key than at Kiawah while mollusk density was lower at Bird Key (Figure 6). On average, all densities were very similar between the spring and fall seasons (Figure 6). Total faunal density was highest in 2007 and, during that year, was significantly higher than overall densities in 2006, 2009 and 2010 (Figure 6). Polychaete density was also highest in 2007 (when they accounted for 98% of overall faunal density) and in that year was significantly higher than in 2009, 2010 and 2011 (when polychaetes

only accounted for 15-54% of overall faunal density). Both total faunal and polychaete densities decreased from 2007 to 2011 in occupied foraging sites. Amphipod density and mollusk density also varied significantly among years, but these measures were lowest in 2006 and 2007 and increased later in the study with amphipod density peaking in 2011 and mollusk density peaking in 2010 (Table 2; Figure 6). Transects through occupied foraging sites on both islands exhibited a similar pattern of

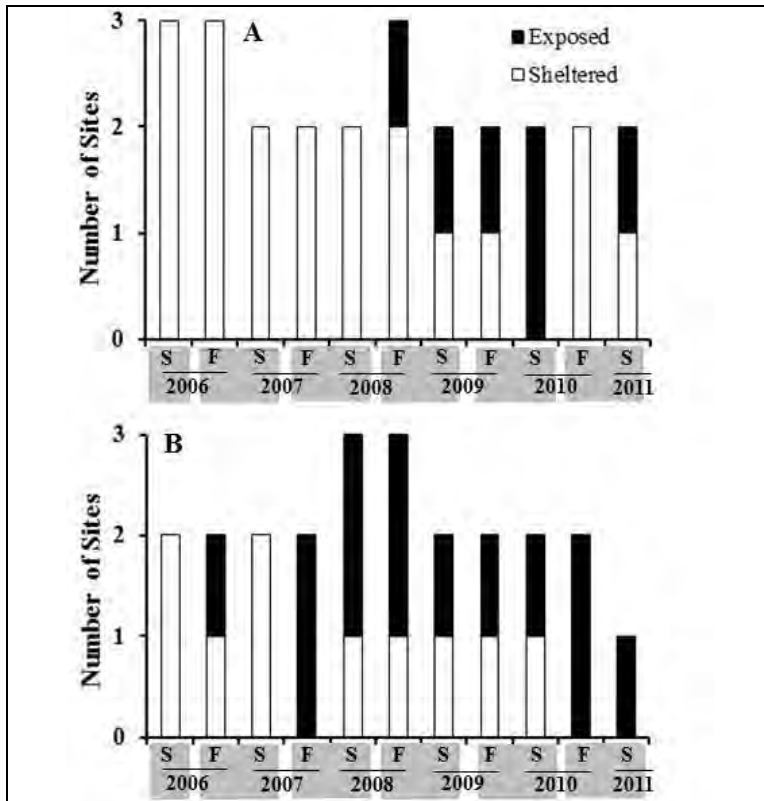


Figure 5. Number of sampled occupied sites on A) Kiawah Island and B) Bird Key that were in sheltered (lagoon or protected flat) or exposed (active beach or river inlet) habitats. S = spring sampling event, F = fall sampling event. Gray boxes along X-axis enclose seasons at the beginning and end of each overwintering/migratory period.

variation through time with both islands having peak abundances of total fauna densities and polychaete densities between fall of 2006 and spring 2008 and peak amphipod and mollusk densities later in the study (Figure 7).

Table 2. Results (p-values) of ANOVAs examining differences in macroinvertebrate communities of occupied foraging habitats. The factors in the models included Island (Kiawah vs. Bird Key), Season (Fall vs. Spring) and Year (2006-2011).

Source	All Fauna	Polychaetes	Amphipods	Molluscs
Island	0.499	0.345	0.515	0.362
Season	0.259	0.801	0.735	0.831
Island X Season	0.227	0.354	0.672	0.330
Year	<0.001	0.002	<0.001	0.002
Island X Year	0.122	0.681	0.182	0.405

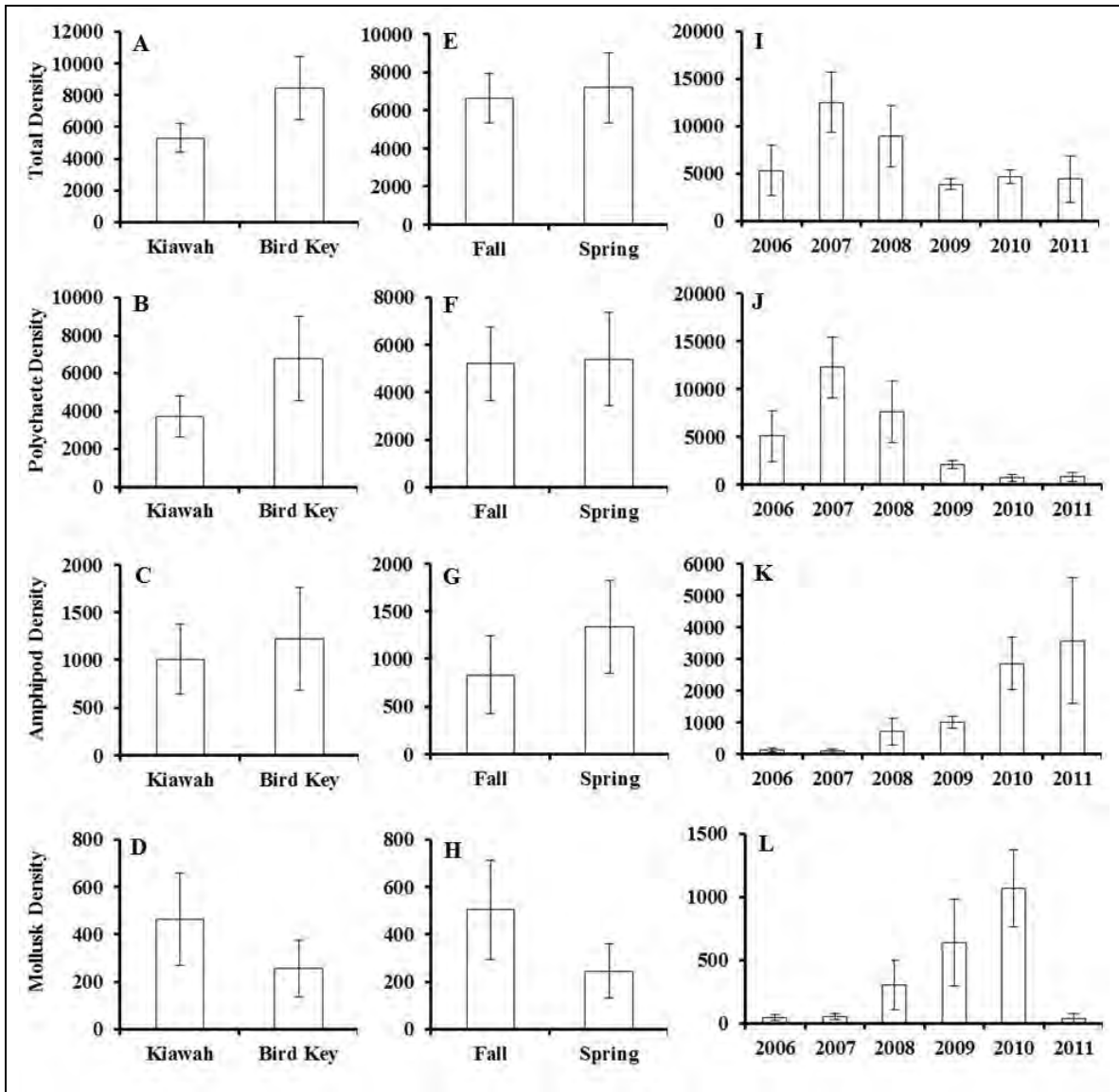


Figure 6. Average (\pm SE) densities (no./m²) of all macroinvertebrate infauna and major taxonomic groups at occupied sites by A-D) island (Kiawah or Bird Key), E-H) season (Fall or Spring), and I-L) year. Replicate cores were averaged within each transect and transects within each island, season and year were averaged prior to calculating the averages shown.

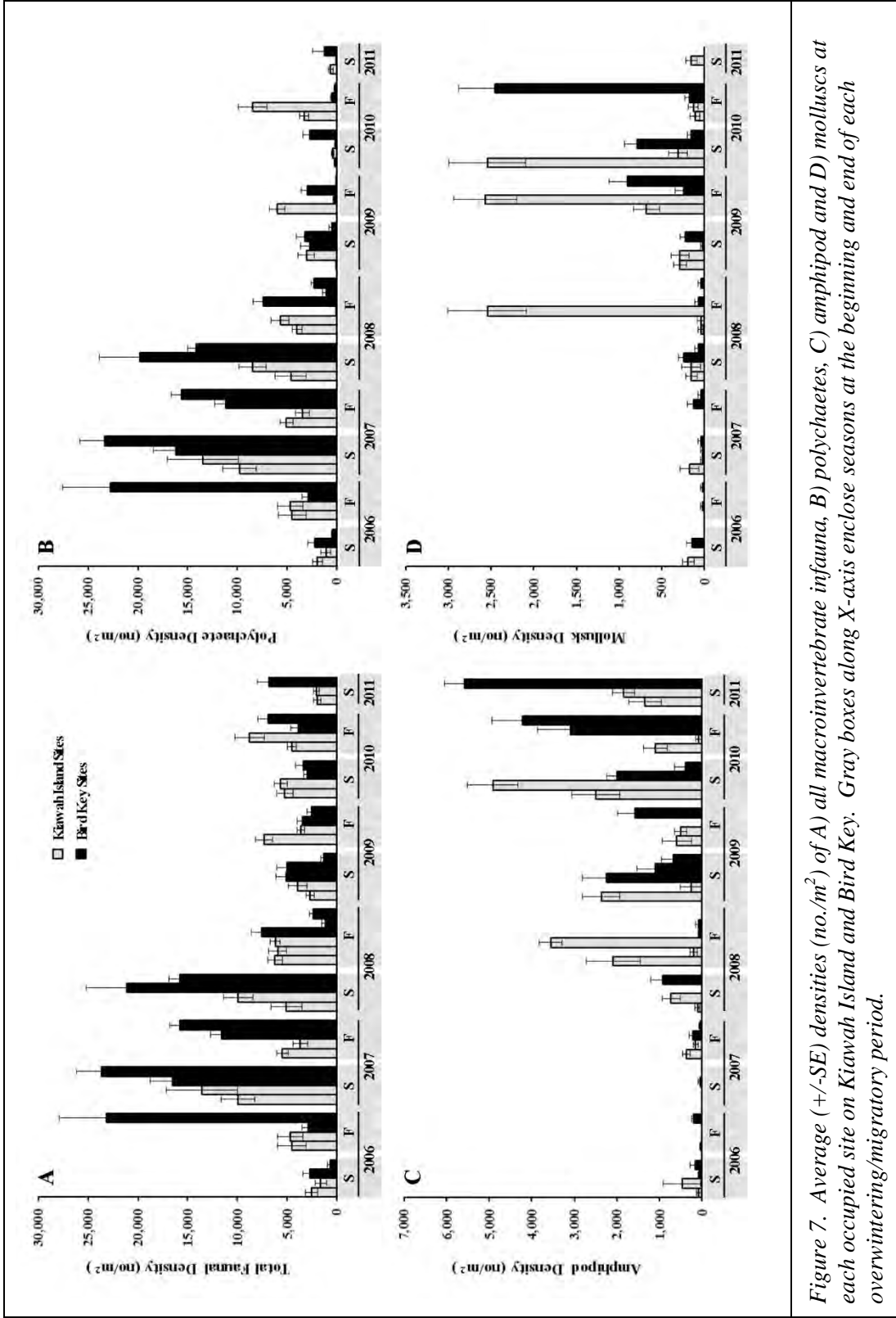


Figure 7. Average (+/-SE) densities (no./m²) of A) all macroinvertebrate infauna, B) polychaetes, C) amphipod and D) molluscs at each occupied site on Kiawah Island and Bird Key. Gray boxes along X-axis enclose seasons at the beginning and end of each overwintering/migratory period.

Piping plover foraging areas generally hosted substantially lower overall macroinvertebrate densities and densities of major macroinvertebrate taxa when abandoned than when occupied (negative values for “density when abandoned minus density when occupied”) (Figure 8). These changes were strongest for total faunal density, polychaete density and amphipod density and weakest for mollusk density (Figure 8). The changes in densities associated with abandonment were not significantly different between the two islands but tended to be slightly more negative at Bird Key than at Kiawah Island (Table 3; Figure 9A-D). The changes were significantly different between seasons in which abandonment occurred for total macroinvertebrate density and polychaete density, but not for amphipod and mollusk densities (Table 3). Foraging sites occupied in the spring and abandoned in the fall experienced greater decreases in total macroinvertebrate densities and polychaete densities than foraging sites occupied in the fall and abandoned in the spring (Figure 9E-H). Total macroinvertebrate density, polychaete density and amphipod density varied significantly by year in which abandonment occurred, but mollusk density did not (Table 3). The most substantial changes occurred coincident with periods in which densities were greatest. For example, total macroinvertebrate density and polychaete density were highest in occupied foraging sites in 2007, and the greatest decreases in these densities associated with abandonment subsequently occurred in 2007 and 2008 (Figure 9I,J). Amphipod densities were greatest during the last couple of years of the study and the greatest decreases in densities of this

Table 3. Results of ANOVAs (p-values) examining the effects of Island (Kiawah vs. Bird Key), Season (Fall vs. Spring) and Year (2006-2011) on the change in foraging habitat macroinvertebrate communities following abandonment.

Source	All Fauna	Polychaetes	Amphipods	Mollusks
Island	0.926	0.855	0.157	0.287
Season of Abandonment	0.005	0.023	0.134	0.565
Island X Season	0.075	0.167	0.305	0.198
Year of Abandonment	0.005	0.014	0.017	0.241
Island X Year	0.087	0.147	0.039	0.371

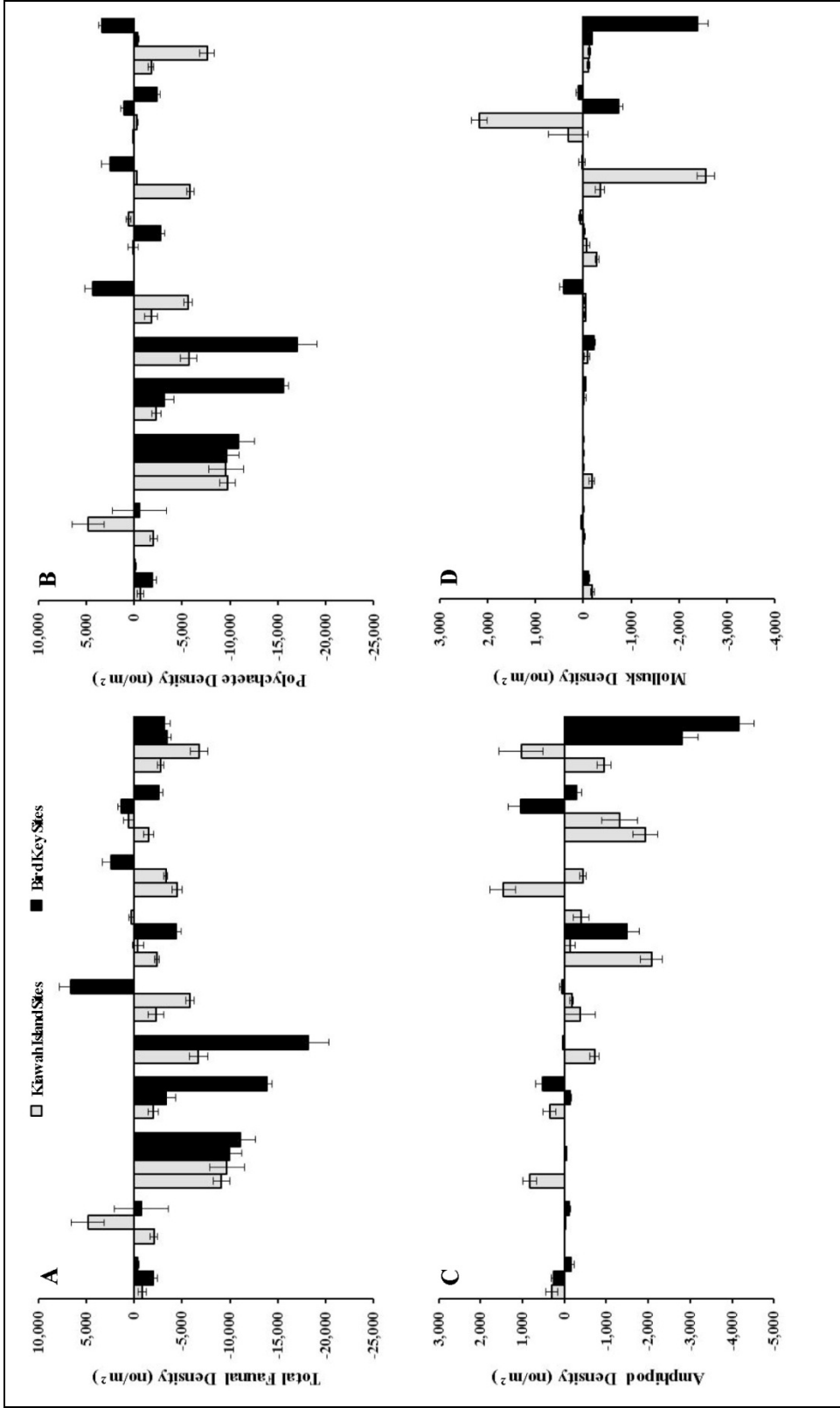


Figure 8. Changes in the average densities (no./m²) of A) all macroinvertebrate infauna, B) polychaetes, C) amphipod and D) mollusks following abandonment of each occupied site on Kiawah Island and Bird Key. Gray boxes along X-axis enclose seasons at the beginning and end of each overwintering/migratory period.

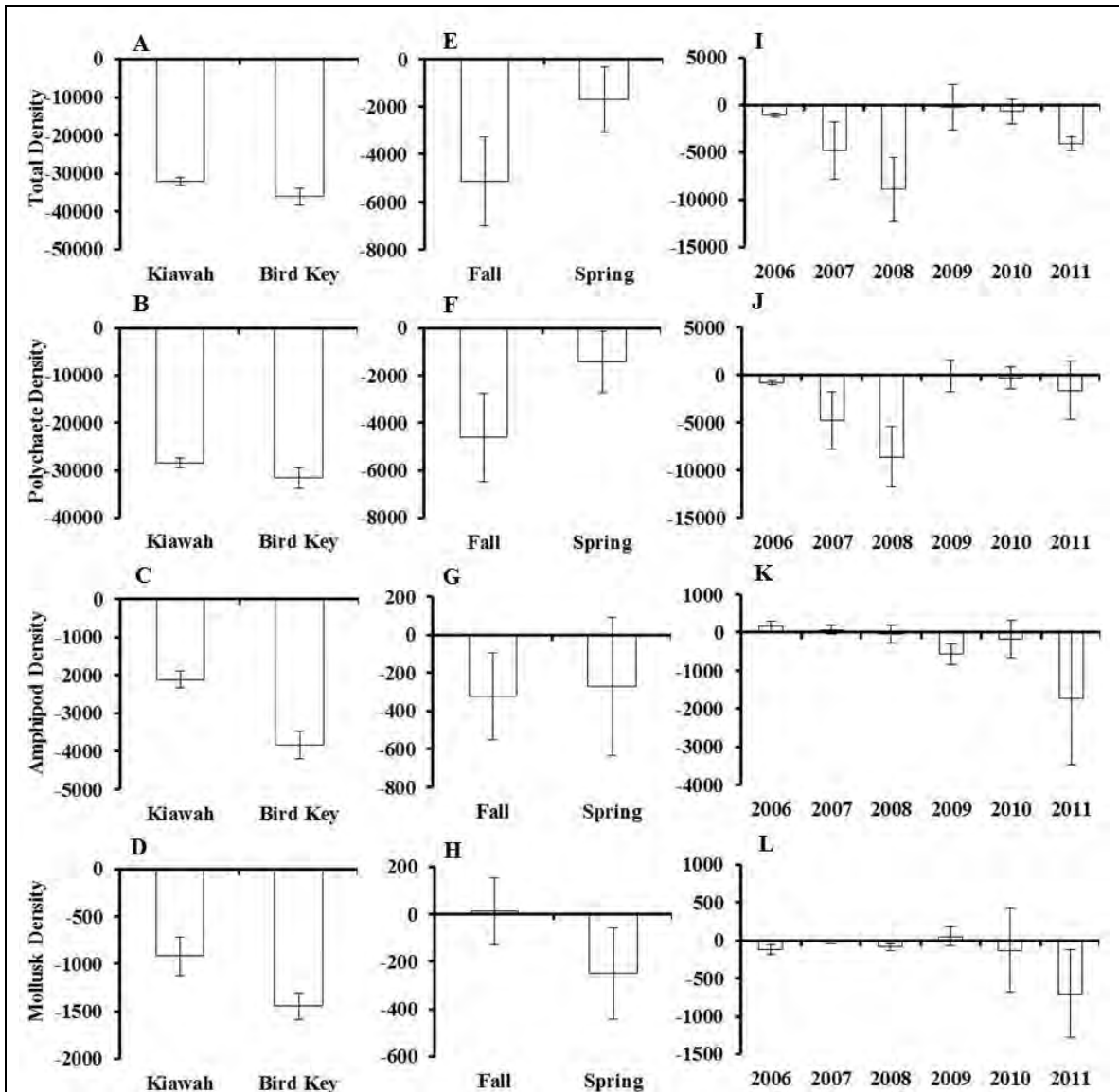


Figure 9. Average (+/-SE) changes in densities (no./m²) of all macroinvertebrate infauna and major taxonomic groups at occupied sites by A-D) island (Kiawah or Bird Key), E-H) season (Fall or Spring), and I-L) year following abandonment of occupied foraging sites. Replicate cores were averaged within each transect, the differences were calculated between the last occupied season and the subsequent abandoned season then then the site differences averaged within each island, season and year prior to calculating the averages shown.

taxon occurred during those latter periods (Figure 9K). Decreases in mollusk densities were also greatest during the latter years of the study, but this was not a significant temporal trend (Table 3; Figure 9K). In general, changes associated with abandonment were similar through time on both islands (no significant Island X Year interaction in Table 3), although amphipod densities were an exception, due to differences occurring in 2010 and 2011 when foraging areas occurred primarily in exposed habitats (Figure 8C).

Multivariate ANOSIM comparing changes in community composition between occupied and abandoned sites identified a marginally significant difference ($R = 0.062$; $p = 0.059$). SIMPER analysis identified a diverse suite of fauna responsible for the dissimilarity between occupied and abandoned sites but the list was dominated by polychaetes (Table 4). All taxa were more abundant at occupied sites than at abandoned sites with the exception of the very long and thin polychaete *Heteromastus filiformis*. Also on the list were three haustoriid amphipods and two mollusk taxa including the common bean clam *Donax variabilis*.

Table 4. All taxa responsible for at least 2% of the dissimilarity between occupied and abandoned sites at Kiawah Island and Bird Key based on similarity percentage (SIMPER) analysis. Higher Taxa: P = polychaete, A = amphipod, M = mollusk, no abbreviation = other. For each taxon, replicate cores were averaged within each transect and fourth root transformed prior to analysis. Densities shown in the table were derived from those transformed data and do not represent absolute densities.

Taxon	Higher Taxon	Average Density in		Percent Contribution to Dissimilarity
		Occupied Sites	Abandoned Sites	
<i>Neohaustorius schmitzi</i>	A	2.92	2.53	4.79
<i>Paraonis fulgens</i>	P	5.38	4.26	4.56
<i>Streblospio benedicti</i>	P	3.76	3.49	4.47
<i>Laeonereis culveri</i>	P	3.51	3.00	4.34
<i>Capitella capitata</i>	P	3.68	3.18	4.31
<i>Donax variabilis</i>	M	2.06	0.59	3.52
<i>Lepidactylis dytiscus</i>	A	2.80	1.78	3.37
<i>Heteromastus filiformis</i>	P	1.97	2.50	3.04
<i>Nereis succinea</i>	P	1.95	1.65	2.82
<i>Mediomastus</i> sp.	P	1.78	1.48	2.78
<i>Tharyx acutus</i>	P	1.45	1.13	2.68
Tellinidae	M	1.35	1.08	2.45
Cirratulidae	P	1.36	1.24	2.31
<i>Eteone heteropoda</i>	P	1.44	0.55	2.17
<i>Leitoscoloplos fragilis</i>	P	1.32	0.69	2.04
<i>Acanthohaustorius</i> sp.	A	0.91	0.71	2.03
Nemertea		1.32	0.52	2.00

When the species matrix was reduced to include only occupied foraging sites, cluster analysis identified six unique and significant clusters (I-VI in Figure 10). When these clusters were delineated on an MDS plot of the sites, two patterns emerged: 1) the two islands were not clearly differentiated in terms of community composition and 2) the communities of the two islands transitioned through time (Figure 11). The occupied foraging sites on Kiawah Island and Bird Key were highly mixed throughout the ordination plot indicating they were very similar throughout the study. Four of the significant clusters formed a series moving from left to right across the ordination plot, roughly representing the time course of the study. Cluster V included periods sampled only in 2006, 2007 and 2008. Clusters III and VI included only sampling periods in 2009

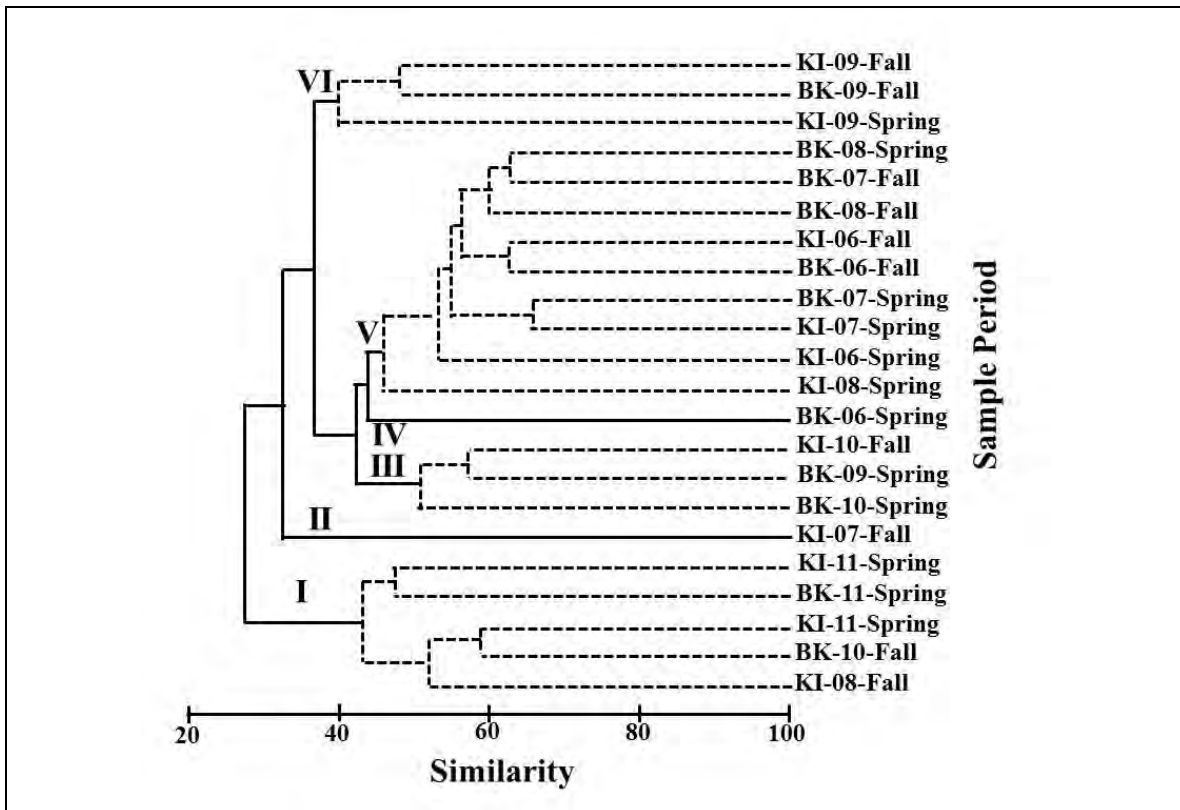


Figure 10. Results of cluster analysis involving only occupied sites in Kiawah island and Bird Key. Individual taxon densities on transects within each island, season and year were averaged prior to analysis to simplify interpretation. Solid lines – significant clusters based on similarity profile permutation tests (SIMPROF), dashed lines—non-significant clusters. Roman numerals identify significant clusters plotted in Figure 11.

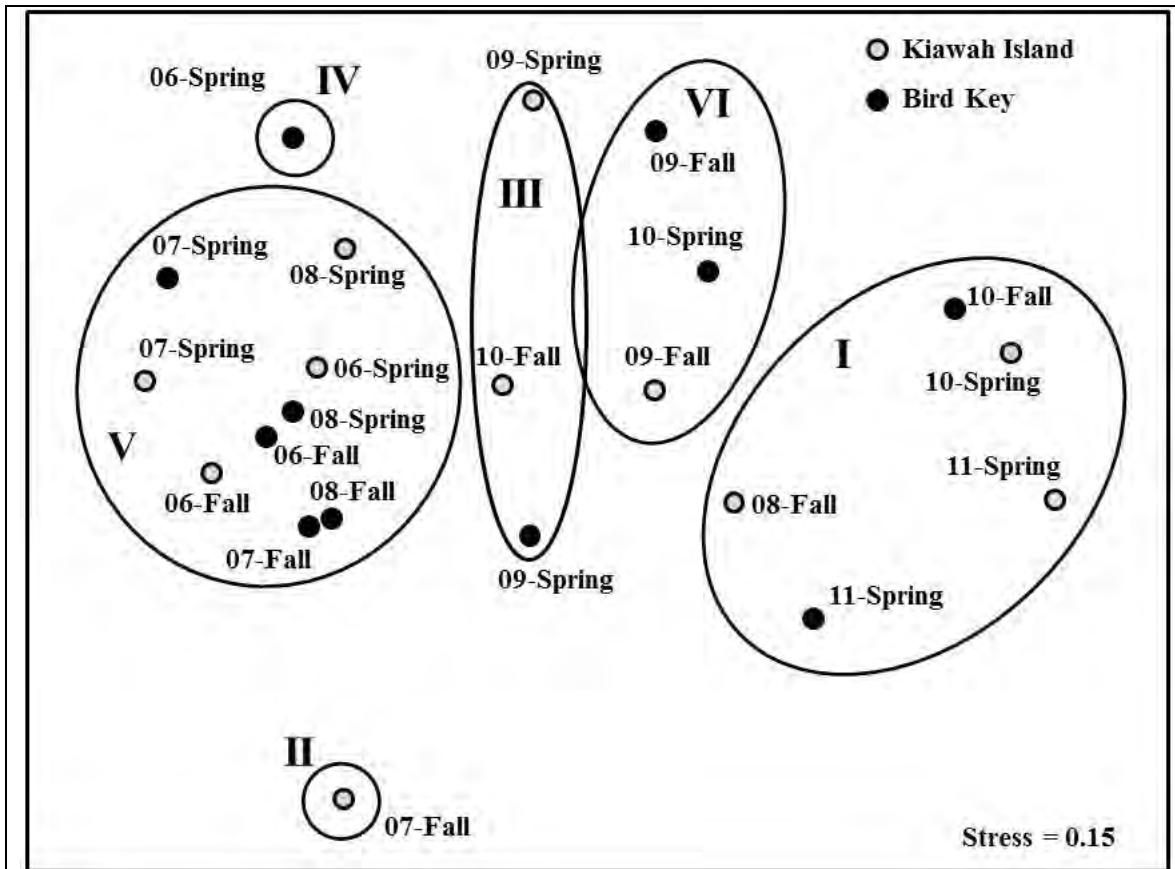


Figure 11. MDS ordination plot of occupied sites on Kiawah Island and Bird Key. Individual taxon densities on transects within each island, season and year were averaged prior to analysis to simplify interpretation. Roman numerals identify significant clusters determined from similarity profile permutation tests (SIMPROF) shown in Figure 10.

and 2010, and cluster I included periods sampled primarily in 2010 and 2011 with the exception of the Kiawah 2008 fall sampling period (Figure 11). Two individual sampling periods formed single point clusters: Bird Key 2006 Spring (IV) and Kiawah Island 2007 Fall (II) sampling periods. These individual clusters were adjacent to cluster V consistent with the general temporal transition seen as one moves from left to right across the plot.

In order to focus the SIMPER analysis on major groupings, the clusters containing a single sampling period were excluded. Between the two most disparate clusters, V and I, an evident shift from polychaetes to amphipods and mollusks occurred over the course of the study (Table 5). All polychaete taxa responsible for at least 2% of the dissimilarity between these clusters were always more abundant during the early sampling periods represented by cluster V. By contrast, all amphipods and molluscs responsible for at least 2% of the dissimilarity between these clusters were more

Table 5. All taxa responsible for at least 2% of the dissimilarity between occupied and abandoned sites at Kiawah Island and Bird Key based on similarity percentage (SIMPER) analysis. Higher Taxa: P = polychaete, A = amphipod, M = mollusk, no abbreviation = other. For each taxon, replicate cores were averaged within each transect and fourth root transformed prior to analysis. Densities shown in the table were derived from those transformed data and do not represent absolute densities.

Taxon	Higher Taxon	Average Density in		Percent Contribution to Dissimilarity
		Cluster V	Cluster I	
<i>Neohaustorius schmitzi</i>	A	0.44	6.83	7.68
<i>Capitella capitata</i>	P	6.16	0.43	6.73
<i>Laeonereis culveri</i>	P	5.83	0.49	6.24
<i>Streblospio benedicti</i>	P	5.23	0.88	5.04
<i>Donax variabilis</i>	M	0.20	4.12	4.49
<i>Nereis succinea</i>	P	3.36	0.00	3.90
<i>Heteromastus filiformis</i>	P	3.34	0.53	3.50
<i>Tharyx acutus</i>	P	2.78	0.00	3.10
<i>Paraonis fulgens</i>	P	6.12	4.82	3.01
Cirratulidae	P	2.46	0.36	2.48
<i>Acanthohaustorius</i> sp.	A	0.32	2.05	2.29
<i>Eteone heteropoda</i>	P	2.29	0.51	2.22
<i>Lepidactylus dytiscus</i>	A	2.39	4.05	2.16
<i>Mediomastus ambiseta</i>	P	2.05	0.00	2.14
<i>Parahaustorius</i> sp.	A	0.00	1.62	2.03

abundant during the latter time periods represented by cluster I. SIMPER produced similar results for comparisons amongst all other pairs of clusters along the left-right temporal axis identified in the MDS ordination (clusters representing earliest to latest sampling periods: V to III to VI to I). When cluster V was compared to cluster III, taxa more abundant in V included only polychaetes (eg. *Capitella capitata*, *Laeonereis culveri*, *Paraonis fulgens*, *Tharyx acutus*, and *Heteromastus filiformis*) while those more abundant in cluster III were primarily amphipods (*Neohaustorius schmitzi* and *Lepidactylus dytiscus*) and molluscs (Tellinidae and *Donax variabilis*) but also the polychaete *Leitoscoloplos fragilis*. The comparison of clusters III and VI was less clearly differentiated based on taxa. Taxa more abundant in cluster III were mostly polychaetes (*P. fulgens*, *L. fragilis*, *Nereis succinea*, *Eteone heteropoda* and *Streblospio benedicti*) but the amphipod *L. dytiscus* was also more abundant in this cluster; taxa more abundant in cluster VI included a mix of amphipods (*Parahaustorius* sp., *Parahaustorius longimerus*, *N. schmitzi*, and *Acanthohaustorius* sp.), mollusks (*D. variabilis* and *M. lateralis*) and polychaetes (*L. culveri*, *T. acutus*, and *C. capitata*). Finally, when cluster VI was

compared to cluster I, the same general pattern held, but again was less clearly differentiated (both clusters included overlapping sampling periods). Taxa more abundant in cluster VI included a mix of polychaetes (*S. benedicti*, *C. capitata*, *Mediomastus* sp., *L. culveri*, *L. fragilis* and *T. acutus*), amphipods (*P. longimerus*, and *Parahaustorius* sp.) and mollusks (*Tellinidae*, *D. variabilis* and *M. lateralis*); taxa more abundant in cluster I included mostly amphipods (*N. schmitzi*, *Acanthohaustorius* sp., *L. dytiscus*) and the polychaete *P. fulgens*.

Macroinvertebrates Identified in Fecal Samples

When the invertebrate community present in foraging sites of Kiawah Island and Bird Key was reduced to just those taxa found in piping plover fecal samples (“consumed” taxa), statistical analysis produced similar results to those obtained using the entire community. The consumed macroinvertebrate community was significantly different among years but not between islands or seasons (Tables 6 and 7). Although not significant, consumed total faunal, polychaete, and amphipod densities tended to be higher at Bird Key than at Kiawah while consumed mollusk density was lower at Bird Key (Tables 6 and 7). On an annual basis, consumed total faunal densities peaked twice: once in 2007 coincident with the peak in consumed polychaete density and again in 2010 and 2011 coincident with peak consumed amphipod density (Table 7). Although among-transect variation was high, the transition among the consumed community from a polychaete dominated assemblage to an amphipod-dominated assemblage was apparent at the transect level (Figure 12B,C). This transition resulted in total faunal densities not changing as substantially through time as the individual taxa (Figure 12A). In general, the two islands followed the same pattern through time, but the interaction between

<i>Table 6. Results (p-values) of ANOVAs using only those taxa identified in piping plover fecal samples and examining differences in the macroinvertebrate communities of occupied foraging habitats. The factors in the models included Island (Kiawah vs. Bird Key), Season (Fall vs. Spring) and Year (2006-2011).</i>				
Source	All Fauna	Polychaetes	Amphipods	Molluscs
Island	0.113	0.127	0.477	0.336
Season	0.855	0.913	0.801	0.269
Island X Season	0.620	0.843	0.693	0.863
Year	0.004	<0.001	<0.001	0.001
Island X Year	0.131	0.007	0.185	0.451

Table 7. Average (SE) densities (no./m²) of major taxa consumed by piping plovers (those identified in fecal samples) in occupied foraging sites by island (Kiawah vs. Bird Key), season (fall vs. spring), and year. Replicate cores were averaged within each transect and transects within each island, season and year were averaged prior to calculating the averages shown.

	Density of			
	All	Polychaetes	Amphipods	Mollusks
Island				
Kiawah	1882 (441)	600 (307)	957 (337)	322 (152)
Bird Key	2886 (670)	1491 (691)	1244 (539)	180 (107)
Season				
Fall	2216 (536)	1045 (486)	801 (364)	371 (161)
Spring	2524 (616)	1047 (590)	1323 (488)	151 (101)
Year				
2006	617 (304)	496 (316)	110 (46)	2 (2)
2007	3891 (1372)	3794 (1405)	94 (52)	3 (3)
2008	1737(522)	808 (427)	715 (420)	214 (214)
2009	1701 (313)	256 (208)	990 (199)	455 (274)
2010	3361 (851)	397 (365)	2275 (813)	688 (280)
2011	3613 (1957)	0 (0)	3575 (1996)	38 (38)

Island and Year was significant for density of consumed polychaetes (Table 6). This significant interaction was due to substantially higher consumed polychaete densities on Bird Key than Kiawah Island during 2007 and 2008 (Figure 12B).

As with the macroinvertebrate community as a whole, piping plover foraging areas tended to host lower densities of consumed taxa when abandoned than when occupied (negative values for “density when abandoned minus density when occupied”) (Table 9; Figure 13). These changes were strongest for total faunal density, polychaete density and amphipod density and weakest for mollusk density (Figure 13). With the exception of total consumed fauna density, the density changes associated with abandonment were not significantly different between the two islands but were more negative at Bird Key than at Kiawah Island (Tables 8 and 9). The changes were not significantly different between seasons in which abandonment occurred (Season) or the Island X Season interaction for any measure (Table 8). The changes in consumed polychaete density, amphipod density and mollusk density following abandonment varied significantly by year in which abandonment occurred, but total consumed faunal density did not (Table 8). The largest decreases in density following abandonment occurred subsequent to periods of peak consumed faunal densities. Polychaete densities decreased

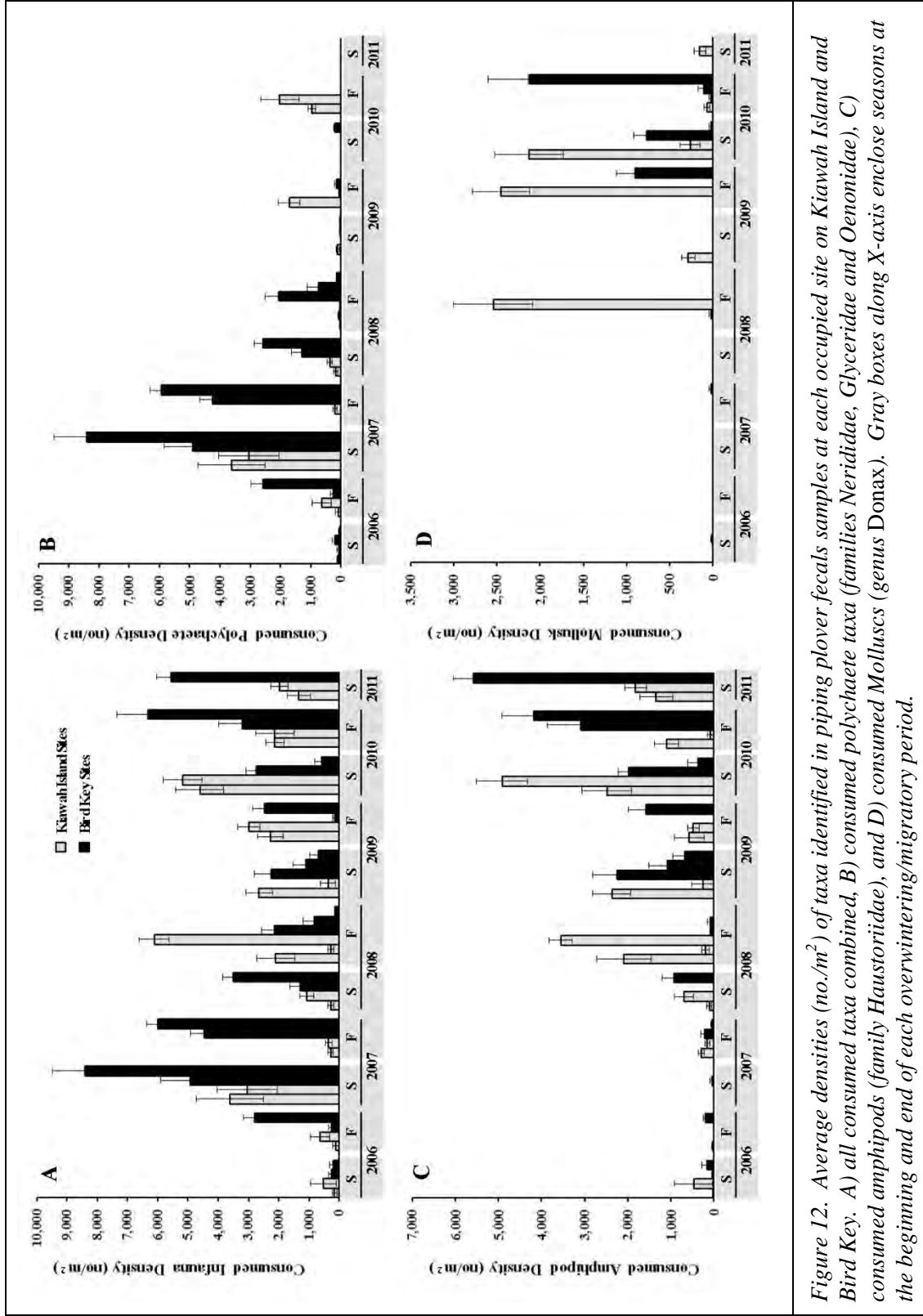


Figure 12. Average densities (no./m²) of taxa identified in piping plover fecals samples at each occupied site on Kiawah Island and Bird Key. A) all consumed taxa combined, B) consumed polychaete taxa (families Nerididae, Glyceridae and Oeononidae), C) consumed amphipods (family Haustoriidae), and D) consumed Molluscs (genus Donax). Gray boxes along X-axis enclose seasons at the beginning and end of each overwintering/migratory period.

the most following peak polychaete densities in 2007 and 2008 and consumed amphipod and mollusk densities decreased the most following their peak densities during the latter portion of the study (Table 9).

Table 8. Results of ANOVAs (p-values) examining the effects of Island (Kiawah vs. Bird Key), Season (Fall vs. Spring) and Year (2006-2011) on the change in foraging habitat macroinvertebrate communities following abandonment.

Source	All Fauna	Polychaetes	Amphipods	Molluscs
Island	0.046	0.308	0.156	0.134
Season	0.362	0.575	0.130	0.861
Island X Season	0.573	0.512	0.299	0.470
Year	0.062	0.042	0.016	0.007
Island X Year	0.159	0.110	0.038	0.005

Table 9. Average (SE) changes in densities (no./m²) of major taxa consumed by piping plovers (those found in fecal samples) between foraging sites being occupied and abandoned. Replicate cores were averaged within each transect, the differences were calculated between the last occupied season and the subsequent abandoned season then then the site differences averaged within each island, season and year prior to calculating the averages shown.

	Change in density of			
	All	Polychaetes	Amphipods	Mollusks
Islands				
Kiawah	-1286 (553)	-855 (609)	-410 (430)	-20 (355)
Bird Key	-2848 (1285)	-1784 (1139)	-760 (725)	-304 (229)
Abandonment Season				
Fall	-1829 (1253)	-1367 (1028)	-603 (724)	141 (299)
Spring	-2305 (715)	-1272 (813)	-568 (439)	-465 (270)
Abandonment Year				
2006	110 (102)	-102 (15)	208 (91)	4 (4)
2007	-2856 (1780)	-3026 (1874)	164 (224)	5 (5)
2008	-2900 (2269)	-2911 (2380)	16 (253)	-5 (5)
2009	-921 (737)	313 (244)	-1156 (549)	-77 (70)
2010	-888 (714)	-400 (457)	-334 (990)	-153 (991)
2011	-5647 (3520)	-1042 (1086)	-3443 (3531)	-1162 (1075)

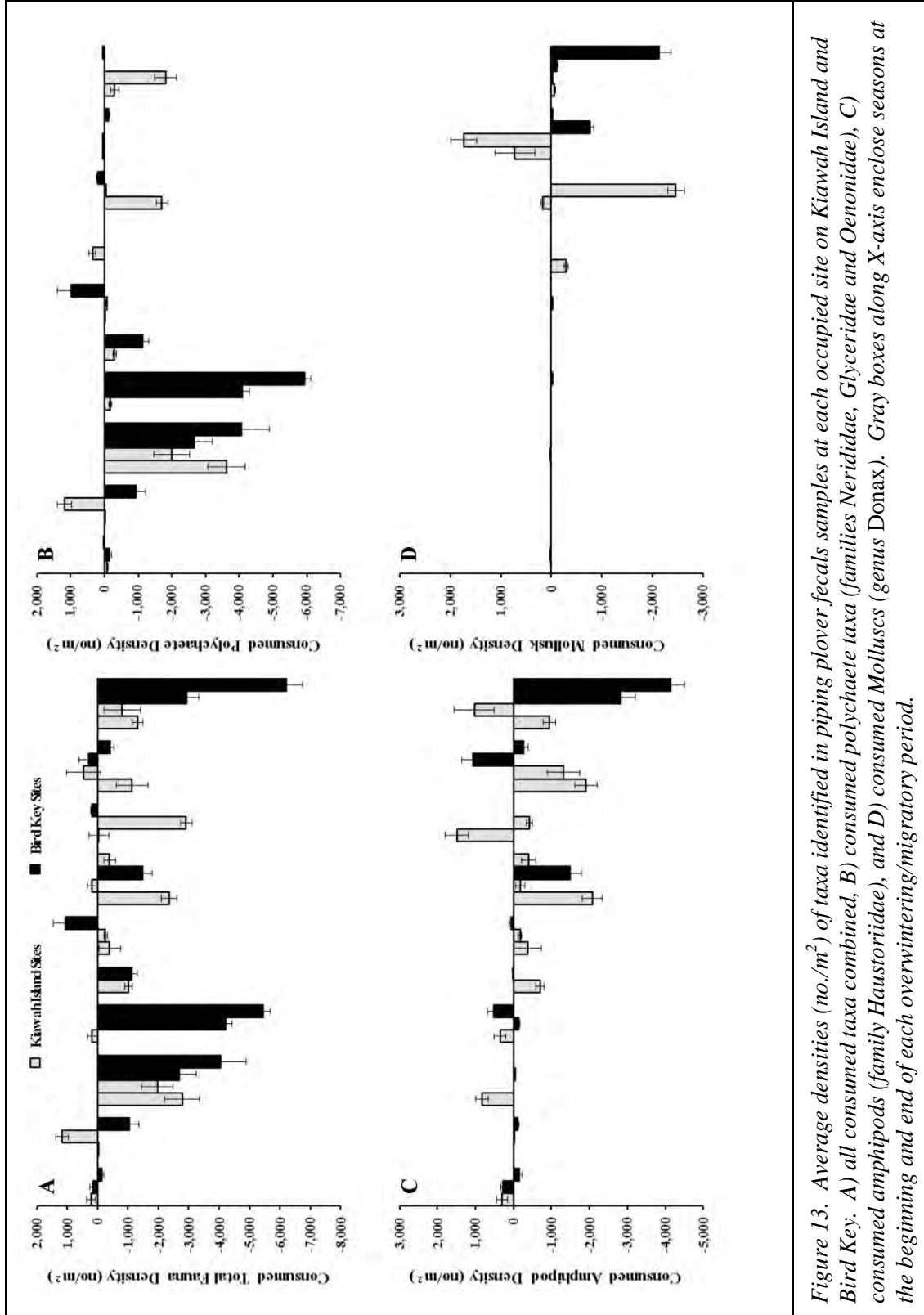


Figure 13. Average densities (no./m²) of taxa identified in piping plover fecals samples at each occupied site on Kiawah Island and Bird Key. A) all consumed taxa combined, B) consumed polychaete taxa (families Nerididae, Glyceridae and Oeononidae), C) consumed amphipods (family Haustoriidae), and D) consumed Molluscs (genus Donax). Gray boxes along X-axis enclose seasons at the beginning and end of each overwintering/migratory period.

DISCUSSION

Caveats regarding impact detection

Whether modification of the lagoon at the east of Kiawah Island significantly impacted macroinvertebrate prey densities in associated piping plover foraging habitats was not clearly resolvable in this study. Limitations in the temporal controls were recognized from the outset, but Before-After comparisons should have been possible using only the spring sampling season data. Modification of the intended control area (Bird Key) prevented a meaningful analysis of even that dataset under a BACI framework. The analyses performed here compared the two islands and examined relative changes in foraging areas on the two islands through time (Island X Year interaction), but it is important to keep in mind that both islands experienced anthropogenic modification at approximately the same time. Under these circumstances, the comparison if the two islands could only identify whether one modified habitat changed differently relative to another modified habitat. Despite these limitations, the dataset still provided the ability to address the two primary study objectives: 1) assess changes in the macroinvertebrate community in piping plover foraging sites around the Kiawah Island lagoon, 2) determine changes in the macroinvertebrate community associated with piping plover foraging site abandonment within the lagoon.

Macroinvertebrate Communities in Occupied Piping Plover Foraging Areas

Based on total faunal and major taxa densities, there was little evidence of differences between foraging sites on the two islands, of differences between seasons, or of the two islands changing differently through time (ie. few Island X Year interactions were detected). The density of polychaete taxa identified in fecal samples (consumed polychaetes) was the only parameter to show a significantly different trend between the two islands through time, and this was due to particularly high polychaete densities on Bird Key during 2007 and 2008. The occupied foraging sites on Kiawah Island also hosted elevated polychaete densities during this same period, but they were much lower than on Bird Key. This depression of polychaete numbers on Kiawah Island relative to those on Bird Key could have been due to a wide range of factors including differential

disturbance from modification, recruitment patterns, interspecific competition or predation pressure.

The most apparent temporal patterns in macroinvertebrate community composition were those that occurred on both islands over the course of the study. Polychaete densities were relatively high on both islands during the 2006-2007 and 2007-2008 overwintering seasons but then declined over subsequent overwintering seasons. While polychaete densities were declining, amphipod densities and, to a lesser extent mollusk densities, were increasing. This same scenario played out at finer taxonomic levels as polychaete taxa including *Laeonereis culveri* and *Nereis succinea* (both nereid polychaetes) were replaced by various haustoriid amphipods such as *Neohaustorius schmitzi* and *Lepidactylus dytiscus* and molluscs such as *Donax variabilis*. This trend was particularly striking as many of the taxa most responsible for the dissimilarities between foraging area communities early in the study and later in the study were taxa also found in piping plover fecal samples. This suggests that the temporal changes occurring in foraging areas impacted the diet of migratory and overwintering piping plovers in the Kiawah Island/Bird Key system.

Piping plovers on Kiawah Island and Bird Key shifted their primary foraging areas from protected lagoon habitats to exposed shoreline habitat (active beach face or inlet channel edges) over the course of the study. Some studies have found communities of greater total invertebrate abundances and biomasses in protected intertidal shorelines than in exposed ocean beach shorelines (Cohen *et al.* 2006). This pattern was not particularly strong in the current study in terms of abundances, but the shift in plover habitat use likely contributed to the concurrent changes observed in the available prey community from polychaetes to amphipods (and mollusks) at occupied foraging sites. Polychaetes tend to be most abundant and diverse in more protected and/or dissipative shoreline environments, while crustaceans (such as amphipods) tend to fare better in more exposed and higher energy environments (McLachlan and Brown 2006). Consistent with this general pattern, the relative abundance of polychaetes was greater in protected foraging areas while the relative abundance of amphipods was greater in exposed habitats on Kiawah Island and Bird Key (Figure 14A,B). When examined by

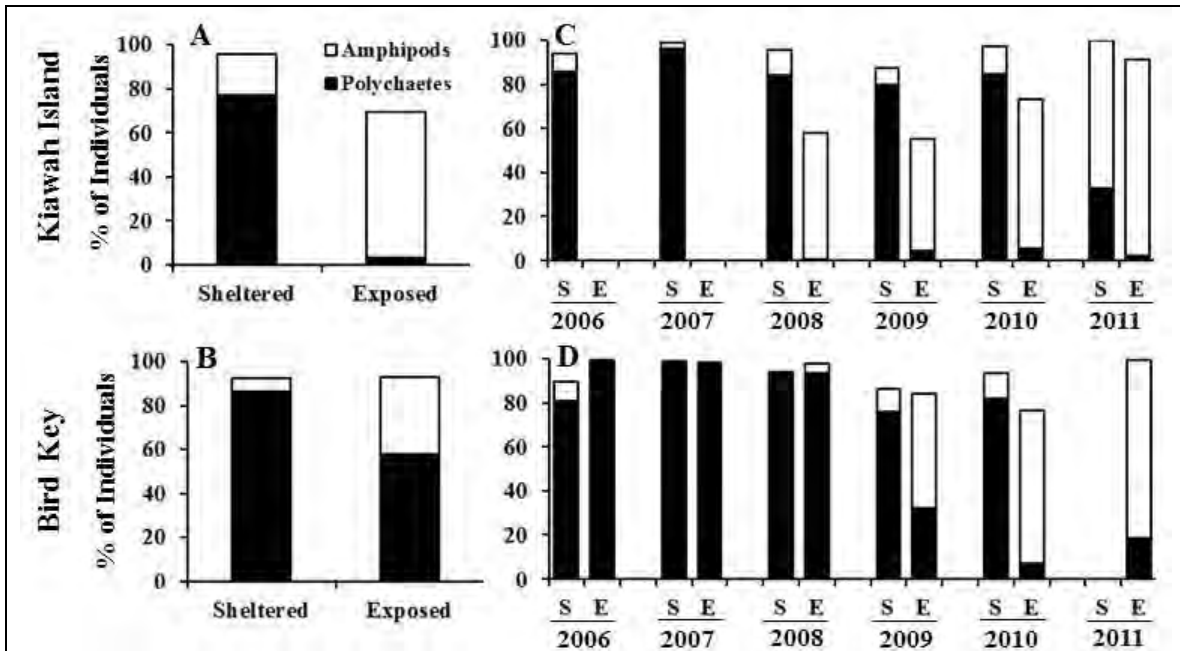
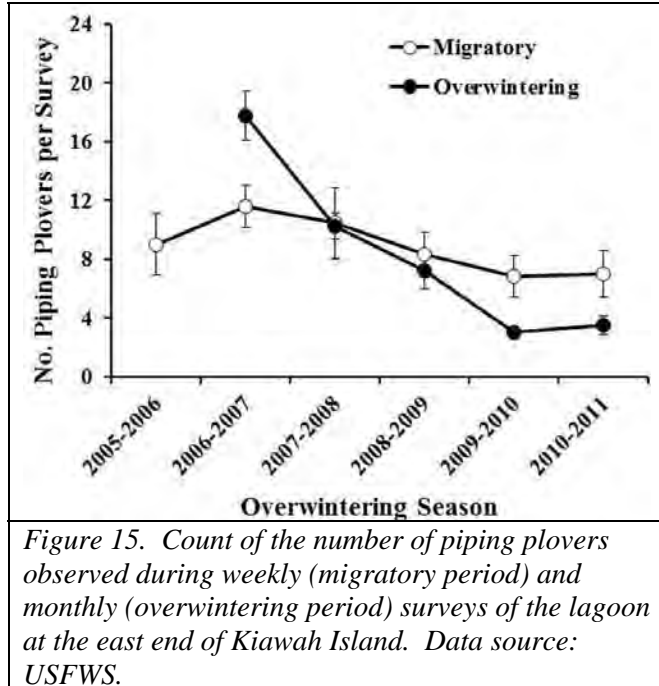


Figure 14. Relative abundances of polychaetes and amphipods in sheltered and exposed habitats overall on A) Kiawah Island and B) Bird Key and by year on C) Kiawah Island and D) Bird Key.

year, relative abundances of polychaetes and amphipods followed this same trend with respect to habitat type, but with some exceptions (Figure 14C,D). The habitat-specific pattern was very consistent on Kiawah Island, except in the spring of 2011 when a sheltered foraging site was dominated by amphipods. On Bird Key, the pattern was less consistent with exposed habitats having very high relative abundances of polychaetes during the years of peak polychaete densities (2006-2008). This suggests that the decline in polychaetes and increase in amphipods over the course of this study reflected a combination of shifting piping plover habitat use and broader change in the relative abundances these taxa at the two islands.

The temporal trend of declining polychaete densities from the earlier to the later portions of the study period was very similar to the trends observed in the piping plover count surveys in the area. The numbers of piping plovers using the lagoon at the east end of Kiawah Island during the migratory period and during the overwintering period were highest during the 2006-2007 period, declined over the next two overwintering periods and remained low thereafter (Figure 15; USFWS, unpublished data). The specific polychaete taxa observed in piping plover fecal samples (Neriidae, Glyceridae, and

Oenonidae) also followed the same temporal trend, becoming almost absent from most foraging sites during the latter portion of the study. Other studies using more formal methodology have documented significant positive correlations between numbers of foraging shorebirds and polychaete densities in migratory stopovers and overwintering habitats (Mercier and McNeil 1994; Muhammad 2009), suggesting these taxa are an



important part of the habitat quality of shorebird stopover and overwintering grounds. Although amphipod densities increased substantially during the latter portion of the study and partially compensated for the polychaete declines in terms of total faunal abundances, plover numbers did not appear to respond.

Macroinvertebrate Communities in Abandoned Foraging Areas

As foraging sites transitioned from being occupied to being abandoned by migratory and overwintering piping plovers, the over-riding trend was a decrease in macroinvertebrate densities. This pattern generally held regardless of island, season of abandonment, year of abandonment, or major invertebrate taxon examined. The majority of the 33 foraging sites that were occupied and subsequently abandoned experienced decreases in total faunal densities (27 sites) and all the major taxa densities. Of the major taxa, polychaetes most consistently decreased following abandonment (25 sites) while amphipods and molluscs decreased at a majority of sites but not as consistently as polychaetes (19 and 20 sites, respectively). In fact, multivariate analyses confirmed that many of the fauna consumed by plovers (haustoriid amphipods, nereid polychaetes, etc.) were among those most responsible for the community changes occurring with abandonment. This suggests that piping plovers were relocating to other foraging sites as prey became scarce and/or as associated environmental conditions (sediment

composition, vegetation distribution, elevation, etc.) became unsuitable for foraging activity or their prey.

The causes of the changes leading up to foraging site abandonment are unclear but they may partially reflect changing environmental conditions over the course of the study. Some intertidal foraging sites transitioned to subtidal or supralittoral habitats (or at least elevated close to the high water mark) at some point leading up to abandonment. These types of changes appeared to be associated with shifting tidal channel locations or with the accumulation of wind and wave-driven sand (Bergquist and Levisen personal observations). Because piping plovers prefer to forage in intertidal habitats, such severely altered sites were no longer suitable foraging habitat for piping plovers or suitable habitat for many intertidal invertebrates. Other foraging areas remained intertidal following abandonment, thus more subtle changes in sediment composition, grain size or penetrability, known to influence invertebrate communities (Gray 1974), may have occurred in these cases. Determining those characteristics on Kiawah Island was outside of the scope of the current study, but sediment samples from a small number of sites (5) were processed and little variation was found in sand content (92.4 - 98.8% of dry mass) or silt and clay content (silt/clay = 1.2 - 7.6% of dry mass). Despite these results, relative compositions of the major taxonomic groups suggest that the physical environment changed in association with abandonment in a somewhat predictable manner. In particular, the change in polychaete density was inversely related to the change in amphipod density following abandonment (Figure 14). The different habitat

preferences of polychaetes and amphipods and the different magnitudes of change of the taxa following abandonment (polychaetes decreased more often and to a greater extent than amphipods), indicate that the changes may be related to sediments becoming coarser or foraging areas becoming more exposed to greater wave action.

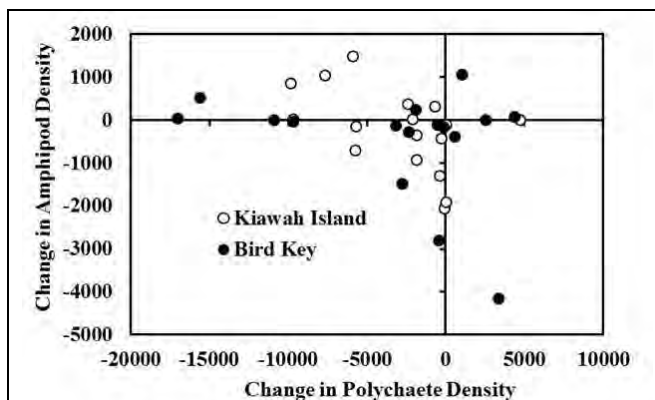


Figure 14. Relationship between the changes in the density (no./m²) of amphipods and density of polychaetes of occupied foraging sites following abandonment.

More detailed physical data on elevation, sediment composition, water flow and wave exposure as well as data on invertebrate recruitment patterns, predatory prey depletion and shorebird behavior are needed to determine the mechanisms driving changes observed in macroinvertebrate communities following foraging site abandonment.

The compositional changes in the macroinvertebrate communities associated with abandonment of foraging sites were similar to the changes that occurred at occupied sites over the course of the study. Occupied foraging sites shifted from relatively high polychaete and low amphipod densities in the early part of the study to relatively low polychaete densities later in the study. Similarly, foraging sites when occupied had higher densities of polychaetes than when later abandoned. In both cases, piping plovers appeared to respond similarly with decreasing numbers of overwintering birds through time in the Kiawah Island/Bird Key system and with abandonment of individual foraging sites on both islands in all years. Interestingly, based on multivariate analyses, practically all of individual taxa responsible for most of the dissimilarity (at least 2% individually) between occupied foraging sites early in the study and occupied foraging sites later in the study were also responsible for the dissimilarity between occupied and subsequently abandoned sites. These taxa included many of those also found in piping plover fecal samples such as the nereids *Nereis succinea* and *Leionereis culveri* and the haustoriid amphipods *Neohaustorius schmitzi*, *Lepidactylus dytiscus* and *Acanthohaustorius* sp. This further reinforces that changes specific to taxa in the diets of migratory/overwintering piping plovers were occurring both within individual foraging sites leading to subsequent abandonment and within the larger Kiawah Island/Bird Key system, perhaps leading to declines in the overwintering population.

Macroinvertebrate Prey as a Component of Migratory/Overwintering Habitat Quality

Migratory birds expend enormous amounts of energy during seasonal migrations of sometimes thousands of miles (Blem 1980; Myers et al. 1987), and up to 90% of the migratory period is spent at stopover sites where migrants refill energy stores (Hedenström and Alerstam 1998). Because of the high energy demands of active foraging during these migratory stopovers (Evans 1976; McWilliams et al. 2004), energy expended during this time may be twice that expended during migratory flight

(Hedenström and Alerstam 1998). Consequently, quantity and quality of prey at stopover and overwintering habitats are critical considerations of overall habitat quality.

Polychaetes form a major part of the diet for many migrant shorebirds (eg. Kalejta 1992; Tsipoura and Burger 1999; Verkuil et al. 2006) including piping plovers (Nichols 1989; Zonick and Ryan 1996). Polychaete densities, including those found to be consumed by piping plovers in South Carolina stopover/overwintering habitats, declined in foraging areas over the course of this study. Coincident with this decrease was an increase in amphipod densities that at least partially compensated for the loss of polychaetes in terms of total invertebrate abundances. Whether the amphipods were capable of providing similar or better quality forage as compared to polychaetes depends on a number of factors including the relative biomasses of these two prey taxa, the assimilation efficiency of the prey items when consumed by piping plovers (the proportion of the ingested prey energy content that is assimilated into the tissues of the predator), and the amount of foraging effort required by plovers to obtain the two different prey taxa. The polychaete taxa found in piping plover fecal samples are substantially larger than the amphipod taxa found in the fecal samples. This indicates that piping plovers must capture many more haustorid amphipods in order to equal the mass available in a single nereid or glycerid polychaete. Most studies indicate intertidal marine invertebrates are assimilated by shorebirds with an efficiency of ~75-85% (Kersten and Piersma 1987; Stillman et al. 2005; Castro 2008), so the greater mass of a polychaete prey item would provide a greater energy gain for the predatory shorebird.

It is not known whether piping plovers forage more successfully on polychaetes or amphipods. In order to determine whether the quality of foraging habitat is undermined by a community shift from a polychaete-dominated to a amphipod-dominated assemblage, more information on the foraging behavior of piping plovers is required. It is currently not known whether piping plovers search for greater lengths of time or successfully capture when foraging on one prey taxon versus the other. Regardless, the relative ubiquity of polychaete remains in piping plover fecal samples and the potentially greater energy content of this prey taxon suggest that the density of large errant polychaetes is an important component of piping plover stopover and overwintering habitat quality. Because piping plovers have a site high fidelity both within and between wintering seasons (Drake *et al.* 2001; Stucker *et al.* 2010) changes in

the condition of wintering habitats in terms of prey composition may have severe consequences for returning migrants.

CONCLUSIONS AND RECOMMENDATIONS

A late start in the monitoring efforts and unexpected modification of the intended control island (Bird Key) inhibited the ability to detect impacts from the Kiawah Island East End Erosion and Beach Restoration Project, but these limitations did not affect the primary study objectives. There was little evidence the macroinvertebrate communities differed between islands or sampling seasons or that they changed differently through time at the two islands, although these between-island comparisons were capable only of indicating whether two human-modified systems changed differently through time. Macroinvertebrate community composition changed significantly through time from a polychaete-dominated assemblage early in the study to an amphipod dominated assemblage later in the study. At least part of this change may be due to a change in piping plover foraging behavior as they foraged primarily in protected habitats during 2006-2008 and foraged more in exposed habitats during 2009-2011, thus the macroinvertebrate community changed from taxa typically of lower-energy environments to those typical of higher energy environments. Many of the taxa found in piping plover fecal samples were among those that changed during this period, the temporal shift in community composition likely affected the diet of migratory and overwintering piping plovers in this system. The decreasing trend in polychaete density was accompanied by a decrease in the number of overwintering piping plovers in the system, suggesting a link between the two. Abandoned foraging sites supported lower densities of practically all taxa. The changes in macroinvertebrate community composition that occurred in association with site abandonment were almost identical to the changes that occurred at occupied feeding areas over the course of the study (these similarities were true at broad taxonomic levels and at the species level). As a result, the potential link between macroinvertebrate prey and overwintering piping plovers was apparent at two different spatial scales: 1) prey changes in individual foraging sites and subsequent abandonment of those sites by piping plovers, 2) prey changes in the larger Kiawah Island/Bird Key system and declines in the overwintering piping plover population. The quantity and quality of prey are often critical during the energetically demanding process of foraging and migration. The relative importance of various prey taxa in meeting the energetic

demands of migrating and overwintering piping plovers will require further study. The data presented here suggest that larger, errant polychaetes such as the families Nereididae, Glyceridae and Oeonidae may be particularly important to piping plovers overwintering in this region.

Based on the findings of this study and the obstacles experienced here, the following recommendations are proposed to improve future investigations and ensure anthropogenic modification does not significantly impair critical shorebird habitats:

- 1) Improve communication and coordination among project participants so that appropriate Before-After-Control-Impact study designs are employed and all data (bird surveys, aerial photography, and physical and biological habitat characterization) are collected to maximize usefulness.
- 2) Perform more thorough monitoring of physical habitat characteristics (including elevation, tidal inundation, sediment characteristics, vegetation, surface microtopography, etc.) recognized by ornithologists as important to migratory and overwintering shorebird habitat choice at spatial scales relevant to piping plover foraging activities.
- 3) Perform more thorough studies of prey community composition (including determining biomasses of key taxa) and piping plover foraging behavior (attack rates, foraging efficiency, etc.) to better determine the relationship between different prey taxa and the energetic costs/benefits of foraging in different migratory stopover and overwintering habitats.

ACKNOWLEDGEMENTS

We wish to thank the staff of the Environmental Research Section at the Marine Resources Research Institute for their hard work and dedication to this project. Patrick Biondo, Stephen Burns, Stacie Crowe, Jordan Felber, Jeremy Grigsby, John Heinsohn, Jared Hulteen, Brooke James, and George Riekerk assisted with field sample collection. Stephen Burns assisted with benthic sample sorting. A very special thanks to Melissa Bimbi at the US Fish and Wildlife Service for her assistance in the field, lessons in shorebird identification, and insight into piping plover ecology. Thanks also to Jim Jordan and Aaron Givens for their assistance identifying foraging areas on Kiawah Island and accessing those areas using many fun, and sometimes memorably troublesome, methods. This project was funded by the Town of Kiawah.

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Appendix 1. Foraging sites sampled on Kiawah Island and Bird Key between 2006 and 2011.

Island	Site	Season	Year	Collection Date	Status	Habitat Type
Bird Key	1	Spring	2006	4/19/2006	Occupied	Protected
Bird Key	2	Spring	2006	4/19/2006	Occupied	Protected
Bird Key	1	Fall	2006	8/21/2006	Abandoned	Protected
Bird Key	2	Fall	2006	8/21/2006	Abandoned	Protected
Bird Key	3	Fall	2006	8/21/2006	Occupied	Protected
Bird Key	4	Fall	2006	8/21/2006	Occupied	Exposed
Bird Key	3	Spring	2007	3/29/2007	Occupied	Protected
Bird Key	4	Spring	2007	3/29/2007	Abandoned	Exposed
Bird Key	5	Spring	2007	3/29/2007	Occupied	Protected
Bird Key	3	Fall	2007	9/5/2007	Abandoned	Protected
Bird Key	5	Fall	2007	9/5/2007	Abandoned	Protected
Bird Key	6	Fall	2007	9/5/2007	Occupied	Exposed
Bird Key	7	Fall	2007	9/5/2007	Occupied	Exposed
Bird Key	6	Spring	2008	4/1/2008	Abandoned	Exposed
Bird Key	7	Spring	2008	4/1/2008	Abandoned	Exposed
Bird Key	8	Spring	2008	4/1/2008	Occupied	Protected
Bird Key	9	Spring	2008	4/1/2008	Occupied	Exposed
Bird Key	8	Fall	2008	9/10/2008	Abandoned	Protected
Bird Key	9	Fall	2008	9/10/2008	Occupied	Exposed
Bird Key	10	Fall	2008	9/10/2008	Occupied	Exposed
Bird Key	11	Fall	2008	9/10/2008	Occupied	Protected
Bird Key	9	Spring	2009	4/1/2009	Occupied	Exposed
Bird Key	10	Spring	2009	4/1/2009	Abandoned	Exposed
Bird Key	11	Spring	2009	4/1/2009	Occupied	Protected
Bird Key	12	Spring	2009	4/1/2009	Occupied	Exposed
Bird Key	9	Fall	2009	9/29/2009	Abandoned	Exposed
Bird Key	11	Fall	2009	9/29/2009	Occupied	Protected
Bird Key	12	Fall	2009	9/29/2009	Abandoned	Exposed
Bird Key	13	Fall	2009	9/29/2009	Occupied	Exposed
Bird Key	11	Spring	2010	4/7/2010	Abandoned	Protected
Bird Key	13	Spring	2010	4/7/2010	Occupied	Exposed
Bird Key	14	Spring	2010	4/7/2010	Occupied	Protected
Bird Key	13	Fall	2010	9/16/2010	Abandoned	Exposed
Bird Key	14	Fall	2010	9/16/2010	Abandoned	Protected
Bird Key	15	Fall	2010	9/16/2010	Occupied	Exposed
Bird Key	16	Fall	2010	9/16/2010	Occupied	Exposed
Bird Key	15	Spring	2011	4/12/2011	Abandoned	Exposed
Bird Key	16	Spring	2011	4/12/2011	Abandoned	Exposed
Bird Key	17	Spring	2011	4/12/2011	Occupied	Exposed
Kiawah	1	Spring	2006	4/19/2006	Occupied	Protected
Kiawah	2	Spring	2006	4/19/2006	Occupied	Protected
Kiawah	3	Spring	2006	4/19/2006	Occupied	Protected

Appendix 1. Foraging sites sampled on Kiawah Island and Bird Key between 2006 and 2011.

Island	Site	Season	Year	Collection Date	Status	Habitat Type
Kiawah	1	Fall	2006	8/22/2006	Abandoned	Protected
Kiawah	2	Fall	2006	8/22/2006	Occupied	Protected
Kiawah	3	Fall	2006	8/22/2006	Occupied	Protected
Kiawah	4	Fall	2006	8/22/2006	Occupied	Protected
Kiawah	2	Spring	2007	3/30/2007	Abandoned	Protected
Kiawah	3	Spring	2007	3/30/2007	Abandoned	Protected
Kiawah	4	Spring	2007	3/30/2007	Occupied	Protected
Kiawah	5	Spring	2007	3/30/2007	Occupied	Protected
Kiawah	4	Fall	2007	9/6/2007	Abandoned	Protected
Kiawah	5	Fall	2007	9/6/2007	Abandoned	Protected
Kiawah	6	Fall	2007	9/6/2007	Occupied	Protected
Kiawah	7	Fall	2007	9/6/2007	Occupied	Protected
Kiawah	6	Spring	2008	4/3/2008	Abandoned	Protected
Kiawah	7	Spring	2008	4/3/2008	Abandoned	Exposed
Kiawah	8	Spring	2008	4/3/2008	Occupied	Protected
Kiawah	9	Spring	2008	4/3/2008	Occupied	Protected
Kiawah	8	Fall	2008	9/11/2008	Occupied	Protected
Kiawah	9	Fall	2008	9/11/2008	Abandoned	Protected
Kiawah	10	Fall	2008	9/11/2008	Occupied	Protected
Kiawah	11	Fall	2008	9/11/2008	Occupied	Exposed
Kiawah	8	Spring	2009	4/2/2009	Abandoned	Protected
Kiawah	10	Spring	2009	4/2/2009	Abandoned	Protected
Kiawah	11	Spring	2009	4/2/2009	Occupied	Exposed
Kiawah	12	Spring	2009	4/2/2009	Occupied	Protected
Kiawah	11	Fall	2009	9/30/2009	Abandoned	Exposed
Kiawah	12	Fall	2009	9/30/2009	Abandoned	Protected
Kiawah	13	Fall	2009	9/30/2009	Occupied	Protected
Kiawah	14	Fall	2009	9/30/2009	Occupied	Exposed
Kiawah	13	Spring	2010	4/8/2010	Abandoned	Protected
Kiawah	14	Spring	2010	4/8/2010	Abandoned	Exposed
Kiawah	15	Spring	2010	4/8/2010	Occupied	Exposed
Kiawah	16	Spring	2010	4/8/2010	Occupied	Exposed
Kiawah	16	Spring	2010	9/17/2010	Abandoned	Exposed
Kiawah	16	Spring	2010	4/13/2011	Abandoned	Exposed
Kiawah	15	Fall	2010	9/17/2010	Abandoned	Exposed
Kiawah	17	Fall	2010	9/17/2010	Occupied	Protected
Kiawah	18	Fall	2010	9/17/2010	Occupied	Protected
Kiawah	17	Spring	2011	4/13/2011	Abandoned	Protected
Kiawah	18	Spring	2011	4/13/2011	Abandoned	Protected
Kiawah	20	Spring	2011	4/13/2011	Occupied	Exposed

Appendix 2. Abundance of benthic species collected at Bird Key and Kiawah Island during Spring 2006. Abundance values represent the number of individuals per push core (0.0043 m² area). Higher taxa codes are P = polychaete, A = amphipod, M = mollusc, and O = other taxa.

SpeciesName	Season	Year	Higher Taxon	Bird Key		Kiawah	
				1	2	1	2
<i>Acanthohaustorius intermedius</i>	Spring	2006	A	0	0	5	0
Actiniaria	Spring	2006	O	0	1	0	0
<i>Aphelochaeta</i> sp.	Spring	2006	P	3	0	0	0
Aricidea sp.	Spring	2006	P	1	0	0	0
<i>Biffarius biformis</i>	Spring	2006	O	1	0	0	0
<i>Boonea impressa</i>	Spring	2006	M	3	0	0	0
<i>Capitella capitata</i>	Spring	2006	P	0	19	39	33
Capitellidae	Spring	2006	P	0	0	1	1
<i>Carinomella lactea</i>	Spring	2006	O	2	0	0	0
Cirratulidae	Spring	2006	P	2	0	2	1
Cirrophorus sp.	Spring	2006	P	0	0	1	0
<i>Cistenides gouldii</i>	Spring	2006	P	1	0	0	0
<i>Clymenella torquata</i>	Spring	2006	P	1	0	0	0
Copepoda	Spring	2006	O	3	1	0	0
<i>Corophium</i> sp.	Spring	2006	A	1	0	0	0
<i>Cyclaspis varians</i>	Spring	2006	O	1	0	0	0
Decapoda	Spring	2006	O	1	0	0	0
<i>Donax variabilis</i>	Spring	2006	M	1	0	0	0
Enchytraeidae	Spring	2006	O	0	1	0	0
<i>Eteone heteropoda</i>	Spring	2006	P	9	0	2	0
Gammaridea	Spring	2006	A	1	0	0	0
<i>Gemma gemma</i>	Spring	2006	M	2	0	10	0
<i>Geukensia demissa</i>	Spring	2006	M	0	0	1	0
<i>Glycera americana</i>	Spring	2006	P	2	0	0	0
<i>Glycinde nordmanni</i>	Spring	2006	P	1	0	0	0
<i>Goniada littorea</i>	Spring	2006	P	1	0	0	0
Haustoriidae	Spring	2006	A	1	0	0	0
<i>Heteromastus filiformis</i>	Spring	2006	P	1	0	36	38
<i>Ilyanassa obsoleta</i>	Spring	2006	M	0	0	1	0
<i>Laeonereis culveri</i>	Spring	2006	P	4	0	5	3
<i>Leitoscoloplos fragilis</i>	Spring	2006	P	0	1	2	0
<i>Lepidactylus dytiscus</i>	Spring	2006	A	0	11	0	32
<i>Magelona</i> sp.	Spring	2006	P	1	0	0	0
<i>Mediomastus ambiseta</i>	Spring	2006	P	2	0	0	0
<i>Mediomastus</i> sp.	Spring	2006	P	13	0	7	0
<i>Mercenaria mercenaria</i>	Spring	2006	M	1	0	0	0
<i>Mulinia lateralis</i>	Spring	2006	M	2	0	0	0
Nemertea	Spring	2006	O	0	0	0	1
<i>Nephtys picta</i>	Spring	2006	P	1	0	0	0

Appendix 2. Abundance of benthic species collected at Bird Key and Kiawah Island during Spring 2006. Abundance values represent the number of individuals per push core (0.0043 m² area). Higher taxa codes are P = polychaete, A = amphipod, M = mollusc, and O = other taxa.

SpeciesName	Season	Year	Higher Taxon	Bird Key		Kiawah	
				1	2	1	2
Nereididae	Spring	2006	P	8	1	0	0
<i>Nereis succinea</i>	Spring	2006	P	0	2	1	1
<i>Oxyurostylis smithi</i>	Spring	2006	O	0	1	0	0
<i>Paraonis fulgens</i>	Spring	2006	P	8	1	7	0
<i>Pinnixa</i> sp.	Spring	2006	O	1	0	0	0
<i>Polydora cornuta</i>	Spring	2006	P	1	0	0	0
<i>Pseudohaustorius caroliniensis</i>	Spring	2006	A	1	0	0	0
Spionidae	Spring	2006	P	3	2	3	0
<i>Spiophanes bombyx</i>	Spring	2006	P	3	0	0	0
<i>Streblospio benedicti</i>	Spring	2006	P	88	2	24	0
Tellinidae	Spring	2006	M	1	0	1	0
<i>Tharyx acutus</i>	Spring	2006	P	0	0	4	0

Appendix 2. Abundance of benthic species collected at Bird Key and Kiawah Island during Fall 2006. Abundance values represent the number of individuals per push core (0.0043 m² area). Higher taxa codes are P = polychaete, A = amphipod, M = mollusc, and O = other taxa.

SpeciesName	Season	Year	Higher Taxon	Bird Key				Kiawah			
				1	2	3	4	1	2	3	4
<i>Acanthohaustorius</i> sp.	Fall	2006	A	0	0	0	6	0	0	0	0
<i>Aricidea</i> sp.	Fall	2006	P	0	0	0	0	0	1	0	0
<i>Capitella capitata</i>	Fall	2006	P	2	2	34	19	41	35	46	103
Cirratulidae	Fall	2006	P	0	0	0	0	0	2	0	1
Copepoda	Fall	2006	O	0	0	0	1	0	0	0	0
Decapoda	Fall	2006	O	0	0	0	0	0	0	1	0
<i>Donax variabilis</i>	Fall	2006	M	1	0	0	0	0	0	0	0
<i>Eteone heteropoda</i>	Fall	2006	P	0	0	3	1	0	0	0	1
<i>Gemma gemma</i>	Fall	2006	M	0	0	0	0	0	0	0	1
<i>Heteromastus filiformis</i>	Fall	2006	P	1	0	1	4	14	89	7	50
<i>Ilyanassa obsoleta</i>	Fall	2006	M	0	0	0	0	0	1	0	0
<i>Laeonereis culveri</i>	Fall	2006	P	1	1	0	94	0	2	2	20
<i>Leitoscoloplos fragilis</i>	Fall	2006	P	1	0	0	2	0	0	0	0
<i>Lepidactylus dytiscus</i>	Fall	2006	A	14	0	0	3	17	0	1	0
<i>Lumbrineris</i> sp.	Fall	2006	P	1	0	0	0	0	0	0	0
<i>Mediomastus</i> sp.	Fall	2006	P	0	0	0	1	0	0	0	0
<i>Mercenaria mercenaria</i>	Fall	2006	M	1	0	0	0	0	0	0	0
Nemertea	Fall	2006	O	0	0	0	2	0	0	0	0
Nereididae	Fall	2006	P	2	1	8	19	0	0	0	4
<i>Nereis succinea</i>	Fall	2006	P	0	1	4	5	0	0	2	5
Paraonidae	Fall	2006	P	0	0	1	0	0	0	2	0
<i>Paraonis fulgens</i>	Fall	2006	P	8	7	0	892	6	0	113	5
<i>Polydora cornuta</i>	Fall	2006	P	0	0	1	0	0	0	1	0
Spionidae	Fall	2006	P	0	0	11	0	0	2	0	0
<i>Spiophanes bombyx</i>	Fall	2006	P	0	0	0	1	0	0	0	0
<i>Streblospio benedicti</i>	Fall	2006	P	0	1	68	1	0	0	32	21
<i>Tellina agilis</i>	Fall	2006	M	0	0	0	1	0	0	0	0
<i>Tharyx acutus</i>	Fall	2006	P	0	0	0	0	0	6	0	3
<i>Tubificoides brownae</i>	Fall	2006	O	0	0	0	1	0	0	0	0
<i>Uca</i> sp.	Fall	2006	O	0	0	0	0	0	1	1	0

Appendix 2. Abundance of benthic species collected at Bird Key and Kiawah Island during Spring 2007. Abundance values represent the number of individuals per push core (0.0043 m² area). Higher taxa codes are P = polychaete, A = amphipod, M = mollusc, and O = other taxa.

SpeciesName	Season	Year	Higher Taxon	Bird Key			Kiawah			
				3	4	5	2	3	4	5
<i>Abra aequalis</i>	Spring	2007	M	0	0	1	0	0	0	0
Actiniaria	Spring	2007	O	0	0	2	0	0	0	0
<i>Aphelochaeta</i> sp.	Spring	2007	P	10	0	26	0	0	0	0
<i>Capitella capitata</i>	Spring	2007	P	143	32	416	17	11	215	150
Capitellidae	Spring	2007	P	0	3	1	0	0	0	0
Cirratulidae	Spring	2007	P	1	1	16	0	2	1	0
<i>Drilonereis</i> sp.	Spring	2007	P	0	1	0	0	0	0	0
<i>Eteone heteropoda</i>	Spring	2007	P	24	3	37	0	4	1	0
Gastropoda	Spring	2007	M	0	0	0	0	0	1	0
<i>Gemma gemma</i>	Spring	2007	M	0	1	0	0	0	0	0
<i>Glycera americana</i>	Spring	2007	P	0	0	1	0	0	0	0
Haustoriidae	Spring	2007	A	2	0	0	0	0	0	0
<i>Heteromastus filiformis</i>	Spring	2007	P	1	3	0	6	2	19	0
<i>Ilyanassa obsoleta</i>	Spring	2007	M	0	0	0	0	0	1	0
<i>Laeonereis culveri</i>	Spring	2007	P	116	73	316	1	24	139	100
<i>Leitoscoloplos fragilis</i>	Spring	2007	P	0	2	3	0	4	0	0
<i>Lepidactylus dytiscus</i>	Spring	2007	A	0	4	0	0	0	0	0
<i>Macoma tenta</i>	Spring	2007	M	0	0	0	0	1	0	1
<i>Mediomastus ambiseta</i>	Spring	2007	P	1	0	5	0	6	1	0
<i>Mediomastus</i> sp.	Spring	2007	P	3	7	15	2	6	0	0
<i>Mercenaria mercenaria</i>	Spring	2007	M	1	0	1	0	1	1	0
Nemertea	Spring	2007	O	1	0	4	0	1	0	1
Nereididae	Spring	2007	P	1	0	0	0	0	1	0
<i>Nereis succinea</i>	Spring	2007	P	106	1	66	0	34	25	39
Oligochaeta	Spring	2007	O	0	0	0	0	1	0	1
<i>Paraonis fulgens</i>	Spring	2007	P	0	870	11	18	2	7	4
Pelecypoda	Spring	2007	M	0	0	0	0	0	5	0
<i>Pinnixa sayana</i>	Spring	2007	O	0	1	0	0	0	0	0
<i>Polydora cornuta</i>	Spring	2007	P	4	5	1	0	6	2	12
<i>Polydora</i> sp.	Spring	2007	P	1	0	0	0	0	0	0
Spionidae	Spring	2007	P	1	0	0	0	0	0	0
<i>Spiophanes bombyx</i>	Spring	2007	P	0	3	1	0	0	0	0
<i>Streblospio benedicti</i>	Spring	2007	P	325	2	131	0	322	35	306
Terebellidae	Spring	2007	P	0	8	0	0	0	0	0
<i>Tharyx acutus</i>	Spring	2007	P	0	0	19	0	0	0	3

Appendix 2. Abundance of benthic species collected at Bird Key and Kiawah Island during Fall 2007. Abundance values represent the number of individuals per push core (0.0043 m² area). Higher taxa codes are P = polychaete, A = amphipod, M = mollusc, and O = other taxa.

SpeciesName	Season	Year	Higher Taxon	Bird Key				Kiawah			
				3	5	6	7	4	5	6	7
<i>Acanthohaustorius millsii</i>	Fall	2007	A	0	0	0	0	0	0	15	6
<i>Biffarius biformis</i>	Fall	2007	O	0	0	0	0	0	0	0	1
<i>Capitella capitata</i>	Fall	2007	P	108	170	212	233	0	82	4	8
Cirratulidae	Fall	2007	P	27	19	1	6	0	0	0	0
Copepoda	Fall	2007	O	0	1	0	0	0	0	0	0
Decapoda	Fall	2007	O	0	1	0	1	0	0	0	1
Donax sp.	Fall	2007	M	0	0	0	0	0	1	0	0
<i>Donax variabilis</i>	Fall	2007	M	0	0	0	1	0	0	0	0
<i>Drilonereis</i> sp.	Fall	2007	P	0	0	0	1	0	0	0	0
<i>Eteone heteropoda</i>	Fall	2007	P	0	0	1	1	0	0	0	0
<i>Glycymeris americana</i>	Fall	2007	M	0	0	1	0	0	0	0	0
<i>Heteromastus filiformis</i>	Fall	2007	P	13	21	4	6	0	19	3	23
Isopoda	Fall	2007	O	0	0	1	0	0	0	0	0
<i>Laeonereis culveri</i>	Fall	2007	P	100	197	188	265	0	42	1	9
<i>Lepidactylus dytiscus</i>	Fall	2007	A	0	0	10	2	0	0	0	0
<i>Mediomastus ambiseta</i>	Fall	2007	P	0	0	0	1	0	0	0	0
<i>Mediomastus</i> sp.	Fall	2007	P	0	0	0	1	0	0	0	0
<i>Mercenaria mercenaria</i>	Fall	2007	M	1	1	4	0	0	0	0	0
Nemertea	Fall	2007	O	0	0	1	1	0	0	0	0
<i>Neohaustorius schmitzi</i>	Fall	2007	A	0	0	0	0	38	0	0	1
<i>Nereis succinea</i>	Fall	2007	P	2	1	6	5	0	6	0	0
<i>Paraonis fulgens</i>	Fall	2007	P	0	0	94	190	0	13	217	118
<i>Parvilucina multilineata</i>	Fall	2007	M	0	0	0	1	0	0	0	0
Pelecypoda	Fall	2007	M	0	0	1	0	0	0	0	0
<i>Rhepoxynius hudsoni</i>	Fall	2007	A	0	0	0	0	0	0	3	0
<i>Sphenia antillensis</i>	Fall	2007	M	0	1	0	0	0	0	0	0
Spionidae	Fall	2007	P	5	5	0	0	0	0	0	1
<i>Spiophanes bombyx</i>	Fall	2007	P	0	0	0	1	0	0	0	0
<i>Spiophanes</i> sp.	Fall	2007	P	0	0	0	1	0	0	0	0
<i>Streblospio benedicti</i>	Fall	2007	P	33	126	1	1	1	14	0	0
Terebellidae	Fall	2007	P	0	0	1	1	0	0	0	0
<i>Tharyx acutus</i>	Fall	2007	P	8	29	0	0	0	0	0	0
<i>Tubificoides wasselli</i>	Fall	2007	O	0	0	0	0	0	0	2	0
<i>Uca</i> sp.	Fall	2007	O	0	0	1	0	0	0	0	0

Appendix 2. Abundance of benthic species collected at Bird Key and Kiawah Island during Spring 2008. Abundance values represent the number of individuals per push core (0.0043 m² area). Higher taxa codes are P = polychaete, A = amphipod, M = mollusc, and O = other taxa.

SpeciesName	Season	Year	Higher Taxon	Bird Key				Kiawah		
				6	7	8	9	7	8	9
<i>Acanthohaustorius millsii</i>	Spring	2008	A	0	0	0	0	0	0	8
<i>Acteocina canaliculata</i>	Spring	2008	M	0	0	0	0	0	0	1
Arachnida	Spring	2008	O	0	1	0	0	0	0	0
<i>Bhawania heteroseta</i>	Spring	2008	P	0	0	0	0	0	0	1
<i>Capitella capitata</i>	Spring	2008	P	54	0	86	131	1	8	0
Capitellidae	Spring	2008	P	0	0	0	2	0	0	0
<i>Carinomella lactea</i>	Spring	2008	O	0	0	0	0	0	0	2
Cirratulidae	Spring	2008	P	1	0	24	3	0	3	3
<i>Corbula contracta</i>	Spring	2008	M	0	0	0	1	0	0	0
<i>Eteone heteropoda</i>	Spring	2008	P	0	0	2	0	0	0	6
Gastropoda	Spring	2008	M	0	0	0	0	0	1	0
<i>Gemma gemma</i>	Spring	2008	M	0	0	0	0	0	0	1
<i>Glycera americana</i>	Spring	2008	P	0	0	0	0	0	3	2
<i>Glycymeris americana</i>	Spring	2008	M	0	0	2	0	0	0	0
Haustoriidae	Spring	2008	A	0	0	0	0	0	1	1
<i>Heteromastus filiformis</i>	Spring	2008	P	3	0	1	3	3	7	0
<i>Ilyanassa obsoleta</i>	Spring	2008	M	0	0	0	0	0	1	0
<i>Laeonereis culveri</i>	Spring	2008	P	7	0	53	117	1	4	15
<i>Leitoscoloplos fragilis</i>	Spring	2008	P	0	0	3	1	0	0	1
<i>Lepidactylus dytiscus</i>	Spring	2008	A	4	0	0	42	21	3	0
Lumbrineridae	Spring	2008	P	0	0	0	0	0	0	1
<i>Mediomastus ambiseta</i>	Spring	2008	P	0	0	12	0	0	0	177
<i>Mediomastus</i> sp.	Spring	2008	P	0	0	15	1	1	3	3
<i>Mercenaria mercenaria</i>	Spring	2008	M	4	0	2	2	0	0	0
<i>Monticellina</i> sp.	Spring	2008	P	0	0	0	0	0	0	13
Nemertea	Spring	2008	O	0	0	0	1	0	0	2
<i>Neohaustorius schmitzi</i>	Spring	2008	A	0	26	0	0	2	0	23
<i>Nereis succinea</i>	Spring	2008	P	1	0	6	1	0	1	0
<i>Oxyurostylis smithi</i>	Spring	2008	O	0	0	0	0	0	3	8
<i>Paraonis fulgens</i>	Spring	2008	P	297	1	1	379	44	156	123
<i>Polydora cornuta</i>	Spring	2008	P	0	0	3	2	0	0	0
<i>Protohaustorius deichmannae</i>	Spring	2008	A	0	0	0	0	0	1	0
<i>Sayella</i> sp.	Spring	2008	M	0	0	3	0	0	0	0
<i>Scolelepis</i> sp.	Spring	2008	P	0	0	0	0	0	2	0
<i>Scolelepis texana</i>	Spring	2008	P	0	0	0	0	0	0	1
<i>Scoletoma</i> sp.	Spring	2008	P	0	0	0	0	0	0	1
Spionidae	Spring	2008	P	0	0	0	0	0	1	0
<i>Spiophanes bombyx</i>	Spring	2008	P	0	0	0	1	0	6	7
<i>Stenothoe</i> sp.	Spring	2008	A	0	0	0	0	0	0	1

Appendix 2. Abundance of benthic species collected at Bird Key and Kiawah Island during Spring 2008. Abundance values represent the number of individuals per push core (0.0043 m² area). Higher taxa codes are P = polychaete, A = amphipod, M = mollusc, and O = other taxa.

SpeciesName	Season	Year	Higher Taxon	Bird Key				Kiawah		
				6	7	8	9	7	8	9
<i>Streblospio benedicti</i>	Spring	2008	P	0	0	67	2	3	18	28
<i>Tellina agilis</i>	Spring	2008	M	1	0	2	0	0	5	5
Tellinidae	Spring	2008	M	0	0	2	0	0	0	0
<i>Tharyx acutus</i>	Spring	2008	P	0	2	630	0	0	0	4
Tubificidae	Spring	2008	O	0	0	3	0	0	0	0
<i>Tubificoides brownae</i>	Spring	2008	O	0	0	0	0	0	0	12

Appendix 2. Abundance of benthic species collected at Bird Key and Kiawah Island during Fall 2008. Abundance values represent the number of individuals per push core (0.0043 m² area). Higher taxa codes are P = polychaete, A = amphipod, M = mollusc, and O = other taxa.

SpeciesName	Season	Year	Higher Taxon	Bird Key				Kiawah			
				8	9	10	11	8	9	10	11
<i>Acanthohaustorius intermedius</i>	Fall	2008	A	0	1	0	0	0	0	0	0
<i>Acanthohaustorius</i> sp.	Fall	2008	A	0	0	0	0	46	0	3	0
<i>Aligena elevata</i>	Fall	2008	M	0	0	0	0	0	0	1	0
<i>Capitella capitata</i>	Fall	2008	P	6	15	8	2	0	9	3	0
<i>Carinomella lactea</i>	Fall	2008	O	0	0	0	0	0	1	0	0
<i>Chiridotea coeca</i>	Fall	2008	O	0	0	0	0	1	0	0	3
Cirratulidae	Fall	2008	P	5	0	0	5	0	0	0	0
Decapoda	Fall	2008	O	0	0	0	1	1	0	0	0
<i>Donax variabilis</i>	Fall	2008	M	0	0	0	0	0	0	1	116
<i>Gemma gemma</i>	Fall	2008	M	0	0	0	0	0	1	0	0
<i>Glycymeris americana</i>	Fall	2008	M	0	0	0	1	0	0	0	0
Goniadidae	Fall	2008	P	0	0	0	1	0	0	0	0
Haustoriidae	Fall	2008	A	0	0	0	0	0	0	2	0
<i>Heteromastus filiformis</i>	Fall	2008	P	5	3	0	3	3	9	4	0
<i>Ilyanassa obsoleta</i>	Fall	2008	M	0	0	0	0	0	2	0	0
<i>Laeonereis culveri</i>	Fall	2008	P	6	91	34	6	1	2	3	1
<i>Leitoscoloplos fragilis</i>	Fall	2008	P	0	0	1	0	0	0	0	0
<i>Lepidactylus dytiscus</i>	Fall	2008	A	0	2	4	0	47	0	3	2
<i>Listriella clymenellae</i>	Fall	2008	A	1	0	0	0	0	0	0	0
<i>Mediomastus ambiseta</i>	Fall	2008	P	0	0	0	2	0	0	0	0
<i>Mediomastus</i> sp.	Fall	2008	P	0	0	0	0	0	16	0	0
<i>Mercenaria mercenaria</i>	Fall	2008	M	1	3	0	0	0	0	0	0
<i>Mulinia lateralis</i>	Fall	2008	M	0	0	0	0	1	0	0	0
Nemertea	Fall	2008	O	0	0	0	0	1	0	1	0
<i>Neohaustorius schmitzi</i>	Fall	2008	A	0	0	0	0	0	0	0	160
<i>Nereis succinea</i>	Fall	2008	P	1	3	0	0	0	1	0	0
Oligochaeta	Fall	2008	O	0	0	0	0	0	1	0	0
Orbiniidae	Fall	2008	P	0	2	1	0	0	0	0	0
<i>Paraonis fulgens</i>	Fall	2008	P	0	223	4	30	180	8	248	0
<i>Paraprionospio pinnata</i>	Fall	2008	P	0	0	0	0	0	1	0	0
Pelecypoda	Fall	2008	M	0	0	0	1	1	0	0	0
<i>Protohaustorius deichmannae</i>	Fall	2008	A	0	0	0	0	2	0	1	0
<i>Pseudohaustorius caroliniensis</i>	Fall	2008	A	1	0	0	0	0	0	0	0
<i>Scoletoma tenuis</i>	Fall	2008	P	0	0	0	0	0	0	2	0
<i>Streblospio benedicti</i>	Fall	2008	P	101	0	2	53	0	73	0	0
<i>Tharyx acutus</i>	Fall	2008	P	4	0	0	3	0	7	0	0
<i>Tubificoides brownae</i>	Fall	2008	O	0	0	0	0	0	14	0	0

Appendix 2. Abundance of benthic species collected at Bird Key and Kiawah Island during Spring 2009. Abundance values represent the number of individuals per push core (0.0043 m² area). Higher taxa codes are P = polychaete, A = amphipod, M = mollusc, and O = other taxa.

SpeciesName	Season	Year	Higher Taxon	Bird Key				Kiawah			
				9	10	11	12	8	10	11	12
<i>Acanthohaustorius</i> sp.	Spring	2009	A	0	1	0	0	11	0	0	0
<i>Acteocina canaliculata</i>	Spring	2009	M	0	0	1	0	0	0	0	0
<i>Ampelisca</i> sp.	Spring	2009	A	0	0	1	0	0	0	0	0
<i>Capitella capitata</i>	Spring	2009	P	1	13	1	8	8	0	1	4
Capitellidae	Spring	2009	P	0	0	2	0	1	0	0	0
<i>Chiridotea coeca</i>	Spring	2009	O	0	0	0	0	1	0	0	0
Cirratulidae	Spring	2009	P	0	13	2	0	0	0	0	0
<i>Cochliolepis parasitica</i>	Spring	2009	M	1	0	0	0	0	0	0	0
Copepoda	Spring	2009	O	0	0	2	0	0	0	0	0
<i>Donax variabilis</i>	Spring	2009	M	0	0	0	0	0	0	13	0
<i>Eteone heteropoda</i>	Spring	2009	P	0	0	0	0	0	0	0	4
<i>Eteone lactea</i>	Spring	2009	P	0	0	1	0	0	0	0	0
Gastropoda	Spring	2009	M	0	0	1	0	0	0	0	0
<i>Gemma gemma</i>	Spring	2009	M	0	1	0	0	0	0	0	1
Haustoriidae	Spring	2009	A	0	2	0	0	5	0	2	0
<i>Haustorius canadensis</i>	Spring	2009	A	0	0	0	0	0	0	7	0
<i>Heteromastus filiformis</i>	Spring	2009	P	0	1	0	0	1	0	0	2
<i>Ilyanassa obsoleta</i>	Spring	2009	M	0	0	0	0	0	0	0	1
<i>Laeonereis culveri</i>	Spring	2009	P	0	59	1	0	0	0	0	0
<i>Leitoscoloplos fragilis</i>	Spring	2009	P	1	2	69	11	0	0	0	0
<i>Leitoscoloplos</i> sp.	Spring	2009	P	0	1	0	0	0	0	0	0
<i>Lepidactylus dytiscus</i>	Spring	2009	A	93	3	49	31	7	0	0	0
<i>Mediomastus ambiseta</i>	Spring	2009	P	0	2	2	0	0	0	0	0
<i>Mediomastus</i> sp.	Spring	2009	P	0	10	3	1	0	0	0	2
<i>Mercenaria mercenaria</i>	Spring	2009	M	0	0	1	0	0	0	0	0
Nemertea	Spring	2009	O	1	8	0	0	0	0	0	0
<i>Neohaustorius schmitzi</i>	Spring	2009	A	7	0	0	0	55	1	96	1
<i>Nephtys picta</i>	Spring	2009	P	0	0	0	0	1	0	0	0
<i>Nereis succinea</i>	Spring	2009	P	0	20	0	1	0	0	0	5
Opheliidae	Spring	2009	P	0	1	0	0	0	0	0	0
<i>Paraonis fulgens</i>	Spring	2009	P	122	69	56	4	89	2	0	1
Pelecypoda	Spring	2009	M	0	0	1	0	0	0	0	0
<i>Pinnixa</i> sp.	Spring	2009	O	0	1	0	0	0	0	0	1
<i>Polydora cornuta</i>	Spring	2009	P	0	16	0	0	0	0	0	1
<i>Protohaustorius deichmannae</i>	Spring	2009	A	0	1	0	0	0	0	3	0
<i>Protohaustorius wigleyi</i>	Spring	2009	A	2	0	0	0	0	0	0	0
<i>Pseudohaustorius caroliniensis</i>	Spring	2009	A	0	0	0	0	0	0	0	11
<i>Scoletoma tenuis</i>	Spring	2009	P	1	0	0	0	0	0	0	0
<i>Spiophanes bombyx</i>	Spring	2009	P	0	6	0	0	1	0	0	0

Appendix 2. Abundance of benthic species collected at Bird Key and Kiawah Island during Spring 2009. Abundance values represent the number of individuals per push core (0.0043 m² area). Higher taxa codes are P = polychaete, A = amphipod, M = mollusc, and O = other taxa.

SpeciesName	Season	Year	Higher Taxon	Bird Key				Kiawah			
				9	10	11	12	8	10	11	12
<i>Streblospio benedicti</i>	Spring	2009	P	0	25	10	0	1	0	0	120
<i>Tagelus divisus</i>	Spring	2009	M	0	2	0	0	0	0	0	0
<i>Tellina agilis</i>	Spring	2009	M	0	0	4	0	0	0	0	0
Tellinidae	Spring	2009	M	0	16	2	0	0	0	0	11
<i>Tharyx acutus</i>	Spring	2009	P	0	11	0	0	0	0	0	2

Appendix 2. Abundance of benthic species collected at Bird Key and Kiawah Island during Fall 2009. Abundance values represent the number of individuals per push core (0.0043 m² area). Higher taxa codes are P = polychaete, A = amphipod, M = mollusc, and O = other taxa.

SpeciesName	Season	Year	Higher Taxon	Bird Key				Kiawah			
				9	10	11	12	11	12	13	14
<i>Acanthohaustorius intermedius</i>	Fall	2009	A	0	0	0	0	0	2	0	0
<i>Acanthohaustorius</i> sp.	Fall	2009	A	0	0	0	0	0	1	18	0
<i>Ampelisca verrilli</i>	Fall	2009	A	0	0	0	0	0	0	1	0
<i>Anadara transversa</i>	Fall	2009	M	0	0	0	0	0	1	0	0
<i>Aricidea</i> sp.	Fall	2009	P	0	9	0	0	0	0	0	0
<i>Biffarius biformis</i>	Fall	2009	O	0	2	0	0	0	0	0	0
<i>Capitella capitata</i>	Fall	2009	P	0	5	20	0	0	1	69	0
Capitellidae	Fall	2009	P	0	0	0	0	0	0	1	0
<i>Carinomella lactea</i>	Fall	2009	O	0	1	0	0	0	0	0	0
<i>Chiridotea coeca</i>	Fall	2009	O	0	0	0	0	0	0	0	1
Copepoda	Fall	2009	O	0	0	0	0	0	0	0	2
Cumacea	Fall	2009	O	0	0	0	0	0	0	0	1
<i>Cyclaspis varians</i>	Fall	2009	O	0	0	0	0	0	0	1	0
Decapoda	Fall	2009	O	0	0	0	0	0	0	0	1
<i>Donax variabilis</i>	Fall	2009	M	0	0	0	41	0	0	0	112
<i>Drilonereis</i> sp.	Fall	2009	P	0	0	0	0	0	1	0	0
<i>Gemma gemma</i>	Fall	2009	M	0	0	2	0	0	0	0	0
<i>Glycera americana</i>	Fall	2009	P	0	1	0	0	0	0	0	0
<i>Glycinde solitaria</i>	Fall	2009	P	0	3	0	0	0	0	1	0
Goniadidae	Fall	2009	P	0	1	0	0	0	0	0	0
Haustoriidae	Fall	2009	A	0	0	1	0	0	0	0	0
<i>Haustorius canadensis</i>	Fall	2009	A	3	0	0	0	0	0	0	0
<i>Heteromastus filiformis</i>	Fall	2009	P	0	0	3	0	0	3	0	0
<i>Ilyanassa obsoleta</i>	Fall	2009	M	0	0	0	0	0	3	6	0
<i>Laeonereis culveri</i>	Fall	2009	P	0	5	1	0	0	20	78	2
<i>Leitoscoloplos fragilis</i>	Fall	2009	P	0	0	0	0	1	1	1	1
<i>Lepidactylus dytiscus</i>	Fall	2009	A	0	0	0	0	0	0	8	0
<i>Lumbrineris</i> sp.	Fall	2009	P	0	0	0	0	0	0	1	0
<i>Mediomastus</i> sp.	Fall	2009	P	0	21	0	0	0	1	6	0
<i>Mercenaria mercenaria</i>	Fall	2009	M	0	0	1	0	0	0	0	0
<i>Metharpinia floridana</i>	Fall	2009	A	0	0	0	0	0	1	0	0
<i>Microprotopus raneyi</i>	Fall	2009	A	0	0	0	0	0	0	0	1
<i>Mulinia lateralis</i>	Fall	2009	M	0	2	0	0	0	3	11	5
Nemertea	Fall	2009	O	0	2	0	0	0	0	0	0
<i>Neohaustorius schmitzi</i>	Fall	2009	A	31	0	0	63	13	1	0	15
Nereididae	Fall	2009	P	0	1	0	0	0	0	0	0
<i>Parahaustorius</i> sp.	Fall	2009	A	0	0	12	9	0	0	0	7
<i>Paraonis fulgens</i>	Fall	2009	P	0	8	1	3	0	102	113	10
Pelecypoda	Fall	2009	M	0	1	0	0	0	2	0	0

Appendix 2. Abundance of benthic species collected at Bird Key and Kiawah Island during Fall 2009. Abundance values represent the number of individuals per push core (0.0043 m² area). Higher taxa codes are P = polychaete, A = amphipod, M = mollusc, and O = other taxa.

SpeciesName	Season	Year	Higher Taxon	Bird Key				Kiawah			
				9	10	11	12	11	12	13	14
<i>Pinnixa</i> sp.	Fall	2009	O	0	2	0	0	0	0	3	0
Platyhelminthes	Fall	2009	O	0	2	0	0	0	0	0	0
<i>Scolelepis</i> sp.	Fall	2009	P	0	3	0	0	0	0	0	0
<i>Scoletoma tenuis</i>	Fall	2009	P	0	0	0	0	0	2	0	0
<i>Scoloplos</i> sp.	Fall	2009	P	0	1	0	0	0	0	0	0
Spionidae	Fall	2009	P	0	1	0	0	0	0	0	0
<i>Streblospio benedicti</i>	Fall	2009	P	0	31	26	0	0	14	3	0
Tellinidae	Fall	2009	M	0	8	0	0	0	1	14	0
<i>Tharyx acutus</i>	Fall	2009	P	0	47	0	0	0	0	0	0
<i>Tiron triocellatus</i>	Fall	2009	A	0	0	0	0	0	1	0	0
<i>Uca</i> sp.	Fall	2009	O	0	0	7	0	0	0	0	0

Appendix 2. Abundance of benthic species collected at Bird Key and Kiawah Island during Spring 2010. Abundance values represent the number of individuals per push core (0.0043 m² area). Higher taxa codes are P = polychaete, A = amphipod, M = mollusc, and O = other taxa.

SpeciesName	Season	Year	Higher Taxon	Bird Key			Kiawah			
				11	13	14	13	14	15	16
Ampharetidae	Spring	2010	P	0	0	0	1	0	0	0
<i>Amphiodia</i> sp.	Spring	2010	O	0	0	0	0	1	0	0
Amphipoda	Spring	2010	A	0	0	0	0	0	1	0
<i>Bathyporeia</i> sp.	Spring	2010	A	0	0	2	0	0	0	0
<i>Capitella capitata</i>	Spring	2010	P	2	0	3	0	0	0	0
<i>Caulleriella</i> sp.	Spring	2010	P	0	0	0	0	1	0	0
<i>Chiridotea coeca</i>	Spring	2010	O	0	0	0	2	0	0	0
<i>Chiridotea stenops</i>	Spring	2010	O	0	1	0	0	0	0	0
Cirratulidae	Spring	2010	P	2	0	0	0	1	0	1
<i>Crassinella martinicensis</i>	Spring	2010	M	0	1	0	0	0	0	0
<i>Donax variabilis</i>	Spring	2010	M	0	35	1	8	0	97	12
<i>Eteone heteropoda</i>	Spring	2010	P	4	0	0	0	0	0	0
<i>Eudevenopus honduranus</i>	Spring	2010	A	0	0	1	0	0	0	0
<i>Glycera americana</i>	Spring	2010	P	0	0	1	0	0	0	0
Haustoriidae	Spring	2010	A	0	4	0	1	0	0	0
<i>Haustorius canadensis</i>	Spring	2010	A	0	0	0	7	0	3	8
<i>Haustorius</i> sp.	Spring	2010	A	0	1	0	0	0	0	0
<i>Laeonereis culveri</i>	Spring	2010	P	1	0	0	0	0	0	0
<i>Leitoscoloplos fragilis</i>	Spring	2010	P	0	0	23	0	0	0	0
<i>Lepidactylus dytiscus</i>	Spring	2010	A	0	1	5	3	0	35	0
<i>Mediomastus ambiseta</i>	Spring	2010	P	10	0	6	0	0	0	0
<i>Mediomastus</i> sp.	Spring	2010	P	41	0	4	0	0	0	0
<i>Melanella intermedia</i>	Spring	2010	M	0	0	0	1	0	0	0
Nemertea	Spring	2010	O	0	0	2	0	0	0	0
<i>Neohaustorius schmitzi</i>	Spring	2010	A	0	31	0	83	3	27	216
<i>Nereis succinea</i>	Spring	2010	P	15	0	8	0	0	0	0
Orbiniidae	Spring	2010	P	0	0	2	0	0	0	0
<i>Pagurus longicarpus</i>	Spring	2010	O	0	0	0	12	0	0	0
<i>Parahaustorius longimerus</i>	Spring	2010	A	0	54	0	0	0	45	0
<i>Parahaustorius</i> sp.	Spring	2010	A	0	0	7	0	0	3	0
<i>Paraonis fulgens</i>	Spring	2010	P	0	7	19	3	0	7	15
Pelecypoda	Spring	2010	M	1	0	3	1	0	0	1
<i>Protohaustorius wigleyi</i>	Spring	2010	A	0	0	3	0	0	0	0
<i>Sabellaria gracilis</i>	Spring	2010	P	0	0	0	3	0	0	0
<i>Scolelepis</i> sp.	Spring	2010	P	0	0	0	0	0	1	0
<i>Scolelepis squamata</i>	Spring	2010	P	0	0	0	0	0	1	0
<i>Scoletoma tenuis</i>	Spring	2010	P	0	0	0	0	0	0	1
<i>Scoloplos rubra</i>	Spring	2010	P	0	0	0	0	0	0	3
<i>Streblospio benedicti</i>	Spring	2010	P	176	0	60	0	0	0	0

Appendix 2. Abundance of benthic species collected at Bird Key and Kiawah Island during Spring 2010. Abundance values represent the number of individuals per push core (0.0043 m² area). Higher taxa codes are P = polychaete, A = amphipod, M = mollusc, and O = other taxa.

SpeciesName	Season	Year	Higher Taxon	Bird Key			Kiawah			
				11	13	14	13	14	15	16
Tellinidae	Spring	2010	M	11	0	3	5	0	19	1
<i>Tharyx acutus</i>	Spring	2010	P	2	0	0	0	0	0	0

Appendix 2. Abundance of benthic species collected at Bird Key and Kiawah Island during Fall 2010. Abundance values represent the number of individuals per push core (0.0043 m² area). Higher taxa codes are P = polychaete, A = amphipod, M = mollusc, and O = other taxa.

SpeciesName	Season	Year	Higher Taxon	Bird Key				Kiawah			
				13	14	15	16	15	16	17	18
<i>Acanthohaustorius</i> sp.	Fall	2010	A	12	4	112	0	2	8	8	0
<i>Amastigos caperatus</i>	Fall	2010	P	0	0	0	0	0	0	0	1
Amphipoda	Fall	2010	A	0	0	0	1	0	0	0	0
Capitellidae	Fall	2010	P	0	0	0	0	0	0	0	2
Cirratulidae	Fall	2010	P	0	0	0	0	0	0	0	1
Cumacea	Fall	2010	O	0	0	0	1	0	0	0	0
Decapoda	Fall	2010	O	0	0	0	0	0	0	0	1
<i>Donax variabilis</i>	Fall	2010	M	0	0	5	97	130	91	3	1
<i>Eteone heteropoda</i>	Fall	2010	P	0	0	0	0	0	0	0	6
<i>Gemma gemma</i>	Fall	2010	M	0	6	0	0	0	0	0	0
Haustoriidae	Fall	2010	A	0	0	1	0	1	0	0	1
<i>Heteromastus filiformis</i>	Fall	2010	P	0	1	0	0	0	0	0	1
<i>Laeonereis culveri</i>	Fall	2010	P	0	1	0	0	1	2	42	87
<i>Leitoscoloplos fragilis</i>	Fall	2010	P	1	1	0	0	0	0	10	2
<i>Leitoscoloplos</i> sp.	Fall	2010	P	0	0	1	0	0	0	0	0
<i>Lepidactylus dytiscus</i>	Fall	2010	A	0	0	5	12	0	10	41	0
<i>Mediomastus ambiseta</i>	Fall	2010	P	0	0	0	0	0	0	0	2
<i>Mediomastus</i> sp.	Fall	2010	P	0	0	0	0	0	0	0	6
<i>Mercenaria mercenaria</i>	Fall	2010	M	0	1	0	0	0	0	0	0
Nemertea	Fall	2010	O	0	0	2	1	0	0	0	1
<i>Neohaustorius schmitzi</i>	Fall	2010	A	127	1	3	178	15	146	1	3
Nereididae	Fall	2010	P	0	0	0	0	1	0	0	0
<i>Nereis succinea</i>	Fall	2010	P	0	2	0	0	0	0	2	5
<i>Ogyrides alphaerostris</i>	Fall	2010	O	0	0	2	0	0	0	1	0
<i>Parahaustorius longimerus</i>	Fall	2010	A	0	0	5	0	6	0	0	0
<i>Paraonis fulgens</i>	Fall	2010	P	54	4	21	9	8	4	95	212
Pelecypoda	Fall	2010	M	0	0	0	1	0	0	2	3
<i>Protohaustorius bousfieldi</i>	Fall	2010	A	0	0	0	0	2	0	0	0
<i>Protohaustorius deichmannae</i>	Fall	2010	A	0	0	0	1	0	0	0	0
<i>Protohaustorius</i> sp.	Fall	2010	A	0	0	15	0	0	0	0	0
<i>Scolelepis bousfieldi</i>	Fall	2010	P	0	0	0	0	2	0	0	0
<i>Scolelepis</i> sp.	Fall	2010	P	0	0	0	0	0	0	0	1
<i>Scoletoma tenuis</i>	Fall	2010	P	0	0	0	0	0	0	0	2
<i>Scoloplos</i> sp.	Fall	2010	P	0	0	0	0	0	0	1	1
Spionidae	Fall	2010	P	0	0	0	0	1	0	0	0
<i>Streblospio benedicti</i>	Fall	2010	P	0	10	1	0	0	0	0	58
Tellinidae	Fall	2010	M	2	5	3	14	0	22	0	2
Tubificidae	Fall	2010	O	0	1	0	0	0	0	0	0

Appendix 2. Abundance of benthic species collected at Bird Key and Kiawah Island during Spring 2011. Abundance values represent the number of individuals per push core (0.0043 m² area). Higher taxa codes are P = polychaete, A = amphipod, M = mollusc, and O = other taxa.

SpeciesName	Season	Year	Higher Taxon	Bird Key			Kiawah		
				15	16	17	17	18	20
<i>Aglaophamus verrilli</i>	Spring	2011	P	0	1	0	0	0	0
<i>Amastigos caperatus</i>	Spring	2011	P	0	1	0	0	0	0
<i>Capitella capitata</i>	Spring	2011	P	0	0	0	3	27	0
Capitellidae	Spring	2011	P	1	0	0	4	0	0
<i>Cirriiformi a sp.</i>	Spring	2011	P	0	1	0	0	0	0
<i>Donax variabilis</i>	Spring	2011	M	0	0	0	0	0	7
<i>Edotia montosa</i>	Spring	2011	O	0	1	0	0	0	0
<i>Eteone heteropoda</i>	Spring	2011	P	0	4	2	0	0	0
<i>Gammarus mucronatus</i>	Spring	2011	A	1	0	0	0	0	0
<i>Glycera americana</i>	Spring	2011	P	0	2	0	0	0	0
<i>Haustorius canadensis</i>	Spring	2011	A	0	0	0	0	0	1
<i>Heteromastus filiformis</i>	Spring	2011	P	0	2	0	6	8	0
<i>Laeonereis culveri</i>	Spring	2011	P	0	0	0	26	9	0
<i>Lepidactylus dytiscus</i>	Spring	2011	A	1	1	14	2	38	7
<i>Mediomastus sp.</i>	Spring	2011	P	0	2	1	4	7	0
<i>Mulinia lateralis</i>	Spring	2011	M	0	2	0	0	0	0
Nemertea	Spring	2011	O	1	3	0	3	0	1
<i>Neohaustorius schmitzi</i>	Spring	2011	A	11	1	239	5	74	57
<i>Nereis succinea</i>	Spring	2011	P	0	0	0	4	0	0
<i>Oxyurostylis smithi</i>	Spring	2011	O	0	0	1	0	0	0
<i>Parahaustorius sp.</i>	Spring	2011	A	0	0	1	0	0	7
<i>Paraonis fulgens</i>	Spring	2011	P	3	141	53	2	11	2
<i>Pettiboneia sp.</i>	Spring	2011	P	0	2	0	0	0	0
<i>Polydora cornuta</i>	Spring	2011	P	0	0	0	2	1	0
<i>Polydora socialis</i>	Spring	2011	P	0	0	0	1	0	0
<i>Protohaustorius wigleyi</i>	Spring	2011	A	0	0	0	0	0	11
<i>Spiophanes bombyx</i>	Spring	2011	P	0	2	0	0	0	0
<i>Streblospio benedicti</i>	Spring	2011	P	0	4	2	17	7	0
<i>Synchelidium americanum</i>	Spring	2011	A	0	0	0	0	0	1
Tellinidae	Spring	2011	M	0	1	0	0	0	0