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Modification of Trophic Links between an Omnivore and Macroinfaunal Prey from Sandy Beaches of differing Physical Regimes

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Modification of Trophic Links between an Omnivore and Macroinfaunal Prey from
Sandy Beaches of differing Physical Regimes

by

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A thesis submitted in partial fulfillment
of the requirements for the degree of
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Abstract

Sandy beach ecosystems have been studied worldwide; however, ecological data are sparse for the extensive barrier islands of Florida. Accordingly, I investigated the feeding patterns of the ghost crab (*Ocypode quadrata*), a dominant omnivore inhabiting beaches along the Floridian coast. Density data was collected for ghost crabs and swash macroinfaunal prey. In addition, I utilized stable isotopes in conjunction with the mixing models IsoSource and SIAR to characterize diets of ghost crabs across three barrier islands in spring and summer 2011. Results showed that ghost crabs at Cayo Costa feed primarily on swash macroinfauna, while those from Anclote Key shifted their diet to one comprised primarily of semi-terrestrial amphipods. However, at Honeymoon Island, ghost crab isotopic signatures were best explained by a mixed diet of both macroinfauna and wrack-associated prey. The unique consumption of wrack fauna at Anclote Key co-occurs with comparatively low infaunal densities and biomass, and modified ghost crab behavior due to trait-mediated effects. My results are novel because they suggest that wrack-associated fauna may be an important food source for ghost crabs in certain beach regimes.

Introduction

Sandy beach ecosystems cover two-thirds of ice-free coastlines worldwide (McLachlan & Brown 2006). Sandy beach habitats are structurally dynamic and strongly influenced by tidal conditions, wave energy and sand. Interactions of waves, tides and sand result in the following morphological beach types: dissipative, intermediate and reflective (Short 1996). Dissipative beaches are characterized by fine sediment, high wave energy, a wide, shallow sloping swash zone, a wide surf zone and are usually macro-tidal. Reflective beaches are typically micro-tidal and are characterized by medium to coarse sand, low wave energy and a narrow, steep swash zone. A range of intermediate beach types exist and exhibit a range of characteristics of both reflective and dissipative beaches.

Sandy beaches are located at the interface of terrestrial and subtidal/offshore systems, and thus represent a transitional zone between terrestrial and marine ecosystems (Polis & Hurd 1996; Spiller et al. 2010). Coastal dunes interact with beaches through exchanges of sand, groundwater, salt spray and organic materials (McLachlan & Brown 2006). Likewise, organic materials are exchanged between the surf zone and beach (Colombini et al. 2000; Rossi et al. 2010). Such exchanges may be diverse and include intertidal invertebrates eaten by land predators (Wolcott 1978; Dugan et al. 2003), stranded marine carrion eaten by terrestrial scavengers, marine macrophyte wrack eaten by insects and semi-terrestrial crustaceans (Colombini et al. 2000; Colombini & Chelazzi

2003), insects blown seaward by wind and eaten by marine animals and other litter blown from the dune to the sea (McLachlan & Brown 2006). Importantly, exchanges of these organic materials between land and sea are major components of sandy beach food webs.

Past studies have described how macroinvertebrate diversity and distribution are strongly influenced by beach morphodynamics and physical and geological properties. This is especially true for those organisms inhabiting the swash zone (designated as the area between the highest wave run-up and area of backwash) as swash climate is coupled to beach morphodynamics (Rakocinski et al. 1991; Defeo & McLachlan 2005; McLachlan & Dorvlo 2005; Celentano & Defeo 2006). The coquina clam, *Donax spp.*, and the mole crab, *Emerita spp.*, represent two taxa that have been reported as dominant in swash zones across broad geographic regions (Dahl 1952; Ansell 1983; McLachlan & Brown 2006). Above the swash, commonly encountered supralittoral species in most temperate and tropical areas worldwide include talitrid amphipods, ocypodid crabs and insects (Dahl 1952; McLachlan et al. 1993; Defeo & McLachlan 2011). In general, wave-driven water movement is thought to be a main factor influencing macrofaunal distribution, behavior and trophic links as it controls faunal movement, transports food and reproductive products (e.g. eggs and larvae) and may limit predation access (Dugan et al. 1994; Ellers 1995; McLachlan & Brown 2006).

Given that sandy beaches are generally located at the interface of terrestrial and offshore habitats, food webs on sandy beaches reflect varying degrees of linkages with adjacent habitats. For example, primary production from marine sources includes phytoplankton, algae, and seagrasses (Griffiths et al. 1983; Campbell & Bate 1987; Dugan et al. 2003), and these sources are known to support bivalves and mole crabs

inhabiting the swash zone (Brusca & Brusca 1990; Colombini & Chelazzi 2003; McLachlan & Brown 2006). Swash macroinvertebrates, in turn, are the main prey for top predators found on beaches and in the shallow intertidal such as birds, fishes and burrowing crabs (Delancy 1989; Defeo & McLachlan 2005; Wolcott 1978). Marine turtle nests and uneaten hatchlings which move offshore also form an important component of food webs in some locales (Bouchard & Bjorndal 2000; Barton & Roth 2008; Tewfik et al. 2011, in review).

Sources of primary productivity from the terrestrial system likely play a reduced role as food for macroinvertebrates, although insect activity on washed up plant material (wrack) may augment nutrition for some beach dwelling fauna (Tewfik et al. 2011, in review). Predatory birds and ghost crabs, who inhabit burrows in sand dunes through to the upper intertidal, obtain prey from supratidal and intertidal areas whereas portunid crabs (including the genera *Arenaeus*, *Ovalipes*, *Matuta* and *Callinectes*) move from the subtidal zone into the intertidal zone. Ghost crabs and birds are the main predators in regions such as India, Southwest Florida and Brazil (Ansell et al. 1978; Gianuca 1983; McLachlan & Brown 2006). In other cases, including Scotland, South Africa, and North Carolina, intertidal fishes are the main predators of intertidal and subtidal benthos (DeLancey 1989; McLachlan & Brown 2006).

While the basic structure of sandy beach food webs is relatively well-established, the specific contribution of different components in food webs is not well described for many regions with the Eastern Cape, South Africa, representing one of the few sandy beach food webs that has been studied in detail (McLachlan & Romer 1990; Heymans & McLachlan 1996; McLachlan & Brown 2006). Reports on sandy beach ecology and food

web studies in particular are sparse for Florida, USA; although, an extensive area of the coastline has substantial barrier island formations. Tewfik et al. (2011, in review) conducted a detailed food web study in southwest Florida, and their study provides a first comprehensive evaluation of ghost crabs (*Ocypode quadrata*) as omnivores utilizing a variety of prey. Their study builds on earlier studies of ghost crabs as a dominant predator on sandy beaches (Wolcott 1978).

Overall, although ghost crabs are widely distributed across broad geographic areas, inhabiting sandy shores of the tropics and subtropics, few studies have examined the trophic structures of ghost crabs (Wolcott 1978; Branco et al. 2010). Little information exists as to the variation in ghost crab diet that might exist as a result of differences in physical setting or the extent of connectivity with inland habitats, including dune systems. If abundances of primary prey (swash invertebrates) of ghost crabs vary across gradients of physical settings of the beach, then ghost crab feeding might also display modification linked to differing abundances of their food resources. Likewise, if extensive connectivity exists between beach systems and inland habitats (such as dunes), ghost crabs may expand beyond the use of the swash zone as a feeding site and incorporate prey items from these adjacent habitats.

In this study, I examine food resource use by ghost crabs on three beaches along the central west Florida coastline and simultaneously investigate patterns of abundance of their well-documented swash zone prey in each location. By using a combination of field surveys and stable isotope analyses of beach consumers and prey, three interrelated questions were investigated: 1) Are dietary stable isotope signatures of omnivorous ghost crabs similar across all three beaches; 2) Is abundance of dominant macroinvertebrate

prey (coquina clams, mole crabs) of ghost crabs similar across beaches; and 3) If stable isotope signatures of ghost crabs differ across beaches, what additional prey are likely candidate food items utilized by ghost crabs?

Study Areas

Site Descriptions

Three barrier islands along the west central coast of Florida were chosen as sampling sites: Anclote Key, Cayo Costa and Honeymoon Island. All sampling locations are relatively undeveloped areas located within the Florida state park boundaries of each island. The three beaches, within a distance of 175 km, represent different geological and hydrological features, levels of human modification and extend of dune/upland fringe (Table 1).

Ghost Crabs: Background Information

Ghost crabs (*Ocypode spp.*) are primarily nocturnal crustaceans that build semi-permanent burrows on the beach from the upper intertidal to the foredunes (Alberto & Fontura 1999), and in some cases, burrows extend into the dunes (Pearse et al. 1942). Ghost crab distribution can be influenced by physical attributes of the beach including beach slope, amount of available space, temperature, grain size and sand moisture (Warburg & Shuchman 1979; Turra et al. 2005; Brown & McLachlan 2006; Lucrezi et al. 2009; Tureli et al. 2009). In addition, ghost crab burrows exhibit a clumped distribution (Valero-Pacheco et al. 2007) with juvenile crabs building burrows closer to the high water mark and larger crabs building burrows further up the beach closer to the foredune (Hill & Hunter 1973; Fisher & Tevesz 1979; Christoffers 1986; Strachan et al. 1999;

Tureli et al. 2009). Such distribution patterns may be linked to juveniles having an increased risk of desiccation and need to wet gills and branchial chambers (Fisher & Tevesz 1979; Chan et al. 2006; Valero-Pacheco et al. 2007) compared to larger sized crabs which can directly take up water from moist sand (Wolcott 1976).

Ghost crabs in the Western Atlantic (*O. quadrata*) inhabit coastal areas from Rhode Island to southern Brazil including the Gulf of Mexico and Caribbean (Felder et al. 2009), and have a lifespan of approximately three years (Haley 1969; Alberto & Fontura 1999), allowing ghost crabs to breed over multiple years. Mating and spawning seasons vary with latitude and appear to correlate with temperature (Christoffers 1986). Ghost crabs breed in the summer months, January to March in the Southern Hemisphere (Negreiros-Fransozo et al. 2002; Antunes et al. 2007) and May to September in the Northern Hemisphere (Haley 1972; Christoffers 1986). Females reach sexual maturity at approximately 26 mm in carapace width and males at 24 mm carapace width (Haley 1969).

Egg-carrying females exhibit behaviors different from males and non-gravid females (Milne & Milne 1946). Egg-carrying females enter the water more frequently, most likely to ensure that oxygen-rich water is available to brooding eggs. In addition, ovigerous females may remain in burrows throughout the brooding process (Negreiros-Fransozo et al. 2002) except when oxygenating eggs. Diaz & Costlow (1972) reared *O. quadrata* from egg release to examine larval development under laboratory conditions. Megalopae appeared after a minimum of 34 d with a high mortality rate (<10% survival to megalopae). Haley (1972) found the entire developmental period was approximately 60 days with a period of 45 days from ovulation to hatching.

Table 1: Study site characteristics.

Site	Anclote Key	Cayo Costa	Honeymoon Island
Location	28° 12'N, 82°51'W	28° 4'N, 82°50'W	26° 40'N, 82°14'W
Beach width (m)	15-20 (avg. 20)	20-30 (avg. 25)	10-20 (avg. 17.5)
Island width (m)	100-150	1,200-2,000	100-150
Extent of dune/upland fringe	Minimal Tidal swamp of black mangrove	Extensive Coastal grasslands and maritime forest	Moderate Coastal grasslands to mangrove fringe
Beach slope (degrees)	1	5	10
Median Grain Size (mm)	0.125	0.500	0.250
Sorting coefficient	0.33 very well sorted	0.95 moderately sorted	1.88 poorly sorted
Human modification/impacts	minimal; lighthouse at southern tip	campsites/restrooms, trash bins	renourished beaches, parking lots, trash bins, restaurants
Annual visitation	194,000	92,000	1,100,000
Pest animals	raccoons	raccoons; feral pigs	raccoons
Accessibility	personal watercraft	personal watercraft; ferry service	roadway

Information compiled from Herwitz (1977), Wright (1972), Inglin (1991), Department of Environmental Protection, Chris Madden (pers. comm.) and field measurements

Early literature on ghost crab feeding behavior stated that ghost crabs were scavengers (Phillips 1940; Pearse et al. 1942; Dahl 1952); however, Wolcott (1978) reported that scavenging accounted for less than 10% of the diet of *O. quadrata* on North Carolina beaches. Rather, approximately 90% of the diet consisted of live prey from the swash zone including the mole crab, *Emerita talpoida*, and the coquina clam, *Donax variabilis*. Fales (1976) also provided anecdotal evidence of ghost crabs preying upon *E. talpoida*. In Southern Brazil, insects comprised a large amount of the diet of *O. quadrata* (Branco et al. 2010) and a similar pattern was seen in *O. cursor* in the Mediterranean (Chartosia et al. 2010). Sea turtle eggs and hatchlings are known prey items of ghost crabs (Bouchard & Bjorndal 2000; Barton & Roth 2008) as well as semi-terrestrial amphipods in some cases (Wolcott 1978; Christoffers 1986). Robertson & Pfeiffer (1982) even found that deposit feeding can be an important component of ghost crab diets in certain environmental conditions. In general, swash zone macroinvertebrates are thought to be the primary prey of ghost crabs (Wolcott 1978; Leber 1982; Christoffers 1986); however, ghost crabs have flexible feeding behaviors and are capable of enduring long periods of starvation (up to three months) (Wolcott 1978).

Methods

Sampling Periods

Sampling was conducted at each of the three sites between late April 2011 and September 2011. Two sets of sample collections, one km apart, were conducted at each island during each of three sampling events. Three sampling dates as well as two sample locations at each site allowed for sufficient material to be collected for isotopic analysis as well as to insure sufficient sample size for isotopic comparison and statistical analyses. In addition, sampling between April and September covered the most active time period for all organisms in this study. The study targeted these months as swash animals move offshore to deeper/warmer water (Leber 1982; Degraer et al. 1999) and ghost crabs become inactive and remain in burrows (Haley 1972) in winter months.

Ghost Crab Burrow Counts

To verify that adult ghost crabs were present on each beach, density and size distribution of ghost crabs were estimated for each site during each sampling event. Transects were laid perpendicular to the shoreline, spanning four meters wide and ran the width of the beach, beginning at the top of the swash zone line to the edge of the dune (Figure 1). If low-lying vegetation (e.g. creeping vegetation morning glory, *Ipomoea spp.*) was present, such as at Cayo Costa, transects ran through the vegetation line up to the dune edge or beginning of marsh grass (vegetation line). Each burrow was flagged

and burrow width as well as position along each transect (e.g. distance from top of the swash zone) was measured.

Ghost crab density estimates were calculated as the number of burrows within a given area (100 m²). Additional information was collected along each transect when present including berm location, wrackline location(s), animal tracks, vehicle tracks, etc. In some cases, transects were extended into the vegetation line to get an estimate of the number of individual crabs utilizing this beach/dune habitat interface.

Six transects were sampled at each site during each of the three time periods for a total of 18 transects throughout the sampling period. Transects were run in sets of three, spaced 50 meters apart to ensure independence. A second set of three transects were sampled one km south of the original sampling location.

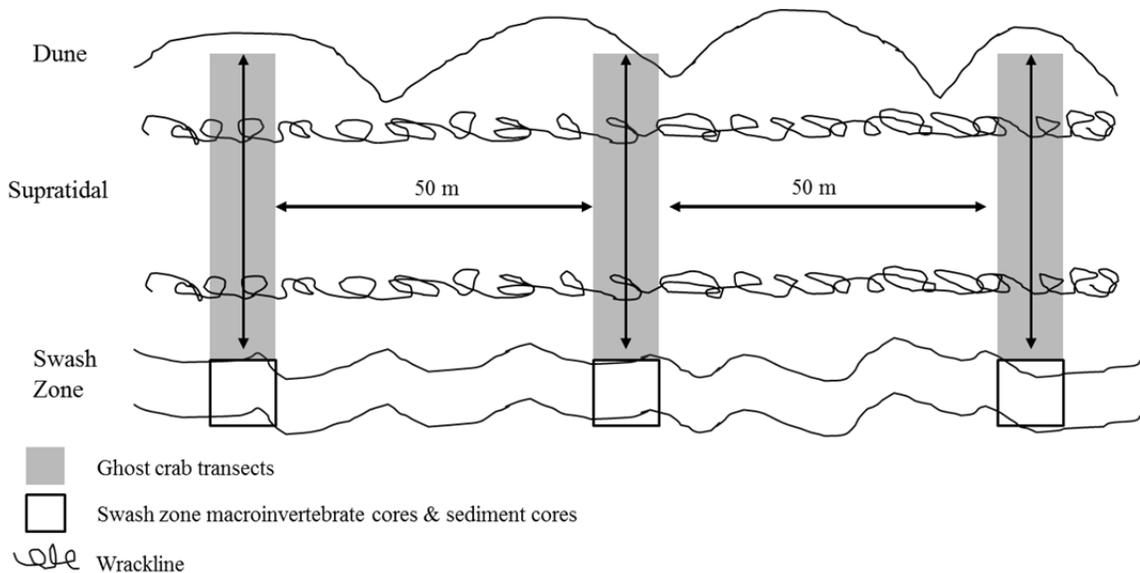


Figure 1: Example of sampling design. Six transects were sampled each time period at each site.

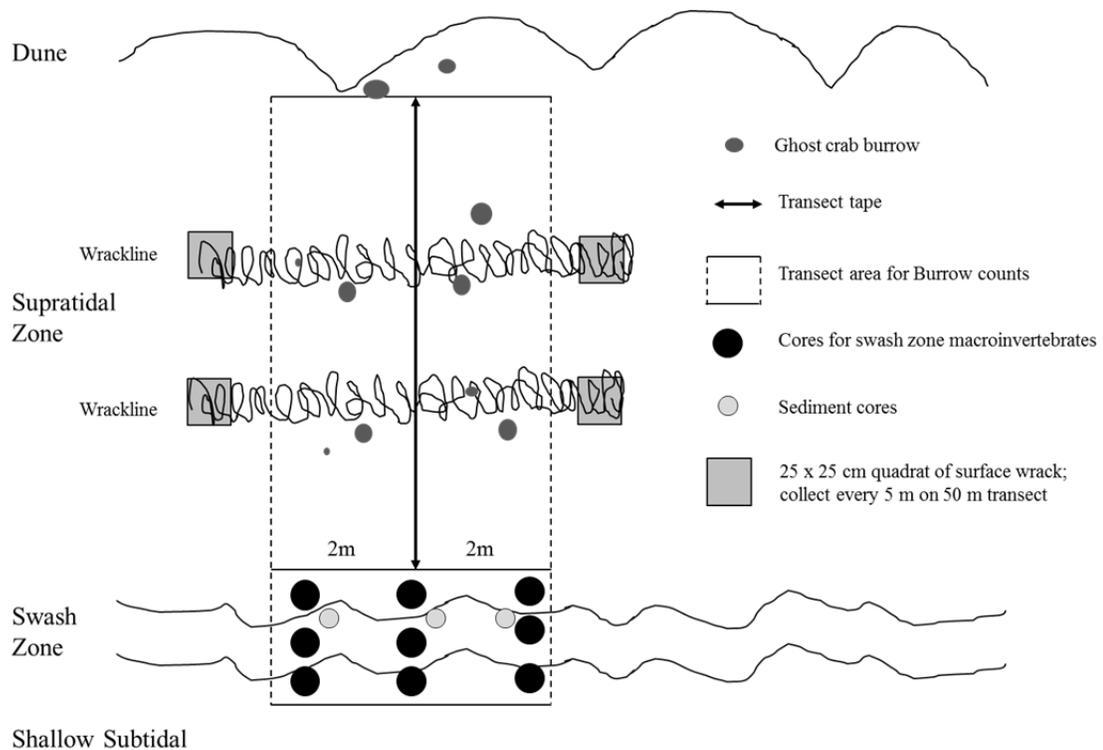


Figure 2: Sample design for one transect (six at each site per time period).

Swash Zone Animal Densities and Biomass

Coquina clams (*Donax variabilis*) and mole crabs (*Emerita talpoida*) were sampled within the swash zone following methods in James and Fairweather (1996). A total of nine cores (each 10 centimeter depth and 10 cm diameter) were taken in the swash zone within each of the six ghost crab transects per site per time period (for a total of 54 cores per sampling period) (Figure 2). Cores were separated by 0.5 to 2 m and sieved in the field through a one millimeter sieve. All cores were taken within two hours of low tide to ensure homogenous sampling. Contents were frozen and brought back to the laboratory for further analysis.

Swash animals were individually picked from each core and counted to estimate density. Density was calculated for each core as the number of coquina clams or mole crabs per square meter (area of coring device is 0.00785 m²).

A length to weight relationship was established for both mole crabs and coquina clams from 100 individuals to calculate biomass and save hours of time. Carapace length was measured for a variety of sizes of mole crabs and individuals were dried for at least 24 hours at 60°C. Once dried, individuals were weighed using a Sartorius Competence Series scale with an accuracy of ±0.01 milligrams. The data points were plotted in Microsoft Excel where a best fit logarithmic trendline was added with an R² of 0.9838. Carapace lengths of remaining mole crabs were measured using digital calipers with an accuracy of ±0.01 millimeters. Biomasses were estimated using the equation from the length to weight relationship. A biomass value per core (g/m²) was estimated for each site.

Coquina clam biomass was estimated using total shell length (mm) and dry weight (g) of all tissue. One hundred individual coquina clams across a size range of three to 25 mm were measured for total length (mm) using a digital caliper with an accuracy of ±0.01 millimeters. Once measured, tissue was removed from the shell and dried for at least 24 h at 60°C. Tissue was then weighed and a best fit logarithmic trendline was added to the data with an R² of 0.9754. Biomass was estimated for the remaining coquina clams from this length to weight equation from which a biomass per core (g/m²) was estimated for each site for each time period.

Wrack Sample Collection

Wrack samples were collected to estimate the relative input of the allochthonous resource at each site (biomass/m²). Fifty meter transects were run through the wrackline, and a 25x25 cm quadrat of surface wrack was collected every 5 m along the transect (beginning at 5 m position on transect) (Figure 2). If multiple wracklines were present, wrack samples were collected from each wrackline. A minimum of two transects were completed at each site during each sampling event (a minimum of 20 wrack samples per site per sampling period).

Wrack samples at Cayo Costa were collected differently during the first sampling event in April 2011. Three 25x25 cm quadrats (0.5 m to two m apart) were collected from the wrackline running through each transect used for ghost crab burrow counts. If multiple wracklines were present, three quadrats were collected from each wrackline. For the April 2011 sample collection, at least 18 quadrats were collected (compared to the transect collection method total of 20 quadrats). The method of wrack collection was changed to the 50 m transect collection method in order for sample collection to be more consistent among sites.

Wrack samples were sorted in the lab and categorized to the finest possible taxonomic unit. Sorted samples were dried at 60°C for a minimum of 24 h and weighed to the nearest 0.01 gram. Wrack samples were then condensed to four main categories: seagrass, macroalgae, terrestrial plant and other (including carrion, garbage, etc).

Collection of Isotopic Material

Ghost crabs were collected via hand-netting after dusk for stable isotope analysis. A total of 18, 13 and 30 crabs were collected from Anclote Key, Honeymoon Island and Cayo Costa, respectively. Two individuals from Anclote Key were collected using pitfall traps.

Additional material was collected by hand from each of the sites. Swash zone animals from cores and wrack material from quadrats were used for isotope analysis. Grasshoppers were caught using hand-nets. Wrack-associated amphipods (beach hoppers) were caught by hand at night while foraging in the moist wrack. All material was frozen until analyzed.

Sample Preparation

Organisms collected were prepared for stable isotope analysis (SIA). Ghost crabs were thawed by running appendages under tap water. Muscle tissue was extracted from one set of limbs, dried at 60°C for 24 h and ground into a powder. Mole crabs were prepared whole, in some cases with up to 10 individuals combined in one sample. All mole crabs were acid washed with 10% HCl solution for one minute and rinsed with distilled water to remove any carbonate sand stuck in crevices in the exoskeleton. Samples were dried at 60°C for 24 h and ground into a powder. Coquina clam muscle tissue was removed from the shell, dried at 60°C for 24 h and ground into a powder.

Grasshoppers were rinsed with distilled water to remove any loose sediment. Individuals were dried whole at 60°C for 24 h and ground into a powder. Wrack-associated amphipods were rinsed in distilled water to remove any carbonate sand. Up to

50 individuals were combined into one sample, dried at 60°C for 24 h and ground into a powder.

Stable Isotope Analysis (SIA)

Stable isotope measurements were made at the USFSI Stable Isotope Lab, Department of Geology, University of South Florida, Tampa, using a Costech ECS Elemental Analyzer with a “zero-blank” autosampler connected to a Thermo Fisher Scientific (Finnigan) Delta V 3 keV isotope ratio mass spectrometer. Measured $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ ratios are reported as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in ‰ relative to the standards, Vienna PeeDee Belemnite carbon and air nitrogen, respectively. The common delta notation is used: $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}})-1]*1000$, where R is respectively $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$.

Statistical Analyses

Because SIA reflects an interpretation of resource use over time and space, density and biomass data from each beach were combined for all time periods. Density differences across time were not important in this study as ghost crabs encountered these density differences throughout the active period. Since isotope signatures are incorporated over time, these signatures should reflect differences in swash zone prey availability. The data were square root transformed ($\sqrt{(x+0.5)}$) in order to reduce heteroscedasticity following methods outlined in Gotelli & Ellison (2004) for count data with high numbers of zeros. Data did not meet the assumptions of homoscedasticity, so Statistica was used to perform a Kruskal-Wallis ANOVA by Ranks to determine

density/biomass differences by site. Mann-Whitney Multiple Comparisons were also performed to determine site specific differences.

Mixing Models

Two mixing models were used to determine dietary composition of ghost crabs at each of my study sites. Four sources were identified as potential components of the ghost crab diet: swash animals (averaged isotope values of *D. variabilis* and *E. talpoida*), semi-terrestrial amphipods (*Talorchestia spp.*), herbivorous insects (e.g. grasshoppers of various spp.), and benthic microalgae. Isotope values for benthic microalgae were estimated from Currin et al. (1995) due to the logistical challenges of acquiring the value ourselves. Herbivorous insect material from Honeymoon Island was not collected, and isotopic values were estimated from material collected from a previous study (Tewfik et al., unpublished). In addition, isotope values from amphipods from Cayo Costa were adjusted from values at Anclote Key. Material has been collected, but will not be processed in time for this publication.

IsoSource software (version 1.3.1) (Phillips and Gregg 2003) was the first model to overcome the limitations of using n isotopes when more than $n+1$ sources are present (Phillips & Gregg 2003; Benstead et al. 2006). In IsoSource, the isotopic signature of the target organism is entered as well as all possible food source signatures (corrected for trophic fractionation). No fractionation adjustment (trophic enrichment factor) was made for $^{13}\text{C}/^{12}\text{C}$ (Peterson & Fry 1987) and $^{15}\text{N}/^{14}\text{N}$ fractionation was determined by averaging the differences between consumers and their respective food sources (3.4, 3.4 and 2.32 for Anclote Key, Cayo Costa and Honeymoon Island, respectively). Once these

parameters were put in the model, the model iteratively creates each possible combination of source proportions that sum to 100% by a small increment (1% in this study). Predicted mixture signatures are compared to the observed mixtures and if they are equal or within a small tolerance ($\pm 0.1\%$ in this study), then the solution is saved in the data set. Thus, the minimum and maximum proportion for each source represents the possible contribution to the diet mixture.

Descriptive statistics for mixed diet analyses including mean (standard deviation) proportion of each source used as well as the range of food source contributions were calculated using IsoSource. Small ranges reflect well-constrained estimates and large ranges may indicate an ambiguous level of contribution to the diet (Benstead et al. 2006). While IsoSource has been the standard software to use when the number of sources is greater than the number of isotopes plus one, it does not allow variability in any parameter including consumers, sources and trophic enrichment factors (Parnell et al. 2010).

I chose to incorporate an additional model, the software package SIAR (Stable Isotope Analysis in R) (Parnell et al. 2008), into my analysis. The SIAR model is a Bayesian mixing model based on Gaussian likelihood (Parnell et al. 2008; Parnell et al. 2010), fitting the model to the data via Markov chain Monte Carlo. The benefit to this model compared to the IsoSource models, is that SIAR allows the user to incorporate variability into the sources as well as trophic enrichment factors (TEF).

I utilized the 'siarsolomcmc4' version of the SIAR model, for isotope data with only a single target organism per group. Analyzing the data in such a way allowed us to compare individual diet variability as well as diet differences among sites. For

consistency with the IsoSource model, a TEF of zero for carbon was used. TEF for Nitrogen was calculated for each site similarly to that for the IsoSource model, averaging all TEFs from consumers and food sources. However, TEFs from ghost crabs and two food sources (herbivorous insects and benthic microalgae) were left out of this calculation as it created too much variation in the data and both are thought to be minimal contributors to ghost crab diets. Standard deviations of $\delta^{15}\text{N}$ TEF were calculated similarly; however, the calculated standard deviation of Cayo Costa was too large for realistic values of fractionation. A realistic standard deviation was set to 0.89, allowing a trophic enrichment factor range of 2.72-3.52.

The SIAR model was run for 100,000 iterations, dropping the first 10,000 iterations and thinning results by 15, giving a final total of 6,000 results. Each of the 6,000 results provided a potential model for each individual ghost crab from each site. These 6,000 results were averaged to provide an average proportion of each food source incorporated into the diet of each crab.

Results

Stable isotope signatures of ghost crabs and potential food sources were examined and modeled to determine dietary composition of ghost crabs. Primary prey (swash macroinvertebrates) and wrack (habitat for alternative amphipod prey) abundances were estimated to verify presence on each beach as well as the availability of each food source to ghost crabs. In addition, ghost crab densities were estimated to ensure presence at each beach.

Ghost crab burrow densities varied among sites, with Anclote Key having mean densities twice as high as Cayo Costa and almost three and a half times higher than Honeymoon Island (Figure 3). Densities at Anclote Key ranged from 0 to 39.3 individuals/100m², with a median of approximately 11.0 individuals/100m². Cayo Costa densities ranged from 1.0 to 19.4 individuals/100m² with a median of 5.5 individuals/100m²; while Honeymoon Island densities ranged from 0 to 13.9 individuals/100m² and a median of 3.1 individuals/100m².

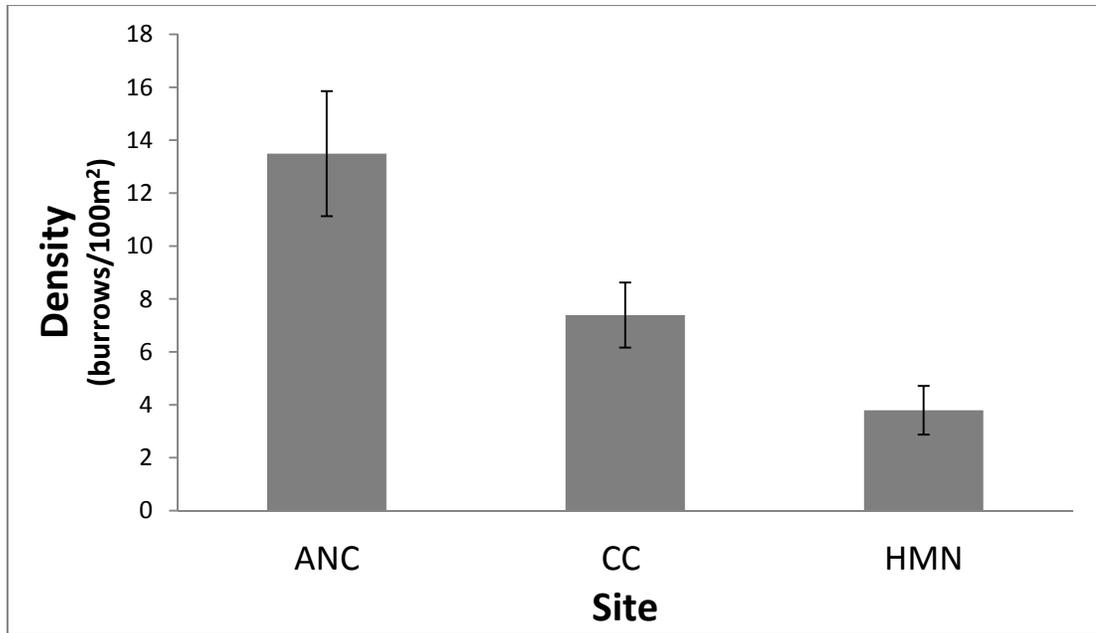


Figure 3: Mean density of ghost crabs (burrows/100m²) at each of the three study sites: Anclote Key (ANC), Cayo Costa (CC) and Honeymoon Island (HMN). Error bars represent standard error of the mean.

Density data from swash zone macroinvertebrates reveal contrasting trends among sites. Swash animal densities varied significantly over the beaches (Figure 4). Based upon multiple comparison tests (post-hoc), densities of coquina clams are significantly different at Honeymoon Island compared to Cayo Costa ($p < 0.001$) and Anclote Key ($p < 0.001$), but not significantly different between Anclote Key and Cayo Costa. Mole crab densities are significantly different among all sites with Honeymoon Island having the highest density. Clearly, however, mole crabs appear to be the dominant swash zone macroinvertebrate at all three sites, existing at densities two to three times higher at all sites.

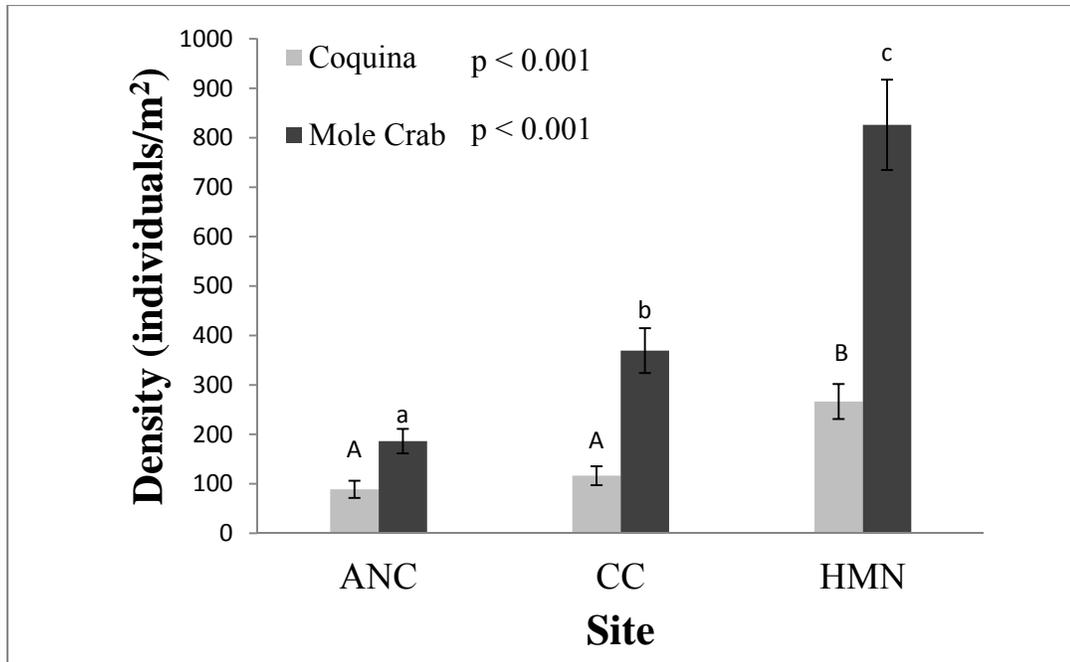


Figure 4: Density of swash zone macroinvertebrates (individuals/m²) at each of the three study sites: Ancote Key (ANC), Cayo Costa (CC) and Honeymoon Island (HMN). Error bars represent standard error of the mean. Sites that are significantly different for each swash zone macroinvertebrate are indicated by letters (capital letters = coquina clams; lower case letters = mole crabs).

Similar to density results, biomass per square meter of swash zone macroinvertebrates were significantly different among all three sites (Figure 5). Post hoc multiple comparison tests showed biomass of coquina clams to be significantly greater at Honeymoon Island compared to Cayo Costa ($p < 0.001$) and Ancote Key ($p < 0.001$), but not significantly different between Ancote Key and Cayo Costa. Mole crab biomass are significantly different among all sites with Cayo Costa having the highest biomass and Ancote Key the lowest ($p < 0.001$). Mole crabs are the dominant macroinfaunal prey by biomass as well with mean biomass three to four times larger than coquina clams at all sites.

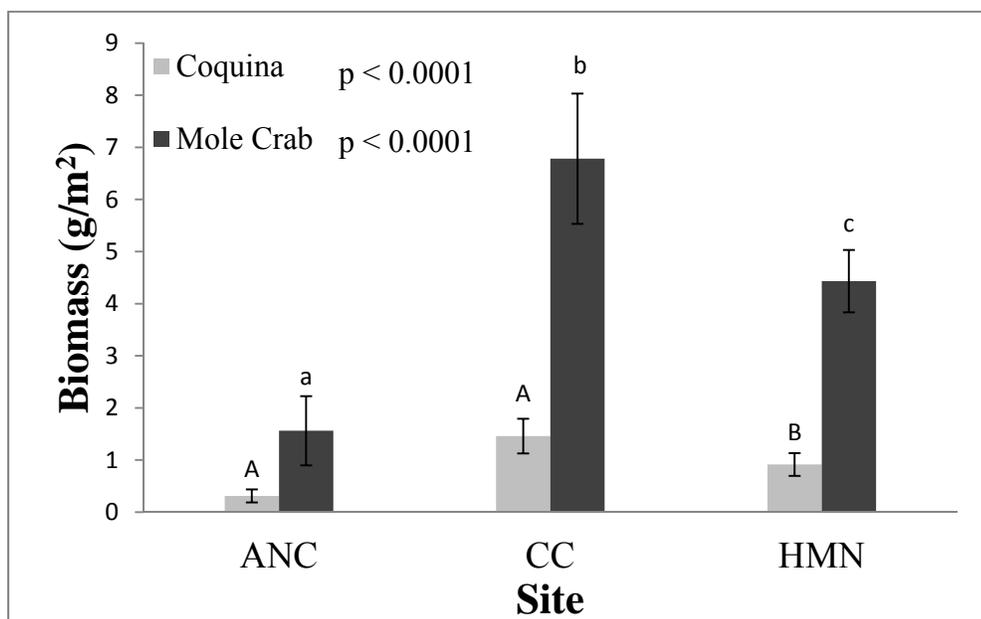


Figure 5: Biomass of swash zone macroinvertebrates (g/m^2) at each of the three study sites: Anclote Key (ANC), Cayo Costa (CC) and Honeymoon Island (HMN). Error bars represent standard error of the mean. Significant differences for each macroinvertebrate are indicated by letters (capital letters = coquina clams; lower case letters = mole crabs).

Wrack biomass per square meter was estimated to determine potential habitat area for macrophyte-associated amphipods (*Talorchestia spp.*), a prey item of the ghost crab. Wrack biomass varied among sites, with Anclote Key having mean densities twice as high as Cayo Costa and Honeymoon Island (Table 2). Biomass at Anclote Key ranged from 40.5 to 326.58 g/m^2 with a mean of 178.64 g/m^2 . Cayo Costa wrack biomass ranged from 7.9 to 217.3 g/m^2 with a mean of 75.4 g/m^2 ; while Honeymoon Island biomass ranged from 13.3 to 396.35 g/m^2 and a mean of 97.23 g/m^2 . High ranges of wrack biomass at Cayo Costa and Honeymoon Island are likely a result of two storm events prior to one sampling event at each site, which resulted in extensive input of this

allochthonous resource. Seagrass was the primary component of beach macrophyte wrack at all sites (Table 2).

Table 2: Mean biomass of wrack, range of wrack biomass and mean percent of wrack components for each site.

Site	Mean biomass (g/m ²)	Range (g/m ²)	Percent wrack composition			
			Seagrass	Macroalgae	Terrestrial Plant	Other
ANC	178.6	40.5-326.6	94.1%	1.3%	3.5%	1.1%
CC	75.4	7.9-217.3*	88.9%	0.5%	7.7%	2.9%
HMN	97.2	13.3-396.4*	72.6%	15.5%	10.5%	1.4%

Note (*) extreme storm events took place at CC and HMN during one sampling event.

Diet polygons were constructed for ghost crabs from each study site (Figure 6) from the IsoSource mixing model. Mean isotope signatures of ghost crabs were enclosed within the boundaries of each polygon indicating that all accessible and utilized resources have likely been included in this study (Benstead et al. 2006). At all sites, swash zone macroinvertebrates and wrack-associated amphipods represented over 90% of the diet. Ghost crabs at Cayo Costa indicated a diet composed primarily of swash zone macroinvertebrates (86%) (Figure 6a). The narrow range in the dietary proportion of swash prey (85-87%) indicates the importance of this prey item in ghost crab diets at Cayo Costa. Amphipods comprised a smaller proportion of the diet, consisting of an average of 13.5% (range of 13-14%), while benthic microalgae (0.2%) and herbivorous insects (0.3%) contributed little to diets (range of 0-1% & and 0-1%, respectively) of ghost crabs at Cayo Costa. In contrast, ghost crabs at Anclote Key had a heavy proportion of amphipods (60.4%) in their diet, while swash zone macroinvertebrates were of

secondary importance (34.8%) (Figure 6b). A narrow range of moderately high diet proportions were observed for amphipods (57-64%), while a wider range was recorded for swash zone prey (24-43%). Herbivorous insects at Anclote Key were of minor importance with an average proportion of the diet being 4.8%, with a range of 0-12%. Benthic microalgae were not an important food source for ghost crabs at Anclote Key (0%). Swash zone prey comprised the largest proportion (62%) of ghost crab diets at Honeymoon Island, while a moderate proportion of the diet consisted of amphipods (32.7%) (Figure 6c). Relatively narrow ranges of diet proportions among both swash zone macroinvertebrate prey and amphipods comprise the majority of the ghost crab diet (56-69% and 28-39%, respectively). Herbivorous insects (3.3%) and benthic microalgae (2.1%) were of little importance in the diet of ghost crabs at Honeymoon Island.

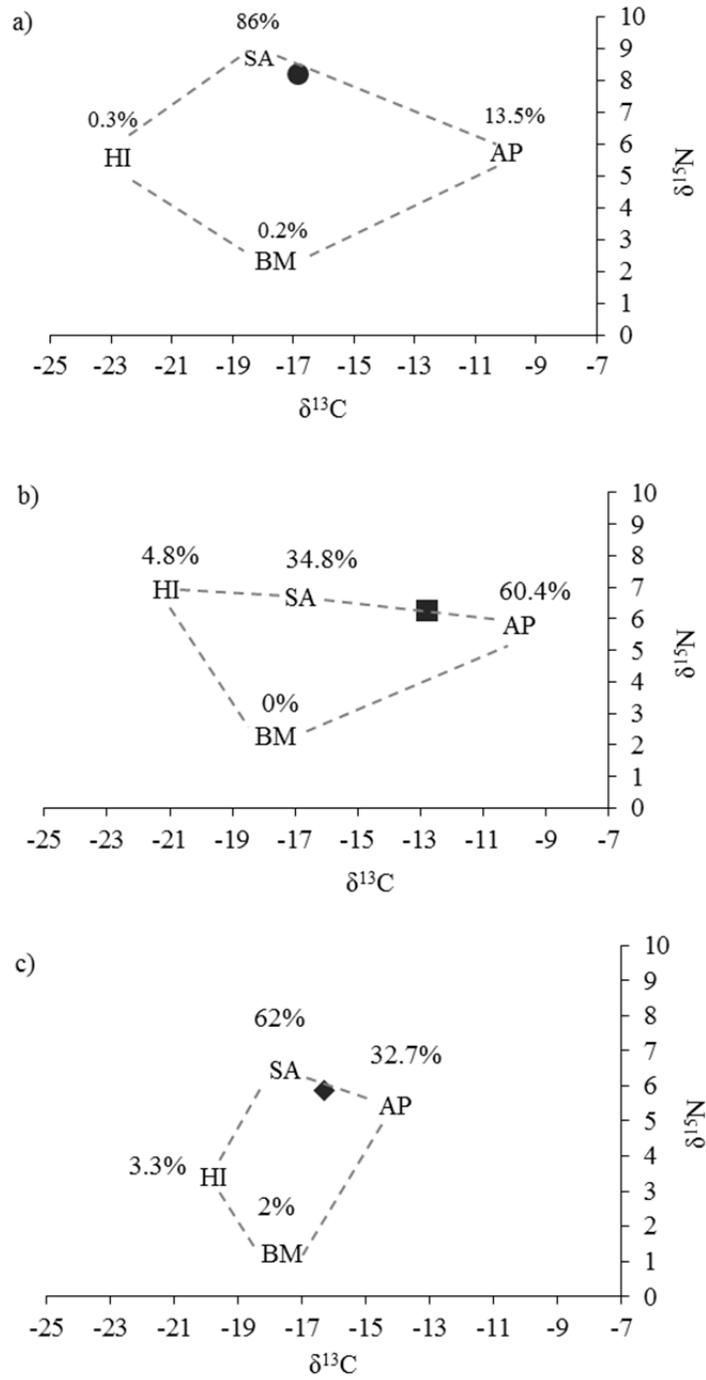


Figure 6: IsoSource model bi-plots of $\delta^{13}\text{C}$ (x-axis) and $\delta^{15}\text{N}$ (y-axis) for resource groups (SA=swash animals; AP=amphipods; HI=herbivorous insects; BM=benthic microalgae) (mean isotope signature and $\delta^{15}\text{N}$ corrected for trophic enrichment) and mean ghost crab

signatures (black shape). Numbers above resources represent percentage of the diet. a) Cayo Costa; b) Anclote Key; c) Honeymoon Island as determined from IsoSource model.

Isotopic box plots of individual ghost crabs and potential food resources (Figures 7A, 7B, 7C) from all three sites display the variability in diets as determined using the SIAR mixing models. Cayo Costa ghost crab isotopic signatures cluster around the isotopic signature of swash animals (Figure 7A) exhibiting little variation in $\delta^{13}\text{C}$ isotope signatures, but a wide range of $\delta^{15}\text{N}$ isotope signatures. In contrast, ghost crabs from Anclote Key have a wide $\delta^{13}\text{C}$ isotope distribution and a narrow range of $\delta^{15}\text{N}$ isotope signatures, with all individuals clustering between swash animals and amphipods (Figure 7B). Honeymoon island ghost crab isotope signatures mainly cluster around swash animal signatures (Figure 7C); however, a moderate level of $\delta^{13}\text{C}$ isotopic variation exists, with some ghost crab signatures clustering near amphipod isotope signatures.

Results from the SIAR mixing models revealed that ghost crabs from Cayo Costa feed primarily on swash zone animals (60.6%), while those from Anclote Key mainly feed on amphipods (64.4%) (Table 3). Amphipods (18.8%) were of secondary importance as a food item at Cayo Costa, while swash animals (20.8%) were of secondary importance at Anclote Key. Ghost crabs from Honeymoon Island exhibit an intermediate diet consisting of similar proportions of swash animals (37.6%) and amphipods (44.3%). Generally, at all sites, the SIAR model suggested that herbivorous insects and benthic microalgae were of minimal importance as was true for the IsoSource analyses. While these trends hold true for most crabs, some individual diet preferences existed. For example, one crab at Cayo Costa appears to feed primarily on herbivorous insects (58.3%), while another ghost crab at Anclote Key utilized amphipods almost exclusively (91.9%).

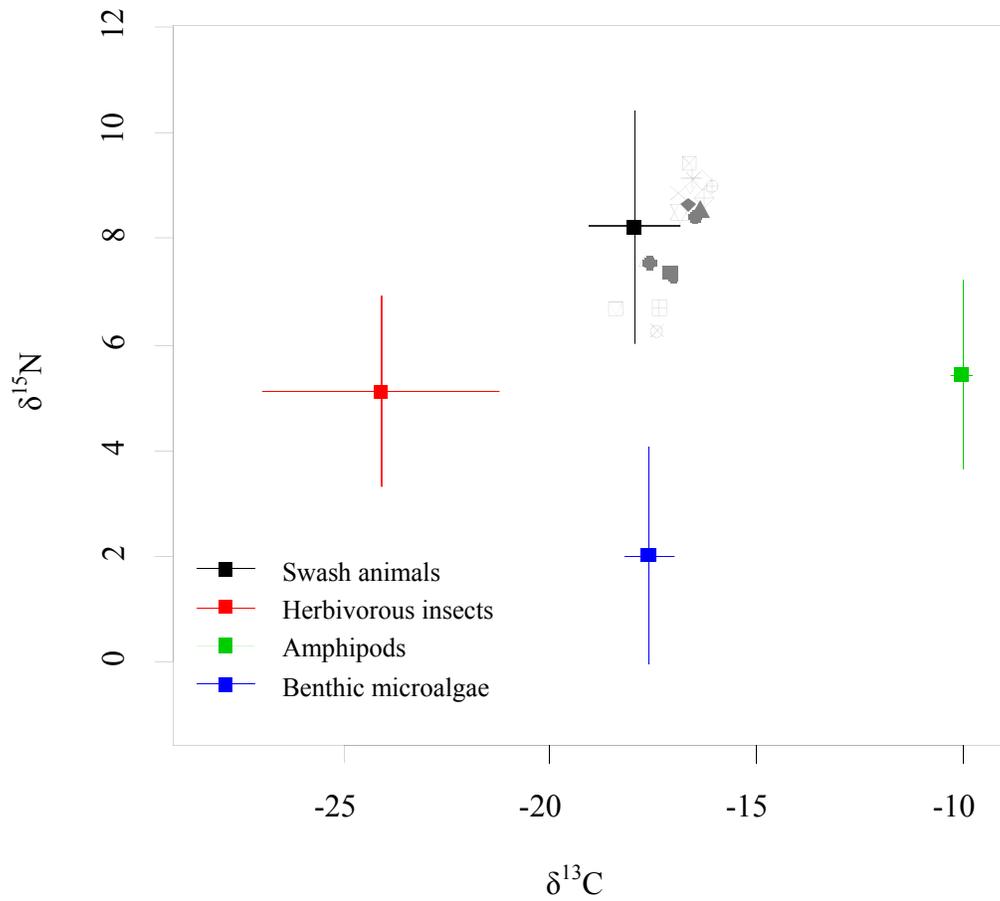


Figure 7A: Cayo Costa SIAR model isotopic bi-plot of *Ocypode quadrata* and potential food sources. The grey symbols represent individual ghost crabs and the colored symbols represent potential food sources adjusted for trophic enrichment. Error bars represent standard deviation.

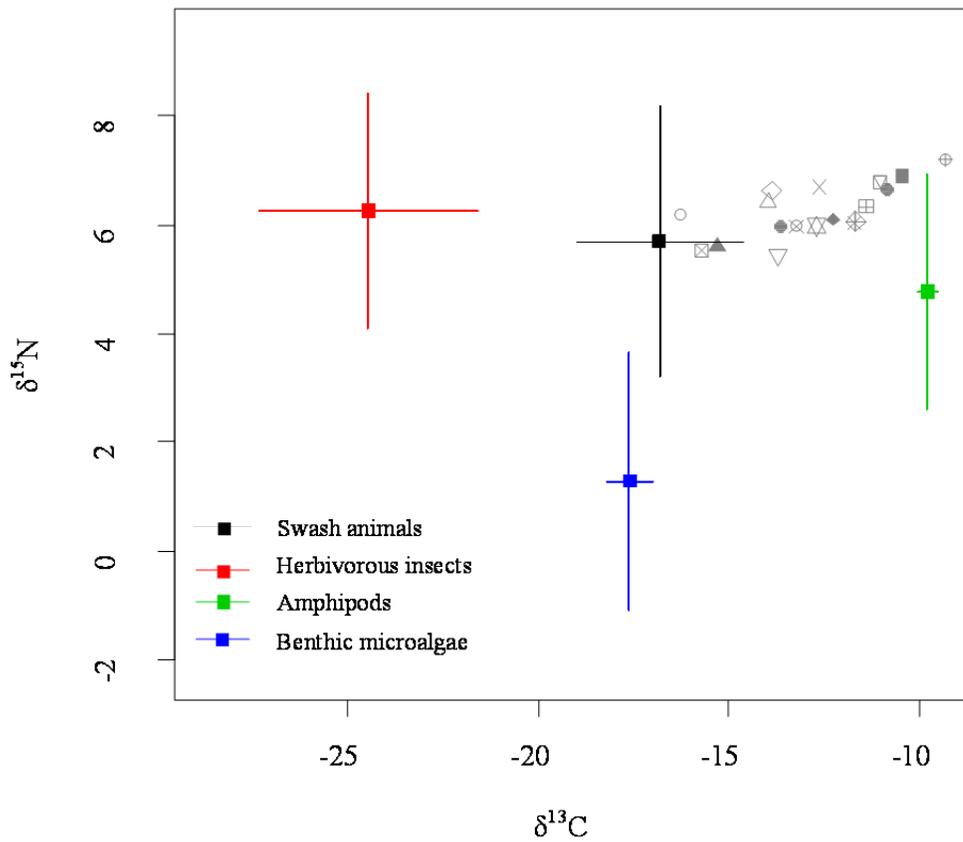


Figure 7B: Anclote Key SIAR model isotopic bi-plot of *Ocypode quadrata* and potential food sources. The grey symbols represent individual ghost crabs and the colored symbols represent potential food sources adjusted for trophic enrichment. Error bars represent standard deviation.

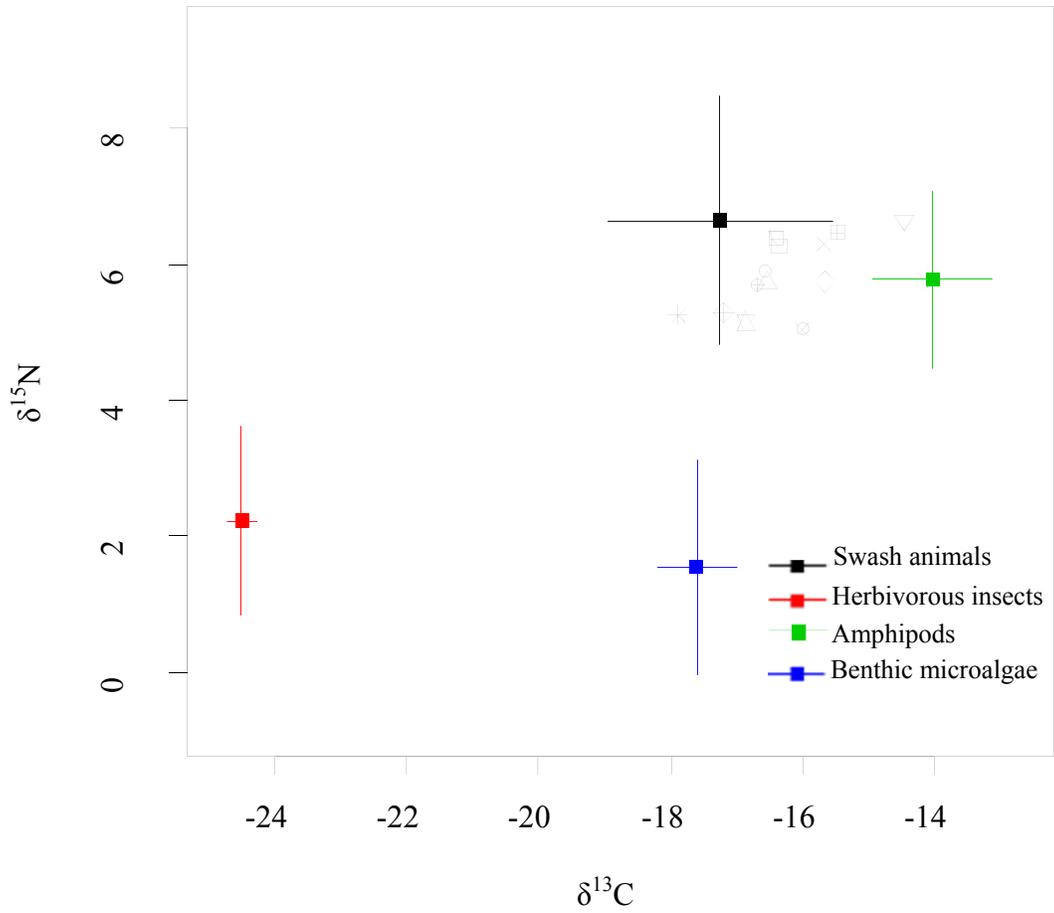


Figure 7C: Honeymoon Island SIAR model isotopic bi-plot of *Ocypode quadrata* and potential food sources. The grey symbols represent individual ghost crabs and the colored symbols represent potential food sources adjusted for trophic enrichment. Error bars represent standard deviation.

Table 3: Summary of SIAR model results.

Site	Statistic	% Swash animals	% Amphipod	% Herbivorous Insect	% Benthic microalgae
CC	mean	60.6	18.8	12.8	7.8
	range	13.2-73.9	7.0-24.7	4.0-58.3	4.0-14.6
ANC	mean	20.8	64.4	8.5	6.3
	range	3.6-34.3	36.3-91.9	0.3-20.0	0.6-12.5
HMN	mean	37.6	44.3	7.6	10.5
	range	14.0-50.7	28.6-79.8	2.4-19.8	3.8-18.6

Mean percent of all ghost crabs and range of individual dietary components for each site.

Discussion

General Results

The present study investigated whether the proportional use of dietary items of the ghost crab (*O. quadrata*), as well as abundances of the crab's primary swash zone prey, were similar across the three study beaches. I found that stable isotope signatures of ghost crabs varied, and significant differences in swash zone macroinvertebrate abundances exist among study sites. Moreover, mixing models for stable isotopes provide evidence that semi-terrestrial amphipods (*Talorchestia spp.*) associated with macrophytes in beach wrack may be an additional food source utilized in some locations and contribute to the differences recorded in prey consumption by the ghost crab.

In general, the mole crab, *E. talpoida*, and coquina clam, *D. variabilis*, are reported to be the primary food source for *O. quadrata* (Wolcott 1978), and results from my study verified their use by ghost crabs at all beaches. Mole crabs are dominant, both in terms of density and biomass, in the swash zone at my study areas, although, abundance levels vary across sites. Diets of ghost crabs at Cayo Costa, the site which supported the highest abundance of swash prey, were comprised mainly (85-87%) of swash animals.

In contrast, the lowest density and biomass of swash animals was recorded at Anclote Key. Stable isotope signatures for ghost crabs diverged from that of animals collected at Cayo Costa. Ghost crabs at Anclote Key appear to shift their diet to one composed mainly of amphipods. Ghost crabs from Honeymoon Island have a dietary signature intermediate to that of crabs from Cayo Costa and Anclote Key, with swash animals and amphipods making up similar proportions of the diet. At all sites, evidence emerged to suggest that microalgae and herbivorous insects (e.g. grasshoppers) were only utilized minimally as food items by crabs, possibly due to inconsistency of their availability in space and time. Ghost crabs are most active at night, at which time benthic microalgae return to interstitial spaces from the surface of sand (where they accumulate and multiply during daytime low tides) (McLachlan & Brown 2006). In addition, grasshoppers, active during the day at the dune fringe, likely return to shelter within vegetation at night. Thus, ghost crabs likely feed on prey items (swash animals and amphipods) most abundant during their nocturnal feeding periods.

In general, both IsoSource and SIAR mixing models provided similar dietary results, even though the SIAR proportional dietary composition displayed some differences. Such discrepancies in the results follow from model features. IsoSource provides a model of diet composition, but does not account for variability in individual ghost crab isotope signatures, food sources or trophic enrichment (Phillips & Greg 2003) as is the case for the SIAR model.

One reason for the marked differences in swash zone prey abundances across beaches may be the variation in median grain size from the intertidal zones, with study sites ranging from ultra-dissipative (very fine sand) (such as Anclote Key) to intermediate

beaches (fine to coarse sand) (including Cayo Costa and Honeymoon Island). Swash zone macroinvertebrates are thought to be best suited to intermediate and dissipative exposed sandy beaches (McLachlan & Brown 2006) than to reflective beaches. Such assemblages are a result of beach morphodynamics and swash zone climate (McLachlan et al. 1981; McArdle & McLachlan 1991; McArdle & McLachlan 1992). Dugan et al. (2000) found *Emerita analoga* to be a substrate generalist, burrowing well into sediments across a broad range of mean grain sizes on exposed sandy beaches in California coasts. Others have reported on *Emerita spp.* as a substrate generalist, but with abundances low in reflective and ultra-dissipative beach types (McLachlan & Brown 2006). However, most studies on *Emerita spp.* have been limited to areas with mean grain sizes larger than 0.2 mm (Dugan et al. 1994; Veloso & Cardoso 1999; Defeo & Cardoso 2002; Cardoso et al. 2003; Celetano & Defeo 2006), sediment sizes almost twice as large as the median grain size at my Anclote Key site. Anclote Key may be characterized as an ultra-dissipative beach in which even *Emerita spp.*, substrate generalists, are not well adapted for long-term survival (McLachlan & Brown 2006).

Low swash zone macroinvertebrate abundances at Anclote Key may have been a contributing factor to the shift in ghost crab diets to wrack amphipods at this site. Other studies have reported similar trends in target organisms shifting their diet due to the variation in abundances of primary prey. For example, Edgar (1990) reported juvenile western rock lobster diets are a result of prey availability, with lobsters in areas with low invertebrate prey shifting to a diet comprised primarily of coralline algae. Remonti et al. (2008) outlined how changes in fish availability resulted in diet shifts in otters (*Lutra lutra*), while Dorn et al. (2011) examined how wetland hydrological conditions resulted in

dietary shifts in the White Ibis (*Eudocimus albus*), likely related to decreased abundances of primary prey. Such studies are aligned with my findings of diet shifts in ghost crabs to alternative in areas where primary prey are in reduced abundances.

An ample supply of amphipod prey may be supported by the high incidence of fresh macrophyte wrack present on all dates at Anclote Key. High densities of amphipods were observed within the wrack at Anclote Key (pers. observation) while very few were observed at Cayo Costa. In addition, the beach morphodynamics at Anclote Key may facilitate high allochthonous input in the form of wrack subsidies. The shallow slope of the beach at Anclote Key may also allow large amounts of wrack that are stranded on the beach to remain moist, thereby providing a substrate utilized by amphipods. Semi-terrestrial amphipods are known to colonize freshly deposited wrack (Colombini et al. 2000) and often occur at high densities (Griffiths et al. 1983; McLachlan 1985). Larger beach slopes at Cayo Costa accompanied by increased wave energy, however, may prevent a constant and fresh input of macrophytes on the beach. Observations on the wrack that did remain onshore at Cayo Costa confirmed that most was typically dry and stranded on the extreme high tide mark, conditions which are suggested to be unsuitable for amphipods (Pelletier et al. 2011) While Honeymoon Island had similar densities of wrack to Cayo Costa, the lower beach slope allows some wrack to remain on the beach and in a moist condition. Note that some evidence for amphipod prey utilization was recorded for ghost crabs at the Honeymoon Island site which supported wrack.

In addition to low swash animal abundances playing a role in diet shift of ghost crabs at Anclote Key, behavioral modification may influence the dietary shifts observed in my study. Raccoons, known predators of ghost crabs (Bouchard & Bjorndal 2000;

Barton & Roth 2008), are present on all islands in this study. However, extremely high densities of raccoons occur on Anclote Key (Chris Berner, pers. comm.). With virtually no human development and an extremely narrow island, few places for raccoons to forage outside of the beach habitat exist. Raccoons may preferentially feed on ghost crabs in many settings (Barton & Roth 2008). At Anclote Key on all sampling occasions, personal observations revealed, raccoon tracks surrounding ghost crab burrows with prints extending from burrow to burrow, along with a dramatically decreased level of nocturnal activity by ghost crabs. While ghost crabs were observed at the opening of their burrows at Anclote Key, very few crabs ventured far from their burrow to forage in the swash zone over the days/nights that observations were made. Ghost crabs at Anclote Key, due to apparent increased predation pressure from raccoons, may display a modified behavior, remaining in or around their burrows which were located amongst the wrackline. If ghost crabs are remaining near their burrows, then food sources in close proximity to the burrows may be highly utilized prey. In the case of ghost crabs at Anclote Key, the high incidences of amphipods in the wrack line may facilitate predation on amphipods by ghost crabs. While this trend exists in the marine environment and in ghost crabs at Anclote Key, raccoons also occur in high abundances at Cayo Costa; however, ghost crabs at Cayo Costa do not exhibit modified behavior, and are readily observed foraging in the swash zone feeding on *E. talpoida* (pers. observation).

Many studies have outlined non-consumptive predator effects on prey similar to those that may be influencing ghost crabs at Anclote Key. McIntosh & Townsend (1996) reported on shifts in mayfly nymph foraging behavior in the presence of two predators. Additionally, considerable shifts in diet occur in roach (*Rutilus rutilus*) and perch (*Perca*

fluviatilis) when separately exposed to high densities of a common predator, the pike (*Esox lucius*) (Sharma & Borgstrom 2008). The lack of such non-consumptive predator effects on ghost crabs at Cayo Costa may be due to the presence of an extensive savannah and maritime forest beyond the beach within which raccoons may forage.

In summary, my results indicate notable differences in diet among populations of ghost crabs inhabiting different islands as reflected in stable isotope values of ghost crabs at three beaches of the Florida Gulf Coast. Dietary differences are most likely a result of reduced primary prey (swash macroinvertebrates) at Anclote Key where ghost crabs utilize alternative prey consisting of amphipods (*Talorchestia spp.*). In all cases, benthic microalgae and herbivorous insects appear to be of little importance in the diet of ghost crabs. Behavioral modification of ghost crabs due to predation pressure from raccoons may also have influenced the diet shift of ghost crabs at Anclote Key. Future studies should aim to manipulate swash prey availability and/or predation pressure in order to establish causal relationships between these environmental factors and behavioral modification of ghost crabs leading to diet shifts.

Implications

Recently, research has focused on the use of ghost crabs as good indicators of anthropogenic effects on sandy beaches (Barros 2001; Neves & Bemvenuti 2006; Magalhães et al. 2009). Extreme coastal development and human activities have led to the destruction and modification of almost every sandy beach worldwide (Schlacher et al. 2008; Defeo et al. 2009). Studies have shown that urban or disturbed beaches have significantly lower densities of ghost crabs than natural or undisturbed beaches (Barros

2001; Maccarone & Mathews 2007; Noriega et al. 2012). Fisher and Tevesz (1979) reported fewer adult ghost crabs on disturbed beaches and reduction in survival to sexual maturity. The use of off-road vehicles (ORVs) directly affects densities of ghost crabs (Moss & McPhee 2006; Schlacher & Lucrezi 2010), but also alters behavior and movement (Turra et al. 2005; Schlacher et al. 2007; Lucrezi 2009a; Lucrezi & Schlacher 2010). Neves and Bemvenuti (2006) reported the vertical distribution of ghost crabs was limited to areas outside of ORV traffic, while Schlacher and Lucrezi (2010) found ghost crabs in areas heavily impacted by ORVs traveled significantly shorter distances, covered smaller areas, but had no difference in the number of turning points.

Overall, it appears that anthropogenic impacts on sandy beaches could be assessed using ghost crab burrows/densities as a proxy. However, managers should be cautious in the use of crabs to assess ecosystem health because human impact on density and size distribution of ghost crabs may be confounded by high environmental variability (Turra et al. 2005) as well as inconsistencies in sampling protocols. Specific causes of environmental impact (patterns observed) cannot always be separated because multiple anthropogenic pressures are altering the sandy beach environment simultaneously (Lucrezi et al. 2009a). The biological responses of organisms (in this case, ghost crabs) to both natural and human factors are poorly understood.

In order for ghost crabs to be utilized in shoreline management decisions, more empirical studies are needed to determine their functional role in the sandy beach ecosystem and how they respond to changes in natural and anthropogenic variables. Because ghost crabs are an important link between marine and terrestrial food webs (Phillips 1940; Wolcott 1978; Barton & Roth 2008; McLachlan 1980), knowledge of

their role in sandy beach food webs is essential for appropriate management plans to be put in place. *Ocypode quadrata* have flexible feeding behavior as indicated by the diverse feeding habits exhibited in this study and throughout its range from preying on swash zone macroinvertebrates (Fales 1976; Wolcott 1978; Christoffers 1986) to amphipods (Wolcott 1978; Christoffers 1986) to insects (Branco et al. 2010) to deposit feeding (Robertson & Pfeiffer 1982). Such information could prove useful if ghost crabs are to be used as bioindicators of the health of beach ecosystems.

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