

Variation in ghost crab trophic links on sandy beaches

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ABSTRACT: Using field surveys and stable isotope analyses of beach consumers and prey, we investigated whether the identity of dominant prey items of ghost crabs *Ocypode quadrata* differed across 3 barrier island beaches along the west coast of Florida, USA. Abundance of potential prey, mole crabs *Emerita talpoida* and coquina clams *Donax variabilis*, was determined from sediment cores collected from the swash zone at Anclote Key (ANC), Honeymoon Island (HI) and Cayo Costa (CC) from late April to September 2011. Concurrently, wrack-associated amphipods were gathered from supra-tidal areas, and ghost crabs were captured from these beaches. Stable isotopic signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of amphipods, mole crabs, coquinas and ghost crabs were identified and diets of ghost crabs compared across beaches using stable isotope analysis in R (SIAR) mixing models. Ghost crabs from CC and HI fed primarily on swash zone animals (mean contribution to diet = 67.6 and 68.4 %, respectively), while those from ANC mainly consumed wrack-associated amphipods (mean contribution = 55.7 %). ANC supported a comparatively low abundance of swash prey, contained moderate amounts of fine-grain sediments and retained a high biomass of seagrass wrack. In contrast, significantly greater abundances of swash prey were found on CC than on other beaches, and a low biomass of wrack was commonly recorded. This new information suggests that wrack may serve as an important marine subsidy and underlie a dietary shift observed for ghost crab consumers on some beaches. In addition to products transported onshore, beach morphology and features of inland habitats may contribute to variability in trophic structure of these subtropical beaches.

KEY WORDS: Food web · Ghost crab · Macroinfauna · Sandy beach · Stable isotope analyses · Subsidy · Swash zone · Wrack

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INTRODUCTION

Sandy beaches represent a widely occurring, crucial and frequently impacted transitional zone between terrestrial and marine ecosystems (e.g. Polis & Hurd 1996). Sediment movement, tidal transport and wave dynamics represent major forces molding not only geomorphology but also ecological structure and function of beaches (e.g. McLachlan & Brown 2006, Bergamino et al. 2011). Strong ecological links are maintained between sandy beaches and adjacent

coastal habitats by the rapid exchange of materials facilitated by physical regimes and biotic activities (e.g. bird and turtle nesting, nearshore and inland foragers) (Stapp & Polis 2003, Crawley et al. 2009). Increasingly, investigations focusing on ecosystem functioning of sandy beaches have recognized that trophic links operating between beach and adjacent inland or coastal waters remain poorly documented (e.g. Rodil et al. 2012).

A current view of sandy beach ecosystems is that food webs are supported by not only local primary

production but also subsidies from adjacent aquatic systems. For example, primary production from marine sources including phytoplankton, algae and seagrasses, often as particulate detritus (Griffiths et al. 1983, Campbell & Bate 1987, Yu et al. 2002, Dugan et al. 2003), is ingested by macroinfauna inhabiting the swash zone (= area of wave run up) (Brusca & Brusca 1990, Colombini & Chelazzi 2003, McLachlan & Brown 2006). Wrack material washed onto beaches may also be consumed by small invertebrates, especially terrestrial arthropods, associated with stranded materials on upper beach zones (Lastra et al. 2008, Olabarria et al. 2009, Colombini et al. 2011). Swash macroinvertebrates, in turn, serve as prey for higher level consumers found on beaches and foraging in the shallow intertidal such as birds, fishes and ghost crabs (Wolcott 1978, DeLancey 1989, Defeo & McLachlan 2005), and in some cases, polychaetes (Bergamino et al. 2011). Marine turtle eggs and hatchlings also represent important subsidies of food webs in some areas (Bouchard & Bjorndal 2000, Barton & Roth 2008). Finally, a limited number of studies have described trophic interactions between marine products washed onto beaches and both terrestrial invertebrates and vertebrates (e.g. Spiller et al. 2010).

Although the basic structure of sandy beach food webs is relatively well established, especially for areas of South Africa (McLachlan & Romer 1990, Heymans & McLachlan 1996, McLachlan & Brown 2006), trophic relationships generally remain understudied for most geographic regions. Some studies investigating food webs have further noted that the relative contribution of individual food items to diets of dominant higher order consumers may be highly variable both spatially and temporally (e.g. Bergamino et al. 2011). Together, these findings suggest a clear need to: (1) expand documentation of trophic interactions on sandy beaches, and (2) develop improved descriptions of diets of dominant high level consumers that couple beach and surrounding habitats.

Ocypodids (i.e. ghost crabs) may be excellent candidates for trophic analyses because these secondary consumers exploit resources over a large spatial expanse of beaches, extending from the dune, and possibly further inland, to the shallow subtidal (Wolcott 1978). Ghost crabs are found circumglobally and within the Western Atlantic, with members of the genus *Ocypode* inhabiting coastal areas from Rhode Island, USA, to southern Brazil, as well as throughout the Gulf of Mexico and Caribbean (Felder et al. 2009). Available information suggests that ghost

crabs consume a broad array of foods, although some early studies viewed ghost crabs only as scavengers (Phillips 1940, Pearse et al. 1942, Dahl 1952). However, swash zone macroinvertebrates, including the mole crab *Emerita talpoida* and the coquina clam *Donax variabilis*, are generally reported as primary prey of these ghost crabs (Wolcott 1978, Leber 1982, Christoffers 1986). Other studies have reported that insects comprise a large proportion of prey consumed by *O. quadrata* in southern Brazil (Branco et al. 2010) and by *O. cursor* in the Mediterranean (Chartosia et al. 2010). Additionally, sea turtle eggs and hatchlings are preyed upon by ghost crabs (Bouchard & Bjorndal 2000, Barton & Roth 2008), as are semi-terrestrial amphipods often found in association with wave-cast macrophyte wrack (Wolcott 1978, Christoffers 1986). Lastly, Robertson & Pfeiffer (1982) reported that ghost crabs may exhibit deposit feeding, ingesting surface phytoplankton in certain beach environments. Ghost crabs therefore represent taxa which may utilize a variety of food items originating from both beach sands and habitats adjacent to beaches.

Given the variety of beach physical settings, the relative contribution of selected food items in ghost crab diets might be expected to vary considerably. Specifically, hydrodynamics directly influence sediment characteristics, and beach macroinfauna often show strong preferences for sediments of a particular range of grain sizes (e.g. Jaramillo & McLachlan 1993). Also, physical setting or exposure to winds and extent of the inland area fringing beaches may impact the extent of beach connectivity with both offshore and inland habitats or the availability of primary production (Bergamino et al. 2011). If abundances of primary prey (swash invertebrates) of ghost crabs vary across gradients of beach physical setting, then ghost crabs might also display modified feeding behavior as food resources become more, or less, available. Likewise, if extensive connectivity exists between beach systems and offshore or inland habitats, ghost crabs may move into, and incorporate prey items from, adjacent habitats. To evaluate any of these suggestions, the contribution of individual prey items to ghost crab diets must be quantified. However, no studies to date have investigated the relative contribution of different prey items to ghost crab diets across multiple sites using techniques, such as stable isotope analyses (SIA), that can provide an integrated assessment of resource use.

In this study, we expand upon studies on sandy beach food webs and examine food resource use by ghost crabs from 3 barrier island beaches along the

Table 1. Characteristics of barrier island beaches that served as study sites. See Fig. 1 for locations

Characteristic	Anclote Key	Cayo Costa	Honeymoon Island
Mean beach width (m)	32.2	15.7	16.0
Beach slope (degree)	3.1	8.8	6.8
Range of island width (m)	100–150	1200–2000	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
Median grain size (mm)	0.19	1.50	0.25
Sorting coefficient	0.33/very well sorted	0.95/moderately sorted	1.88/poorly sorted

central west coast of Florida, USA. We simultaneously investigate patterns of abundance of ghost crabs and their well-substantiated macroinfaunal prey inhabiting the swash zone in each location. Using a combination of field surveys and SIA of beach consumers and prey, we investigate whether the identity of dominant prey items of ghost crab diets differs across the suite of beaches and, if so, explore what factors might explain such shifts in trophic structure.

MATERIALS AND METHODS

Three barrier island beaches along the west central coast of Florida, USA, were chosen as sampling sites: Anclote Key (ANC), Cayo Costa (CC) and Honeymoon Island (HI) (Fig. 1). All sampling locations are relatively undeveloped beaches located within the Florida State Park boundaries of each island. The 3 beaches, located within a distance of 175 km, display different geological and hydrological features (Table 1), but all support swash macroinfauna and ghost crab populations.

Faunal sampling was conducted at each of the 3 beaches during 3 sampling events from late April to September 2011, when swash animals and ghost crabs are most active and available in the swash zone. Swash animals move offshore to deeper and/or warmer waters (Leber 1982, Degraer et al. 1999), and ghost crabs become inactive and remain in burrows (Haley 1972) in colder months (October–March). Transects were run at 2 locations separated by approximately 1 km along each beach site. For each location, 3 belt transects, 4 m wide, were laid perpendicular to the shoreline, with at least 50 m between each transect. Transects extended the width of the beach from the top of the swash zone to the edge of the dune. All ghost crab burrows (>7 mm) within a transect were then enumerated to estimate ghost crab density (no. of burrows per 100 m²).

Coquina clams *Donax variabilis* and mole crabs *Emerita talpoida* were sampled within the swash zone following James & Fairweather (1996). During a sampling event, at each beach, 9 cores (10 cm deep; 10 cm diameter) were taken in the high, mid and low swash zone at the end of each of the 3 ghost crab transects (n = 162 cores per beach). All cores were taken within 2 h of low tide, and the contents were sieved (1 mm) in the field. Contents retained on sieves were placed on ice, brought back to the laboratory and stored at 0–4°C until further analysis. Additionally, three 60 ml cores for sediment analyses were collected during each sampling event in all swash zone locations from which infaunal samples were taken (n = 54 cores per beach). Sediment size class analysis was conducted on these core samples, which were returned to the laboratory, dried for 24 h at 60°C and then analyzed for mean grain size and sorting using the software Gradistat (Blott & Pye 2001).

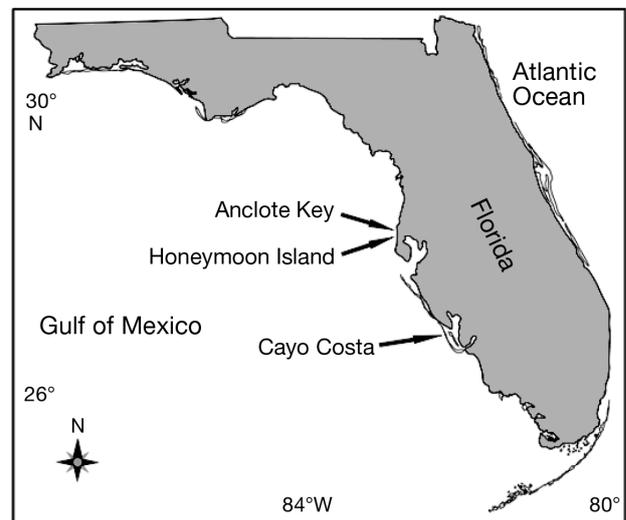


Fig. 1. Location of 3 barrier island beaches (Anclote Key, Honeymoon Island, and Cayo Costa) along the west coast of Florida, USA, that served as study sites

In the laboratory, swash animals were identified and enumerated from each core. Carapace length was measured for mole crabs using digital calipers (± 0.01 mm accuracy). A randomly selected subset of 100 individuals was then dried for at least 24 h at 60°C and subsequently weighed (± 0.01 mg). Coquina clams were measured for shell length (mm) using digital calipers (± 0.01 mm) and a randomly selected subset of 100 individuals was selected for further analyses. Tissue material was removed from each of the 100 individual coquina clams, dried for at least 24 h at 60°C and weighed (± 0.01 mg). Length–weight relationships were established for both mole crabs ($N = 100$) and coquina clams ($N = 100$) using a best-fit logarithmic trend line for biomass (y) and length (x). The resultant equations were: mole crabs, $y = 1.39955\ln(x) - 4.4678$ ($R^2 = 0.9838$); and coquina clams; $y = 1.2065\ln(x) - 5.2035$ ($R^2 = 0.9754$). Using these equations, biomass (g dry weight m^{-2}) was then estimated for both taxa at each of the 3 beaches.

To characterize macroinfauna, information on densities and biomass of mole crabs and coquinas was combined across events and locations for each beach. This approach was adopted given the following: (1) our study examined ghost crab diets via SIA (see below), which reflect an integration of resource use over time (months) and space (Peterson & Fry 1987, Fry 2006); (2) ghost crabs were obtained for trophic analyses from the same beaches from which macroinfauna were collected, although capturing ghost crabs required moving 10s to 100s of meters beyond the beach locations used for macroinfaunal sampling; and (3) during an individual nightly foray, ghost crabs can move up to 800 m (Wolcott 1995). Therefore, comparison of macroinfaunal abundance within swash zones among beaches was based upon the total set of cores from each beach. Prior to statistical analyses, data for mole crab and coquina biomass and density were square root transformed [$\sqrt{(x + 0.5)}$] because of the high number of zero values (Gotelli & Ellison 2004). A Kruskal-Wallis ANOVA by ranks (Statistica) was used to determine whether density/biomass differed by beach. The data met all the assumptions of the Kruskal-Wallis test. If differences were detected by ANOVA, a 2-tailed Dunn's test (multiple comparisons) was performed to determine significant differences among beaches.

Biomass of washed-up wrack, representing an allochthonous resource, was estimated from collections at all 3 beaches. Transects, 50 m in length, were surveyed across the wrack line, and all wrack within a 25 × 25 cm quadrat was collected at 5 m intervals.

Two transects of 10 samples each were collected at each beach during each sampling event. Wrack samples were sorted in the laboratory, contents were categorized to the lowest possible taxon and all taxa were then grouped into 4 categories: seagrass, macroalgae, terrestrial plant and other. Samples were dried at 60°C for a minimum of 24 h and weighed to the nearest 0.01 g.

Stable isotope analyses

Ghost crabs were collected for SIA at all beaches via hand-netting after dusk. A total of 18, 13 and 30 crabs were collected from ANC, HI and CC, respectively, over all sampling events. Two individuals from ANC were collected using pitfall traps. Only individuals of 35–45 mm carapace width were used for SIA. Additionally, individual prey items for SIA were recovered from cores (swash animals) and wrack material (amphipods). Amphipods foraging in the moist wrack were caught by hand at night. All material was frozen (0–4°C) until analyzed.

In preparation for SIA, ghost crabs were thawed, and muscle tissue was extracted from one set of walking legs, dried at 60°C for 24 h and ground into a powder for subsequent analyses. All mole crabs and wrack-associated amphipods were washed with 10% HCl solution for 1 min and rinsed with distilled water to remove any $CaCO_3$ sand particles. Mole crabs were prepared using the entire animal and, depending on size, up to 10 individuals were combined in a sample ($n = 5$ samples per beach). Likewise, up to 50 individual amphipods were combined into an individual sample ($n = 2$ samples per beach). For coquinas, muscle tissue was removed from the shell for analyses ($n = 5$ samples per beach). Mole crab, amphipod and coquina materials were then processed as for ghost crab tissue described above.

Stable isotope measurements were made at the University of South Florida (USF) Stable Isotope Laboratory, using a Costech ECS Elemental Analyzer with a 'zero-blank' autosampler connected to a Thermo Fisher Scientific (Finnigan) $\Delta V 3$ k eV isotope ratio mass spectrometer. Measured $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios are reported as $\delta^{13}C$ and $\delta^{15}N$ values in ‰ relative to the standards, Vienna PeeDee Belemnite carbon and air nitrogen, respectively. The common δ notation is used: $\delta^{13}C$ or $\delta^{15}N = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where R is, respectively, $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Between-sample variation was $\pm 0.1\%$ based upon a B-2155 protein certified standard.

Mixing models

The mixing model stable isotope analysis in R (SIAR) (Parnell et al. 2008) was used to determine dietary composition of ghost crabs collected from each beach. Three prey sources were identified as potential major components of the ghost crab diet: coquina clams *Donax variabilis*, mole crabs *Emerita talpoida* and semi-terrestrial amphipods (*Talorchestia* spp.). The SIAR model is a Bayesian mixing model (Parnell et al. 2008, 2010) that allows the user to incorporate variability into the sources as well as trophic enrichment factors (TEF). We utilized the 'siaisolomcmc4' version of the SIAR model for isotope data with only a single target organism per group. Analyzing the data in this way allowed comparison of individual ghost crabs as well as overall trophic differences among beach sites. No fractionation adjustment (TEF) was made for $^{13}\text{C}/^{12}\text{C}$ (Peter-

son & Fry 1987), and $^{15}\text{N}/^{14}\text{N}$ fractionation adjustment was determined by averaging the differences between consumers and their respective food sources (3.24, 3.33 and 2.14 for ANC, CC and HI, respectively). Standard deviations for $\delta^{15}\text{N}$ TEF were calculated similarly (0.77, 0.94 and 0.76 for ANC, CC and HI, respectively).

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 6000 results. Each of the 6000 results provided a potential model for each individual ghost crab from each site. These 6000 results were then averaged to provide a mean proportion of each food source incorporated into the diet of each crab.

RESULTS

Ghost crab densities, inferred from burrow densities in beach surveys, varied among sites, with mean densities on ANC approximately twice those on CC and almost 3.5 times those on HI (Fig. 2). Across transects at each of the 3 beaches, the highest densities of burrows were found in quadrats located within 1 m of the wrack line (Fig. 2). Likewise, densities of swash zone macroinvertebrates displayed contrasting trends among sites (Fig. 3A). Mole crabs were the dominant swash zone macroinvertebrate at all 3 study sites, although the total number of swash zone macroinvertebrates was comparatively low at ANC. When all samples at each beach were combined, both mole crab and coquina densities varied significantly by beach (Kruskal-Wallis ANOVA; Table 2, Fig. 3). A Dunn's multiple comparison test further indicated that densities of coquina clams were significantly higher at HI compared with CC and ANC but were not significantly different between ANC and

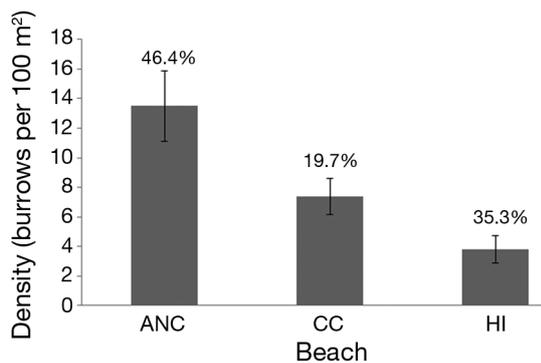


Fig. 2. *Ocyropsis quadrata*. Mean density of ghost crabs assessed from burrow counts at each of the 3 study sites: Anclote Key (ANC), Cayo Costa (CC) and Honeymoon Island (HI). Error bars represent SEM; n = 18 transects (each 100 m²) per site. Percent of burrows within 1 m of wrack line is indicated above each bar

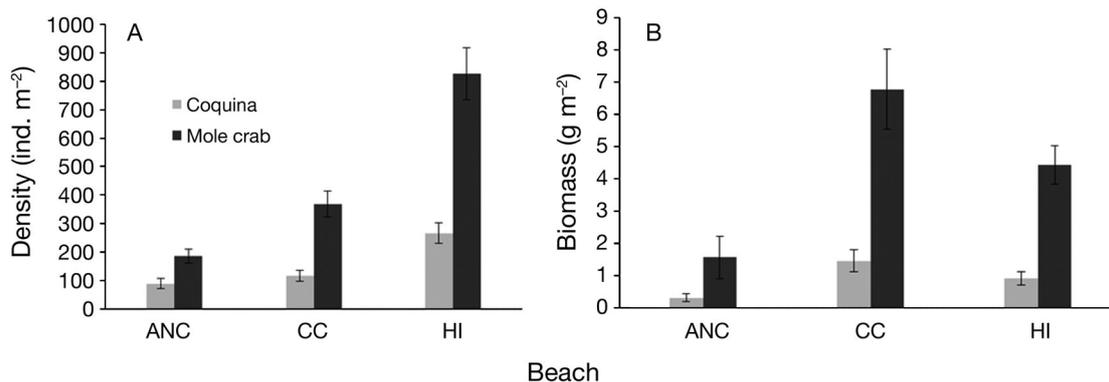


Fig. 3. (A) Density and (B) biomass of swash zone macroinvertebrates at each of the 3 study sites: Anclote Key (ANC), Cayo Costa (CC) and Honeymoon Island (HI). Error bars represent SEM; n = 162 samples per site

CC (Table 2). Mole crab densities were significantly different between all 3 study sites, with HI having the highest, and ANC the lowest, density (Table 2).

Mole crabs were the dominant macroinfaunal prey by biomass across all beaches, with a mean biomass 3–4 times that of coquina clams at all sites (Fig. 3B). As was found for density, biomass per m² of swash zone macroinvertebrates differed significantly among beaches (Kruskal-Wallis test; Table 2). Biomass of coquina clams was significantly greater at CC compared with that from HI and ANC, but coquina biomass was not significantly different between HI and ANC (Dunn's multiple comparison test; Table 2). Mole crab biomass was significantly different among all sites, with CC having significantly higher biomass than HI and ANC, the latter being significantly lower than all other study sites (Dunn's multiple comparison test; Table 2).

On all 3 beaches, seagrasses composed the majority (ca. 73–94%) of washed-up wrack; macroalgae were sometimes abundant on HI (Table 3). Mean wrack biomass at ANC was greater than that at other beaches, although biomass values displayed a wide range on all beaches (Table 3). Patterns of wrack biomass were likely influenced by 2 storms that passed immediately prior to a sampling event at both CC and HI.

Examination of isotopic bi-plots of individual ghost crabs and potential food resource sites constructed from the SIAR mixing models (Fig. 4) revealed vari-

ability in ghost crab diets across beaches. Isotopic signatures of ghost crabs from CC were closely aggregated around the isotopic signatures of swash animals (Fig. 4A), exhibiting low variation in $\delta^{13}\text{C}$ isotopic signatures (2–3 δ units) but a moderate range of $\delta^{15}\text{N}$ isotopic signatures (4+ δ units). In contrast, a wide $\delta^{13}\text{C}$ isotopic distribution (8 δ units) and a narrow range of $\delta^{15}\text{N}$ isotopic signatures (<2 δ units) were present in ghost crabs from ANC, and isotopic signatures of individual ghost crabs were intermediate to those of swash fauna and amphipods (Fig. 4B). Isotopic signatures of ghost crabs from HI were strongly aggregated around the values associated with swash animals (Fig. 4C); however, a moderate level of $\delta^{13}\text{C}$ isotopic variation was recorded (4 δ units), and some ghost crab signatures were aligned with isotopic signatures of amphipods.

Further examination of trophic signatures based upon results from the SIAR mixing models revealed that ghost crabs from CC and HI displayed isotopic signatures aligned with a diet based primarily on swash zone animals (mean contribution to diet = 67.6 and 68.4%, respectively), while those from ANC had a diet with the greatest contribution by amphipods (mean contribution = 55.7%; Table 4). Additionally, isotopic signatures from ghost crabs revealed that amphipods were of secondary importance (mean contribution = 31.6%) at CC and HI; the same was true for swash animals (mean contribution = 44.3%) at ANC. But some individual crabs had remarkably unique diets. Specifically, one crab at CC displayed isotopic signatures suggesting a preponderance of coquina clams in the diet (92.5%), while another at ANC appeared to utilize primarily swash animals (47.9% mole crabs and 36.5% coquina clams).

Table 2. Kruskal-Wallis nonparametric ANOVA for data shown in Fig. 3. Values from beach sites that are not significantly different from one another (2-tailed Dunn's multiple comparison test) are indicated by continuous underlining. HI: Honeymoon Island; CC: Cayo Costa; ANC: Anclote Key

Parameter	Kruskal-Wallis $H_{2,486}$	p-value	Dunn's multiple comparison test
Coquina density	29.29	<0.001	<u>HI</u> <u>CC</u> <u>ANC</u>
Coquina biomass	23.93	<0.001	<u>CC</u> <u>HI</u> <u>ANC</u>
Mole crab density	81.07	<0.001	<u>HI</u> <u>CC</u> <u>ANC</u>
Mole crab biomass	65.22	<0.001	<u>CC</u> <u>HI</u> <u>ANC</u>

DISCUSSION

The present study provides the first detailed information on food source utilization by ghost crabs *Ocyropsis quadrata* across a suite of subtropical sandy beaches. Furthermore, by simultaneously examining

Table 3. Mean biomass of wrack, range of wrack biomass and mean percent composition of wrack by major category for each site. DW: dry weight

Site	Mean biomass (g DW m ⁻²)	Range (g DW m ⁻²)	Wrack composition (%)			
			Seagrass	Macroalgae	Terrestrial plant	Other
Anclote Key	178.6	40.5–326.6	94.1	1.3	3.5	1.1
Cayo Costa	75.4	7.9–217.3	88.9	0.5	7.7	2.9
Honeymoon Island	97.2	13.3–396.4	72.6	15.5	10.5	1.4

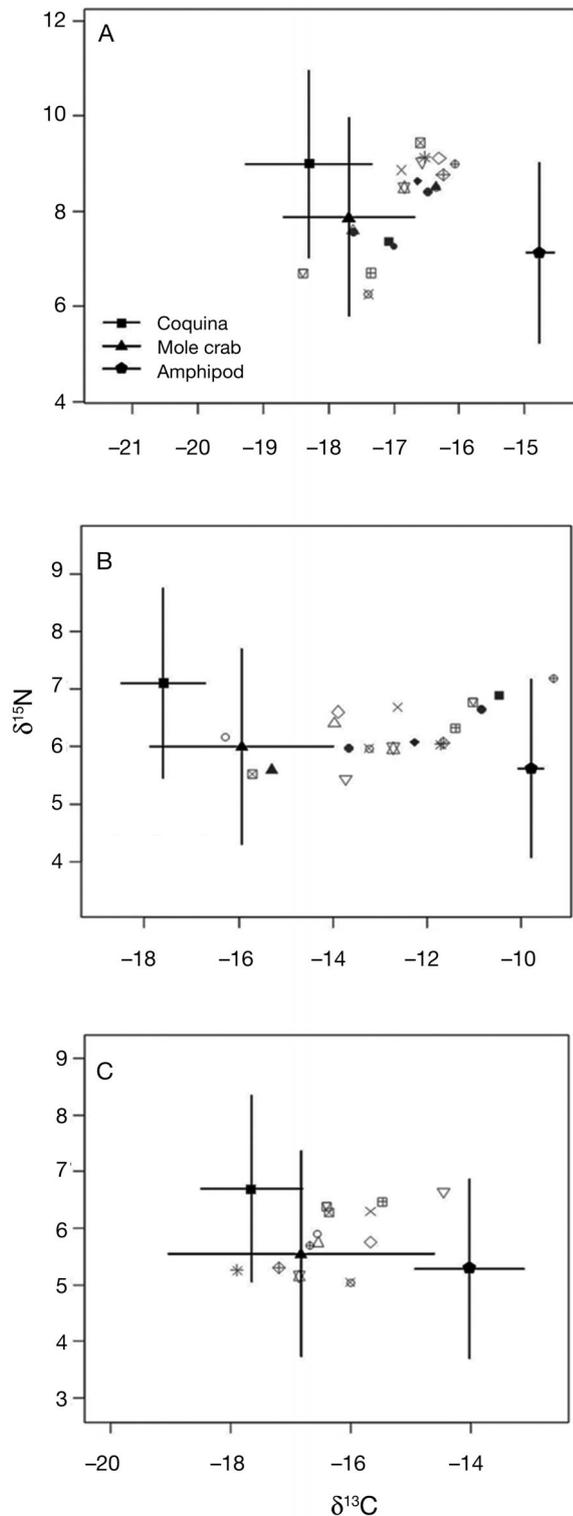


Fig. 4. SIAR model isotopic bi-plot of *Ocypode quadrata* and potential food sources at (A) Cayo Costa, (B) Anclote Key and (C) Honeymoon Island. Black symbols (mean \pm SD) represent potential food sources adjusted for trophic enrichment; all other symbols represent values for individual ghost crabs

Table 4. Mean (\pm SD) percent of major food items in ghost crab diets as determined from the SIAR model for all 3 study sites

Site	Mole crab (%)	Coquina (%)	Amphipod (%)
Cayo Costa	32.5 (12.5)	35.1 (14.6)	32.5 (15.3)
Anclote Key	24.4 (13.5)	19.9 (12.6)	55.7 (25.6)
Honeymoon Island	35.1 (8.2)	33.3 (8.5)	31.6 (14.9)

stable isotope signatures of ghost crabs and their food sources, both differences and similarities in ghost crab diets were identified. The SIAR mixing models used for trophic analyses revealed dissimilarities in primary food sources of ghost crab diets and is an attractive method because variability in any parameter, including consumers, sources and trophic enrichment factors, could be included in the analyses (Parnell et al. 2010). Specifically, while evidence suggested that swash zone infauna were indeed consumed by ghost crabs, SIAR mixing models provided evidence that semi-terrestrial amphipods, associated with macrophyte beach wrack, served as an important additional food source for this beach consumer. The lowest contribution of swash infauna to ghost crab diets was recorded at ANC, the beach with markedly reduced abundances of swash zone macro-invertebrates but the highest densities of ghost crabs. Thus, data on infaunal abundances across the barrier island beaches, in conjunction with dietary analyses of the ghost crab, offer initial insight into features of the subtropical beach food webs examined here.

Dietary shifts by consumers as a result of variation in abundance of primary prey have been reported in trophic studies from diverse settings (e.g. rock lobsters and invertebrate prey, Edgar 1990; otters and fish, Remonti et al. 2008; invertebrates and white ibis, Dorn et al. 2011), and our findings now provide an example from a sandy beach ecosystem. When diets of ghost crabs from all 3 beaches were compared, distinctly different patterns of prey utilization were apparent. Specifically, diets of ghost crabs at CC, the site which supported the highest abundance of swash prey and specifically the highest biomass of mole crabs, reflected mainly consumption (67–73%) of swash animals. Ghost crabs from HI had diets similar to that of crabs from CC, with swash animals (68–69%) making up comparable proportions of the diet. Therefore, at these 2 beaches, diet composition verified the dominance of swash zone organisms as prey, as suggested by reports from other geographic areas (Wolcott 1978, Leber 1982). In contrast, stable isotope signatures for ghost crabs at ANC suggested a

diet composed mainly of amphipods (55–61%), possibly related to the low abundance of swash animals at this beach. Such reduced swash faunal abundances, in turn, may reflect the comparatively finer grain sediments at ANC, which are not preferred by these taxa, especially mole crabs (e.g. Rodil et al. 2012).

Our findings suggest an important role of wrack as a trophic subsidy on beaches, as has been noted in earlier investigations on beach food web structure. However, the significance of wrack subsidies has generally been limited to examples of wrack supporting terrestrial consumers such as lizards or spiders (e.g. Ince et al. 2007, Paetzold et al. 2008, but see Porri et al. 2011). At ANC, the use of seagrass wrack-associated amphipods as a common food source by ghost crabs, along with the relatively high availability of seagrass wrack, underlies the diet shift of ghost crabs at this beach. Semi-terrestrial amphipods are known to colonize freshly deposited wrack (Colombini et al. 2000, Porri et al. 2011) and often at high densities (Griffiths et al. 1983, McLachlan 1985). Therefore, an ample supply of amphipod prey may be supported by the high incidence and large biomass of fresh macrophytes at ANC. High densities of amphipods were observed within the wrack during collections at ANC (K. Morrow pers. obs.), while very few organisms were observed in the field or in the laboratory to be associated with wrack at CC. In addition, the shallow beach slope at ANC may facilitate retention of allochthonous input in the form of wrack subsidies and provide suitable habitat (moist wrack) for amphipods. Compared with ANC, greater beach slopes accompanied by increased wave energy (larger grain size of sediments) at both CC and HI may prevent stranding of a constant and fresh input of macrophytes on the beach. In fact, wrack that remained on beaches at CC and HI was often dry and located at the extreme high tide mark (K. Morrow pers. obs.), conditions that are suggested to be unsuitable for amphipods (Pelletier et al. 2011). Note that some evidence for amphipod prey utilization was recorded for ghost crabs at both CC and HI, although the dietary contribution was comparatively lower than that at ANC. This last finding suggests that some wrack and associated amphipods may remain on CC or HI outside the window of our sampling events.

In addition to prey availability, behavioral modification or non-consumptive effects may contribute to ghost crab dietary shifts at ANC. Studies from other marine settings have reported non-consumptive predator effects on prey (Matassa 2010, Gosnell & Gaines 2012). Ghost crab behavior may be related to predation threats from raccoons on ANC, as raccoons

feed preferentially on ghost crabs in some settings (Bouchard & Bjorndal 2000, Barton & Roth 2008). This suggestion is supported by field observations of raccoon tracks surrounding and extending between ghost crab burrows only at ANC across all sampling dates. Moreover, visual inspection revealed high numbers of ghost crabs near openings of their burrows, but noticeably only a low incidence of nocturnal forays by ghost crabs and low capture rate of ghost crabs at night by researchers at ANC when compared with ghost crab activity patterns at CC and HI. Finally, at ANC, nearly 50% of ghost crab burrows were located amongst the wrack line in our transect surveys (Fig. 2), and accordingly, amphipods on wrack represent the food source in closest proximity to any ghost crab remaining within, or very near, a burrow. Combined, these data and observations offer one possible explanation for the high proportion of amphipods in ghost crab diets from ANC as indicated by isotopic signatures: restricted ghost crab movement in response to predator activity. If so, then use of subsidies delivered to subtropical barrier islands and habitat utilization and behavior of higher level consumers (predators on ghost crabs) are both topics that merit more attention.

In summary, our results indicate notable differences in diet among populations of ghost crabs at 3 Floridian beaches, as reflected in stable isotope values of ghost crabs and accompanying results from mixing models. Dietary differences were associated with reduced abundance of primary prey (swash macroinvertebrates) at ANC and concomitant greater utilization of alternative amphipod prey by ghost crabs than at the 2 other beaches investigated. Our results suggest that, in addition to well-known factors such as sources of primary productivity, both products transported onshore and features of inland habitats that provide suitable habitat for high level consumers may contribute to variability in trophic structure of beach food webs. Human activities that result in removal of wrack subsidies and/or modification of inland landscapes adjacent to beaches may therefore have implications for sandy beach ecosystem functioning via impacts on trophic links of a major consumer.

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