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Distribution of Parasitic Isopods on Caridean Shrimp in South Florida Seagrass Beds

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Distribution of Parasitic Isopods on Caridean Shrimp in South Florida Seagrass Beds

By

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Submitted to the Faculty of Nova Southeastern University Oceanographic Center in partial fulfillment of the requirements for the degree of Master of Science with a specialty in:

Marine Biology

Coastal Zone Management

Nova Southeastern University

July 2013

Thesis of

Sarah Briggs

Submitted in Partial Fulfillment of the Requirements for the Degree of

Masters of Science:

Marine Biology and

Coastal Zone Management

Nova Southeastern University

Oceanographic Center

July 2013

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Acknowledgements

Abstract

Caridean shrimp are a prominent element of seagrass faunal communities and play an important role in the energy transfer between trophic levels. They are a food source for other organisms and play an integral role in the ecosystem by feeding on algae and assisting with the breakdown of organic matter. Carideans are also fundamental to the marine fishery industry in that they are a food source for potentially valuable juvenile commercial fish. Ectoparasitic isopods (Cymothoida: Bopyridae) that infest caridean shrimps decrease the energy level of the shrimp, resulting in slower reaction time, greater predation rate, slower growth rate, and/or reduced egg production. However, in South Florida, little is known about the distributions and effects of parasitism among caridean shrimp in seagrass habitats. This research investigates the relationship of caridean shrimps and ectoparasitic isopods throughout several marine and brackish basins of coastal South Florida ranging from Lostmans River on the lower southwest mangrove coast through Florida Bay and Biscayne Bay. Samples were collected at the end of the wet season in 2010 and the dry season in 2011 using a 1-m^2 throw-trap. Relations among isopods, carideans and environment were determined based on a series of biotic (host preference and availability) and abiotic (salinity, temperature, turbidity, water depth) factors. Bopyrid isopods were most abundant in Manatee Bay and Barnes Sound adjacent to the C-111 canal located in southern Biscayne Bay region and predominantly associated with *Hippolyte* spp. Logistical regression revealed that the likelihood of parasite presence is associated with higher temperatures, lower salinity, increasing depth, less seagrass coverage and greater macroalgae coverage. The results suggest that increased stressors in an environment, such as anthropogenic runoff, may also negatively impact host resistance to parasitism.

Keywords:

Bopyridae, parasitic isopods, caridean shrimp, seagrass beds, South Florida

Table of Contents

List of Figures

List of Tables

1.0 Introduction

Shrimps belonging to decapod crustacean Infraorder Caridea are abundant and important invertebrates in South Florida seagrass beds. Caridean shrimp play an integral role in the seagrass beds as important food resources for economically valuable organisms (Williams 1984; Anderson 1985; Bauer 2004). These crustaceans are known to carry ectoparasitic isopods belonging to family Bopyridae. The isopods can have long-lasting effects on shrimp reproduction and decreased response to potential predators. They often take advantage of their host's energy, which often reduces host growth, respiration, metabolism and survival (Anderson 1972; Opplinger and Clobert 1997). Bopyrids appear to include parasitic castrators that may partly or completely shut down host reproduction, while others show little or no effects on host reproduction (Williams and Boyko 2012).

1.1 *Caridean shrimp*

Infraorder Caridea (Dana 1852) is the largest group of shrimplike crustaceans and includes over 3,438 named species in 28 families and 389 genera throughout the world with new genera and species continually being described (Bowman and Abele 1982; Holthuis 1993; Bauer 2004; De Grave and Fransen 2011). They are distinguished most easily from other shrimplike decapod crustaceans in having the second abdominal pleura overlapping both the first and third. They differ from penaeoid shrimps in having phylobranchiate gills, and in brooding eggs on the abdominal pleopods. They also lack chelae, or claws, on the third pair of walking legs, which distinguishes them from both penaeoid and stenopodid shrimps (Williams 1984; Anderson 1985; Bauer 2004). Carideans vary in form, but always have one pair of stalked eyes, although they may be

1

covered by the carapace, as in Alpheidae. Alpheids have unique asymmetrical claws, of which the larger is used to produce loud snapping sounds for stunning prey (Chace and Abbott 1980; Bauer 2004). Adult carideans range in size from species that are a few millimeters long to others, such as *Macrobrachium rosenbergii*, that can grow longer than 30 centimeters (Poore and Ahyong 2004; Chace and Abbott 1980).

Carideans range from freshwater to marine and from shallow coastal to deep ocean habitats at all latitudes from tropical to polar regions (Dolmen et al. 2004); they include both pelagic and benthic forms, with the latter found on soft and hard substrates, as infauna and epifauna (Chace and Hobbs 1969; Williams and Chace 1982; Chace 1993; Bauer 2004; McLaughlin et al. 2005; Rintelen et al. 2012). Carideans are typically omnivorous; however, there are variations in feeding and diets particular to specialized feeding methods. Their first two pairs of clawed pereopods, referred to as chelipeds, are used to assist with finding and handling food, defense, and grooming (Bauer 2004). Snapping shrimps use a shock wave created by the snap of their claw to stun prey (Anker et al. 2006). Filter feeding carideans use the setae on their legs as sieves to collect particles from the water column. Some carideans use their chelae to scrape algae from rocks or, in the case of cleaner shrimp, to remove and feed on parasites and dead tissue from reef fish (Chace and Abbott 1980, Bauer 2004). In addition to their wide range of habitats and diets, carideans also form mutualistic associations with other organisms such as corals (Pratchett 2001), sponges (Fransen 2003), sea anemones (Knowlton and Keller 1983) and echinoderms (Criales 1984).

Carideans are important to the overall ecology of coastal ecosystems and aquatic resources, although they have little value as food to humans (Anderson 1985). The

majority of seagrass dwelling carideans are omnivorous, consuming other fauna, such as zooplankton, small crustaceans or polychaetes, as well as plant material (Odum 1972; Morgan 1980; Hieb 1999). They play an integral role in seagrass communities by feeding on algae and assisting with the breakdown of organic matter. They also serve as an essential link for transferring energy to higher trophic levels as prey for fish, crabs, and other invertebrates including the pink shrimp, *Farfantepenaeus duorarum,* a commercially important penaeid shrimp in South Florida (Welsh 1975; Anderson 1985; Pung et al. 2002). Some burrowing carideans are especially important in tropical and subtropical coastal habitats where they promote bioturbation and aerate the sediment. In mangrove forest systems, burrowing alpheid carideans are important consumers of litter material and aid in the recycling of nutrients to support productivity and seagrass production in these areas (Vonk et al. 2008).

Although most carideans are not directly linked to commercial fisheries, they can be credited for an indirect contribution to economically important fisheries. Caridean shrimp are considered fundamental to the fishery industry as a food source for juvenile fish that are commercially harvested as adults (Hieb 1999). Grass shrimps, *Palaemonetes* spp., are an important part of diets of a large number of commercial and recreational fishery species. These shrimps are often consumed by killifish and other small foraging fish which are then eaten by larger commercially important fish (Anderson 1985) such as sheepshead, seatrout, and red drum (Corey and Reid 1991).

Nevertheless, a few caridean shrimp species are harvested for human consumption in some parts of the world. Freshwater, *Macrobrachium dacqueti,* is cultivated in Asia and Africa (Sunier 1925). In the United States, caridean fisheries are

dominated by cold-water shrimps in family Pandalidae in the north Atlantic and Pacific oceans (Bracken 2008).

1.1.1 *Parasites*

Caridean shrimp host a variety of parasitic organisms. The most common are coccidia, microsporidians, trematode flatworms, and isopods (Anderson 1985). Coccidia and Microspora are both single-celled, spore-forming intracellular parasites. The former are apicomplexan protists, a group that includes the causative agent of malaria, while the latter are now classified as Fungi. Grass shrimp are an intermediate host for the coccidian, *Eimeria funduli,* which feeds on the liver and pancreas of estuarine killifish (Solangi and Overstreet 1980). Grass shrimp also serve as secondary intermediate hosts for the coastal marsh trematode, *Microphallus turgidus*. Shrimp heavily infected by this trematode can have altered swimming abilities, increasing the likelihood they will be eaten by a predator (Heard and Overstreet 1983; Pung et al. 2002). Microsporidians can cause a white appearance in the affected muscular tissues and are thought to damage reproductive capabilities of the infected shrimp (Overstreet and Weidner 1974). Among caridean parasites, the isopod, *Probopyrus pandalicola*, is well-documented on host *Palaemonetes* spp. (Anderson 1972; Anderson 1977; Anderson 1990; Cash and Bauer 1993; Bass and Weis 1999; Sheehan et al. 2011). Increased abundances of parasites, such as isopods, could possibly serve as indicators of environmental stress (Sheehan et al. 2011).

1.1.2 *Contaminated habitats*

Like all other organisms, carideans must provide energy for maintaining fitness necessary for survival prior to exerting energy towards reproduction. Disturbed

environments and those with higher exposure to concentrations of contaminants are often considered more stressful and provoke higher maintenance expenditures in order to avoid toxicity (Rowe 2002). Many parasites are sensitive to changes in environment, but others may be more resistant than their hosts and are thus likely to increase in numbers as levels of pollution rise (Mackenzie 1999). Parasite infection is considered an acceptable indicator of anthropogenic pollution due to decreased host defense mechanisms and fitness. Energy resources are redirected to stress tolerance for fighting low oxygen levels or repairing physiological damage from pollutants (Lafferty 2008; Penha-Lopes et al. 2011). Parasitic isopod, *Pseudione elongata africana,* has been reported as a biological indicator of sewage polluted mangrove habitats due to the much higher rate (at least 30%) of parasitism in contaminated areas compared to more pristine environments (Penha-Lopes et al. 2011; Williams and Boyko 2012). The grass shrimp, *Palaemonetes pugio*, has also been used as a bioassay organism in toxicity studies for water quality. They can be used as an indicator of sediment pore water quality and toxicity levels from point and nonpoint sources of petroleum, chemicals, and insecticide contamination in coastal areas (Anderson 1985; Lewis and Foss 1999) because they are often more sensitive to contaminants such as sewage and agricultural runoff than estuarine fish (Williamson et al. 2009).

      1.1.3 *Abiotic*

      Temperature and salinity, either independently or in combination, can play a major role in affecting the function and distribution of both marine and estuarine organisms, including caridean shrimp (Vernberg and Piyatiratitivorakul 1998). Alon and Stancyk (1982) found that life-history patterns of *P. pugio* located in a region with lower

salinity differed from a region with higher salinity, indicating the possibility that salinity has an effect on growth pattern. A population of *P. pugio* inhabiting a higher salinity environment typically grew more rapidly, had shorter life spans, and smaller clutch sizes than a population living in a less saline environment (Alon and Stancyk 1982). Temperature is a major factor in reproduction, although at lower temperatures (15-16°C), energy normally allocated to reproduction is instead used for metabolism in shrimp. Higher temperatures increase molting frequency, which may be partially attributed to higher respiratory rates at higher temperature (Hartnoll 1982; Allan et al. 2006). Grass shrimp, *Palaemonetes* spp., devote the majority of their ingested energy to reproduction and respiration during their adulthood (Alon and Stancyk 1982). Salinity has less of an effect on the reproduction effort of shrimp than temperature, but models predict that reproductive effort is higher in a low salinity population than in high salinity, likely due to less optimal conditions in the latter (Vernberg and Piyatiratitivorakul 1998).

1.2 *Isopods*

Isopoda is the most species-rich group in the crustacean superorder Peracarida and it includes approximately 10,000 named species ranging in length from 0.5 mm to 500 mm. Isopods are found in nearly all terrestrial and aquatic environments and include both free-living and symbiotic forms, particularly on fishes and crustaceans (Brusca and Wilson 1991; Poore and Bruce 2012). Symbiotic species are typically assumed to be parasitic, but the nature of these relationships is often unclear, i.e., they might be parasitic, commensal or phoretic. They fill a variety of niches as micrograzers, predators, detritovores, and parasites, and so contribute key elements to the energy cycle within specific habitats. More than 4,500 species are marine or estuarine and are typically

benthic dwellers (Brusca and Wilson 1991). Members of suborder Cymothoida are often

carnivores, predators, or parasites (Brusca and Wilson 1991; Brandt and Poore 2003;

Poore and Bruce 2012). Their mouthparts are reduced to form a cone with sharp stylets

(Kensley and Schotte 1989) for piercing the cuticle of the host (Williams and Bokyo

2012).

Members of the superfamilies Bopyroidea, Cryptoniscoidea, and Cymothooidea

are parasites in the isopod suborder Cymothoida, which attach to their hosts either

permanently or during their larval stages (Williams and Bokyo 2012). Bopyroids and

cryptoniscoids, informally referred to as epicarideans, are primarily ectoparasites that

feed on blood or ovarian fluids of marine crustacean hosts. They are the only isopods

parasitic on crustaceans rather than on fishes, and the only ones parasitic for their entire

lives, requiring crustacean hosts for all stages of their life (Kensley and Schotte 1989;

Williams and Bokyo 2012). They remain on their intermediate host, calanoid copepods,

until they reach their final larval stage and are ready to find a definitive decapod host.

They mature into adulthood while attached to their final hosts and remain there until

death (Anderson 1990; Williams and Bokyo 2012).

1.2.1 *Bopyridae*

Bopyridae, also known as bopyrid isopods, are commonly found on caridean

shrimp in South Florida. They have several physical and morphological differences

compared to free-living isopods (Stromberg 1971). Bopyrid isopods exhibit external

fertilization resulting in broods of thousands of eggs smaller than those of free-living

isopods (0.05-0.2 mm diameter) (Bourdon 1968; Stromberg 1971; Beck 1980a) and

develop through three larval stages into adulthood after leaving the brood pouch

(Kaestner 1970; Beck 1980a). In contrast, free-living isopods fertilize internally (Barnes 1974; Beck 1980a) with broods normally consisting of fewer than 100 larger eggs (0.3->1.0 mm diameter) (Stromberg 1971; Beck 1980a), and develop directly into a smaller version of the adult isopod while still in the brood pouch (Kaestner 1970; Beck 1980a). Bopyrid isopods also exhibit extreme sexual dimorphism (Schultz 1969; Beck 1980a), while free-living isopod females are only slightly larger than males (Kaestner 1970; Beck 1980a). In addition, adult female bopyrid isopods have an asymmetrical body shape with partial to complete loss of eyes and mouthparts modified for piercing and sucking (Kaestner 1970; Beck 1980b). In contrast, free-living adult female isopods exhibit a symmetrical body shape with well-developed eyes and their mouthparts are used for chewing (Kaestner 1970; Beck 1980a). Unlike female bopyrid isopods which have a male attachment for life, both genders of free-living isopods live separately from one another (Kaestner 1970; Beck 1980a).

Within Bopyroidea, members of family Bopyridae are usually ectoparasites on decapod crustaceans (Dale and Anderson 1982; Markham 1986) and can alter reproductive capability of their hosts by modifying external sexual characteristics, reducing gametogenesis or completely sterilizing the host (Beck 1980b). Bopyridae contain at least 80% of the described species of superfamilies Bopyroidea and Crytoniscoidea (Williams and Madad 2009) and contains at least 590 species which parasitize not only shrimp but a variety of hermit crabs, porcelain crabs, and lobsters (Markham 1986; Chaplin-Ebanks and Curran 2007; Williams and Madad 2009; Anyong 2011). Larval bopyrids are ectoparasites of calanoid copepods until they reach their final larval stage and choose decapods as their definitive hosts where they remain for the

remainder of their lives (Markham 1985; Williams and Bokyo 2012). An adult must remain on its host, as its pereopods are reduced, its eyes most likely have little to no function and most of its energy is devoted primarily to producing multiple broods of offspring (Markham 1986).

Bopyridae is divided into nine subfamilies; six are found in the northwestern Atlantic Ocean and each is almost exclusively restricted to hosts in a single decapod infraorder (Markham 1985,1986). The majority of species belong to the following subfamilies: Pseudioninae, Argeiinae, Bopyrinae, Ioninae, and Orbioninae. They infest their hosts' branchial chambers and typically attach to the cephalothorax of the host beneath the carapace, which produces an obvious lump or deformation in the hosts' exoskeleton (Dale and Anderson 1982; Bass and Weis 1999). The branchial chamber, which contains the gills of a caridean shrimp, is enclosed by the branchiostegite, an extension of the carapace (Bauer 2004). Subfamilies Phyllodurinae, Athelginae, and Hemiarthrinae are the second largest group of bopyrids and are all abdominal parasites. Subfamily Entophilinae are the only known internal bopyrids and infest the host's visceral cavity (Markham and Dworschak 2005). Unlike the branchial parasites which leave an obvious bulge in the carapace of the host, abdominal parasites leave no visible sign of their presence once they are removed (Markham 1986). Attachment positioning on the host is only definitive for the adult parasite, whereas the larvae may attach to a variety of locations (Markham 1972). Most species that appear to be abdominal parasites attach to the host ventrally; however, a single species, *Metaphrixus intutus* attaches to the dorsal side of the host's abdomen (Bruce 1965).

Bopyrids usually reside in fairly shallow waters, although a few species penetrate below 4000 meters. The greatest diversity of bopyrids is found in the northwest Pacific Ocean. Distribution patterns of these isopods are thought to be influenced by the distributions of both definitive and intermediate host species, but few data are available to fully justify the primary mechanisms of distribution (Williams and Bokyo 2012). Bopyridae are rarely, if ever, host species-specific; however, suitable host calanoid copepod and decapod species must be available in order for the isopod to survive (Markham 1986; Williams and Boyko 2012).

Carideans serve as hosts to the bopyrid subfamilies of Pseudioninae, Argeiinae, Bopyrinae, and Hemiarthrinae (Markham 1986). Bopyrinae and Hemiarthrinae are exclusively hosted by caridean shrimps. Several species of both Bopyrinae and Hemiarthrinae infest carideans in the Western Atlantic Ocean, including coastal South Florida seagrass beds. Of the 37 known species from the northwestern Atlantic, 23 are found in Florida waters, both fresh and marine (Markham 1985).

1.2.1.1 *Bopyrid life cycle*

Life cycles of bopyrids vary slightly, but typically follow a similar pattern. An adult female parasite matures on the host and upon becoming gravid, she expands with eggs, which are released when the host molts its exoskeleton (Beck 1980a). Bopyrids pass through three larval stages once released from the host marsupium (Beck 1980b; Jay 1989). The first, a free-swimming epicaridium larva characterized by a stout, segmented body, swims using its antennae and pleopods to find and attach to an intermediate host, such as a calanoid copepod (Dale and Anderson 1982). The microniscus stage, distinguished by the loss of swimming function of the antennae and pleopods, is reached

10

quickly as the larva develops and increases in size while on the copepod (Beck 1980b).

After the isopod metamorphoses into its final larval stage, cryptoniscus, characterized by

a more elongate body and seven pairs of pereopods modified as holdfasts, it detaches

from the copepod and seeks its definitive decapod crustacean host (Beck 1980b; Dale and

Anderson 1982). The isopod often attaches to its juvenile caridean host and grows with

the shrimp (Anderson 1975; Beck 1980; Cash and Bauer 1993). After initial attachment

to its final host, the cryptoniscus will begin to develop into a female isopod. The next

isopod that attaches to the same individual host will develop into a dwarf male and join

the female for reproduction (Jay 1989; Kensley and Schotte 1989; Cash and Bauer 1993).

Male isopods attach to the females but are not known to feed on the hosts (Williams and

Boyko 2012).

All epicarideans show sexual dimorphism with the smaller dwarf males lacking

asymmetrical bodies displayed by adult females (Williams and Boyko 2012). Host

carapace length is highly positively correlated with female isopod length suggesting the

isopod attaches to the host early in life and grows with the shrimp (Cash and Bauer 1993;

Roccatagliata and Lovrich 1999; Paradiso et al. 2004). As bopyrids normally die prior to

their hosts, larger crustacean individuals are often found unparasitized (Pike 1960; Beck

1980b). Hosts may be found with stretched or lumpy carapaces over their branchial

chambers without an isopod inside indicating a previous infestation (Paradiso et al.

2004).

1.2.1.2 *Impacts on benthic fauna*

Parasitic isopods influence several commercially important hosts such as

brachyuran crabs, king crabs and shrimp (Markham 1985; Williams and Boyko 2012).

Parasites often take advantage of their host's energy, which often reduces host growth, fecundity, and survival (Opplinger and Clobert 1997), making them more vulnerable to predation. They can delay the ability of the host to respond to predation, leading to decreased survival rates (Bass and Weis 1999). *Probopyrus pandalicola* reduces respiration and metabolism in its host shrimp (Anderson 1972). Predator-prey studies demonstrate higher prey capture rates in stressed prey because they are more vulnerable to predation. Substandard individuals are usually an easier target for predators, because they have a harder time escaping or defending themselves. Predators also exert less energy while capturing weaker prey (Temple 1987). A behavioral study on *P. pugio* parasitized by *P. pandalicola* resulted in lower host activity levels and reduced prey capture relative to non-parasitized shrimp (Bass and Weis 1999).

Some bopyrids are considered partial parasitic castrators, because they have not been proven to completely shut down the reproduction of the host. Other bopyrids show little or no effects on reproduction, while some others appear to be complete parasitic castrators (Williams and Boyko 2012). Species such as *P. pandalicola* can cause castration and prevent reproduction in shrimp and crab species (Lafferty and Kuris 2009). The energy drained from the host may result in the sacrifice of reproductive organs (Pike 1960; Lafferty and Kuris 2009). Another bopyrid, *Eophyrxus lysmatae,* parasitizes the simultaneous hermaphroditic caridean, *Lysmata seticaudata*, but only induces castration in females (Calado et al. 2005).

Native parasites do not normally have significant impacts on host populations; however, parasitic isopods introduced to new areas have been known to create negative effects on the host populations living there. The bopyrid, *Orthione griffenis,* was

introduced from Asia to the northwest coast of the United States during the late 1980's

(Williams and An 2009; Chapman et al. 2011; Williams and Boyko 2012). This parasite

is thought to have caused the collapse of mud shrimp populations after its introduction to

the area. The host shrimp was a key player that influenced sedimentation, which in turn

impacted the stability of the commercial bivalve fisheries (Williams and Boyko 2012).

Bopyrids do not cause a threat to humans but can create a negative effect on the infected

hosts which are no longer as aesthetically pleasing (Paradiso et al. 2004).

1.3 *Seagrass ecosystems*

Estuarine and bay ecosystems are some of the world's most productive habitats

for a wide range of organisms (Lirman et al. 2008) and occur in coastal areas worldwide.

Many coastal areas support abundant seagrasses, mangroves, or macroalgae that act as a

filter between the land and the ocean, trapping both anthropogenic and natural runoff

from river input (Qiu et al. 2010). Seagrass beds, which are found worldwide in

temperate and tropical climates (Orth et al. 2006), are an important aspect of coastal

marine environments and provide habitat for commercially important fish and

invertebrates and foraging grounds for coastal birds (Beck et al. 2001; Fourqurean et al.

2001). These flowering plants live fully underwater and strongly influence the physical,

chemical, and biological conditions of the coastal environments that they inhabit

(Costanza et al. 1997; Orth et al. 2006). Seagrasses can modify nutrient cycling, trophic

levels, and water flow (Hemminga and Duarte 2000). They can also decrease wave

energy, improve sediment stability and improve water clarity (Fourqurean et al. 2001).

Seagrass root systems help stabilize the sediment and are also an important part of the

carbon cycle as they produce substantial amounts of organic carbon (Fourqurean et al.

2001). Although coastal areas are subject to changes from natural freshwater and nutrient influxes (Hefner and Brown 1985), rapid alterations to seagrass ecosystems have also occurred due to increased nutrient runoff, hydrological alterations, overfishing, and introduction of invasive species (Orth et al. 2006).

1.4 *Coastal South Florida*

South Florida is part of a subtropical climate region with two distinct seasons: wet and dry (Hela 1952; Tabb et al. 1962). The area experiences an increased amount of rainfall during the wet season, May through November. The dry season, December through May, has significantly lower amounts of precipitation and milder temperatures (Sutula et al. 2003). The freshwater flow through the Everglades is naturally influenced by the season and, therefore, causes changes in abiotic water properties, such as temperature and salinity, where it empties into Florida Bay (Sutula et al. 2003). As the end of rainy season approaches, organic decomposition is highest, producing low dissolved oxygen levels that often drive fish and invertebrates out of shallow waters (Tabb et al. 1962).

1.4.1 *Lower Southwest Coast*

On the southwest region of the Everglades, approximately 50 km west of Miami, freshwater flows through the Shark River Slough and drains into the Gulf of Mexico via various rivers (Bolster and Saiers 2002). The majority of flow through Shark River Slough dumps freshwater as far north as approximately Lostmans River which connects directly to the Gulf of Mexico and south to approximately Whitewater Bay protected from the gulf by Cape Sable. The Shark River Slough is considered a true estuary because it experiences tidal mixing of fresh- and sea-water (Tabb et al. 1962) causing

basins in this region to experience a range of salinity caused by tidal fluxes and seasons.

Shark River Slough is mostly a meter or less deep and is chiefly lined with organic mud

over limestone rock (Bolster and Saiers 2002). Whitewater Bay and Oyster Bay, located

between Cape Sable and the mainland, averages roughly one and a half meters and two

meters, respectively, in water depth (Tabb et al. 1962). Core samples reveal marine

sediments overlying freshwater mud, which was deposited on bedrock and freshwater

peat approximately 4,000 years ago. The sequence reflects the sea level rise that

inundated the margins of the Everglades, creating the shallow coastline of southwestern

Florida that is now dominated by mangrove forests (Scholl 1964).

Salinity is one of the most influential environmental factors affecting the

communities in the lower southwest coast of Florida. Whitewater Bay has experienced

significant fluctuations in salinity beginning in the 1920's due to anthropogenic

development. Altered water flow through Shark River Slough caused local salinities to

double on average (Tabb et al. 1962). Due to the swift currents created by tidal flux in

Whitewater and Oyster Bays, the substrate is only sparsely covered with vegetation. Red

algae (Rhodophyta) such as *Dasya* spp. and *Gracilaria* spp. become dominant during

periods of high salinity. Species of *Caulerpa* (Chlorophyta), *Laurencia* and

Acanthophora spp (Rhodophyta) dominate in channels. During the dry season, when

salinities are higher, macroalgae are most abundant and serve as shelter for large numbers

of carideans, *Palaemonetes* spp. and *Leander* spp., and small fish including *Gobiosoma*

robustum (Gobiidae) and *Chasmodes saburrae* (Blenniidae) (Tabb et al. 1962).

1.4.2 *Florida Bay*

Florida Bay, a shallow lagoon notable for its seagrass-covered mud banks, lies between the southern tip of mainland Florida and the Florida Keys (Holmquist et al. 1989). Its sediment is 95-99% locally generated biogenic carbonate (Prager and Halley 1999). Seagrasses are a common feature of shallow coastal waters all around the world, but not many areas have such widespread fields as Florida Bay (Iverson and Bittaker 1986; Zeiman et al. 1989). Because the bay is so shallow, winds are a major factor in water circulation. Turbulence created by the wind is a significant source of the typically high levels of turbidity (Tabb et al. 1962). However, water circulation is restricted by carbonate mud banks that divide the bay into smaller basins, creating environmental and biological gradients along transects from southwest to northeast (Robblee et al. 1991b). Mud banks covered in the seagrasses *Thalassia testudinum*, *Halodule wrightii*, and *Syringodium filiforme* provide a habitat with much greater biomass than the rest of the basin (Holmquist et al. 1989). The seagrass rhizomes are thought to bind and hold sediments, while organisms living among the seagrasses contribute to the sediment budget (Prager and Halley 1999). This area is an ecologically important nursery for a variety of organisms, including commercial and recreational fishes, shrimp, and crabs (Fourqurean and Robblee 1999). Carideans are especially abundant in *Thalassia* environments. Palaemonids such as *Periclimenes longicaudatus* and *Periclimenes americanus* and the hippolytids *Tozeuma carolinensis*, *Thor floridanus*, and *Hippolyte pleuracanthus* are some of the most abundant (Tabb et al. 1962).

Salinity is a major environmental factor affecting flora and fauna communities in Florida Bay and surrounding areas (Tabb et al. 1962). Freshwater flows into Florida Bay

through Taylor Slough, and water conditions range between brackish and hypersaline depending on runoff volume (Robblee et al 1991). Taylor Slough is much narrower than Shark River Slough and empties freshwater into central Florida Bay. Within the past several decades, significant habitat changes have occurred due to droughts, seagrass die-offs, increased turbidity, and, during 1987-1991, algal blooms (Fourqurean and Robblee 1999). Most modifications were due to anthropogenic changes of natural water flow through the Everglades associated with increased development and agriculture. Man-made canals and altered waterways significantly decreased water flow through Taylor Slough into Florida Bay (Sutula et al. 2003) which altered salinity and overall ecology, and negatively affected resident organisms, including carideans. During the 1990's, restoration projects were initiated with the intent to return Florida Bay to its unaltered state (Fourqurean and Robblee 1999).

1.4.3 *Biscayne Bay*

Biscayne Bay, another shallow, subtropical southern Florida lagoon, lies immediately southeast of the highly populated, urban Miami area, which makes it susceptible to anthropogenic activities and changes in water quality (Lirman et al. 2008). This rectangular-shaped carbonate estuary covers approximately 700 km^2. Maximum depth is four meters, except where it has been dredged to allow large ships into the Port of Miami (Caccia and Boyer 2005). The northern portion of Biscayne Bay extends from Dumfoundling Bay south to the Rickenbacker causeway; including the Port of Miami and the Miami River. This area is highly urbanized and subject to harmful runoff and chemical leaching (Corcoran et al. 1984) which can affect the water quality of the ecosystem (Bhat and Stamatiades 2003). This area suffers from habitat loss, high

turbidity, sewage pollution, and excessive nutrient loading (Caccia and Boyer 2005, 2007). The central section of the bay extends from Rickenbacker causeway south to Featherbed Bank in Black Point and is the transition between the highly urbanized north and the less developed south (Corcoran et al. 1984). The majority of pollution problems in this area result from localized problems at marinas (Caccia and Boyer 2005). The southern section of the bay includes the area south of Featherbed Bank through Card and Barnes Sounds which is just south of Turkey Point power plant (Caccia and Boyer 2007; FDEP 2011). The majority of southern Biscayne Bay is located in Biscayne National Park and generally experiences better water quality than other parts of the bay (Caccia and Boyer 2007); however, this area contains several canals draining landfills and agricultural areas (Caccia and Boyer 2005). For this study, Biscayne Bay region, which will be referred to throughout as simply Biscayne Bay, also included Manatee Bay and Barnes Sound.

The bay supports benthic communities of seagrass, macroalgae, and hard bottom with sponges and corals (Lirman et al. 2008) and provides habitat for a wide variety of invertebrates, fish, and shorebirds, as well as the endangered manatee and American crocodile. Like Florida Bay and other coastal wetlands globally, this area has also experienced changes such as hypersalinity, pollution, loss of some species, and seagrass die-offs due to increased population growth and harmful watershed, especially in the northern region of the Bay adjacent to the Port of Miami. Turbidity in the northern region has also become a problem, and some benthic communities have been affected by dredging (Caccia and Boyer 2005).

Seagrass beds in Biscayne Bay composed of *T. testudinum, H. wrightii,* and *S. filiforme* cover more than 70% of the bottom, providing essential habitat for fish and invertebrates. Freshwater runoff influences seagrass distributions in the bay. *H. wrightii* tolerates low salinity better than the other two seagrass species and can dominate nearshore habitats more influenced by freshwater discharge. *T. testudinum* and *S. filiforme* may not be as productive in areas of lower salinity (Lirman and Cropper 2003).

1.5 Objectives

The primary objectives of this study are: (1) to determine the occurrence of parasitic isopods on carideans and their distribution in coastal seagrass beds in South Florida, and (2) to identify which shrimp species are most often parasitized and by which isopod species. Possible factors involved in isopod distribution and abundance may be host availability, salinity, temperature, water depth, turbidity and type of vegetative (or lack of) ground cover.

Hypotheses

- *Community diversity and density of caridean shrimp and associated isopods differ spatially among South Florida estuaries.*

From the Lower Southwest Coast through Florida Bay to North Biscayne Bay on the east coast of Florida, a range of bottom sediment types, flora, and canopy height create different habitats specific for certain organisms. Shrimp densities are thought to differ in regions of the study area in response to biotic and abiotic factors, such as salinity and benthic vegetation. Marine isopods associated with the shrimp are also likely to have compositional and density differences based on host location.

- *Isopod density differs between sampling seasons.*

South Florida has distinct wet and dry seasons, typically with increases in abundances and densities of both flora and fauna during the wet, rainy season. Therefore, isopod densities may also fluctuate with temperature, salinity, water depth and/or vegetation.

- *Isopod density and composition vary based on the caridean community at each location.*

Debate exists about bopyrid specificity relative to host carideans. Hutton (1964) and Hutton and Sogandares-Bernal (1960) reported that bopyrid parasites are commonly host specific whereas Markham (1986) reported that host species-specificity is rare among the Bopyridae. This study will test levels of isopod/caridean host specificity and will examine whether parasite community composition and density correlates with those of host shrimp species.

2.0 Materials and Methods

The carideans (and their isopod parasites) studied in this project were provided by the South Florida Fish and Invertebrate Assessment Network (FIAN) project (Robblee and Browder 2012). Samples were collected by FIAN at the end of the rainy season in September and October 2010 and at the end of the dry season in April and May 2011.

2.1 *Field locations*

Carideans were collected at current FIAN sites in 19 different basins in three regions of South Florida nearshore waters (Figure 1): Biscayne Bay, Lower Southwest Coast, and Florida Bay. Lower Southwest Coast sites (Figure 2) included Oyster Bay (OYS), Lostmans River (LOS), Ponce de Leon Bay (PON), and Whitewater Bay (WHT). Florida Bay sites (Figure 3) included Rabbit Key Basin (RAB), Johnson Key Basin

(JON), Eagle Key Basin (EAG), Rankin Lake (RAN), Duck Key Basin (DUK), Crane Key Basin (CRA), Whipray Basin (WHP), and Calusa Key Basin (CAL). Biscayne Bay sites (Figure 4) included North Biscayne Bay (NBB), Port of Miami (POM), North Black Point (NBL), South Black Point (SBL), Barnes Sound (BAR), Manatee Bay (MAN), and Card Sound (CAR) (Robblee and Browder 2012). Lower Southwest Coast, Florida Bay and Biscayne Bay regions will be referred throughout as simply Lower Southwest Coast, Florida Bay, and Biscayne Bay. Variations in benthic vegetation among the sampling sites can be roughly clustered into three groups. The four Lower Southwest Coast sites, OYS, LOS, PON and WHT, cluster within mangrove habitat. NBB and POM from Biscayne Bay and JON, RAB, and RAN from Florida Bay cluster together based on similar compositions of mixed seagrasses and taller canopy heights (>30 cm). The remaining basins typically have shorter canopy heights (<30 cm) (Robblee and Browder 2009).
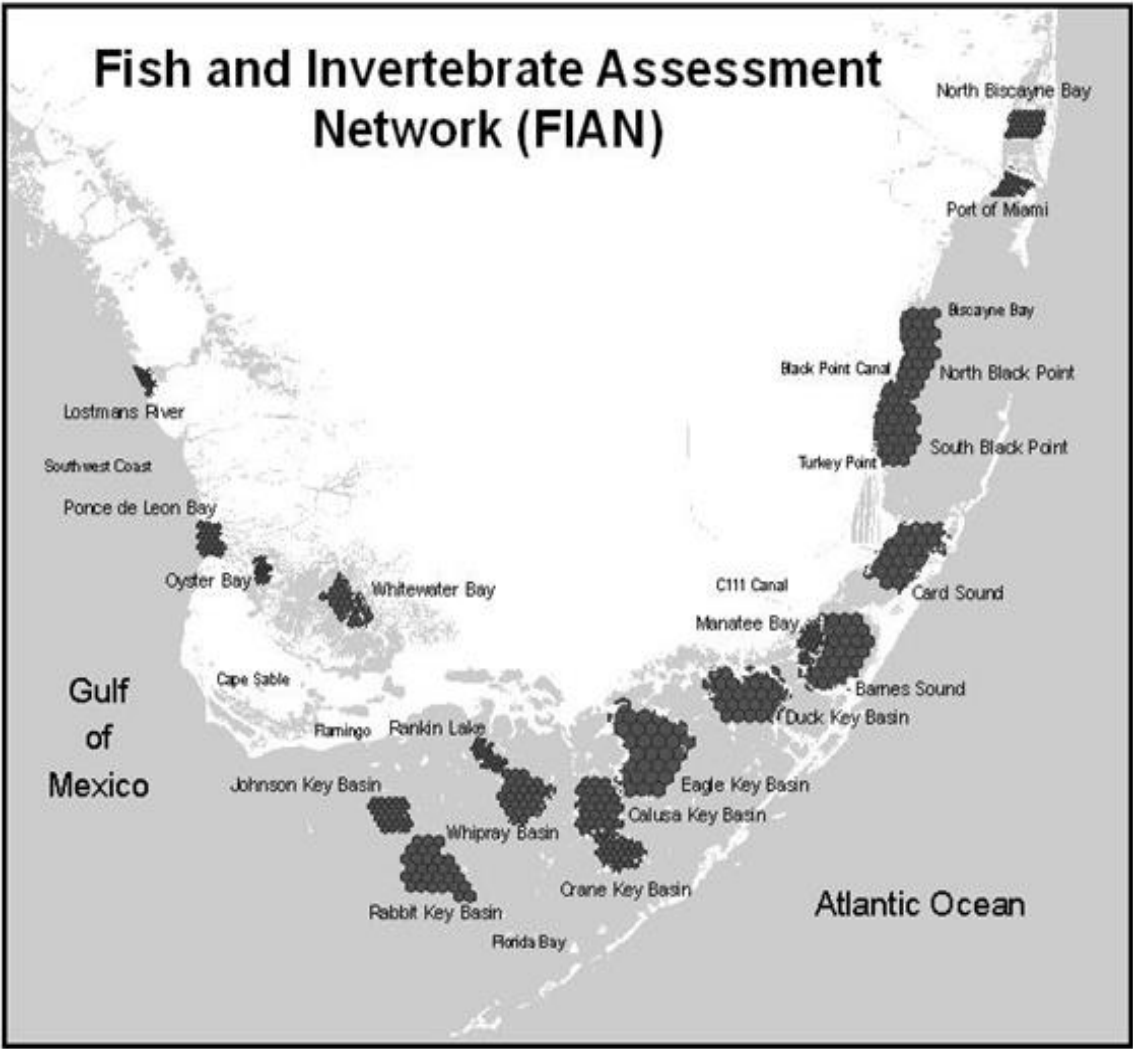
Figure 1. Overall study area (Robblee and Browder 2012).

Lower Southwest Coast Region
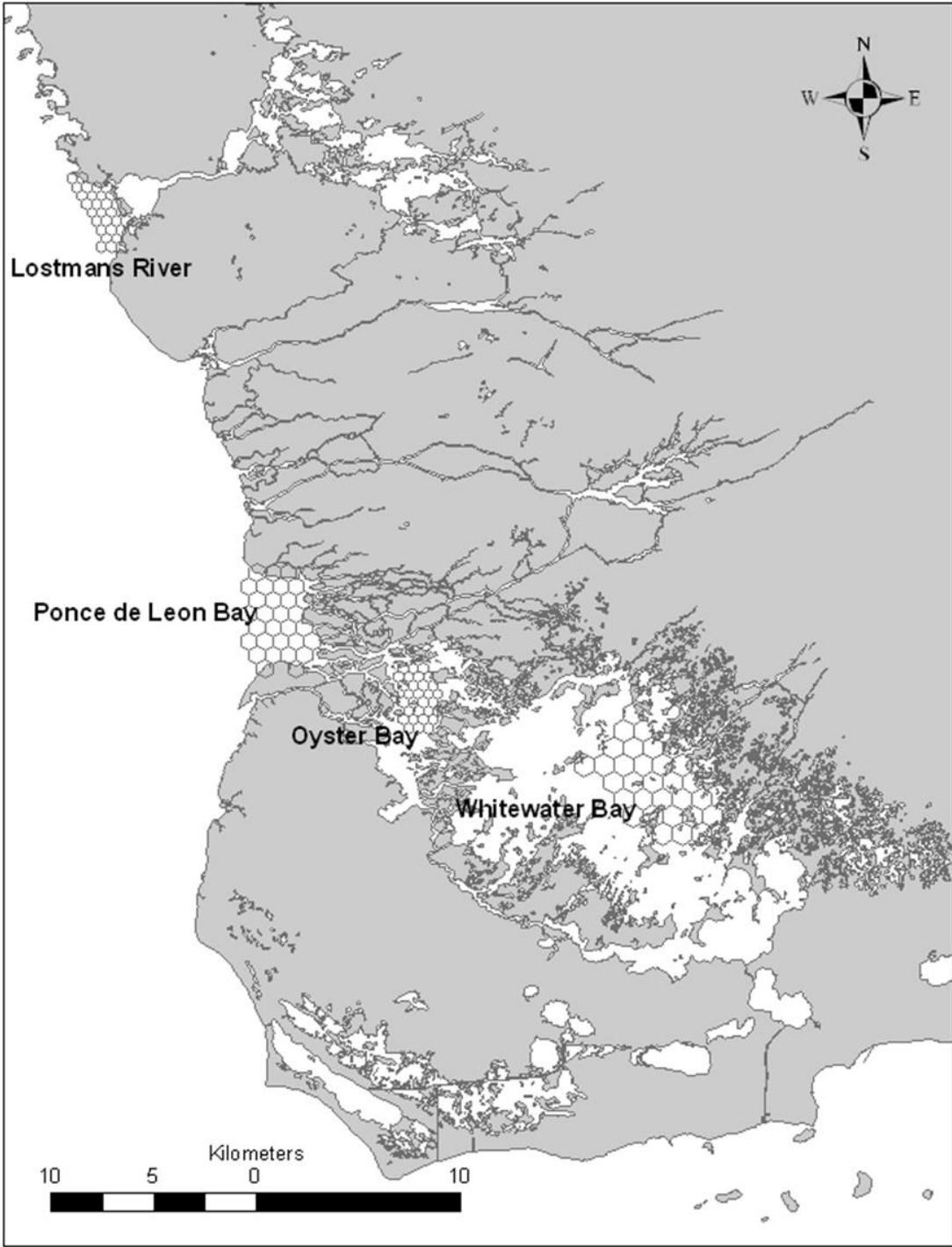
Figure 2. Basins in Lower Southwest Coast sampling areas include Whitewater Bay (WHT), Oyster Bay (OYS), Ponce de Leon Bay (PON), and Lostmans River (LOS) (Robblee and Browder 2012).
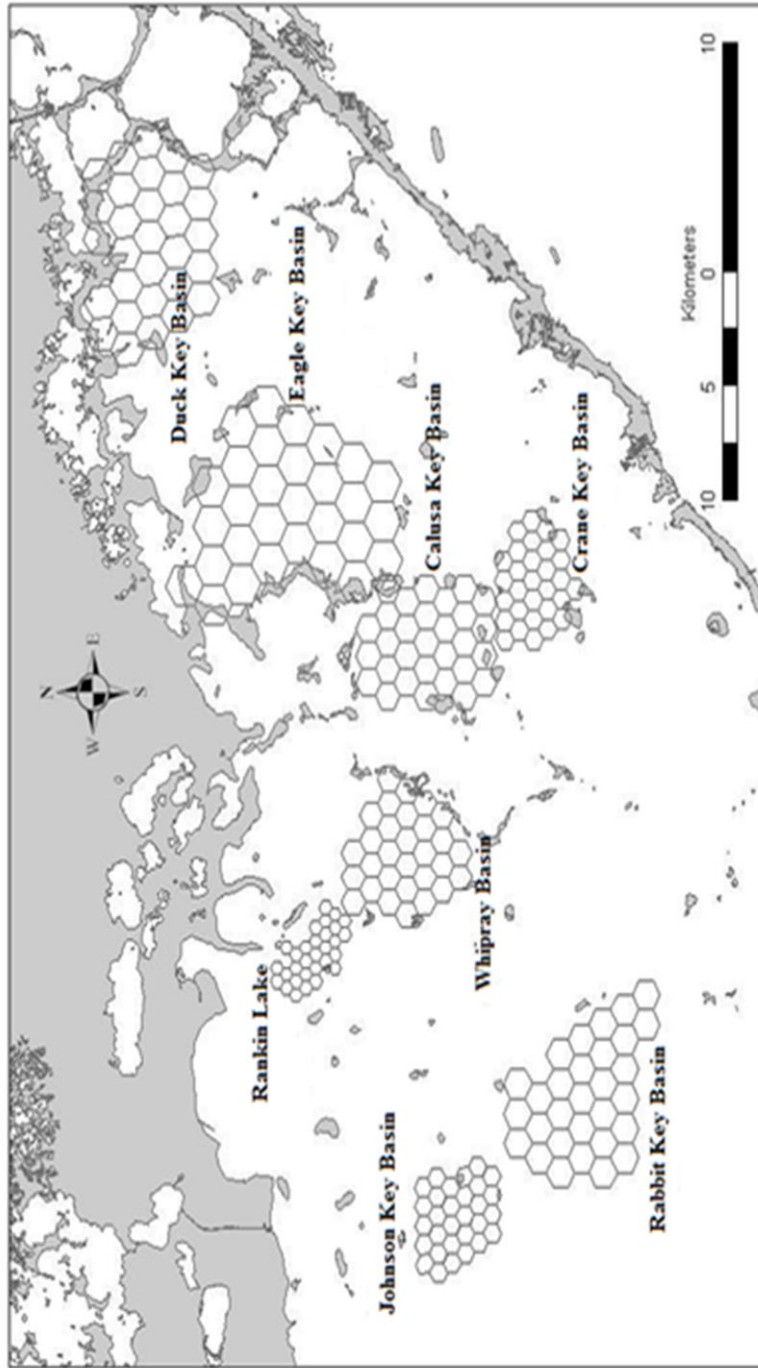
Figure 3. Basins in Florida Bay sampling areas include Duck Key Basin (DUK), Eagle Key Basin (EAG), Calusa Key Basin (CAL), Crane Key Basin (CRA), Whipray Basin (WHP), Rankin Lake (RAN), Johnson Key Basin (JON), and Rabbit Key Basin (RAB) (Robblee and Browder 2012).
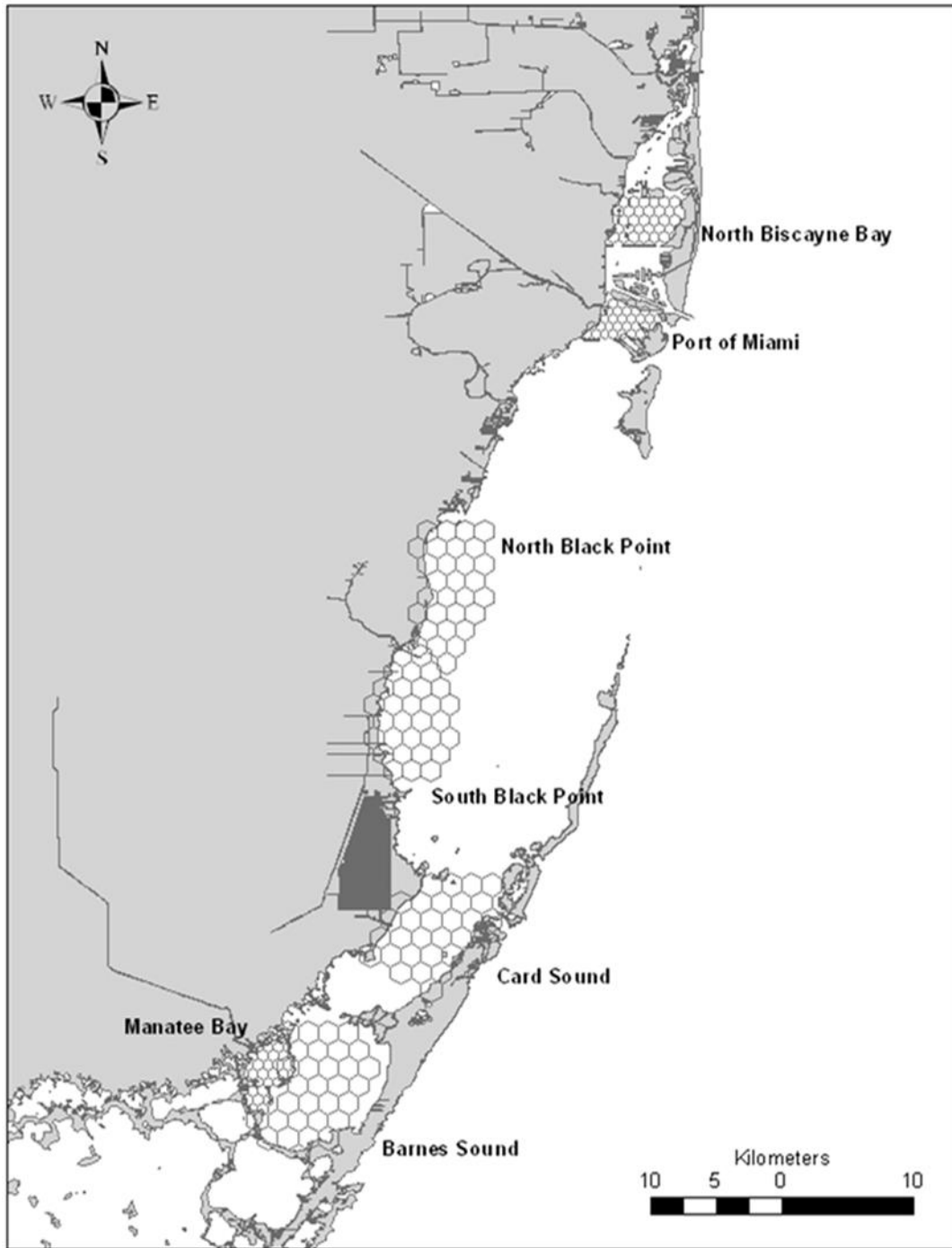
Figure 4. Basins in Biscayne Bay sampling areas include Port of Miami (POM), North Biscayne Bay (NBB), North Black Point (NBL), South Black Point (SBL), Card Sound (CAR), Barnes Sound (BAR), and Manatee Bay (MAN) (Robblee and Browder 2012).

Where feasible, basins were defined by geomorphic features such as islands, channels and banks. Sampling grids of 30 equal-sized hexagonal cells were fitted over each basin sampled using GIS. The size of the grid varied among basins depending on geomorphic features but was of a size sufficient to encompass gradients of environmental conditions and benthic vegetation characterizing each basin. The area sampled among the seven basins in Biscayne Bay covered 210 m^2. The area sampled among the eight basins in Florida Bay encompassed 240 m^2. The four basins sampled in Lower Southwest Coast covered 120 m^2. The grids only encompass waters that are accessible to a shallow-draft boat (Robblee and Browder 2009). One GPS-based sampling site in each of the 30 grid cells in all 19 sampling basins were randomly generated by computer for a total of 570 sites sampled in each of the sampling periods. At each site, water quality was observed and sampled, specimens collected, and seabed flora assessed.

2.2 *Abiotic factors*

Water depth was estimated using a 3-m polyvinyl chloride pole (PVC) marked with 1-cm increments. Sediment depth was also recorded at each sampling site using a 3-m (PVC) rod (1/2 inch diameter) marked in 1-cm increments. Salinity and temperature were taken at the surface and bottom water of each sampling site using a handheld WTW 330i Conductivity Field Meter (Robblee and Browder 2009). Water samples from each site were collected in separate bottles, stored on ice in a cooler, and transported to the laboratory for turbidity analysis using an HF Scientific DRT-15CE portable turbidimeter with measurements in nephelometric turbidity units (NTU).

2.3 *Caridean sampling*

A single, randomly located caridean shrimp sample was collected in each of the 30 grid-cells established for each basin. Samples were collected using the 1-m^2 throw-trap method reported by Kushlan (1981) to be highly quantitative and efficient for collection in shallow areas. The throw-trap method captured organisms during the FIAN project with 95% efficiency (Robblee et al. 1991a; Browder et al. 2005). The 1-m^2 throw-trap is a 45-cm deep aluminum box with openings at both ends (Figure 5). Curtain nets, panels of weighted mesh netting, large enough to cover the trap were attached at the top (Robblee and Browder 2009). The throw-trap was tossed into the water followed by two divers using a hookah device developed by the U.S. Geological Survey: a surface-supplied air source with two regulators and hoses attached to a cylinder. The hoses are on a reel that can be wound or unwound to give appropriate slack to the divers. The deepest site sampled was 6.4 m; however, typically sampling sites were shallower than ~3 m. Sites shallow enough for researchers to stand with head above water were completed without the hookah.

Once the trap had settled on the sediment, the divers made a pass with a sweep net in a vertical chopping motion from one side to the other to collect specimens in the trap. The sweep nets were 1-m wide (0.16-mm mesh) with hinged frames to allow the net to be folded in half to eliminate loss of collected animals while being returned to the boat. The divers then swept the trap with a second sweep net in the same manner but in the opposite direction. The throw-trap was covered with the mesh panels after each sweep to contain organisms. This process was performed a total of five times, alternating sweep direction each time, at each site. As noted above, 30 samples were collected from each of the 19

sampling basins for a total of 570 samples per sampling season (Robblee and Browder 2012).

Figure 5. Throw-trap used for sampling fish and invertebrates associated with the seagrass canopy. Curtain nets located on two parallel sides of the trap covered between sweeps to prevent animals from escaping.

After the divers returned each sweep net to the boat, another researcher on the boat rinsed the contents of the sweep net over a 1-mm sieve. The contents were then transferred to a mesh collection bag (0.16-mm stretch mesh) and securely fastened, tagged with site location and date, and stored on ice in a cooler for future analysis. Samples were preserved in a 10% formalin solution upon return to the dock until they were analyzed in the lab (Rehage and Loftus 2007; Robblee and Browder 2009). Samples were stored in formalin for at least 96 hours. A small portion of samples from Rabbit Key Basin during the 2011 dry season were preserved in denatured formalin

causing some animals to deteriorate and likely affecting the representation of shrimp in the sites in that basin.

2.4 *Benthic Vegetation*

At each site, a researcher assessed the algae and seagrass coverage using the Braun-Blanquet cover-abundance method, which involves identifying a specific area (e.g., quadrat or plot) based on the plant community being sampled, classifying all species represented in that area, and then assigning each one a numerical code based on its abundance in the given area (Braun-Blanquet 1932). Vegetation abundance coverage contributes distributional, as well as structural data that are important for habitat assessments (Wikum and Shanholtzer 1978). Abundance codes were used to quantify the amount of vegetation in each sample area (Table 1). Vegetation was identified using Littler and Littler (2000) and Littler et al. (1989).

Table 1. Braun-Blanquet abundance codes based on vegetative cover in given quadrat.

Abundance Code	Amount of Coverage
0.1	Solitary
0.5	Sparse
1	~5%
2	5-25%
3	25-50%
4	50-75%
5	75-100%

Abundance codes can be considered somewhat subjective; however, they provide a reasonable estimate of vegetative cover to aid in abundance determination and community structure. The precision of results increases with the number of sample areas examined and the results provide a more accurate account of species distribution

throughout the entire community (Braun-Blanquet 1932). This method, or similar

methods, allow a larger area to be quantified in less time (Wikum and Shanholtzer 1978).

At each site, species of vegetation were recorded within a 0.25-m^2 quadrat at six

locations surrounding the boat. Five of the locations created a semi-circle around the

perimeter of the boat (portside to starboard) and the sixth was located immediately to the

top right corner relative to the side farthest from the boat. Vegetation could not be

measured directly inside the trap because an uncovered trap would have allowed

organisms to escape (Robblee and Browder 2009). For this study, the mean of all six

replicate samples per site was used for analyses.

2.5 *Laboratory procedures*

Following preservation, samples were rinsed under running fresh water to remove

formalin residue. When in contact with formalin or formalin residue, gloves, respirator,

and protective eyewear were always used. Each sample was sorted and all carideans

were removed, counted, identified and stored in 70% ethanol. Specimens were chiefly

identified to genus due to the vast sample size and lengthy process of identification to

species. In particular, gender identification is required to determine between female

Hippolyte pleuracanthus and male *Hippolyte zostericola* (Chace 1972). For this study,

genus identifications proved sufficient for analyses because isopods were specific to a

particular genera rather than species. Carideans with an isopod occurrence were further

identified to species level if they were not damaged or missing vital body parts required

for identification. Shrimp with any deformities caused by parasitism were also separated

for further analysis and identification to species.

Carideans were identified chiefly to genus using Williams (1984) and Abele and Kim (1986) and personal communications with Laura Petteway, NOAA Fisheries/USGS. Additional sources for identification of shrimp species with an isopod or evidence of a previous isopod included McClure and Wickesten (1997), Chace (1972), d'Udekem d'Acoz (2007) and Holthius (1952).

2.6 *Parasitic isopod procedures*

An isopod occurrence is defined as isopod presence on an individual shrimp, a free-floating parasitic isopod, or an individual shrimp showing a deformed carapace that a parasitic isopod once occupied. Shrimps found with an isopod occurrence were measured to the nearest 0.01mm with a handheld caliper using carapace length from eye orbital to dorsal posterior edge of carapace. Any isopod found on the shrimp was removed, identified and its length measured. Total length of female isopods were also to the nearest 0.01 mm using a handheld caliper, along the longest line from the anterior end to the posterior edge of the pleotelson following Cash and Bauer (1993). For shrimp with only a lump in the exoskeleton indicating a previous infestation, the lump was measured from one edge to the other edge to estimate the length of the previous isopod. Only adult isopods were collected and analyzed, because juvenile isopods were often not large enough to be recognized. Isopods were identified using Markham (1985) with personal communication and verification from Dr. Christopher Boyko, Dowling College, NY. The location of attachment, e.g., left (sinistral) or right (dextral) side of branchial chamber or abdomen was also documented (Walker 1977; Bass and Weis 1999).

2.7 *Statistical analyses*

All data were analyzed using statistical analysis software SPSS (2011). Kruskal-Wallis tests were used to compare total shrimp counts among regions and also among basins between seasons. Nonparametric tests were used since data was extremely skewed and could not be normalized with data transformation, possibly due to the high variance of shrimp counts among basins. A chi-square analysis was used to determine whether significant population differences existed among each shrimp genus between seasons.

From all parasitized shrimp collected, a chi-square analysis was used to determine whether significant differences existed in host selected. Regressions of parasite size on host size were calculated using the least squares method (Wilkinson 1988; Cash and Bauer 1993). Two sample T-tests, assuming unequal variance, were utilized to determine differences among abiotic variables between sites with parasites compared to sites without parasites. Braun-Blanquet data from sites with parasites were compared to sites without using Mann-Whitney U test (non-parametric t-test) due to the ordinal nature of ranked vegetation abundance codes. Proportions were calculated to determine whether there was a difference between the proportions of shrimp found parasitized during the wet season versus the dry season. Mann-Whitney U test was also used to compare the proportion of each genus of shrimp parasitized between seasons. Finally, logistical regressions were used to determine significance among variable(s) relative to site location as a factor for presence of isopods. Examining regressions enable one to predict the likelihood of finding particular isopods in a given location based on available environmental parameters.

A series of t-tests were used to test for differences in abiotic as well as biotic variables between wet and dry season. One-way ANOVA was used to test for any significant differences relative to region, basin, and environmental conditions (temperature, salinity, depth, and turbidity). Post-hoc results were reported to reveal where, if any, significant differences between region and/or basin occurred. Also, two-way ANOVA and nested ANOVA were used to examine relationships and interactions among the combination of season, region and basin for each abiotic and biotic variable. Due to the irregularity of sample areas (unequal sized hexagonal cells dependent on basin size), non-parametric tests were considered for analysis. However, due to the large sample size and numerous data points, normality was not determined to be an issue when running analysis with ANOVA. Although the majority of data was reported using parametric analysis, non-parametric tests such as Kruskal-Wallis, Mann-Whitney U test, and Wilcoxon rank-sum test were also run to ensure homogeneity between the results. When non-parametric tests and ANOVA resulted in same p-values, the latter was utilized and reported. Levene's homogeneity of variance test (Levene 1960) was also evaluated on all abiotic and biotic variables in regards to basin, region, and season. In cases where significance was found, indicating unequal variances among data values from the mean value, an adjusted F value was used to account for variance. Post-hoc tests assuming unequal variances were also used in cases where appropriate.

3.0 Results

3.1 *Environmental and habitat conditions*

Temperature, salinity, water depth and turbidity measurements were taken at every site in each basin. The value for each abiotic factor in the basin was calculated

based on the average value of 30 sites in the basin (Table 2). Overall vegetation coverage

was also estimated using Braun-Blanquet method and reported based on corresponding

abundance codes.

Table 2. Average abiotic data measurements of 30 sites in each of the 19 basins. Mean abiotic measurements listed ± standard deviation for temperature (° C), salinity (‰), turbidity (ntu), and water depth (cm).

Region	Basin	Season	Temperature (°C)	Salinity (‰)	Turbidity (ntu)	Water Depth (cm)
Biscayne Bay	NBB	Wet	28.44±0.52	28.06±2.72	2.19±1.66	186.53±113.70
		Dry	28.07±0.41	36.07±1.91	4.19±3.10	159.90±67.30
		AVG	28.26±0.50	32.06±4.62	3.19±2.63	173.22±92.82
	POM	Wet	28.98±0.53	32.00±1.48	2.05±0.82	183.57±70.02
		Dry	27.82±0.49	37.00±0.48	1.70±0.63	188.87±74.53
		AVG	28.40±0.76	34.50±2.72	1.88±0.74	186.22±71.15
	NBL	Wet	29.57±0.31	27.29±3.66	1.50±0.70	223.00±58.75
		Dry	26.71±0.53	35.56±1.99	1.97±0.92	177.70±56.46
		AVG	28.14±1.49	31.43±5.05	1.74±0.84	200.35±61.01
	SBL	Wet	30.65±0.47	24.02±6.38	1.26±0.44	187.27±64.20
		Dry	26.90±0.71	38.95±4.91	1.67±0.48	131.47±41.78
		AVG	28.78±1.97	31.49±9.33	1.47±0.50	159.37±60.12
	CAR	Wet	31.33±0.56	33.39±0.94	1.61±0.69	260.27±105.66
		Dry	27.15±0.39	36.76±0.42	3.92±3.03	235.10±96.09
		AVG	29.24±2.14	35.08±1.83	2.77±2.45	247.69±100.08
	BAR	Wet	31.10±0.33	31.72±1.67	1.29±0.38	294.43±54.38
		Dry	26.59±0.41	32.43±0.72	3.54±1.43	255.03±62.36
		AVG	28.85±2.30	32.08±1.32	2.42±1.53	274.73±60.80
	MAN	Wet	30.52±0.36	26.90±2.52	3.85±2.61	179.23±28.49
		Dry	26.64±0.81	29.77±1.59	4.11±1.37	144.97±35.94
		AVG	28.58±2.04	28.34±2.52	3.98±2.05	162.10±36.19
	Avg Region	Wet	30.08±1.11	29.05±4.47	1.96±1.52	216.33±85.56
		Dry	27.13±0.78	35.22±3.62	3.01±2.13	184.72±76.56
		AVG	28.61±1.76	32.14±5.10	2.49±1.92	200.53±82.71

Table 2. Continued.

Region	Basin	Season	Temperature (°C)	Salinity (‰)	Turbidity (ntu)	Water Depth (cm)
Florida Bay	DUK	Wet	29.24±0.66	32.97±1.83	2.76±1.12	166.23±18.75
		Dry	27.71±0.67	34.78±0.34	4.31±2.03	135.83±18.93
		AVG	28.48±1.01	33.88±1.58	3.54±1.79	151.03±23.96
	EAG	Wet	28.67±0.26	25.07±3.17	3.11±1.82	199.60±23.78
		Dry	27.67±0.75	31.85±0.84	5.04±2.95	168.43±21.27
		AVG	28.17±0.75	28.46±4.09	4.08±2.59	184.02±27.11
	CAL	Wet	28.13±0.30	33.56±1.73	3.76±1.28	211.73±43.76
		Dry	30.25±0.40	39.39±2.24	3.04±0.64	195.63±26.22
		AVG	29.19±1.12	36.48±3.51	3.40±1.06	203.68±36.37
	CRA	Wet	27.76±0.19	36.91±0.61	4.37±2.18	213.13±50.27
		Dry	29.98±0.64	40.94±0.44	3.74±2.04	184.87±51.14
		AVG	28.87±1.20	38.93±2.08	4.06±2.10	199.00±51.82
	RAN	Wet	28.29±0.39	34.31±1.73	0.95±0.20	132.40±16.71
		Dry	28.35±1.03	46.83±0.94	1.83±0.92	103.77±21.36
		AVG	28.32±0.76	40.57±6.41	1.39±0.79	118.09±23.68
	WHP	Wet	28.83±0.63	36.54±1.64	2.07±0.87	171.33±39.81
		Dry	27.26±0.61	44.69±0.56	3.13±3.15	147.47±36.27
		AVG	28.05±1.00	40.62±4.25	2.60±2.33	159.40±39.30
	JON	Wet	28.48±0.56	36.73±0.46	0.91±0.36	129.30±32.32
		Dry	27.37±1.34	44.20±2.34	2.47±1.18	103.03±30.29
		AVG	27.93±1.16	40.47±4.25	1.69±1.16	116.17±33.48
	RAB	Wet	28.17±0.62	37.28±1.44	1.73±0.92	188.73±44.83
		Dry	28.42±0.54	42.80±1.49	2.90±3.00	178.63±66.77
		AVG	28.30±0.59	40.04±3.11	2.32±2.26	183.68±56.14
	Avg Region	Wet	28.45±0.65	34.12±4.13	2.46±1.71	176.56±46.78
		Dry	28.38±1.33	40.68±5.00	3.31±2.36	152.21±49.82
		AVG	28.42±1.05	37.40±5.63	2.89±2.11	164.39±49.83
Southwest Coast	LOS	Wet	27.15±0.53	24.20±2.50	12.31±4.08	103.10±34.78
		Dry	28.52±1.70	35.56±0.14	12.68±2.62	182.67±39.00
		AVG	27.84±1.42	29.88±5.94	12.50±3.38	142.89±53.88
	PON	Wet	26.22±0.64	24.60±1.86	8.80±4.53	198.73±97.02
		Dry	27.85±0.47	34.74±1.38	15.36±11.12	205.63±84.43
		AVG	27.04±0.98	29.67±5.32	12.08±8.97	202.18±89.48
	OYS	Wet	26.56±0.05	21.15±1.38	4.36±1.16	196.33±20.91
		Dry	28.74±0.34	34.24±2.02	9.26±2.98	219.67±24.62
		AVG	27.65±1.13	27.70±6.76	6.81±3.31	208.00±25.31
	WHT	Wet	27.24±0.32	8.79±1.44	2.15±0.43	171.07±15.58
		Dry	28.08±0.35	27.67±3.64	2.31±0.51	143.67±20.00
		AVG	27.66±0.53	18.23±9.82	2.23±0.47	157.37±22.32
	Avg Region	Wet	26.79±0.62	19.69±6.68	6.90±4.98	167.31±64.99
		Dry	28.29±0.97	33.05±3.81	9.90±7.59	187.91±56.22
		AVG	27.54±1.11	26.37±8.62	8.40±6.59	177.61±61.63

3.1.1 *Water depth*

Recorded water depth ranged between 2 and 640 cm for all basins; $\bar{X}=189.26 \pm$ 70.40 cm during wet season and $\bar{X}=171.70 \pm 64.46$ cm during dry season (Table 2) and were significantly deeper during the wet season (t (1,138) = 4.39, $p < 0.01$). Biscayne Bay and Florida Bay were significantly deeper during the wet season (t (400.65) = 15.50, $p < 0.01$; t (478) = 5.51, $p < 0.01$), respectively. However, Lower Southwest Coast was significantly deeper during the dry season (t (238) = 2.62, $p = 0.01$).

Water depth varied among regions during the wet and dry seasons (Table 2). Overall, Biscayne Bay was significantly deeper than Florida Bay and the Lower Southwest Coast (*Welch F* (2, 278.92) = 21.43, p < 0.01) during the wet season. Overall, during the dry season, Lower Southwest Coast was significantly deeper than Biscayne Bay and Florida Bay (F (2, 567) = 20.35, $p < 0.01$).

Water depth also differed significantly among basins during the wet season (*Welch F* (18, 203.33) = 35.43, $p < 0.01$). BAR was significantly deeper ($p \leq 0.004$) than the other basins in the entire study area. Water depth also differed significantly among basins during the dry season (*Welch F* (18, 203.58) = 39.70, $p < 0.001$). Again, BAR was significantly deeper that all other basins in the entire study area ($p \leq 0.05$) except for CAR, which was only slightly shallower.

A two-way ANOVA found a significant interaction between the effects of season and region on water depth (F (2, 1,134) = 13.49, $p < 0.001$, partial $\eta^2 = 0.02$). Simple main effects analysis showed greater water depths during wet season in Biscayne Bay and Florida Bay ($p < 0.001$) but greater dry season depths than in Lower Southwest Coast ($p = 0.01$). There were also significant interactions between the effects of season and

basin on water depth (F (18, 1,102) = 4.57, $p < 0.001$, partial $\eta^2 = 0.07$). Simple main

effects analysis showed significantly greater depths during wet season in the following

basins: NBL, SBL, BAR, MAN, DUK, EAG, CRA, and RAN. Depths were significantly

greater during the dry season only in LOS ($p < 0.001$).

3.1.2 *Temperature*

Bottom and surface water temperatures were taken at each site and no significant

differences were detected between averaged bottom temperatures ($\bar{X}$=28.30 ± 1.45 °C)

and averaged bottom and surface temperatures ($\bar{X}$=28.30 ± 1.42 °C) ($p = 0.10$, DF=

2,278). Temperature ranged from 24.90° C to 33.15° C ($\bar{X}$=28.70 ± 1.49 °C) during the

wet season and between 25.10° C and 36.90° C ($\bar{X}$=27.90 ± 1.23 °C) during the dry season

(Table 2). An independent-samples t-test showed temperature of all basins during the

wet season significantly higher ($\bar{X}$=28.70 ± 1.49 °C, Median=28.55) than dry season

($\bar{X}$=27.90 ± 1.23 °C, Median=27.85) (t (1,138) = 9.92, $p < 0.01$). Only Biscayne Bay (p

< 0.01) and Lower Southwest Coast ($p < 0.01$) were significantly different in temperature

between seasons. In Biscayne Bay, average water temperature was significantly higher

during the wet season than the dry (t (373.78) = 31.53, $p < 0.01$) but Lower Southwest

Coast had significantly higher temperatures during the dry season (t (238) = 14.24, $p <$

0.01) (Figure 6).

Due to the seasonal differences in temperature, variations in each region were

analyzed separately for both the wet and dry seasons. To account for unequal variances

in temperature values during the seasons, an adjusted *F* statistic was calculated and

resulted in significant differences among the three regions during both the wet season

(*Welch F* (2,316.12) = 618.90, $p < 0.001$) and dry season (*Welch F* (2,307.20) = 109.26, p

< 0.001). During the wet season, Biscayne Bay was significantly warmer than Florida

Bay ($p < 0.001$), which was significantly warmer than Lower Southwest Coast (p

<0.001). Temperature during the dry season in Biscayne Bay was significantly lower

than in the other two regions ($p < 0.001$).
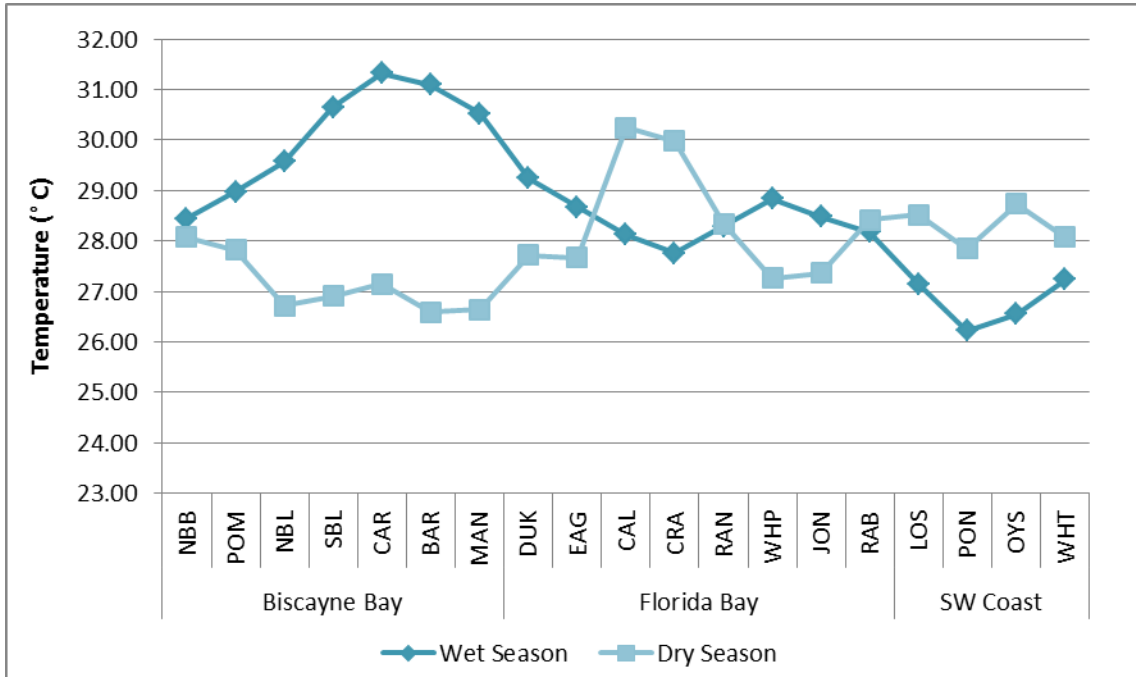
Figure 6. Seasonal mean temperature values observed for each basin.

Significant differences in temperature were also found among the basins during

the wet season (*Welch F* (18, 203.64) = 396.02, $p < 0.001$) and dry season (*Welch F* (18,

203.80) = 121.83, $p < 0.001$). Games-Howell post-hoc results generally showed warmer

water temperature for basins during the wet than the dry season. Basin data are

synopsized in Table 2.

A two-way ANOVA indicated a significant interaction between season and region

(F (2, 1,134) = 460.63; $p < 0.01$, partial $\eta^2 = 0.45$). Simple main effects analysis showed

that wet season temperatures were significantly higher than those during the dry season in

Biscayne Bay ($p < 0.01$), and dry season temperatures were significantly higher in Lower

Southwest Coast ($p < 0.01$). A two-way ANOVA was also used to examine the effects of season and basin on temperature differences ($F_{(18, 1,102)} = 193.96$; $p < 0.01$, partial $\eta^2 = 0.76$). Simple main effects analysis showed that wet season temperatures were significantly higher than those during the dry season for 11 out of 19 basins. Dry season temperatures were higher in six basins ($p < 0.01$).

3.1.3 *Salinity*

Bottom and surface salinities were taken at each site and no significant differences were detected between average bottom salinity ($\bar{X}=33.21 \pm 7.45‰$) and averaged bottom and surface salinity values ($\bar{X}=33.14 \pm 7.51‰$) ($p = 0.82$, DF=2,278) (Table 2). Salinity values recorded during the wet season ranged between 5.95‰ and 39.70‰ ($\bar{X}=29.22 \pm 7.30‰$). Dry season values ranged between 21.45‰ and 57.10‰ ($\bar{X}=37.0 \pm 5.35‰$) (Figure 7). An independent-samples t-test indicated that, overall, salinity was significantly lower during the wet season ($\bar{X}=29.22 \pm 7.30‰$) than the dry season ($\bar{X}=37.06 \pm 5.35‰$); ($t_{(1,138)} = 20.70$, $p < 0.001$). Every region had higher salinities during the dry season: Biscayne Bay ($t_{(400.65)} = 15.50$, $p < 0.001$); Florida Bay ($t_{(461.53)} = 15.65$, $p < 0.001$); and Lower Southwest Coast ($t_{(189.07)} = 18.95$, $p < 0.001$).

Salinities recorded per region and basins for wet versus dry seasons were compared separately due to the significant seasonal differences. To account for unequal variances, an adjusted F statistic was calculated (*Welch F* $_{(2,277.19)} = 257.56$, $p < 0.01$), and significant differences in salinity values were found among all three regions during the wet season, ($p < 0.01$). Florida Bay had the highest salinity and Lower Southwest Coast had the lowest (Table 2). An adjusted F statistic was also calculated for dry season

salinity to account for unequal variances, (*Welch F* (2, 321.68) = 144.18, $p < 0.01$) and

significant differences were found among each of the regions ($p < 0.01$). During the dry

season, salinity was lowest in the Lower Southwest Coast, followed by Biscayne Bay.

Florida Bay had the highest salinity (Table 2).
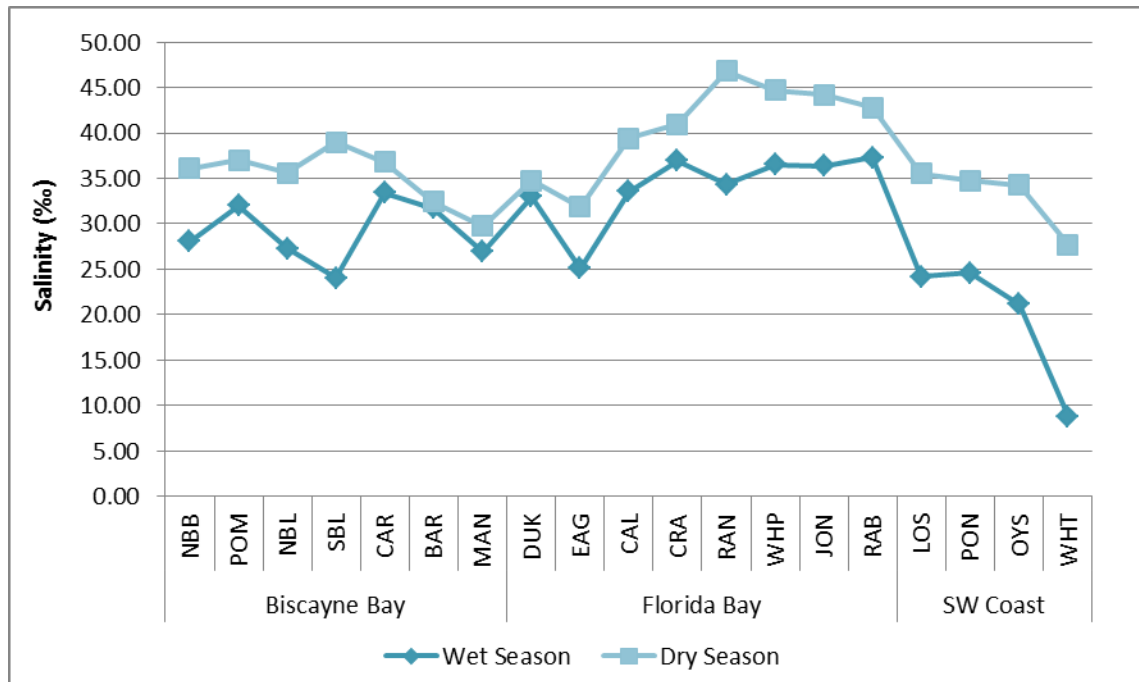
Figure 7. Seasonal mean salinity values observed for each basin.

Significant differences in the mean salinities were also found among basins

during the wet season (*Welch F* (18, 202.48) = 813.07, $p < 0.01$). Post-hoc tests showed

greater variability among basins in Biscayne Bay and Lower Southwest Coast during the

wet season than the dry. Every basin in Biscayne Bay, except for three, had significantly

higher salinities than Lower Southwest Coast ($p < 0.01$). Basins in Florida Bay had

significantly higher salinities than Lower Southwest Coast except for one ($p < 0.01$).

WHT had the lowest salinity of every other basin in entire study area ($p < 0.01$). Salinity

varied significantly among basins during the dry season (*Welch F* (18, 200.31) = 988.05,

$p < 0.01$). In Biscayne Bay, BAR and MAN had significantly lower salinities than the

other basins in the region ($p < 0.01$). RAN had the highest of all basins in every region. WHT also had the lowest salinity during the dry season ($p < 0.01$) among all other basins except for MAN in Biscayne Bay region.

A two-way ANOVA to examine the effect of season and region on salinity found a significant interaction (F (2, 1,134) = 54.55, $p < 0.01$, partial η^2 = 0.09). Simple main effects analysis showed that wet season salinities were significantly lower than those in the dry season in every region ($p < 0.01$). A two-way ANOVA also found a significant interaction between the effects of season and basin on salinity (F (18, 1,102) = 70.50, $p < 0.01$, partial η^2 = 0.54). Dry season salinities were significantly higher in every basin except: BAR, RAB and RAN (Figure 7, Table 2).

3.1.4 *Turbidity*

Overall wet season turbidity values ($\bar{X}$=3.21 ± 3.32 ntu) were significantly lower than those in the dry season ($\bar{X}$=4.59 ± 4.87 ntu) (t (1138) = 5.58, $p < 0.001$) (Figure 8). Biscayne Bay, Florida Bay and Lower Southwest Coast all had significantly lower turbidities during the wet season (t (377.54) = 5.81, $p < 0.001$; t (436.12) = 4.51, $p < 0.001$; t (238) = 18.95, $p < 0.001$), respectively.

Wet season turbidity values ranged from 1.96 ntu on the eastern coast of Florida to 6.90 ntu on the west coast (Table 2). Biscayne Bay had significantly lower turbidity than Florida Bay (*Welch F* (2, 258.66) = 56.79, $p = 0.004$). The Lower Southwest Coast had significantly higher turbidity values than both of the other regions ($p < 0.001$). Dry season turbidity values were higher than those of the wet season and ranged from 3.01 ntu to 9.90 ntu (Table 2). Turbidity was significantly higher in Lower Southwest Coast than the other two regions (*Welch F* (2, 257.32) = 46.81, $p < 0.001$).

Mean turbidity values were compared during the wet season and significant differences were found among the basins (*Welch F* (18, 202.22) = 57.74, $p < 0.001$). During the wet season, the Lower Southwest Coast showed the highest turbidity values; LOS ($\bar{X}$=12.31 ntu) and PON ($\bar{X}$=8.80 ntu). The basins with the lowest turbidity were found in Florida Bay: RAN ($\bar{X}$=0.95 ntu) and JON ($\bar{X}$=0.91 ntu). During the dry season significant turbidity differences were also found among the basins (*Welch F* (18, 202.97) = 50.81, $p < 0.001$). Turbidity values were highest in LOS ($\bar{X}$=12.68 ntu±2.62), PON ($\bar{X}$=15.36 ntu), and OYS ($\bar{X}$=9.26 ntu). Lowest turbidity values were found in POM ($\bar{X}$=1.70 ntu), SBL ($\bar{X}$=1.67 ntu), and RAN ($\bar{X}$=1.83 ntu). (Figure 8, Table 2).

Two-way ANOVA analysis was used to examine interaction effects of season and region on turbidity (F (2, 1134) = 8.59, $p < 0.001$, partial $\eta^2 = 0.02$). Simple main effects analysis returned the same results as the t-tests reported above that wet season had significantly lower turbidity values than dry season in all three regions: Biscayne Bay ($p = 0.002$), Florida Bay ($p = 0.007$), and Lower Southwest Coast ($p < 0.001$). A significant interaction was also found when examining effects of season and basin on turbidity (F (18, 1,102) = 7.03, $p < 0.001$, partial $\eta^2 = 0.10$). Effects analysis showed wet season turbidity values were significantly higher in the following basins: NBB, CAR, BAR, DUK, EAG, JON, PON, and OYS.
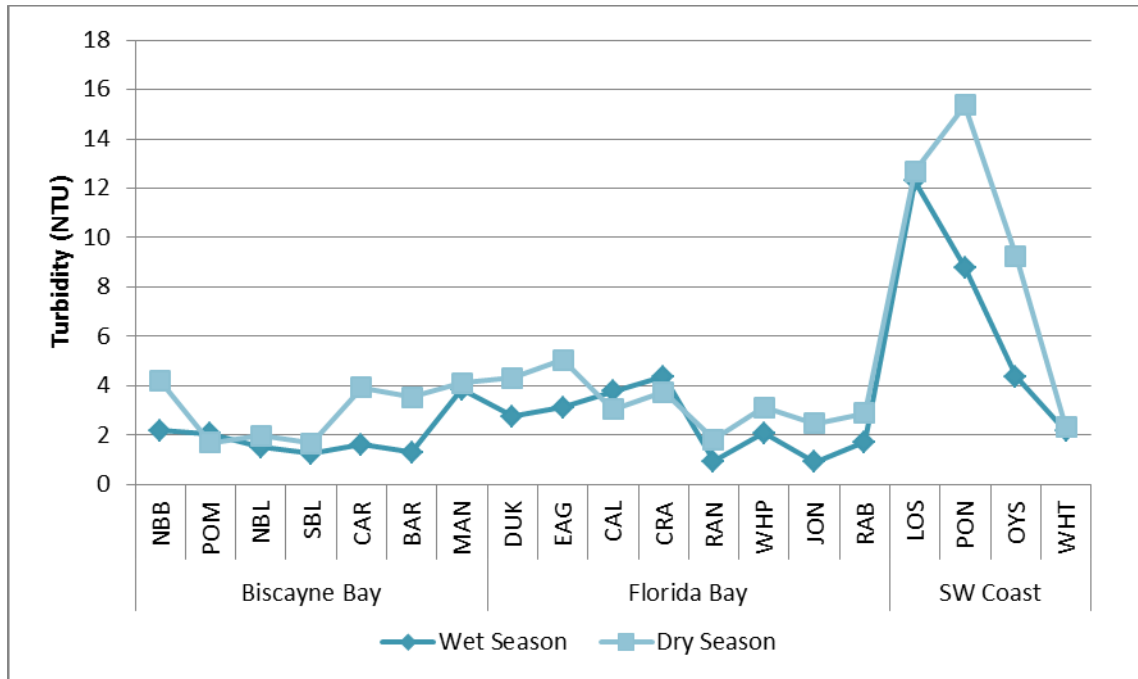
Figure 8. Seasonal mean turbidity values observed for each basin.

3.1.5 *Macroalgal coverage*

Vegetative cover of both macroalgae and seagrass were determined for each site within a basin based on the Braun-Blanquet abundance codes (Table 1). The codes ranged from 0 (no cover) to 5 (complete cover of the quadrat). Maximum macroalgal coverage were 4.8 ($\bar{X}$=0.87 ± 0.85) during the wet season and 4.7 ($\bar{X}$=1.16 ± 0.89) during the dry season (Figure 9). Mann-Whitney U tests used to compare abundance codes among regions and basins during both seasons found significantly higher overall macroalgal coverage during the dry season (U (n=1,140) = 121,179.50, z = 7.44, *p* < 0.001).

Due to significant differences between seasons, wet and dry season were analyzed separately. During the wet season, Biscayne Bay had significantly greater macroalgal coverage than the other two basins, and Florida Bay had the least (χ^2(2) = 20.26, *p* < 0.001). Biscayne Bay also had significantly greater macroalgal coverage than the other

43

regions during the dry season. Lower Southwest Coast region had significantly lower

coverage than both other regions ($\chi^2(2) = 59.57$, $p < 0.001$).

During the wet season, macroalgal coverage differed among basins: Biscayne Bay

($\chi^2(6) = 29.31$, $p < 0.001$), Florida Bay ($\chi^2(7) = 53.22$, $p < 0.001$), and Lower Southwest

Coast ($\chi^2(3) = 64.76$, $p < 0.001$). In Biscayne Bay, SBL and MAN had the highest

overall coverage and NBB had the least. In Florida Bay, the greatest coverage was found

in CAL and CRA and JON had the least. In Lower Southwest Coast, OYS and WHT had

significantly greater macroalgal coverage than LOS and PON. During the dry season,

significant differences in coverage were found among basins in each region ($\chi^2(18) =$

188.81, $p < 0.001$): Biscayne Bay ($\chi^2(6) = 38.05$, $p < 0.001$), Florida Bay ($\chi^2(7) = 45.00$,

$p < 0.001$), and Lower Southwest Coast ($\chi^2(3) = 47.33$, $p < 0.001$). In Biscayne Bay,

CAR had significantly greater coverage than any other basin ($p < 0.001$) and MAN and

NBB had the least coverage. In Florida Bay, WHP had significantly greater coverage

than any other basin in the region ($p < 0.001$), and RAB had the least ($p < 0.001$). In

Lower Southwest Coast, WHT had the greatest coverage among other basins in the

region ($p < 0.001$) and PON had the least ($p \leq 0.02$).

3.1.6 *Seagrass coverage*

Overall seagrass coverage ranged between 0 and 5 during both the wet ($\bar{X}=1.77 \pm$

1.44) and dry ($\bar{X}=1.84 \pm 1.40$) seasons (Figure 9). Total seagrass coverage during the wet

season was not significantly different than in the dry season (Mann-Whitney U (n=1140)

= 156,235.00, z = 1.12, $p = 0.26$), therefore, seagrass coverage among regions and basins

were not separated by season. However, a significant difference was found among the

three regions ($\chi^2(2) = 449.94$, $p < 0.001$), with Florida Bay having the highest seagrass

coverage and Lower Southwest Coast having the least. Due to variations among the

regions, basins in each region were evaluated separately. The basins in Biscayne Bay had

significant differences ($\chi^2(6) = 106.98$, $p < 0.001$). NBB had significantly more seagrass

than any other basin in the region and BAR had the least ($p < 0.001$). Significant

differences in seagrass coverage were also found among the basins in Florida Bay ($\chi^2(7)$

$= 320.87$, $p < 0.001$), with RAB containing the most coverage ($p < 0.001$). Coverage also

differed significantly among Lower Southwest Coast ($\chi^2(3) = 93.31$, $p < 0.001$). WHT

had the most seagrass of the four basins in the region ($p < 0.001$), while PON and OYS

had significantly less than the other two ($p < 0.001$).
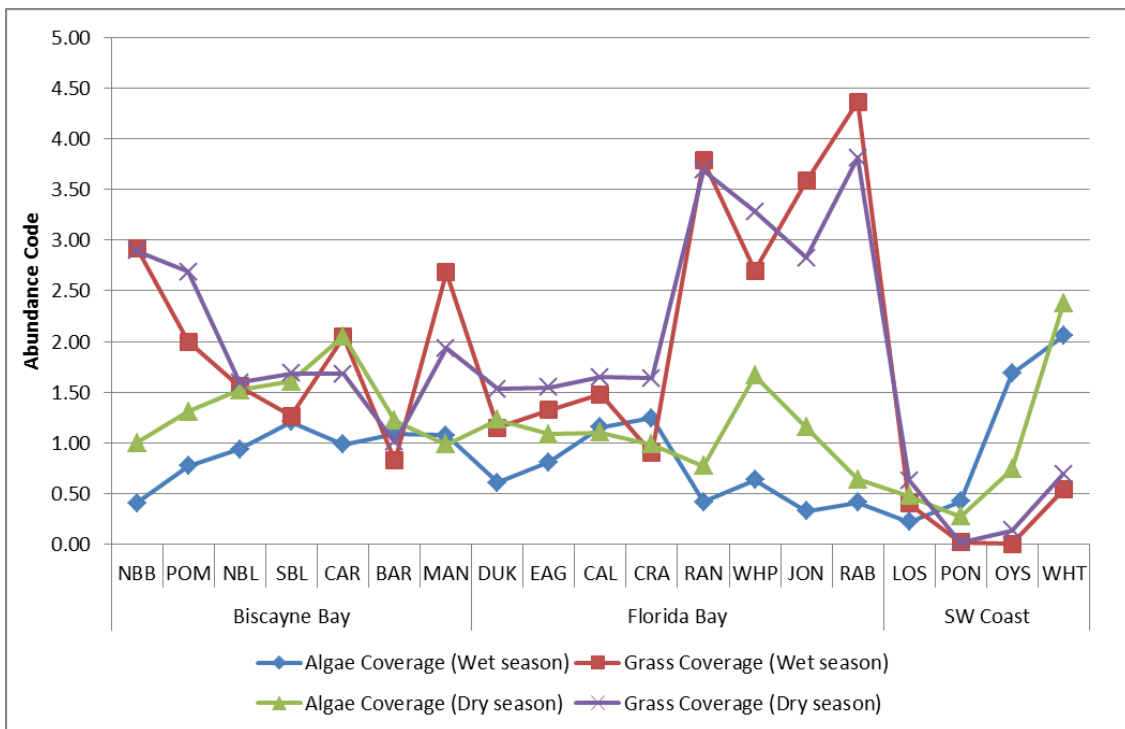
Figure 9. Macroalgae and seagrass coverage between seasons based on Braun-Blanquet abundance codes (0.1=solitary, 0.5=sparse, 1=~5%, 2=5-25%, 3=25-50%, 4=50-75%, 5=75-100%).

3.1.7 *Total vegetation coverage*

Overall average vegetation coverage was significantly higher during the dry

season ($\bar{X}=2.42 \pm 1.40$) than the wet ($\bar{X}=2.19 \pm 1.33$); (Mann-Whitney U (n=1,140) =

147,590.50, z = 2.68, $p = 0.007$). The three regions differed significantly by season with Florida Bay sites supporting greater coverage overall than either Biscayne Bay or Lower Southwest Coast during both wet (χ^2 (2) = 99.02, $p < 0.001$) and dry seasons (χ^2(2) = 142.97, $p < 0.001$). Overall, basins with more seagrass coverage typically had less macroalgae based on a Pearson correlation, indicating a significantly negative correlation between algae and seagrass ($r = -0.28$, $p < 0.001$).

3.5 *Caridean shrimp community*

A total of 44,474 shrimp belonging to 12 genera and 5 families (Alpheidae, Hippolytidae, Palaemonidae, Ogyrididae and Processidae) was collected and examined; wet season $n = 18,496$ and dry season $n = 25,978$.   Total shrimp density was compared with an independent samples t-test assuming unequal variances. Caridean population size differed significantly between wet season and dry season (t (860.22) = 2.79, $p = 0.005$), with the dry season having significantly more shrimp than the wet season (Table 3). The majority of shrimp collected were found in Florida Bay ($n = 25,585$) followed by Biscayne Bay ($n = 13,840$). Lower Southwest Coast had the fewest shrimp ($n = 5049$).

Regions differed significantly during both wet (Kruskal-Wallis H (2) = 13.98, $p < 0.001$) and dry seasons (Kruskal-Wallis H (2) = 14.79, $p = 0.001$). During the wet season, Biscayne Bay had significantly more shrimp than Lower Southwest Coast ($p < 0.001$) and Florida Bay had significantly more shrimp than Biscayne Bay ($p = 0.02$). In the dry season, Florida Bay again had significantly more shrimp than Biscayne Bay ($p < 0.006$) and Lower Southwest Coast ($p < 0.001$).

Given the significant seasonal differences in numbers of carideans, wet and dry season shrimp counts were separated and Kruskal-Wallis tests were used to analyze

differences among basins. Significant differences were found among the basins during

both wet (Kruskal-Wallis $H(18) = 217.42$, $p < 0.001$) and dry seasons ($H(18) = 223.57$,

$p < 0.001$). EAG, in Florida Bay, had the fewest shrimp ($n = 131$) and JON, also in

Florida Bay, had the most ($n = 3,228$) during the wet season. In the dry season, the

fewest were again found in EAG ($n = 75$) and the most in RAN ($n = 6,350$) (Table 3).

Table 3. Caridean shrimp collected in each basin by season.

Region	Basin	Wet Season 2010 No. of shrimp	Dry Season 2011 No. of shrimp
Biscayne Bay Region	POM	1,066	1,015
	NBB	1,867	5,554
	SBL	605	401
	NBL	614	511
	CAR	843	293
	BAR	416	173
	MAN	329	153
	Region Total	5,740	8,100
Florida Bay Region	CRA	240	110
	CAL	513	205
	JON	3,228	4,450
	RAB	2,331	2,784
	EAG	131	75
	DUK	241	224
	RAN	1,397	6,350
	WHP	1,284	2,022
	Region Total	9,365	16,220
SW Coast	WHT	605	880
	LOS	999	519
	OYS	1,011	145
	PON	776	114
	Region Total	3,391	1,658
	TOTAL	18,496	25,978

Table 4 outlines caridean taxonomic composition by basin. Florida Bay and

Biscayne Bay assemblages were predominately composed of *Thor* spp. and *Hippolyte*

spp. *Thor* spp. was the most abundant genus in seven of the eight Florida Bay basins, and

accounted for 85.2-96.1% of shrimps in the four western basins (RAN, WHP, JON and

RAB). *Hippolyte* spp. accounted for 63.9% in EAG and was the second most abundant

genus in the remaining seven basins (3.2-39.6%). In Biscayne Bay, *Thor* spp. and

Hippolyte spp. were again the most abundant, accounting for 20.3-79.0% and 16.2-56.6%

of carideans, respectively, with *Thor* spp. dominating in the central three basins (NBL,

SBL, CAR) and *Hippolyte* spp. in the southern two (BAR, MAN). By contrast,

Periclimenes spp. was the most abundant genus in three of the four Lower Southwest

Coast basins (45.8-51.5%) and the second most abundant in one (35.6%). *Alpheus* spp.

accounted for 42.7% in one basin (PON) and 34.1% in another (OYS). *Thor* spp. never

accounted for more than 2.8% in any basin, and *Hippolyte* spp. was the second most

common shrimp in only one (LOS).

Table 4. Dominant caridean genera and percentage of total caridean assemblage by basin.

Region	Basin	Dominant shrimp (% of total community)	Secondary shrimp (% of total community)
Biscayne Bay	NBB	*Thor* spp. (79.0%)	*Hippolyte* spp. (19.7%)
	POM	*Hippolyte* spp. (52.7%)	*Thor* spp. (20.3%)
	NBL	*Thor* spp. (60.0%)	*Hippolyte* spp. (36.2%)
	SBL	*Thor* spp. (73.8%)	*Hippolyte* spp. (22.3%)
	CAR	*Thor* spp. (56.5%)	*Hippolyte* spp. (16.2%)
	BAR	*Hippolyte* spp. (52.9%)	*Alpheus* spp./*Thor* spp. (22.4%)
	MAN	*Hippolyte* spp. (56.6%)	*Thor* spp. (30.5%)
Florida Bay	DUK	*Thor* spp. (52.4%)	*Hippolyte* spp. (39.6%)
	EAG	*Hippolyte* spp. (63.9%)	*Thor* spp. (18.5%)
	CAL	*Thor* spp. (69.1%)	*Hippolyte* spp. (21.5%)
	CRA	*Thor* spp. (41.6%)	*Hippolyte* spp. (29.9%)
	RAN	*Thor* spp. (96.1%)	*Hippolyte* spp. (3.2%)
	WHP	*Thor* spp. (88.6%)	*Hippolyte* spp. (9.8%)
	JON	*Thor* spp. (92.4%)	*Hippolyte* spp. (5.9%)
	RAB	*Thor* spp. (85.2%)	*Hippolyte* spp. (13.5%)
SW Coast	LOS	*Periclimenes* spp. (45.8%)	*Hippolyte* spp. (23.9%)
	PON	*Alpheus* spp. (42.7%)	*Periclimenes* spp. (35.6%)
	OYS	*Periclimenes* spp. (49.3%)	*Alpheus* spp. (34.1%)
	WHT	*Periclimenes* spp. (51.5%)	*Palaemonetes* spp. (25.4%)

Table 5 itemizes total numbers of shrimp collected in each genus by season. A

Pearson's chi-square test found that overall densities of different shrimp genera differed

between seasons ($\chi^2(12) = 2{,}903.77$, p < 0.001). Mann-Whitney U tests were used in

accordance with the chi-square results to determine specifically which shrimp genera

were different between seasons. *Alpheus* spp. (U = 126,573.50, Z = -7.86, *p* < 0.001),

Leander spp. (U = 159,309.00, Z = -2.86, *p* < 0.001), *Periclimenes* spp. (U = 146,891.00,

Z = -3.74, *p* < 0.001), and *Tozeuma* spp. (U = 158,492.00, Z = -2.86, *p* < 0.001) had

higher densities during the wet season, whereas *Thor* spp. (U = 146,241.00, Z = -3.10, *p* <

0.001) had a higher overall density during the dry season. The most abundant caridean

shrimps found throughout entire sampling area were *Thor* spp., *Hippolyte* spp., and

Periclimenes spp. For both the wet and dry sampling collections, *Thor* spp. (*n* = 31,507)

proved to be the dominant caridean species overall, followed by *Hippolyte* spp. (*n* =

6,910).

Table 5. Total numbers of carideans in wet and dry seasons.

Shrimp	Collection		Total Count
	Wet 2010	Dry 2011	
Alpheus spp.	1,569	282	1,851
Hippolyte spp.	2,829	4,081	6,910
Latreutes spp.	70	48	118
Leander spp.	34	2	36
Leptochela spp.	3	0	3
Ogyrides spp.	127	102	229
Palaemon spp.	1	0	1
Palaemonetes spp.	259	149	408
Periclimenes spp.	1,969	866	2,835
Processidae	42	19	61
Thor spp.	11,367	20,140	31,507
Tozeuma spp.	23	21	44
Unknown spp.	203	268	471
Total	18,496	25,978	44,474

3.6 *Parasitic isopods*

A total of 365 isopod occurrences were recorded, 138 were found during the wet

season (0.75% of shrimp) and 226 found during the dry season (0.87% of shrimp). The

total included 109 adult female parasites associated with a host shrimp, five unattached

adult females (free-floating) and 251 host shrimp with evidence of prior parasitism. The

114 parasites represented 13 species, 12 genera and 2 subfamilies (Bopyrinae and

Hemiarthrinae) all from family Bopyridae. A chi-square analysis returned a statistically

significant difference in frequency among host species parasitized (χ^2 (16) = 1,496.10, p

< 0.001). *Bopyrina abbreviata*, hosted by *Hippolyte* spp., was the most common and

accounted for 37.7 % of all isopods found (Tables 6 and 7). The second most common

species, *Diplophryxus* spp. accounted for only 15.8% (Table 7). Of the ten carideans

identified to species, six hosted only a single parasite species, whereas three hosted two

species and *Alpheus heterochaelis* hosted three (Table 6).

Table 6. Isopod species with associated host shrimp and location found.

Isopod Species	Occurrence in Sample	Orientation	Host Shrimp
Probopyria alphei	2	Branchial	*Alpheus heterochaelis* *Alpheus* spp.
Parabopyrella richardsonae	3	Branchial	*Alpheus heterochaelis*
Parabopyriscus stellatus	1	Branchial	*Alpheus heterochaelis*
Ovobopyrus alphezemiotes	1	Branchial	*Alpheus floridanus*
Eophrixus subcaudalis	1	Abdominal	*Alpheus normanni*
Parabopyrella lata	1	Branchial	*Alpheus normanni*
Bopyrina abbreviata	43	Branchial	*Hippolyte zostericola* *Hippolyte obliquimanus* *Hippolyte* spp.
Metaphrixus carolii	5	Abdominal	*Hippolyte zostericola*
Diplophryxus spp.	18	Abdominal	*Periclimenes americanus*
Schizobopyrina urocaridis	1	Branchial	*Periclimenes longicaudatus*
Probopyrus pandalicola	6	Branchial	*Palaemonetes intermedius*
Bopyrinella thorii	17	Branchial	*Thor floridanus* *Thor manningi*
Loki circumsaltanus	15	Abdominal	*Thor floridanus*

A total of 68.8% of parasite occurrences were cases of an individual shrimp with a deformed carapace that a parasitic isopod had previously occupied. The majority of isopods were found in the branchial chamber of the host, either on the left or right side. A simple t-test found no significant difference in parasite attachment location between left or right side. Significantly fewer abdominal parasites were found (t (364) = 9.86, $p <$ 0.01). However, evidence of abdominal parasitism is not visible once the isopod is gone and may account for the lower number.

Table 7. Occurrence of parasite species found in sample collections.

Isopod species	Count	Percent (%) of total occurrences	Percent (%) of total isopods
Lump in carapace / no parasite present	251	68.8	
Bopyrina abbreviata	43	11.8	37.7
Diplophryxus spp.	18	4.9	15.8
Bopyrinella thorii	17	4.7	14.9
Loki circumsaltanus	15	4.1	13.1
Probopyrus pandalicola	6	1.6	5.3
Metaphrixus carolii	5	1.4	4.4
Parabopyrella richardsonae	3	0.8	2.6
Probopyria alphei	2	0.5	1.8
Eophrixus subcaudalis	1	0.3	0.9
Ovobopyrus alphezemiotes	1	0.3	0.9
Parabopyrella lata	1	0.3	0.9
Parabopyriscus stellatus	1	0.3	0.9
Schizobopyrina urocaridis	1	0.3	0.9
Total number of parasites present	114	31.2	100
Total occurrences	365	100	

Of the 12 caridean shrimp genera observed (Table 5), only six hosted parasitic isopods, with *Hippolyte* spp. representing 59.5% of the total (Table 8) and *Hippolyte*

zostericola accounting for 49.6% (Table 9). *Thor* spp. comprised 26.3% of total

parasitized shrimp with *Thor floridanus* accounting for 20.8% of parasitized shrimp

identified to species (Table 9). Only a single specimen of *Tozeuma* spp. was found with

evidence of parasitism.

Table 8. Parasite occurrence among each of the shrimp host genera.

Shrimp genus	Count	Percent (%)
Alpheus spp.	15	4.1
Hippolyte spp.	217	59.5
Palaemonetes spp.	10	2.7
Periclimenes spp.	21	5.8
Thor spp.	96	26.3
Tozeuma spp.	1	0.3
No host	5	1.4
Total	365	100.0

Table 9. Parasite occurrence among host shrimp species.

Shrimp Species	# Parasitized	% of total parasitized
Alpheus floridanus	1	0.3
Alpheus heterochaelis	9	2.5
Alpheus normanni	3	0.8
Alpheus spp.	2	0.5
Hippolyte obliquimanus	23	6.3
Hippolyte pleuracanthus	2	0.5
Hippolyte zostericola	181	49.6
Hippolyte spp.	11	3.0
Periclimenes americanus	19	5.2
Palaemonetes intermedius	9	2.5
Periclimenes longicaudatus	2	0.5
Palaemonetes spp.	1	0.3
Tozeuma carolinense	1	0.3
Thor floridanus	76	20.8
Thor manningi	10	2.7
Thor spp.	10	2.7
No host	5	1.4
Total	365	100

Total length (Y) of adult female parasitic isopods correlated strongly with host shrimp carapace length (X) (Figure 10). The regression equation calculated for length was $Y = 0.645x + 0.66$ ($r = 0.90$, $n = 360$).
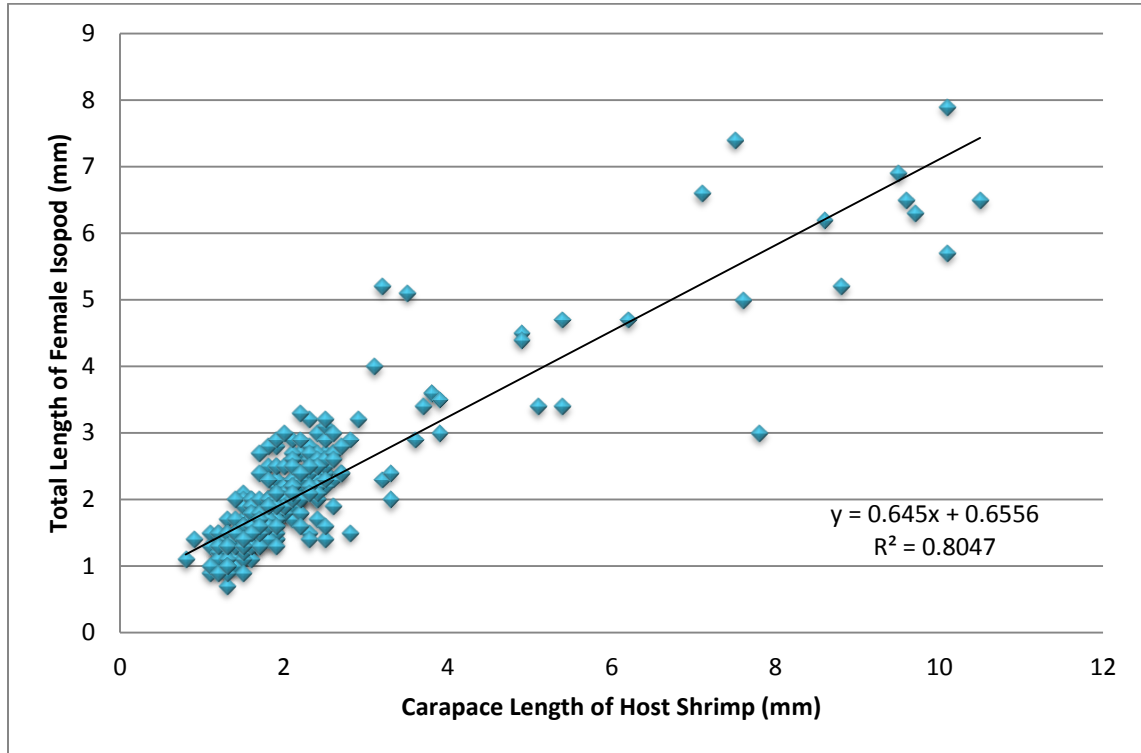
Figure 10. Total length of adult female isopods relative to host shrimp carapace length.

3.7 *Factors influencing isopod presence*

Two-sample t-tests were performed to determine if there were differences in abiotic factors between sites with and without isopods. A preliminary test for the equality of variances indicated that variances between the temperatures of sites with parasites and sites without parasites differed significantly (Levene F (364, 44,292) = 1.77, $p < 0.01$). Therefore, a two-sample t-test was performed assuming unequal variance. The mean temperature for sites with parasites (28.37 ± 1.61° C, n=365) was significantly higher than the mean temperatures for sites without parasites (28.17 ± 1.21° C, n=44,293) (t (367) = 2.37, p = 0.02). An F-test for the equality of variances between

salinities of sites with and without parasites was also significant (Levene F (364, 44,292) = 0.66, $p < 0.01$); therefore, a t-test assuming unequal variance was used to compare salinity. The mean salinity for sites with parasites (33.00±6.27 ‰, n=365) was significantly lower than mean salinity for sites without parasites (37.18±7.73 ‰, n=44,293) (t (373) = 12.69, $p < 0.01$). An F-test for the equality of variances between water depths of sites with and without parasites was also significant (Levene F (364, 44,292) = 1.28, $p < 0.01$); therefore, a t-test assuming unequal variance was used to compare water depths. The mean water depth for sites with parasites (167.72±64.35 cm, n=365) was significantly higher than mean depth for sites without parasite presence (135.45±56.96 cm, n=44,293) (t (368.72) = 9.55, $p < 0.01$). Mann-Whitney U tests were used to compare vegetation abundance between sites with and without parasite presence. Mean rank sums of algal coverage were higher for sites with parasites than sites without ($Z = 7.82$, $p < 0.01$). Mean rank sums of total seagrass was much lower for sites with parasites than sites without ($Z = 7.62$, $p < 0.01$). However, presence of total vegetation was also much lower for sites with parasite occurrences than sites without parasites ($Z = 5.59$, $p < 0.01$).

A logistical regression was also performed for the presence/absence of isopods based on the independent variables temperature, salinity, turbidity, and water depth. Two biotic factors—total algae and seagrass abundances—were also independent variables in the model. The model was statistically significant as evidenced by the chi-square test (χ^2 (6) = 171.62, $p < 0.001$). More specifically, the analysis found that temperature (Wald's $\chi^2 = 4.28$, $p = 0.04$, OR = 1.09), salinity (Wald's $\chi^2 = 31.07$, $p < 0.001$, OR = 0.96), water depth (Wald's $\chi^2 = 45.36$, $p < 0.001$, OR = 1.01), total algal abundance (Wald's $\chi^2 =$

13.64, $p < 0.001$, OR = 1.23) and seagrass total (Wald's χ^2 = 0.03, $p < 0.001$, OR = 1.008) were significant predictors of the presence of parasites. However, turbidity (Wald's χ^2 = 0.14, $p = 0.71$, OR = 0.99) was not significantly associated with the presence of parasites.

Analysis of the above variables in a logistical regression model in conjunction with a Pearson correlation test returned the following positive correlations with presence of a parasite: temperature ($r = 0.02$, $p = 0.002$), algae total ($r = 0.03$, $p < 0.001$), and depth ($r = 0.05$, $p < 0.001$). Turbidity was also positively correlated with parasite presence but was not significant ($r = 0.001$, $p = 0.80$). By contrast, both salinity ($r = -0.05$, $p < 0.001$) and total seagrass ($r = -0.04$, $p < 0.001$) correlated negatively with parasite presence. Salinity and water depth showed the strongest correlations with parasite presence and were therefore the best predictors of the likelihood of a parasite being present at a particular location. The negative correlation with salinity allows us to infer that every 1 ppt increase in salinity is associated with a ~4% reduction in the probability of having a parasite present (95% CI=0.94, 0.97). Also from the model, one can predict that every 1 cm increase in water depth increases the odds of a parasite presence by up to 1% (95% CI=1.004, 1.008). An increase in temperature by 1°C increases the likelihood of a parasite being present on the host shrimp by 1.09 times (95% CI= 1.005, 1.189). We can infer that a 1°C increase in temperature has at least a 1% increase and at most a 19% increase in the probability of having a parasite present. An increase in total algae by one unit (or up to a 25% increase in algal coverage) increases the likelihood of parasite presence by 23%. A 95% confidence interval for the effects on odds of parasite presence per increase in algae (1.10, 1.37) infers that the odds of a

parasite present increase by at least 10% and at most 37%. Because seagrass total was also negatively correlated with parasite presence, the model predicts that every unit increase (or up to 25% increase in seagrass coverage) is associated with about a 9% reduction in the probability of having a parasite present.

3.8 *Percentages of carideans parasitized by season*

Percentages of shrimp parasitized were calculated for the wet and dry seasons to compare differences between two independent percentages. In the wet season, 18,496 carideans were collected with 139 parasitic isopods. During the dry season, 25,978 carideans had 226 parasitic isopods. Percentages of parasitized shrimp did not differ significantly between seasons ($z = 1.37$, $p = 0.17$). The five adult female isopods found unattached from their host shrimps were not included in the ratios calculated. Although overall percentages of parasitized carideans did not differ significantly between seasons, chi-square analyses found significant differences in percentages parasitized among regions and basins between wet and dry seasons. Florida Bay was the only region which had a significant seasonal difference, with a greater percentage of parasitized shrimp in the dry season ($\chi^2 (1) = 9.74$, $p < 0.01$). Both Biscayne Bay ($p = 0.72$) and Lower Southwest Coast ($p = 0.27$) regions showed no significance in percentages of parasitized shrimp between seasons.

In Biscayne Bay, POM, NBB, and CAR showed no seasonal differences in percentages of parasitized carideans; however, NBL ($\chi^2 (1) = 8.57$, $p < 0.01$), SBL ($\chi^2 (1) = 5.21$, $p = 0.02$), BAR ($\chi^2 (1) = 10.11$, $p < 0.01$), and MAN ($\chi^2 (1) = 9.92$, $p < 0.01$) had higher percentages during dry season. Shrimp populations were smaller in all of these basins during the dry season. In Florida Bay, JON, EAG, and WHP showed no

significant seasonal differences in percentages of parasitized carideans; however, DUK (χ^2 (1) = 4.29, p = 0.04), CAL (χ^2 (1) = 30.75, $p < 0.01$), CRA (χ^2 (1) = 18.61, $p < 0.01$), and RAB (χ^2 (1) = 8.32, $p < 0.01$) had higher percentages during the dry season. RAN was the only basin in Florida Bay that had higher percentages of parasites during the wet season (χ^2 (1) = 22.74, $p < 0.01$). All of these basins had smaller shrimp populations during the dry season except for RAB and RAN, which had less shrimp during the wet season. In Lower Southwest Coast, OYS and PON had no significant differences in percentages of parasitized carideans between seasons; however, LOS had a higher percentage parasitized during the dry season (χ^2 (1) = 13.41, $p < 0.01$) but also a smaller shrimp population than in the wet season. WHT had more parasites (χ^2 (1) = 6.43, p = 0.01) and fewer shrimp collected during wet season.

Percentages of each caridean genus parasitized were compared between wet and dry seasons using Mann-Whitney U non-parametric tests. *Alpheus* spp., *Hippolyte* spp., and *Periclimenes* spp. all showed greater percentage of parasites during the dry season (Figure 11). However, the differences were only significant for *Hippolyte* spp.: 3.97% parasitized during the dry season and 1.94% during the wet season (U (19) = 268, z = 2.54, p = 0.01). The differences for the other two were not significant: *Alpheus* spp. (1.42% dry season, 0.70% wet season (U (19) = 165.50, z = 0.42, p = 0.67). *Periclimenes* spp. (1.15% dry season, 0.56% wet season) (U (19) = 206.50, z = 0.74, p = 0.46). By contrast, two genera had more parasitized shrimp during the wet season but without significant differences (Figure 11): *Palaemonetes* spp. (2.70% wet season, 2.03% dry season) (U (19) = 190, z = 0.26, p = 0.79) and *Thor* spp. (0.47% wet season, 0.21% dry season) (U (19) = 167.50, z = 0.36, p = 0.72). Finally, *Tozeuma* spp. also had a greater

percentage parasitized during the wet season (4.35%) and 0% during the dry season; however, this was based on a single parasitized shrimp out of only 23 during the wet season making the percentage very high due to the small sample size.
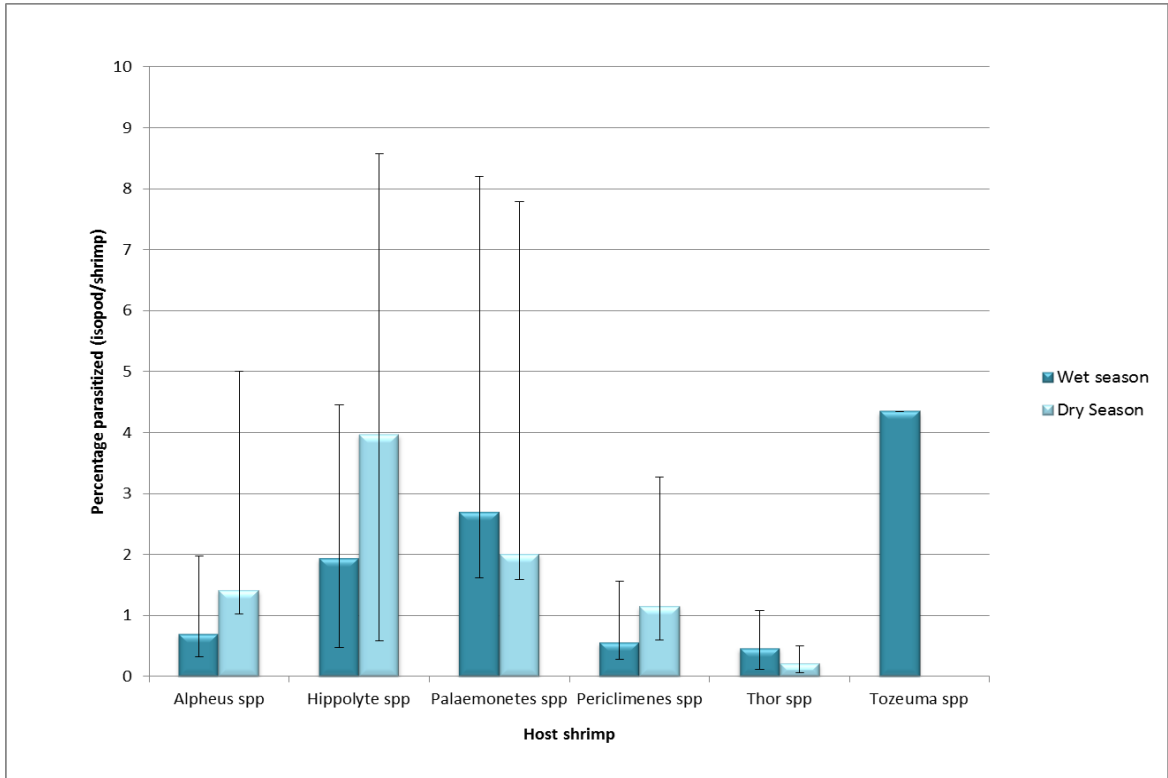
Figure 11. Percentages of shrimp parasitized in wet and dry seasons. Error bars indicate a 95% confidence intervals computed using a modified Wald method (Agresti and Coull 1998).

3.9 *Isopod distribution*

When testing for differences in isopod distributions among region and basin, wet and dry season were not separated, because total percentages of carideans parasitized did not differ significantly by season. A one sample chi-square test showed a significant difference in percent parasitism by region ($\chi^2 (2) = 370.73$, $p < 0.01$) with Biscayne Bay highest. Percent parasitism also varied significantly among the 19 sampled basins ($\chi^2 (18) = 933.03$, $p < 0.01$). Proportionally, MAN and BAR had the highest percentages of parasitized shrimp in both wet and dry seasons (Figure 12).
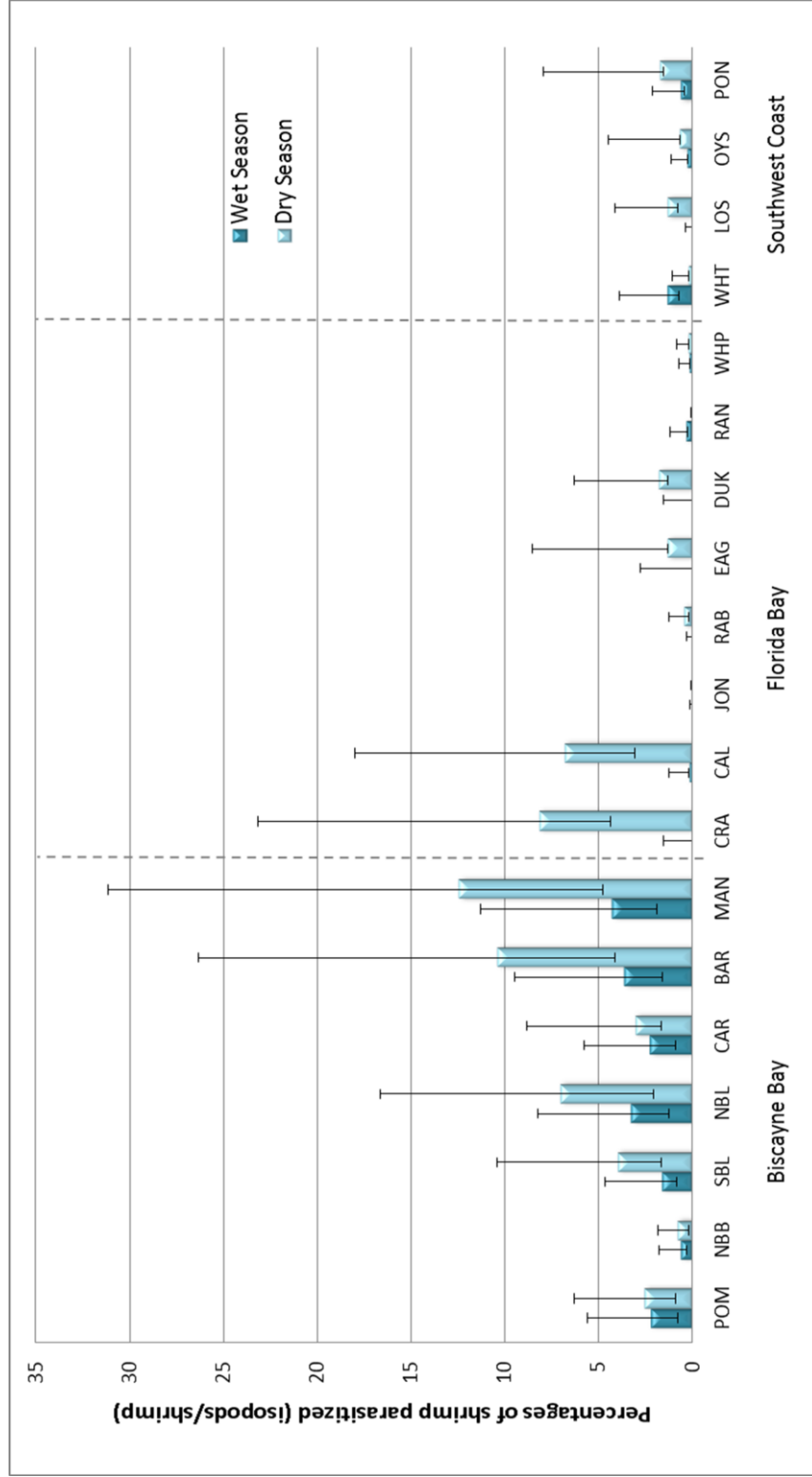
Figure 12. Percentages of shrimp parasitized for each of the 19 sampled basins during wet and dry seasons. Error bars indicate 95% confidence intervals (Agresti and Coull 1998).

Because the majority of isopods were collected from Biscayne Bay, this region was analyzed separately from the other regions to eliminate variances due to regional differences. Simple t-tests were performed to recognize any differences in mean temperatures, salinity, water depth, turbidity, and seagrass and algae coverage among sample sites with and without parasites. Temperature was not significantly different between sample sites with or without parasites (t (288.57) = 0.77, p = 0.44). Average salinity (t (13,910) = 4.22, $p < 0.01$) and seagrass coverage (Z = 6.18, $p < 0.01$) were both significantly lower at sites with parasites, while water depth (t (13,910) = 5.99, $p < 0.01$), turbidity (t (290.05) = 5.07, $p < 0.01$) and algal coverage (Z = 2.80, p = 0.005) were all higher at sites with parasites.

In Biscayne Bay region, Manatee Bay (MAN) and Barnes Sound (BAR) had the highest percentages of parasites during both the wet and dry seasons. In BAR, salinity, water depth and turbidity did not differ significantly between sites with versus without parasites (p = 0.71, p = 0.54, p = 0.46, respectively); however, temperature was significantly lower at sites where parasites were found (t (593) = 2.64, p = 0.01). Sites with parasites also had less algal coverage (Z = 2.44, p =0.02), but seagrass coverage was not significantly different (p = 0.32). MAN also only showed a significant difference in temperature between sites with versus without parasites. Temperature was significantly lower at sites with parasites (t (493) = 3.22, p = 0.01). Salinity (p = 0.11), water depth (p = 0.09), and turbidity (p = 0.81) were not significantly different between sites with versus without parasites. Although MAN had more seagrass coverage than BAR, sites in MAN with parasites versus sites without did not have significant differences in algal coverage (p = 0.21) or seagrass coverage (p = 0.89).

4.0 Discussion

4.1 *Caridean shrimp distribution*

Distributions of estuarine organisms are regulated by a combination of factors such as salinity and habitat complexity (Sheridan and Minello 2003, Barba et al 2005, Lirman et al. 2008, Robblee and Browder 2009). Submerged aquatic vegetation habitats in coastal south Florida typically shelter the most diverse and greatest densities of caridean shrimp, although some species can also be found on soft substrates lacking vegetation (Robblee and Browder 2009). Species of *Hippolyte* and *Palaemonetes* are reported to tolerate the greatest salinity range (meso-euhaline, 5-40 ‰); however, *Hippolyte* spp. are more associated with seagrass or macroalgal habitats, while *Palaemonetes* spp. do not seem to have a habitat preference and can be found in vegetation or soft substrates without vegetation (Barba et al. 2005). *Palaemonetes pugio* and *Palaemonetes vulgaris* can tolerate salinities of 55‰ and 51‰, respectively, which is higher than tolerated by *Palaemonetes intermedius,* also commonly found in the same habitats (Anderson 1985). *P. pugio* is thought to be a phase in the evolution between marine and freshwater habitat shrimps (Knowlton and Kirby 1984; Rowe 2002). *Periclimenes americanus* and *Periclimenes longicaudatus* are most commonly associated with macroalgae or seagrass and are found in poly-euhaline conditions (18-40 ‰) (Barba et al. 2005). *P. americanus* has also been reported in salinities of up to 61‰ (Rouse 1970; Williams 1984). Members of the family Hippolytidae, excluding *Hippolyte* spp., as well as several *Alpheus* spp. are most commonly restricted to euhaline conditions (18-30 ‰) (Barba et al. 2005).

Shrimp population density was greatest in Florida Bay during both seasons (Table 3). Density differences between regions must be viewed with caution, because unequal numbers of basins were sampled from each region, and Florida Bay contained the most sampled basins. However, when looking at individual basins, each with an equal number of sample points, more basins in Florida Bay had greater densities of shrimp than in Biscayne Bay or Lower Southwest Coast. Florida Bay basins JON, RAB, RAN, and WHP all had high shrimp densities during both seasons. Total shrimp densities overall were higher during the dry season, which may indicate either better environmental conditions or greater numbers of recruits. On average, the dry season was associated with lower temperatures, higher salinities, shallower water, higher turbidities (Table 2), and higher vegetation coverage than the wet season. In tropical coastal regions, marine invertebrates typically have access to larval food supplies during the entire year, allowing them to reproduce year-round (Bauer 1989). Bauer (1989) reported that caridean reproduction occurred all year in Puerto Rico seagrass beds but recruitment of juveniles was episodic, peaking in May, June and August and dropping significantly in July and January. Also in Puerto Rico, Bauer (1985) showed that *Latreutes* spp*., Periclimenes* spp., *Thor manningi, Alpheus normanni, Hippolyte* spp*., Processa* spp*.,* and *Leander tenuicornis* exhibited highest densities in late spring and summer and also in December to January. Bauer (1985) found lowest densities of these genera in October to November and also in February and March. In the current study, *Hippolyte* spp. and *Thor* spp. followed this trend but had lowest densities only during October, although samples were not collected from every month of the year. However, *Periclimenes* spp. and *Alpheus* spp. had lowest population densities during the spring (Table 5). Shrimp populations can

vary in tropical climates since many species spawn year-round. Depending on conditions and recruitment cycles, there may be influxes in population and greater densities during certain months which vary from year to year (Sastry 1983, Bauer 2004).

The most common caridean genera collected during this study (*Thor, Hippolyte, Alpheus,* and *Periclimenes*) displayed greatest densities in varying locations (Table 4). The most common shrimp, *Thor* spp., had the greatest densities in RAN, WHP, JON, and RAB in western Florida Bay and NBB in Biscayne Bay. *Hippolyte* spp. had the greatest densities in POM, BAR, and MAN in Biscayne Bay and in EAG in Florida Bay. *Alpheus* spp. occurred in highest densities in Lower Southwest Coast region, in PON and OYS. Greatest densities of *Periclimenes* spp. were also found in Lower Southwest Coast, in LOS, OYS, and WHT.

Although *Thor* spp. was the most abundant caridean shrimp in the study, *Hippolyte* spp. was the most commonly parasitized host. Gill cleaning is important to allow sufficient amounts of oxygen into the gills. Carideans have setal filters at the entrance of their gill chambers; however, the filters do not completely prevent bacteria, protozoans, and invertebrate larvae from entering so they must use other mechanisms to clean their gills. Some caridean shrimp families use specialized grooming chelae lined with tufts of setae which is more effective for removal of fouling organisms. Common internal grooming methods include reversal of water current flow through the gill chamber and scraping with setae on the chelipeds (Bauer 2004).

Many species of Hippolytidae and Palaemonidae have specialized grooming chelipeds to clean their gills. The grooming chelipeds are not completely effective, as parasitic isopods can still invade and survive. Once an isopod is in place, the host often

treats it as part of its own body, brushing and grooming the isopod as if it were part of its own gills. Female carideans also groom their eggs for aeration and have been documented grooming abdominal isopods in place of their eggs. Another method of anti-fouling in the Caridea is the epipod-setobranch system which utilizes tufts of setae on upper portions of their limbs. When the shrimp walks or feeds, the setae passively jostle the gill chamber to enhance cleaning. However, this is a much less efficient means of grooming than chelipedal setae (Bauer 2004). Typically in Caridea, only one major method of gill cleaning is utilized, either grooming chelipeds or epipod-setobranch, and is generally a characteristic at the family level. Hippolytidae is an exception, possessing both mechanisms; however, their epipod-setobranch systems are reduced compared to others (Bauer 1979). Although no literature was found confirming that species of *Hippolyte* collected in the current study are less adapted to gill cleaning, higher levels of parasitism among this genus compared to others may suggest that they are less efficient groomers; however, this may be dependent on habitat and amount of fouling organisms in a particular location.

4.2 *Seasonal variations*

Seasonal variations in percentages of parasitized carideans were generally not significant in this study. A similar study, examining parasite distribution on *Palaemonetes pugio* among several locations in southwestern Alabama also failed to showed significant differences in parasite abundance between seasons (Sheehan et al. 2011). However, *Hippolyte* spp. did exhibit a significant difference in percentage of parasitized carideans between seasons in the current study ($p < 0.01$) (Figure 11). Parasites were more frequent during the dry season, but there were also significantly

higher caridean numbers. MAN, BAR, and NBL did not follow this trend and had greater percentages of parasitized carideans during the dry season despite lower shrimp densities. The results of the current study suggest that parasitism may increase with host availability but is not directly specific to season.

Although seasonal variation cannot accurately be elucidated with only one year (2 seasons) of data, total shrimp counts of the dominant genus, *Thor* spp., which had occurred in greater overall density during the dry season, followed the trend reported by Robblee and Browder (2009) in 2008. The second most common caridean genus, *Hippolyte* spp., had also occurred in greater density during the dry season, but unlike the greater wet season density reported by Robblee and Browder (2009). By contrast, *Periclimenes* spp. occurred in lower dry season densities in the current study and higher densities in the Robblee and Browder (2009) study. However, when examining several years of shrimp population data, Robblee and Browder (2009) found that the dominant genera, *Thor* and *Hippolyte*, showed varying seasonal densities among years and did not always follow the same pattern in the same basins. Thus year-to-year variability obscures any possible seasonal signal influencing caridean populations.

Variations in life spans and reproduction are also likely to influence populations between seasons from year to year. Typically, tropical carideans mature at about two months and live 6-13 months (Alon and Stancyk 1982). *Thor* spp. is thought to live only to about five months (Bauer and VanHoy 1996). Carideans that live through the winter months are likely to spawn early in the year and die before the following winter. Their offspring often spawn later in the year once they reach maturity (Anderson 1985).

Females from the summer generation usually only live 6-8 months and produce the young of the overwintering generation (Bauer 2004).

Seasonal variation in water temperature generally correlate with latitude and is an important factor in the reproductive pattern of many nearshore marine invertebrates; however, in the tropics, warm water and adequate food supply allows year-round breeding (Sastry 1983, Bauer 1992, and Bauer 2004). In tropical coastal regions, marine invertebrates typically have access to larval food supplies for production throughout the year (Bauer 1989). Bauer (1989) reported that although carideans reproduced all year in seagrass beds in Puerto Rico, recruitment of juveniles was episodic, peaking in May, June and August and dropping significantly in July and January. Interestingly, recruitment patterns followed the same patterns for the nine shrimp sampled, suggesting they were all being influenced by the same factors (Bauer 1989).

Growth and molting rates of crustaceans can be affected by temperature and salinity (Vernberg and Piyatiratitivorakul 2011). Alon and Stancyk (1982) reported that *P. pugio* grew more quickly, had shorter life spans and smaller clutch sizes in higher salinity environments. MAN and BAR in Biscayne Bay had the highest percentage of parasitism during both seasons. Also in Biscayne Bay, NBL had the third most parasitized shrimp during the wet season, only behind MAN and BAR, but ranked fourth during the dry season, behind MAN, BAR, and CRA (Figure 12). These locations did not have significant differences in salinity among sites with or without parasites; however, temperature was significantly lower in sites with parasites (Table 2). Hartnoll (1982) reported temperature as the most important factor affecting intermolt periods in crustaceans, with only minimal effects by salinity except for extreme high or lows.

Higher temperatures increased molting frequency, which may be partially attributed to higher respiratory rates at higher temperature, although weight gain and growth were lower in crustaceans at high temperature (Hartnoll 1982; Allan et al 2006). More frequent molting associated with increased temperature may contribute to less parasitism. Although not common, parasites can be shed during molting (Cash and Bauer 1993).

Some hippolytids tend to decrease reproductive output with increasing latitude (Clark 1987). Terossi et al. (2010) also reported this trend among *Hippolyte obliquimanus*. However, latitude cannot account for all reproductive variability, thus, local and regional conditions must be considered as they may contribute greatly to adaptions in decapod reproductive biology (Terossi et al. 2010). Temperature is a major factor in reproduction and at lower temperatures (15-16°C) energy normally allocated to reproduction is instead used for metabolism in grass shrimp. Salinity has less of an effect on caridean reproduction, but models predict that reproductive effort is higher in a low salinity population (Vernberg and Piyatiratitivorakul 1998). Changes in reproductive effort might also affect immunity to pathogens, making the shrimp more susceptibility to parasitism.

4.3 *Host selection*

The majority of parasitized carideans collected in this study showed signs of infestation but no longer had a parasitic isopod. Of the 365 parasitized shrimp; only 109 had an isopod attached. Isopods may have become separated from their host during collection, preservation or sorting, as they can easy become dislodged, especially once dead. Also, carideans typically outlive their parasitic isopods, it is possible that some parasites may have died and fallen off before collection (Pike 1960). Van Wyk (1982)

documented that branchiostegites of previously infected hosts keep their swollen shape through several molts after the parasite has been removed. Jay (1989) reported that approximately 10% of the *Crangon francisorum* collected in his study showed signs of parasitic isopod infestation but had lost the parasite before they were sorted. In the current study, 68.8% of the carideans showed evidence of prior infestation. Reasons for parasite mortality are impossible to determine by simply observing a previously parasitized chamber; however, molting of the host is a possible cause since the cuticle surrounding the isopod is shed during a molt (Cash and Bauer 1993). However, Cash and Bauer (1993) found that less than 3% of parasitic isopods did not survive the molt of the host shrimp. They observed female isopods immediately clinging to newly exposed cuticle and wriggling through the old thin cuticle lining as was being sloughed off by the host. Although the exact reason for high numbers of lost parasites in this study cannot be determined, loss during collection may have been an important contributor.

Previous studies have shown high positive correlations between sizes of female parasitic isopods and host shrimp, indicating that the host is most likely infected early in life. The parasitic isopod continues to grow with the host and remains there for the duration of either life (Beck 1980a, Schuldt and Rodrigues 1985, Pike 1960, Cash and Bauer 1993). Although carideans typically outlive their attached parasite, if the caridean dies first, the isopod cannot live on its own (Pike 1960). The current study also supports this trend, based on the positive size correlation found between parasite (or swollen lump on formerly occupied branchial chambers) and host (Figure 10). However, caution must be used when making any assumptions on correlation due to large number of parasitized shrimp lacking isopod presence. Exact lengths of lost parasites could not be determined;

however, because isopods fit tightly into the branchial chambers, estimates based on size of carapace lumps should be fairly close.

Levels of parasitism are also likely to vary between years, at least in part depending on host shrimp availability as well as intermediate host availability. Several species of bopyrid isopods have only been documented on single host species; however, intermediate copepod hosts may also influence bopyrid distributions. Little information is known about interactions between bopyrids and their intermediate copepod hosts (Boyko and Williams 2009). Availability of cryptoniscus larvae may also have an influence on bopyrid prevalence in seagrass beds. Owens and Rothlisberg (1995) suggested that the cryptoniscus stage of the bopyrid is affected more by environmental factors such as salinity, temperature, depth and turbidity rather than intermediate host abundance, as both cryptonisci and copepod hosts responded to the same environmental variables in the same way. Additional years of data would be required in order to identify any trends (or lack thereof) between seasons or among years in the current study area.

Populations of intermediate and definitive hosts may be spatially separated from each other implying that the cryptoniscus larvae must be able to seek out their desirable final host. For example, the calanoid copepod, *Acartia tonsa,* an intermediate host, is holoplanktonic; however, caridean larvae are often meroplanktonic, creating a possible wide spread between the two organisms in an estuary. Laboratory experiments focusing on *Probopyrus pandalicola* and its host, *Palaemonetes pugio* found that cryptoniscus larvae typically swam at random or with the direction of current; however, when water concentrated with host shrimp crude extract was added, the larvae swam upstream toward

the source. However, when water was added that only previously contained host shrimp, there was not a significantly strong tendency for cryptonisci to swim upstream anymore (Anderson and Dale 1989). In contrary, Beck's (1979) study suggested that cryptoniscus larvae can swim relatively substantial distances, at least 13 km, upstream from the location of the intermediate host in an estuary to the definitive host in a freshwater environment. Nielson and Stromberg (1973) suggest that the isopod larvae must use well-developed chemosensory responses to make the transition between intermediate and definitive hosts successfully. It has also been suggested that chemoreception may be used to attract potential male bopyrids to female parasites already established on the host (Markham 1974).

Hutton (1964) and Hutton and Sogandares-Bernal (1960) reported bopyrid parasites as commonly being host specific. However, some parasitize a range of hosts, and Markham (1986) reports that definitive host species-specificity is rare. For example, *Probopyrus pandalicola*, is a common gill chamber ectoparasite on 16 species of palaemonid shrimp (Walker 1977, Beck 1979). On the other hand, *Bopyrinella thorii*, a common branchial bopyrid parasite in South Florida, is found only on *Thor floridanus* (Markham 1972). According to Hutton and Sogandares-Bernal (1960) and Markham (1985), other documented isopod/shrimp host pairs are *Bopyrina abbreviata* on *Hippolyte* spp., *Bopyrella richardsonae* on *Alpheus heterochaelis*, and *Schizobopyrina urocaridis* hosted by *Periclimenes longicaudatus*. In the current study, parasitic isopods were not host-species specific, although they were specific at the genus level (Table 6). As examples, *B. abbreviata* was found on two different species of *Hippolyte* only. Although bopyrid parasites are commonly host specific (Hutton 1964), host species-specificity is

70

fairly uncommon (Markham 1986). *Alpheus heterochaelis*, hosted three different branchial parasites in this study: *P. alphei, P. richardsonae,* and *P. stellatus. Probopyrus pandalicola* has a variety of palaemonid shrimp species hosts (Cash and Bauer 1993, Walker 1977) but was only found to infect *Palaemonetes intermedius* in this study. Interestingly, *P. pandalicola*, has the greatest range of any bopyrid in the Atlantic Ocean (Markham 1974; Beck 1979; Beck 1980) and is the only bopyrid known that can live in fully fresh water (Markham 1986). Markham (1985) suggested that *H. pleuracanthus* may be the only host for *M. carolii*; however, were only found on *H. zostericola* during the current study (Table 6).

Latitude correlates with number of host species for a given parasite species. Bopyrids living in high latitudes typically have numerous hosts while those in warmer water are usually restricted to a maximum of three hosts, usually from the same genus. Warmer waters typically have greater species diversity of both decapods and bopyrids which may be why bopyrids in low latitudes parasitize fewer hosts. However, *Alpheus* spp. and *Synalpheus* spp. are an exception: six bopyrid species infest *Alpheus* (two of which infest three host species) and ten species infest *Synalpheus* (three of which have three different host species) (Markham 1986).

Thor floridanus was the only species in the genus, *Thor*, collected with abdominal isopods (Table 6). *Thor floridanus* hosted *Loki circumsaltanus* abdominally and *Bopyrinella thorii* in the branchial chamber. Markham (1972) reported four species of *Thor* spp. in Florida; however, is fairly certain *L. circumsaltanus* is host specific to *T. floridanus*. *L. circumsaltanus* was also found only on *T. floridanus* in this study. *T.*

dobkini and *T. manningi* were also collected; however, no *T. dobkini* were found

parasitized and *T. manningi* only hosted the branchial isopod, *B. thorii*.

Prior to this study, *Diplophryxus* spp. had not been documented on *Periclimenes*

americanus. Previously, *Dicropleon periclimenes* was the only known species hosted by

P. americanus in the western Atlantic (Markham 1985). However, the abdominal isopod

species found on *P. americanus* in this study appears to be an undescribed species of

Diplophryxus. Previous descriptions of these isopods may have been missing important

features or could be a new species altogether (Boyko 2012, personal communication).

Diplophryxus has a circumglobal distribution in temperate and tropical latitudes (Boyko

2012).

4.4 *Environmental conditions*

Salinity is a major abiotic factor contributing to species composition distributions

in estuarine habitats (Heck and Wetstone 1977, Barba et al. 2005, Allan et al. 2006,

Lirman et al. 2008, Rozas and Minello 2011). In the current study, variations in water

temperature did not fluctuate as greatly between basins as salinity, which may reflect the

greater effect of salinity on hosts and parasites (Table 2). Higher temperatures during the

wet season and higher salinities during the dry season follow historical patterns for water

quality in the Biscayne Bay area (Caccia and Boyer 2005). Average temperature

measured during the 2010 wet season in Biscayne Bay ($\bar{X}= 30.08$°C) was higher than the

2011 dry season ($\bar{X}= 27.13$°C). Higher wet season mean temperature corresponds to

historic data collected from 1994-2003 in the same region (Caccia & Boyer 2005).

Temperature across South Florida in 2010 was considered extreme relative to

normal averages. The year began cool and wet followed by the hottest summer on record

and ending with the record coldest December for South Florida. South Florida also

recorded the highest summer temperatures lasting more days than normal (NOAA et al.

2010b). Following the summer months, South Florida experienced a cooler winter,

between December 2010 and February 2011, that averaged two to three degrees below

normal (NOAA et al. 2011b). The colder than average winter temperatures were

primarily caused by the strongly negative North Atlantic Oscillation and Arctic

Oscillation, which forces Arctic air masses from Canada into the southeastern U.S.

including Florida. The flip in weather happens when the oscillations are in a strong

negative phase and are believed to have an even stronger effect than the longer-term

ENSO phase, La Niña, which was also occurring at the same time (NOAA et al. 2010b).

In 2010, the wet season began May 16th and ended October 3rd. During the wet

season, Miami International Airport recorded 43.30 inches of rainfall, which was 8.39

inches over the normal average. The dry season began October 4th, thirteen days earlier

than the average start date (NOAA et al. 2010a). The 2010 dry season experienced record

temperatures with December the coldest and April the warmest months on record. In

addition, South Florida experienced the driest conditions in 80 years between October

2010 and February 2011 (Molleda 2010). The 2010-2011 dry season continued until

June 8th, giving the 2011 wet season start date the latest on record since 1956 (NOAA et

al. 2011a).

Variations in abiotic factors among basins in the same region can be attributed to

location, amount of runoff and mixing. Shallow mud banks in Florida Bay divide the bay

into relatively distinct basins that restrict circulation and mixing between basins, which

lessen regional tidal range and current speeds (Boyer and Fourqurean 1997) and likely

restricts larval shrimp transport into the eastern interior portion of bay (Robblee et al. 1991a, 1991b; Browder et al. 2002). The majority of Biscayne Bay is sheltered by land barriers (Figure 4); however, it does not have banks separating individual basins to the extent of Florida Bay. In the Lower Southwest Coast, WHT and OYS are also enclosed by land, whereas PON and LOS have direct access to the Gulf of Mexico (Figure 2).

The regions are unique and distinct from one another in bottom sediment type, vegetation, salinity and temperature. Freshwater input sources and areas of runoff can affect temperature, salinity, and nutrient loading for particular areas. Major freshwater runoff sources from the northern portion of Biscayne Bay include Snake Creek, Arch Creek, Little River, and the Miami River Canal. The central portion of Biscayne Bay receives freshwater input from the Coral Gables Waterway, Snapper Creek, and Cutler Drain, while the southern portion of the bay receives input from Military Canal, Mowry Canal, Black Creek, and Princeton Canal. During 1994-2003, an annual mean canal input into Biscayne Bay was 2071.5 $ft^3 sec^{-1}$, with freshwater flow for all areas of the bay always greater and usually 2-3 times higher during the wet season (Caccia & Boyer 2005). In addition to the increased rainfall during the wet season, Larsen (1995) also found that less freshwater input reached Biscayne Bay due to lower groundwater levels and reduced terrestrial storage.

Florida Bay and Lower Southwest Coast regions are very compartmentalized due to shallow water and local geomorphology (Tabb et al. 1962, Holmquist et al. 1989, Robblee et al. 1991b). Florida Bay receives its freshwater runoff primarily from Taylor Slough in the Everglades and C-111 canal at the northeast side of the bay (Tabb et al. 1962; Boyer and Fourqurean 1997). However, due to the restrictions between basins,

sources of freshwater runoff can be difficult to quantify exactly from nonpoint sources of

Everglades runoff (Boyer and Fourqurean 1997). The water column is generally

oligotrophic and historically phytoplankton biomass has been fairly low throughout the

system (Fourqurean and Robblee 1999). Florida Bay also experiences prolonged periods

of hypersalinity in the coastal embayments (Fourqurean et al. 1993). In addition, past

studies have shown animal density and diversity decreases from west to east in the Bay

(Fourqurean and Robblee 1999).

The Lower Southwestern Coast including Whitewater and Oyster Bays

experiences freshwater influx from streams and rivers originating from Shark River

Slough in the Everglades. The brackish water flows through the mangrove-lined coasts

and into the Gulf of Mexico (Boyer and Fourqurean 1997). This region is less influenced

anthropogenically as it is more remote compared to the heavily populated Miami area on

the eastern side of south Florida.

Salinity and water depth were most strongly correlated with parasite presence.

Increased salinity seemed to decrease the likelihood of parasite presence in a particular

location, as parasites were found at fewer sites with higher salinities. Sheehan et al.

(2011) suggested that bopyrids seemed to be more prevalent in locations with

consistently lower salinity. Although the regression found parasites more likely under

certain parameters, the conditions that may have occurred over longer periods of time

must be considered (Mackenzie 1999), as the data only shows the water quality at that

particular time but parasitism happens over time when conditions may have been

different. In Florida Bay, salinity values are typically highest values in the central

portion of the bay (Boyer and Fourqurean 1997). The eastern portion of the bay has the

largest salinity range (~50 ‰) depending on year and season (Boyer et al. 1997) with the northeastern portion varying the most in response to freshwater runoff (Boyer and Fourqurean 1997). The central portion of the bay typically has higher salinity due to less freshwater runoff and more restricted circulation. The restricted water movement can result in a long residence time, and the area can even experience hypersaline conditions during the summer months (Boyer and Fourqurean 1997).

Although every collection site was relatively shallow, water depths of sites with parasites in each basin were deeper than sites without parasite presence. Shallower water is typically found closer to the shoreline and often experiences higher temperatures and salinities, unless directly next to an area of freshwater runoff. Although parasites were found most often at sites with higher temperatures, they were also found in locations with lower salinities, which is not always the case in shallow water. Moving away from the shore, sites are more likely to be deeper and less saline.

Although turbidity was not significantly different between sites with or without parasitic isopods, there were differences in turbidity between seasons as well as regions. Contrary to this study, past data for this area did not show significant differences in turbidity levels with season (Caccia and Boyer 2005). Variances in turbidity between seasons were most likely caused by shallow depths and wind speeds. Wind speed in the Miami area is on average slightly higher during the wet season than the dry. April and May average 10.5 and 9.5 mph wind speeds, respectively, whereas September and October average 8.2 and 9.2 mph (SERCC 2007). It was expected that increased wind speeds might contribute to higher turbidity levels during the dry season, and results found significantly greater turbidity values during the dry than the previous wet season. On

average, water depths were also significantly deeper during the wet season. The slightly shallower water depths during the dry season may have also contributed to the significantly higher turbidity values due to mixing from the winds (SERCC 2007). Regardless of season, higher turbidities found in the Lower Southwest Coast can be attributed to stronger tidal currents in less sheltered areas open to Gulf of Mexico, increased mixing in the water column, less vegetation to stabilize sediment, and highly particulate water originating from the mangrove estuaries.

4.5 *Vegetation*

Less seagrass and higher algae coverage at a particular site seemed to increase the likelihood of parasite being present. Populations of flora and fauna in Florida Bay and surrounding areas fluctuate with season due to salinity and temperature changes. Greatest organism densities occur when salinity is between 30.0-45.0 ppt (Tabb et al. 1962). Seagrass development declines from highest in the western portion of Florida Bay to lowest in the east. Pink shrimp density is higher in western Florida Bay following the patterns of seagrass abundance (Browder et al. 2002), which also seems to be true for carideans (Table 3).

Biscayne Bay contains a mixture of seagrass and macroalgae giving carideans a habitable environment. However, in the current study, higher macroalgal cover overall was associated with the increased chance of parasitism and may be a factor regarding the greater parasitism in the Biscayne Bay area. Habitat quality may not be ideal for carideans in Biscayne Bay and the added habitat stress from runoff and eutrophication may lower their resistance to parasitism. In the Bahamas, areas of coral that were most

altered by algal growth typically had the highest parasite loads (Boyko 2012, personal communication).

4.6 *Parasitic isopod distribution*

      Spatial heterogeneity seems to have a stronger influence on regional parasite percentages than seasonal variances. MAN and BAR had the greatest percentages of parasitized carideans for both the wet and dry seasons, followed closely by NBL. Parasite ratios were higher for all three of these basins during the dry season. MAN, BAR, and NBL are all located in Biscayne Bay and are grouped into a short-canopy seagrass cluster, characterized by reduced density and canopy height, based on Bray-Curtis similarity cluster analysis in the FIAN network (Robblee and Browder 2012). The short-canopy seagrass cluster is associated with shallow sediment depths, which decrease from west to east through Florida Bay into Barnes and Card Sound (Robblee and Browder 2009, Browder et al. 2002). Shrimp species composition in BAR was 53% *Hippolyte* spp. and roughly 22% each of *Alpheus* spp. and *Thor* spp. MAN was also mainly comprised of *Hippolyte* spp. with almost 57% from that genus followed by 31% *Thor* spp. NBL did not follow the same pattern, with 60% *Thor* spp. and only 36% *Hippolyte* spp. (Table 4).

      Parasitic isopods have been used as biological indicators of disturbed habitats (Williams and Boyko 2012). Many types of parasites are sensitive to changes in environment but others can be more resistant than their hosts and are likely to increase in population as levels of pollution rise. For example, eutrophication has been documented to increase parasite abundance on hosts for the following parasite taxa: Monogenea, Nematoda, Digenea, Cestoda, and Acanthocephala. Ectoparasites are constantly in

contact with the environment and have developed resistance to some natural changes and therefore are often more tolerant than their hosts (Mackenzie 1999).

Human interaction with an environment can significantly affect the transmission of a parasite to its definitive host. Hanzelova (1992) reported that species composition and seasonal dynamics of copepods changed drastically following the drainage of a freshwater reservoir in Czech Republic. Because the copepods were intermediate hosts for a rainbow trout cestode parasite, infection of trout decreased by 97% following drainage (Hanzelova 1992). Copepods are also intermediate hosts for bopyrid isopods and are likely subject to population variations due to environmental conditions and alterations.

Point source contamination from canal water containing urban and agricultural waste enters Biscayne Bay in several locations. In the northern portion of the region, the major tributaries include Miami River, Arch Creek, Snake Creek, and Biscayne Canal (Lietz 1999, Fike 2002). High levels of coliform bacteria, ammonia, and DO have been found in discharges from these sources (Fike 2002). In the southern portion of Biscayne Bay region, high levels of ammonia nitrogen and nutrient concentration have been documented in Goulds Canal and Black Creek presumably due to the adjacent South Dade Landfill (Lietz 1999, Meeder and Boyer 2001, Fike 2002). As a result of contaminated runoff, nutrient enrichment is often an issue in this area. Heavy nutrient loading can cause eutrophication, algal blooms and high phytoplankton productivity which can negatively affect seagrass communities and the fauna, such as caridean shrimp, relying on the seagrass for their habitat (Lietz 1999). Crustaceans are very sensitive to hypoxia and when DO falls below ideal levels they require physiological and behavioral

adaptations to achieve necessary oxygen (Salvato et al. 2001, Bernatis et al. 2007, González-Ortegón et al. 2012). The adaptations required often reduce amount of energy supplied for growth and reproduction of the organism (Das and Stickle 1994). Hypoxic conditions also lower an organisms' tolerance to environmental stresses such as pollutants (Vaquer-Sunyer and Duarte 2008, González-Ortegón et al. 2012).

Two southern Biscayne Bay basins, MAN and BAR, supported the highest percentages of parasites during both the wet and dry seasons, and are located closest to the output of the C-111 canal. This canal is the southernmost of the Central and South Florida canal system, which was established to provide flood protection and drainage for agriculture areas near Homestead. The highest levels of phosphorus in Taylor Slough in northeastern Florida Bay are concentrated within 0.4 km of the C-111 canal (Wright et al. 2008). Although water flowing through Taylor Slough likely has less nutrient loading as it must pass through the wetland area before entering the bay, much of the water which historically drained southwest through Taylor Slough and Everglades National Park currently seeps into the C-111 Canal to the east instead. This causes extreme water fluctuations to the south Florida coastal ecosystem (Wimbrough and Collis 2011). The northeastern portion of Florida Bay also experiences higher nitrogen concentrations than the rest of the bay, most likely from terrestrial sources, along with freshwater runoff (Boyer et al. 1997). Since the C-111 canal flows directly into MAN and BAR, fluctuations in salinity and temperature along with increased nutrient runoff most likely create an environment more susceptible to parasitism.

5.0 Conclusion

The primary objectives of this study were: (1) to determine the occurrence of symbiotic isopods on caridean shrimp and their distribution throughout coastal seagrass beds in South Florida, and (2) to identify which shrimp species are infested most often and by which type of isopod. The first hypothesis stated that the occurrence of carideans and associated isopods would differ spatially among sampling regions. The second hypothesis stated isopod density would differ temporally between sampling seasons. The final hypothesis stated that isopod density would vary based on the caridean population at each location.

The first hypothesis was accepted due to significant differences in densities between regions. The occurrence of carideans and associated isopods differed spatially between regions and basins in each region. Caridean populations varied among the three regions ($p < 0.001$); Florida Bay supported the greatest densities during both seasons, followed by Biscayne Bay and the Lower Southwest Coast. Basins in each region also differed significantly in shrimp populations ($p < 0.001$). In Biscayne Bay, NBB contained the most shrimp in the region for both wet and dry season. In Florida Bay, JON consistently had the most shrimp for the region except for RAN during the dry season. Among the basins of the Lower Southwest Coast, shrimp populations were overall higher during the wet season with OYS having the greatest density in the wet season and WHT having the greatest density during the dry season. The most abundant shrimp, *Thor* spp. had highest densities in RAN, JON, and RAB in Florida Bay and NBB in Biscayne Bay. *Hippolyte* spp. had greatest densities in NBB and POM in Biscayne Bay and in RAB in Florida Bay.

Isopod density also differed significantly among regions ($p < 0.001$) and also among basins in each region ($p < 0.001$). Biscayne Bay had a significantly higher percentage of shrimp parasitized than the other two regions. In Biscayne Bay, the highest percentage of isopods were found in MAN and BAR during both the wet and dry season. Based on the overall regression for the presence/absence of isopods among all regions using temperature, salinity, turbidity, water depth, algal coverage, and seagrass coverage as independent variables, all variables except for turbidity were significantly associated with the presence or absence of parasites. However, in MAN and BAR, sites with parasites had significantly lower temperatures than sites without parasites. These two basins, which are adjacent, had lower average temperatures during the dry season with higher percentages of parasites. MAN and BAR also had fewer shrimp in the dry season than during the wet season. In addition, it is likely that parasite presence increases in areas with added stress on the shrimp. Biscayne Bay experiences more runoff from urbanized areas than the other two regions. MAN and BAR are located at the mouth of the C-111 canal, which regulates water flow from areas near Homestead. Constant changes in freshwater flow and nutrient loading in this area may help explain the higher parasitism levels.

This study failed to accept the second hypothesis, which stated that percentage of shrimp parasitized would differ temporally between the wet and dry seasons. Overall, percentages of parasitized shrimp did not differ significantly between the wet and dry season regardless of the higher populations of shrimp found during the dry season. *Hippolyte* spp. had a higher percentage of parasitized individuals during the dry season and was the only host species that exhibited a significant difference in parasitism between

seasons. However, when evaluating number of parasitized shrimp between wet and dry season based on individual regions and basins, the hypothesis can be accepted since there were temporal differences among individual locations. Florida Bay had a higher percentage of shrimp parasitized during the dry season (also more shrimp collected during that season) but was the only region which had a significant difference in number of parasitized shrimp between wet and dry season. When looking at individual basins between wet and dry seasons, the majority of basins exhibited significant differences: NBL, SBL, BAR, MAN, DUK, CAL, CRA, RAB, and LOS all had higher percentages of parasitism during the dry season. RAN and WHT had higher percentages of parasitism during the wet season.

The final hypothesis stated that isopod density will vary based on the local population of caridean shrimps. Parasitic isopods collected during this study were host-specific within a shrimp genus. Isopod species known to parasitize specific caridean genera or species, most likely exhibit greatest density in areas with higher concentrations of those shrimp. This hypothesis cannot be accepted, as the isopods were not necessarily found in the locations with the highest density of that particular host. Instead, isopod distributions were more heavily based on location and not as much on areas with higher caridean densities. Out of 12 shrimp genera, only six were associated with isopods during this study: *Alpheus* spp., *Hippolyte* spp., *Palaemonetes* spp., *Periclimenes* spp., *Thor* spp., and *Tozeuma* spp. About 60% of all isopod occurrences were associated with *Hippolyte* spp. and 26% with *Thor* spp.

Shrimp collected with the greatest densities (*Thor, Hippolyte, Alpheus,* and *Periclimenes*) were found in highest densities in varying locations. The most common

shrimp, *Thor* spp., had the greatest densities in RAN, WHP, JON, and RAB in western Florida Bay and NBB in Biscayne Bay and was most common during the dry season. *Hippolyte* spp. had the greatest densities in POM, BAR, and MAN in Biscayne Bay and in EAG in Florida Bay and had highest densities during the dry season. *Alpheus* spp. occurred in highest densities in Lower Southwest Coast region, in PON and OYS during the wet season. Greatest densities of *Periclimenes* spp. were also most dominant during the wet season and were found in Lower Southwest Coast, in LOS, OYS, and WHT.

MAN and BAR contained the highest proportion of isopod to shrimps during both seasons. Neither of these basins contained the greatest density of shrimp in Biscayne Bay; however, the composition of shrimp in those basins contained over 50% of the most commonly parasitized shrimp, *Hippolyte* spp. In addition to shrimp host availability, isopod density also depends on other variables such as availability of intermediate hosts, environmental conditions, and water quality.

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