FISHERIES AND AQUACULTURE POTENTIAL OF THE CARIBBEAN SPIDER CRAB *MAGUIMITHRAX SPINOSISSIMUS* AROUND ELEUTHERA, THE BAHAMAS

by

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Abstract

The Caribbean spider crab *Maguimithrax spinosissimus* is the largest brachyuran crab in the Caribbean. In this thesis I investigated the population characteristics of *M. spinosissimus* on the island of Eleuthera, The Bahamas, as well as the potential of this crab to remove biofouling on marine aquaculture pens. In chapter 2 I investigated the size ranges of crabs at patch reefs, a blue hole and an anchialine pond in Eleuthera (January to June, 2018). Males reached larger mean carapace widths than females at all sites. Principal component analysis and hierarchical cluster analyses were used to determine size at maturity; males reached morphological and behavioural maturity at larger carapace widths than females. Haemolymph BRIX levels were used as an indicator of general condition, the levels were relatively high and not dissimilar between sites. The meat yield from male crabs was higher than that of females and comparable to other decapods. In chapter 3, I showed spider crabs exhibited a nocturnal pattern of activity in laboratory tanks. The crabs consumed 3.91 ± 0.35 and 6.97 ± 0.73 % of their bodyweight of algae in 22 - 24°C and 26 - 28°C water, respectively, and although the species is primarily herbivorous they also readily consumed whole fish. Spider crabs were placed on a heavily fouled, offshore aquaculture cage (SeaStation 3000) in confined mesh enclosures to determine if they could be used to remove biofouling organisms. They effectively removed 40 and 90 % of fouling organisms after two and four weeks, respectively, while showing no discriminatory feeding preferences. The crabs were more effective at removing fouling than manual diver scrubbing. The survival rates of crabs inside the aquaculture cage varied between 66.6% and 73.9% during 3 to 6 month trials. The data gathered for this species could be used to establish management plans for an artisanal fishery in the Bahamian archipelago, it also demonstrated the potential of the crab as an effective, environmentally friendly biofouling removing alternative for sustainable aquaculture.

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List of Abbreviations and Symbols

AF	Abdomen Flexibility
ANOVA	Analysis of Variance
AW	Abdomen Width
BRIX	Dissolved Solid Content
BRIX-TC	Dissolved Solid Content – Temperature Compensated
BW	Bodyweight
°C	Degrees Celsius
ChD	Chela Depth
ChH	Chela Height
ChL	Chela Length
ChW	Chela Width
CL	Carapace Length
CW	Carapace Width
FAO	Food and Agriculture Organisation
g	Grams
GLM	General Linear Model
m	Meters
n or n_x	Number of
P_b	Percentage of Black Pixels
P_t	Total Number of Pixels
PCA	Principal Component Analysis
PNA	Percent Net Aperture
PNO	Percent Net Occlusion

R^2	Coefficient of Determination
RI	Refractive Index
SEoM	Standard Error of the Mean
T_c	Total Consumption
TC-RI	Temperature Compensated Refractive Index
W_i	Initial Weight
W_f	Final Weight

Co-Authorship Statement

The work described in the present thesis was conducted by Logan Zeinert with guidance from Dr. Iain J. McGaw. Logan Zeinert was responsible for all field and laboratory data collection. Statistical analysis for each chapter was conducted by Logan Zeinert. All chapters were written by Logan Zeinert with intellectual and editorial input by Dr. Iain J. McGaw, Cyr Couturier and Dr. Ian A. Fleming.

Any publication in primary literature resulting from work in chapter 2 and from complementary work not presented in this thesis will be co-authored by Logan Zeinert, Dr. Iain J. McGaw, Dr. Meghan Burchell and Dr. Nathan J. Robertson.

Any publication in primary literature resulting from work in chapter 3 and from complementary work not presented in this thesis will be co-authored by Logan Zeinert, Dr. Iain J. McGaw, Annabelle Brooks, and Cyr Couturier.

Chapter 1: General Introduction

Global Aquaculture Production

Worldwide fisheries landings are in decline, with many wild finfish fisheries close to, or exceeding, full exploitation (FAO, 2016) and unable to meet the rising seafood demands (FAO, 2016). In contrast, the aquaculture sector is increasing rapidly (Troell et al., 2009). World per capita fish supply reached 20 kg in 2014, largely due to increases in the aquaculture sector which provided 50% of the seafood consumed by humans (FAO, 2016).

Aquaculture provided over 80 million tonnes of fish (finfish: 54 million tonnes; molluscs: 17 million tonnes; crustaceans: 7.8 million tonnes), and 30 million tonnes of aquatic plants in 2016 (FAO, 2018). Regionally, Asia leads production (71 million tonnes), followed by the Americas (3.3 million tonnes) and Europe (2.9 million tonnes). To date over 360 finfish species are produced; the top 20 account for over 84% of production volume, with major species including carps (*Ctenopharyngodon idellus, Hypophthalmichthys* spp, *Cyprinus carpio*) and tilapias (*Oreochromis* spp) (FAO, 2018). Over 100 species of molluscs are produced commercially, the top three (oysters (*Crassostrea* spp.), Japanese carpet shell (*Ruditapes philippinarum*) and scallops (*Pectinidae*)) account for 64% of farmed mollusc species. Farmed crustacean species number over 60, with whiteleg shrimp (*Penaeus vannamei*) accounting for just over half of the total worldwide production volume.

In general, higher value species such as salmonids, tunas, shrimp, and prawns, are traded in high volume in more prosperous markets. For example, the demand for high value fish such as Atlantic salmon, primarily comes from markets in Europe, the United States of America, and Japan. Today the majority of salmon that is consumed originates from aquaculture producers in Norway and Chile, and to a lesser degree from smaller producers in Europe, North America, and Australasia (FAO, 2018). Lower value fish, such as small pelagic species and herbivorous freshwater species, are largely produced in and exported to developing economies (FAO, 2018).

Fisheries and Aquaculture in The Bahamas and Wider Caribbean

In The Bahamas major fisheries include spiny lobster, queen conch, and reef fish including groupers (Epinephelidae), snapper (Lutjanidae) and grunts (Haemulidae). Fisheries management in The Bahamas is complicated by the wide spatial scale and large number of islands (Sherman et al., 2018), as well as the cultural status of some species such as queen conch, spiny lobster and Nassau grouper (*Epinephelus striatus*), which are iconic delicacies throughout the Bahamian islands. Restrictions on such iconic fisheries may cause social outcry, especially where subsistence fishing is an important source of livelihood and food security. Management can also be a complex multi-national issue when species (e.g., spiny lobster) have pelagic larval stages or are exclusively pelagic, resulting in a multi-country dependency on recruitment and migration (Cochrane and Chakalall, 2001).

Historically, fisheries have focused on large, long lived, high trophic level species (Pauly et al., 1998). However, a need for new resources due to declining finfish populations (Anderson et al., 2008; Pauly et al., 2002) has meant that invertebrate fisheries have increased in importance (Anderson et al., 2008). Demand for protein with growing human population size (Clarke, 2004; FAO, 2016), and increased availability after release from finfish predation (Baum and Worm, 2009; Worm and Myers, 2003) have been major drivers in the expansion of invertebrate exploitation. Many of these emerging invertebrates fisheries were previously only used for local subsistence in developing countries (Kaczynski and Fluharty, 2002). This increased fishing pressure has led to declines in invertebrate populations in several regions (Hobday et al., 2000) due to lack of regulation of the fisheries (Anderson et al., 2011a) and a lack of understanding in the population dynamics of the species in question (Anderson et al., 2008). The decline in invertebrate populations has had unintended ecological impacts because many are keystone species in marine coastal communities, or serve as ecosystem engineers (Arnberg et al., 2018; Peterson et al., 2003).

Although the Latin American and Caribbean region has a high export of wild fisheries products (3.9 million tonne), the Caribbean contributes much less (7000 tonnes) to aquaculture production worldwide (FAO, 2018). This is likely due to a multitude of factors including the limited history of aquaculture in the region compared to Asian and European countries, limited land and freshwater resources (Alvarez-Lajonchère and Ibarra-Castro, 2013), and ecologically sensitive areas (Gentry et al., 2017). With increasingly exploited fisheries this may change in the future, forcing a move from wild fishery harvest to aquaculture in order to supplement lost revenue and food supply. Recently, Thomas et al (2019) estimated that further development of offshore mariculture operations could produce over 34 million tonnes of cobia (*Rachycentron canadum*) in the region. Currently, aquaculture in the Caribbean focuses on land-based production of tilapia, pond culture of white legged shrimp (Thomas et al., 2019), with some offshore cage-culture of cobia (Welch et al., 2019). Pompano (Carangidae spp.) and red drum (*Sciaenops ocellatus*) also show potential for offshore aquaculture (Benetti et al., 2006), whilst nearshore species including queen conch (*Lombatus gigas*), Caribbean king crab (*Maguimithrax spinosissimus*) spiny lobster (*Panulirus argus*), and some molluscs (*Argopecten gibbus*) have had mixed success in aquaculture (Creswell, 2007; Sarkis et al., 2006).

The Open Blue aquaculture facility in Panama has been producing cobia, 13 km offshore, since 2009. Considered one of the world’s first truly offshore facilities, it produced 1400 tonnes of cobia in 2018 (Welch et al., 2019). The farm has up to 20 individual Ocean

Spar 6,400 m^3 Sea Station cages operational at a given time. Depths at the site range between 55 to 65 m, with cages submerged at least 10m below the surface, as measured from the top of the cage. Because the cages are located over deeper water with a good water flow there are no significant reductions in dissolved oxygen (DO_2), or changes in chlorophyll-*a*, particulate organic carbon or nitrate and nitrite in the water column (Welch et al., (2019). The sea cages are accessed by boat and are only raised to the surface for maintenance, cleaning, and harvest.

Potential Effects of Aquaculture on the Environment

In recent years, consumers have become increasingly interested in the origin of their food and how it is produced. Many will pay a premium for food that is organically or sustainably raised. Although there have been vast improvements in practices over the last 20 years (Price and Morris, 2013), intensive aquaculture operations still have a number deleterious effects on the environment, especially in marine sea cage farming. Some of these include, but are not limited to, the introduction of organic materials and chemicals into the environment, and the escape of farmed animals.

Organic input into environment

In poorly sited or managed farms, (uneaten) food and faeces descending from cages without adequate water movement can accumulate beneath and surrounding the site. The build-up of solid material can smother the seabed and the subsequent degradation by bacteria can lead to anoxic dead zones under the cages (Price and Morris, 2013). The excessive input of nutrients can also lead to blooms of toxic algae and dinoflagellates, which can kill fish and invertebrates (Davidson et al., 2009). These effects can be reduced through fallowing of sites to allow for biomineralization, or through establishment of sites in deeper, well flushed locations.

Chemicals

A number of chemicals used in aquaculture, including antibiotics and parasiticides, metals, disinfectants, and anaesthetics, can potentially find their way into the environment. The biggest concerns surrounding antibiotic use are residual antibiotics in farmed fish, risking both fish and human health (Cabello, 2004). Additionally, the more an antibiotic is used, the greater the risk of the emergence of bacterial resistance to multiple antibiotics (Aarestrup, 2006). Parasiticides are commonly used to treat sea-lice, and other ecto-parasites. However, these treatments lack specificity and may affect non-target species, especially crustaceans (Burridge et al., 2010), thus the release of these compounds has been identified as a major environmental concern (Nash, 2003). Disinfectants are frequently used on nets to control the spread of bacterial infections (Burridge et al., 2010). Their use is largely unregulated; subsequently the effects in the marine environment are poorly studied (Burridge et al., 2010).

Metals, most commonly copper and zinc, primarily enter the marine environment from antifoulants or from feed ingredients (Burridge et al., 2010). In their ionic forms they can be toxic to marine organisms, especially those with delicate larval stages.

Escape of farmed animals

Escapes of farmed fish, especially salmon are relatively common. These escapees may transfer new disease to wild fish. They can also compete for both food and habitat with both wild conspecifics and other native species. There is evidence that the cultured stocks tend to be less locally adapted so if they interbreed with wild fish it will result an inferior animal for life in nature. This can be important if it results in genetic modification of traits that confer advantages to that area or watershed (Besnier et al., 2015; McGinnity et al., 2003).

Biofouling

One problem that is often overlooked, especially in marine pen aquaculture, is biofouling, the accretion of organisms on submerged surfaces (De Nys and Guenther, 2009). Biofouling can have direct effects on production rates, and thus needs to be controlled, but the control or removal of these encrusting organisms, e.g. hydroids, tunicates, algaes, and molluscs (Guenther et al., 2011; LeBlanc et al., 2007; Qian et al., 2007), can have indirect effects on the environment.

Biofouling is conservatively estimated to cost the industry up to 15% of production (Adams et al., 2011; Lane and Willemsen, 2004). The impacts vary based on the amount and type of fouling present, ranging from negative effects on the structure of the enclosure and support systems, functioning of mechanical structures, and health of species within the facility. In both shellfish and finfish culture, fouling can compromise cage structure and mooring hardware (Swift et al., 2006), which can lead to cage deflection and deformation, resulting in devastating effects such as cage collapse and fish escapement (Jensen et al., 2010; Lader et al., 2008; Swift et al., 2006). Furthermore, fouling can decrease the flow of water by as much as 50% (Gansel et al., 2012; Gormican, 1989; Madin et al., 2010), reducing oxygen availability for fish and concomitantly reducing removal of nitrogenous waste products from within the cage (Lader et al., 2008). Fouling organisms themselves can compete with stock for space and food, reducing effective cage volumes (Aarsnes et al., 1990) and inhibiting growth of the farmed species (Adams et al., 2011). In addition, some fish diseases, (e.g., netpen liver disease) (Kent, 1990) and parasites (e.g., *Gilquinia squali,* *Cardicola forsteri*) (Cribb et al., 2011; Kent et al., 1991) can be attributed to the consumption of fouling organisms by the fish.

Commercial farming operations generally use a combination of three broad categories of control to mitigate the effects of biofouling on nets and cages. These include net changing and cleaning, chemical antifoulants, and biological controls (Fitridge et al., 2012). Net changing and cleaning frequency is dependent on latitude, season, and mesh size. This can vary from every eight days (Hodson and Burke, 1994) to once per year (Sutterlin and Merrill, 1978). Net changing is used to prevent both damage from structural fatigue and deformation, and the impact of biofouling occlusion on the health of target species (De Nys and Guenther, 2009). The net is partially raised out of the water, a clean net is unravelled underneath the current one, attached, and the fouled net removed while fish are in the cage (De Nys and Guenther, 2009). This is labour intensive and expensive, requiring numerous nets, net-changing equipment and cleaning teams, while also potentially impacting feeding regimes and risking loss of stock. (Hodson et al., 1997). As an alternative, *in situ* net cleaning can be completed by SCUBA divers using pressurised water hoses (Cronin et al., 1999), and in larger operations this is almost fully automated using remotely operated vehicles (ROVs) (Fitridge et al., 2012). This method is expensive and can trigger larval release (Carl et al., 2011) or leave remnants of fouling organisms which regrow (Moss and Marsland, 1976). Furthermore, *in situ* cleaning can damage nets, increasing numbers of loose filaments which create additional settlement locations for fouling species (Geffen, 1979). This suggests that while cleaning events may reduce fouling biomass, fouling species may re-populate netting more rapidly than initial rates. Fish have exhibited stress behaviours during cleaning events, which may leave them prone to infections; for example, the breakdown of the hydroid *Ectopleura larynx* with power washers has been associated with reduced gill health of farmed salmon (Bloecher et al., 2018). While the fate of excess feed and faecal matter into the environment are reasonably well documented (Kutti, 2008; Torrissen et al., 2011), fouling material dispersal and deposition from net pen cleaning has not received as much attention, but could have similar impacts, creating anoxic dead zones around the farms (Bannister et al., 2016; Floerl et al., 2016; Reid et al., 2009).

Chemical antifoulants are also commonly used to deter larval settlement on netting, and work by leaching a layer of biocide around the net (De Nys and Guenther, 2009). In most developed countries, such as Canada, Norway and the European Union (Floerl et al., 2016; Sandberg and Olafsen, 2006), the introduction of hazardous chemicals directly into the environment is highly regulated, requiring registration of biocides under law or a regulatory agency (Thomas and Brooks, 2010). Although these chemicals are regulated in their use, the release of chemicals and materials from *in-situ* cleaning, e.g. from fragmentation during high-pressure cleaning, or the degradation of these materials over time is not as well regulated, potentially due to the lack of studies on the release of antifouling biocides (Thomas and Brooks, 2010). Copper-based treatments (including copper core netting) are frequently used on marine nets because they are toxic to most settling marine organisms (Oliva et al., 2007). However, bioaccumulation in sediments (Miller, 1998) and tissues (Chou et al., 2003, 2000; Zhu et al., 1990), and leeching through the water column (Brooks, 2000; Thomas and Brooks, 2010) may negatively impact various non-target organisms such as macro- and micro-algae (Bond et al., 1999; Lim et al., 2006), fish (Mochida et al., 2006; Oliva et al., 2007), molluscs (Zhu et al., 1990), lobster (Chou et al., 2000) and urchins (Chou et al., 2003). In general, best management practices combined with enforced regulation have reduced copper contamination risks (Nash et al., 2005). One such example of release rate regulation occurs in Denmark, where copper paints with a release rate of > 200 µg cm^{-2} after

14 days and 350 μg cm^{-2} after 30 days are prohibited on small vessels (Thomas and Brooks, 2010).

A global move to find biocides that are both effective and ‘eco-friendly’ is underway (Fitridge et al., 2012); this would reduce the environmental impacts and enhance public perceptions of aquaculture (Sandberg and Olafsen, 2006). Such chemicals are currently used during times of heavy fouling and the environmental impact is considered to be minimal as nets and lines must be removed from the water during treatment. Short term less-toxic alternatives include acids (e.g., acetic, silicic, formic and citric acids) (Denny, 2008; Guenther et al., 2011; LeBlanc et al., 2007; Piola et al., 2009) and bases (e.g., sodium hypochlorite (bleach)) (Denny, 2008). Acetic acid has been shown to remove between 55 – 100% of fouling species (Denny, 2008; Piola et al., 2009), while bleach use was equally successful, removing 75 – 100% of fouling organisms (Denny, 2008; Piola et al., 2009). A novel experimental method by Da Gama (2001) involved the crude extraction of natural biofouling chemicals from three species of seaweed and showed some potential antifouling properties in one species.

Finally, researchers have investigated the effectiveness of various species as biocontrol agents to remove organisms through natural grazing on the netting. Sea urchins have been the primary species used, with trials on oyster, mussel and scallop farms (Lodeiros and García, 2004; Ross et al., 2004; Sterling et al., 2016; Zhanhui et al., 2014). All found significant differences between fouling amounts at the end of trials, regardless of the density of urchins used. Whilst Sterling et al., (2016) used photographs to determine percent net occlusions, other studies (Lodeiros and García, 2004; Ross et al., 2004; Zhanhui et al., 2014) used the weight of nets at the end of the trial period to determine success of epibiont removal. In addition to removal of fouling organisms on the cage structure, researchers also investigated the removal of epibionts from the shells of the bivalve crop. Removal of growth from the shells themselves showed mixed success – some grazers had no effect on shell fouling, while others reduced shell fouling. In overall support of this method the co-cultured grazing species had little to no impact on the survival and growth of the farmed species (Lodeiros and García, 2004; Ross et al., 2004).

Crabs have also been used in a number of preliminary trials in oyster farms. Various sizes of rock crabs *Cancer irroratus* were added to oyster trays (Hidu et al., 1981). The larger crabs caused losses in the cultured oysters, but smaller crabs removed fouling mussels resulting in reduced oyster mortality. In addition, the foraging activity of the crabs was thought to reduce the build-up of silt within the oyster trays (Hidu et al., 1981). Other crustaceans such as hermit crabs (Ross et al., 2004), shrimp (Dumont et al., 2009), and gastropod molluscs (Enright et al., 1983) have shown some success at removing fouling from scallop and oysters, and promoting growth.

The majority of biocontrol studies in aquaculture have been preliminary in nature or have focused on small scale bivalve operations (Fitridge et al., 2012). A major limitation of biological control is that grazing species often show a preference for specific prey items. This could lead to removal of competitors, allowing ungrazed fouling species to flourish and form successful monocultures on nets (Fitridge et al., 2012). It also brings into question as to where one obtains the biological control stock; if they are harvested from the wild there is potential to deplete natural resources, and use of wild stock could also lead to the transfer of pathogens or disease (Treasurer, 2012). These two problems could be negated by raising of the control animals in a separate aquaculture operation, as is being done for lumpfish to control sea lice infestations (Powell et al., 2018). At present, the use of grazing animals to control biofouling on large commercial finfish operations has received little attention. However, in the future biocontrol may be a low cost, labour saving method (Ross et al., 2004) that could use a marketable organism to improve farm profits as a form of polyculture, or integrated multitrophic aquaculture (Ahlgren, 1998; Ross et al., 2004).

Assessment of Wild Stock

Today commercial fishery stocks are typically managed with landing quotas, gear restriction and vessel size and/or numbers fishing. Behind these management practices is a complex fishery science designed to provide knowledge of population dynamics and thus inform sustainable harvesting practices. Compared to conventional finfish stocks, management of crustaceans differs as growth and catchability are drastically different (Penn et al., 2019). Growth in particular differs as crustaceans undergo a series of moults which incrementally increase the size of individuals, whereas finfish can be modelled using continuous growth models. This method of growth requires that crustaceans lose the exoskeleton, which adds complexity to stock assessments as they cannot be easily aged because no internal skeleton is maintained, and the moulting process frequently causes loss of tags. Further, some species undergo a terminal moult, where growth ceases. Thus crustacean age is often estimated by observing changes in size-frequency of year-classes (Penn et al., 2019). However new techniques such as gastric mill sectioning (Kilada et al., 2012; Leland et al., 2011) may provide more accurate size-at-age estimates, allowing more accurate life history models, and therefore better fishery management. This is especially important in fisheries with varying latitudinal growth rates. Terminal moult is, in some crab species, reached in conjunction with sexual maturity (e.g. Majidae crabs, Hartnoll, 1983), however in other species sexual maturity is reached in the stages prior to the terminal moult (e.g.

Carcinidae and Portunidae crabs, Hartnoll, 1983). Sexual maturity, in conjunction with age, is one of the more important parameters for stock managers (Hall et al., 2006). The knowledge of the size, moult increment, and age of when males and females in a stock reach maturity allows managers to determine a minimum harvest size which will allow reproductive contribution to a population. Maturity in crabs is often reached in conjunction with a change in allometric growth, where often in males the chela increases in size, and in females, the abdomen increases in size (Somerton, 1980).

In crab and lobster fisheries, basic management strategies often involve a legal minimum size, protection of spawning females, or a catch quota. These work well for temperate and cold water crabs, but fast-growing tropical crabs present additional difficulties as recruitment is often more variable (Penn et al., 2019). In these cases alternative methods such as controlling fishing efforts through limitations on vessel numbers, gear size, gear numbers, and fishing time have been adopted. Most exploited crustacean populations require complex year-to-year assessments to determine an allocated catch amount, as the exploitable biomass can be highly variable due to spawning stock abundance, subsequent recruitment success, and climate (Penn et al., 2019).

In addition to exploitation of stocks for direct sale to market, some crustacean aquaculture operations utilise wild caught juveniles, e.g. crabs (Wu et al., 2010) and shrimp (Coman et al., 2006), while panulirid lobster are grown out from wild caught puerulus larvae (Penn et al., 2019). These methodologies are known to have several issues, including quality and quantity variations, as well as potential introductions of pathogens into farms (Coman et al., 2006; Jang et al., 2009; Meng et al., 2009). In addition, excessive removal of adult crustaceans for broodstock may have an impact on natural recruitment, and therefore the overall production of the fishery. Selection and use of a domesticated stock for a hatchery may promote sustainable development of an aquaculture industry, whilst also promoting genetic selection of desirable traits such as growth rate, reproductive potential and pathogen resistance.

The Study Species

The Caribbean King Crab *Maguimithrax spinosissimus* (previously *Damithrax spinosissimus*, *Mithrax spinosissimus* (Hurtado-Alarcón et al., 2018; Klompmaker et al., 2015; Windsor and Felder, 2014)) hereafter referred to as "spider crab," ranges from North Carolina, USA, through the Caribbean to Venezuela (Baeza et al., 2012). The spider crab is the largest brachyuran crab in the Western Atlantic, with males reaching larger mean carapace widths (Panama: 91.7 ± 2.1 (SE) mm sexes combined (Guzman and Tewfik, 2004); Florida Keys: males 65.4 ± 25.6 (SD) mm, females 57.5 ± 19.3 (SD) mm (Baeza et al., 2012); Colombia: males 121 ± 23.2 (SD) mm, females 119 ± 22.4 (SD) mm (Campos et al., 2015)) and masses than females (Colombia: male max 3800 g, female max 3100 g (Campos et al., 2015)). The larger mass of males is principally due to the larger chelipeds (Campos et al., 2015), arguably making them more marketable (Brownell et al., 1977). The species is a nocturnal omnivore, primarily feeding on encrusting algae (Butler IV and Mojica, 2012), with grazing rates exceeding most Caribbean herbivorous fish (Butler IV and Mojica, 2012).

Current exploitation of spider crabs appears to be made up from incidental catches, primarily in the Panama Canal, Panama, and Pedro Bank, Jamaica (Creswell et al., 1989; Guzman and Tewfik, 2004; Munro, 1983), where it is taken for subsistence rather than commerce. Winfree and Weinstein (1989) suggest that the species has not become commercially important as marketable sizes are infrequently caught in traps. This is likely due to the low densities of the crab (> 0.1 crabs/m^2 (Butler IV and Mojica, 2012; Francis et al., 2019)), which are restricted by crevice abundance and availability (Hazlett and Rittschof, 1975) as well as the herbivorous nature of their diet which makes them unlikely to enter baited traps.

A number of preliminary studies have suggested that the spider crab shows potential for aquaculture because it has a short larval phase with benthic settlement occurring within five to six days post-hatch (Brownell et al., 1977). Growth rates have been shown to be 0.1 – 0.2 mm carapace length (CL) per day as juveniles, up to over 0.5 mm CL/day as adults indicating a grow-out period of 12 - 15 months to a similarly sized marketed species (Adey and Farrier, 1989). The species could also be considered “sustainable” as it could be raised on turf algae rather than more costly commercial feed containing fish meal or oil (Rubino and Stoffle, 1990). The large size of this crab and high quality flesh coupled with increasing demand for seafood (Halwart et al., 2007), suggests that the Caribbean spider crab may be suited for a controlled hand-capture fishery prior to development of an aquaculture operation.

Aims and Hypothesis of Thesis

In this thesis, firstly I investigated the characteristics of a number of populations of the spider crab *Maguimithrax spinosissimus* in Eleuthera, The Bahamas and the potential for the development of an artisanal fishery. Secondly, I determined if this species would be a good candidate for removal of biofouling organisms on marine aquaculture cages.

Chapter 2:

Aim: Determine the size, health and estimate the size at maturity of groups of spider crab from 3 sites around Eleuthera.

Hypothesis: The population size as well as individual size and sex ratios of spider crabs will differ among sites around Eleuthera.

Prediction: Spider crabs will be larger, both on average and overall, for both males and females at the patch reefs, where populations are more dispersed, algae has greater variety and a larger biomass. This will be reflected in haemolymph measurements, where crabs will have higher BRIX measurements, reflecting higher diet variety, quality, and availability.

Chapter 3:

Aim: Determine the feeding rates of adult spider crabs and whether they could be used as a biological control agent to remove biofouling in marine aquaculture pens.

Hypothesis: Crabs will graze on fouling organisms on marine aquaculture cages, removing organisms at a sufficient rate to negate the use of other methods.

Prediction: Crabs will graze all organisms from the nets. Larger crabs will eat more than smaller animals. This may result in a worthwhile future path for sustainable aquaculture or integrated multi-trophic aquaculture (IMTA).

Chapter 2: Population structure and size at maturity of the Caribbean spider crab *Maguimithrax spinosissimus* around Eleuthera, The Bahamas

Abstract

The Caribbean spider crab *Maguimithrax spinosissimus* is the largest crab in the western Atlantic, reaching 3 kg in weight and 170 mm carapace width (CW). At present there is no established fishery for *Maguimithrax spinosissimus*, however its short larval stage and herbivorous nature could make this species a potential candidate for aquaculture. The present study investigated the size ranges of crabs at patch reefs, a blue hole and an anchialine pond in Eleuthera, The Bahamas (January to June, 2018). A total of 392 individuals were collected; males comprised 42.1% of the population with a mean CW of 107.7 ± 1.48 mm, while the mean CW of females was 94.3 ± 0.87 mm. Principal component analysis and hierarchical cluster analyses were used to determine size at maturity: morphological maturity was reached in males at 96.2 mm CW and in females at 72.3 mm, while behavioural maturity was reached at 80.1 and 72.1 mm CW for males and females respectively. On average the meat yield of the wet mass of male and female crabs was 14.07 ± 1.07% and 10.9 ± 0.71% respectively, which is comparable to other decapods. I also used the gastric mills to determine the age of crabs by sectioning the ossicles and looking for rings of seasonal growth. The data gathered for this species could be used to establish management plans for an artisanal fishery in the Bahamian archipelago.

Introduction

Fisheries management in The Bahamas is complicated by the extent of ocean area encompassed by the country (Buchan, 2000; Sherman et al., 2018). Remote islands, small populations, and limited infrastructure makes policing and surveying of marine resources problematic. Spiny lobster (*Panulirus argus*), queen conch (*Lobatus gigas*) and Nassau grouper (*Epinephelus striatus*) are iconic in The Bahamas, forming a large part of the diet and providing income for thousands of people (Cushion and Sullivan-Sealey, 2008). Declines of queen conch, have been observed across the Caribbean (Stoner et al., 2018; Tewfik and Guzman, 2003), whilst the spiny lobster has been designated as “data deficient” on the IUCN Red list (Butler et al., 2013), and the Nassau grouper has been classified as critically endangered by the IUCN. Uncertainty in various population estimates and illegal, unreported and unregulated fishing making up large proportions of all landings (36%, Medley and Gittens, 2012) makes sustainable management of the various fisheries challenging. With numerous treasured Bahamian icons threatened, several new fisheries have emerged. Parrotfishes (Scarinae), previously taken as bycatch or bait, have become more common in local landings, which may be of concern due to the ecological role that parrotfishes play as grazers on coral reefs sites (Dahlgren in Sherman et al. 2018). Sea cucumbers (*Holothuria mexicana* and *Astichopus multifidus*) have also become a potentially economically valuable export (Sherman et al., 2018). However, like parrotfish, they provide an ecologically important role as bioturbators and detritus processors (Dahlgren et al., 1999). Due to their density dependent reproduction, sea cucumber fisheries have proven to be difficult to manage worldwide (Anderson et al., 2011b). Exploration of new species such as the Caribbean spider crab *Maguimithrax spinosissimus,* along with sustainable implementation of an artisanal fishery, could be used to alleviate pressure on other at-risk stocks.

The Caribbean Spider Crab *Maguimithrax spinosissimus* (previously *Damithrax spinosissimus, Mithrax spinosissimus*; Hurtado-Alarcón et al., 2018; Klompmaker et al., 2015; Windsor and Felder, 2014)) hereafter the spider crab, ranges from North Carolina, USA, through the Caribbean to Venezuela (Baeza et al., 2012). It is the largest brachyuran crab in the Western Atlantic, reaching over 3 kg and 170 mm carapace width (Winfree and Weinstein, 1989). This species is a nocturnal omnivore showing preference for fleshy macroalgae but also grazes on calcareous algae (Butler IV and Mojica, 2012), as well as consuming some animal material (Winfree and Weinstein, 1989). The per capita grazing rates of individual crabs have been shown to exceed most herbivorous fish in the Caribbean (Butler IV and Mojica, 2012).

Current exploitation of spider crabs appears to be made up from incidental catches, primarily in the Panama Canal, Panama, and Pedro Bank, Jamaica (Creswell et al., 1989; Guzman and Tewfik, 2004; Munro, 1983), where it is taken for home consumption rather than commerce due to a lack of an organised market for the crab and low catch rates (Munro, 1983). A number of preliminary studies have suggested that the spider crab shows potential for aquaculture because it has a short non-feeding larval phase, with benthic settlement occurring within five to six days post-hatch (Brownell et al., 1977). Growth rates have been shown to be initially 0.1 – 0.2 mm carapace length (CL) per day, up to over 0.5 mm CL/day, indicating a grow-out period of 12 - 15 months (Adey and Farrier, 1989) in culture on an algal turf diet. Because this species does not have to be raised on more costly commercial feed, it can also be considered a sustainable aquaculture species (Rubino and Stoffle, 1990). The final product also has the potential to be highly marketable because it looks and tastes like the Alaskan King Crab *Paralithodes camtschaticus* (Rubino and Stoffle, 1990). Nevertheless because of its large size and high quality flesh coupled with increasing demand for seafood (Halwart et al., 2007), it is possible that the Caribbean spider crab may be suited for a controlled fishery prior to development of an aquaculture operation.

Spider crabs belong to the superfamily Majoidea, a family which display a diverse variety of morphologies, sizes, and behaviours (Baeza et al., 2010). Growth is discontinuous in brachyurans; the rate depends on the size gained at each moult and the frequency of these moults (Hartnoll, 1978). Structures that grow proportional to body size are isometric, while those growing faster or slower are positively or negatively allometric, respectively. Following each moult the relationship between structures may change, indicating different life phases (Hartnoll, 1978). For example, the claws of male crabs often increase disproportionately relative to body size, and are used for agonistic interactions (Hartnoll, 1969), whilst for females a rapid increase in the size of the abdomen is related to an increase in clutch size (Crawford and De Smidt, 1922). Most majoid species have three phases of development after the larval stages: the juvenile, prepubertal, and the adult phase (Carmona-Suárez, 2003; Sampedro et al., 1999) whilst a smaller number of species exhibit two growth phases (Baeza et al., 2012; Barón et al., 2009; Cobo and Alves, 2009). *Maguimithrax spinosissimus* falls into the latter category. The transition between each phase is determined by a critical moult (Hartnoll, 1978), which has not been determined for *Maguimithrax spinosissimus*. Baeza (2012) observed shifts in allometry at 64.85, 60.1, and 45.2 mm CW in males, and 58.77, 69.7, and 71.2 mm CW in females, depending on the variables used in the analysis. Mean size for both sexes varies throughout the Caribbean, with males averaging 65.4 mm and 129 mm in the Florida Keys and Cartagena, Colombia respectively, and females averaging 57.5 mm and 115 mm (Baeza et al., 2012; Campos et al., 2015).

Spider crabs that attain large body sizes such as *Maja squinado, Chionoecetes opilio,* and *Paralithodes camtschatica* are commercial fishery targets (Chilton et al., 2011; Sainte-Marie et al., 1995; Sampedro et al., 1999) and have thus been subject to life history examinations (Conan and Comeau, 1986; Paul, 1992; Sampedro et al., 1999), which includes estimations of size at maturity. These estimations are essential to inform management of the respective fisheries (Alunno-Bruscia and Sainte-Marie, 1998; González-Gurriarán et al., 1995; Paul, 1992; Sainte-Marie et al., 1995) and are often used to establish minimum landing sizes (Corgos and Freire, 2006). Such practices allow juveniles to reach maturity, ensuring future contribution to the respective population.

While previous studies have examined the distributions of size frequencies between sexes (Baeza et al., 2012; Campos et al., 2015; Guzman and Tewfik, 2004) as well as size at maturity (Baeza et al., 2012) of *Maguimithrax spinosissimus*, none have investigated the species in The Bahamas, nor have any compared sites with wide environmental variability. Given the potential of this large crab species for future exploitation, the aims of this study were to determine the size ranges present, physiological condition, meat yield, age, and size at maturity of both sexes of this species across three different locations in Eleuthera, The Bahamas. The hypotheses for this chapter are:

1. The carapace width sizes of spider crabs will differ among sites around Eleuthera.
2. The physiological condition of spider crabs will be similar between sites around Eleuthera.
3. Size at maturity of both sexes of spider crab will differ, with males maturing at a larger carapace width.

These data will provide important current information that may allow sustainable implementation of an artisanal or commercial fishery.

Materials and Methods

Sampling sites of *Maguimithrax spinosissimus*

The study was conducted at the Cape Eleuthera Institute (CEI) (GPS: 24°49'46"N, 76°19'41"W), Eleuthera, The Bahamas. *M. spinosissimus* were collected from three locations: patch reefs northeast of CEI (GPS: 24°50'N, 76°14'W), a blue hole (GPS: 24°47'01"N, 76°13'39"W) northwest of the town of Greencastle, and Sweetings Pond (GPS: 25°21'52"N, 76°31'07"W) (Figure 2.1).

The patch reefs are naturally formed reefs of similar depth (3 – 4 m), separated by areas of sand, seagrass, and soft coral (Smith et al. 2017). Reefs vary from between 17 - 570 m^2 (Tamburello and Côté, 2015) and rise to around 1.3 m above the seabed. Benthic cover includes macroalgae (36.6% ± 21.4% SD), turf algae (17.1% ± 13.2), coral (25.7% ± 18.9%) and sponge cover (11.3% ± 9.1%) (Francis et al., 2019). Various species of herbivorous fish are present diurnally, whilst herbivorous macroinvertebrates (crustaceans and echinoderms) are predominant nocturnally. Various predatory fish species such as snappers, grunts, groupers, and eels are abundant.

Greencastle Blue Hole was a minimum of 1 km away from any of the patch reefs that were used for collection. The hole measures approximately 35 x 12 m and reaches depths exceeding 18 m. Unlike other blue holes, the Greencastle hole appears to be formed by collapsed sub-sea tunnels. The water current in the hole is linked to tidal cycles. Water temperature in the hole was noted to be 1 - 2°C cooler than surrounding waters (Zeinert, 2018, personal observation). Turf algae was the predominant vegetation in the hole, which declined with depth and was not observed below 15 m (Zeinert, 2018, personal observation). Fish abundance was noticeably lower than on the patch reefs, but similar assemblages of fish species were present. Although this location is close to shore and a town, there appeared to be little fishing pressure likely due to local legends surrounding blue holes and the mythical “Lusca” – a half shark half octopus - that inhabits them.

Sweetings Pond is an anchialine lake in the north of Eleuthera (Rose et al., 2016). The pond has a surface area of 0.92 km^2 and a maximum depth of 15 m (Aronson, 1989). Water temperature, salinity, dissolved oxygen, and pH are largely the same as the water in the Bight of Eleuthera due to its tidal link, however visibility is lower due to flocculent matter suspended in the pond (Aronson and Harms, 1985). The benthos is made up of a sand-silt substrate that is easily disturbed. The algal species *Caulerpa sp*. and *Cladophora sp*. dominate the benthos. Fish abundance and diversity, especially of predatory fishes is low in the pond (Aronson and Harms, 1985). The area is surrounded by karstic limestone, the weathering of which produces overhanging ledges around the perimeter of the lake. The majority of crabs were collected from beneath these ledges (depth < 1 m). Subsistence harvest of crabs, especially the larger individuals, from the pond also occurs (O. O’Shea, personal communication, 2018).

Crabs were collected at night by freediving at the patch reefs and SCUBA diving in the blue hole, whilst crabs collected at Sweetings Pond were collected during the day and measured on site, before being returned to the pond. Crabs from the patch reefs and the blue hole were transported to the CEI wet lab in coolers within two hours of collection. They were held at CEI in flow-through tanks for no longer than a week (diameter = 1.5 m, depth = 0.7 m, filled to 50% of capacity). All crabs were measured and haemolymph samples were collected. One subset was sacrificed for meat yield, gastric mill, and gonad sampling, whilst another was used in a mark-recapture study. The remainder were returned alive.

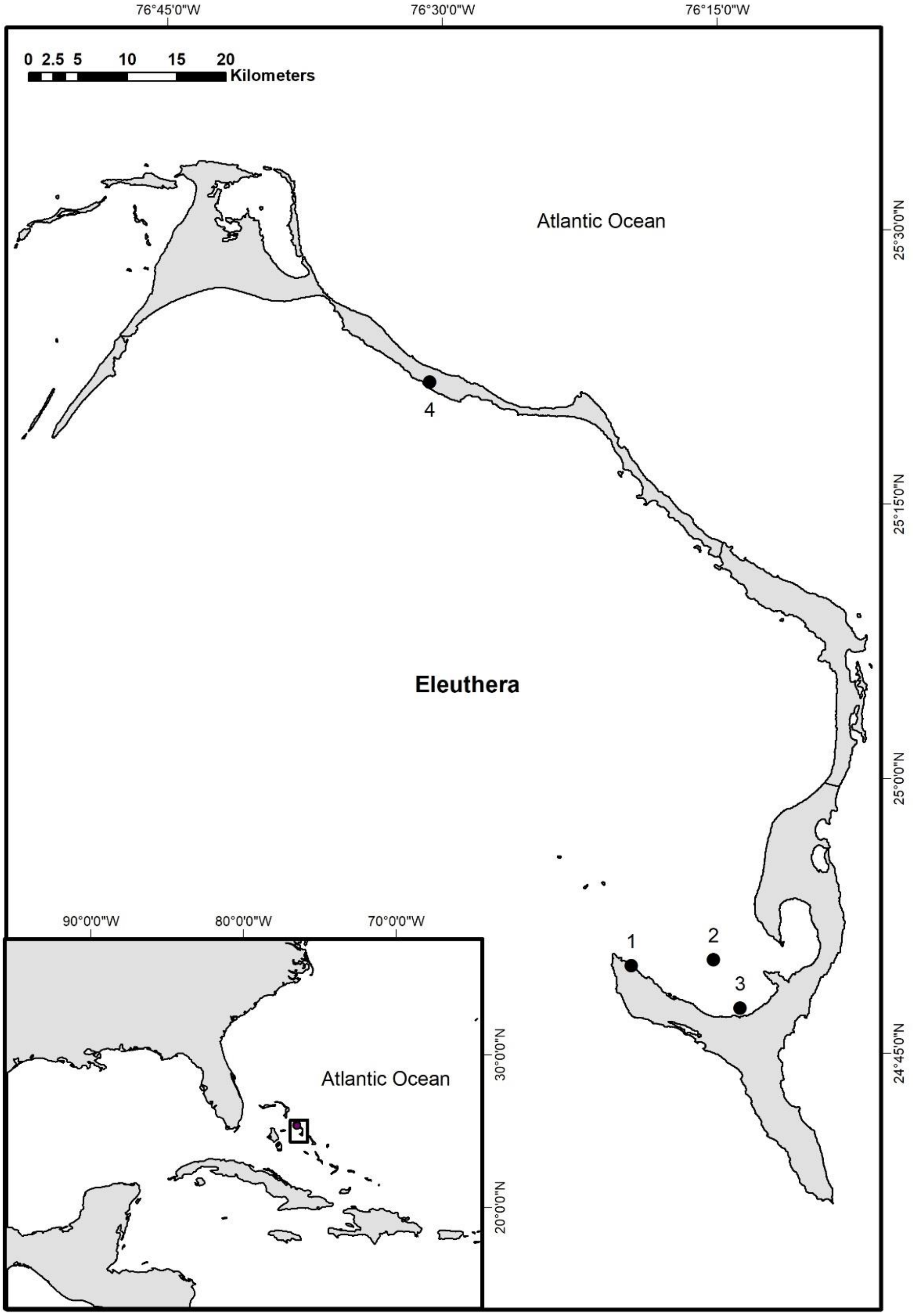

Figure 2.1. Eleuthera in relation to the southern United States of America. (1) The Cape Eleuthera Institute, (2) Coral Patch Reefs, (3) Greencastle Blue Hole, (4) Sweetings Pond.

Morphometric Measurement of *Maguimithrax spinosissimus*

Crab sex was determined by observation of the abdomen, which is broad in females and triangular in males. Mass in grams and any limb loss were recorded. The carapace width (CW), carapace length (CL), right chela length (ChL), chela height (ChH), chela width (ChW) and chela diagonal (ChD; the distance between the dactyl and the insertion point into the base of the propodus) were measured to the nearest mm using calipers (Figure 2.2A, B). Abdomen flexibility (AF) (whether fixed or unfixed from the sternum) was tested in both sexes using a probe (Figure 2.2D). In females, the abdomen width (AW) at its widest point was measured in mm and presence or absence of eggs noted (Figure 2.2C). However, presence of eggs was not used as an indicator of maturity because larger morphometrically mature females often had no eggs present due to their mode of continuous reproduction throughout the year (Adey and Farrier, 1989; Baeza et al., 2012).

Abdomen flexibility is associated with behavioural maturity (Baeza et al., 2012); both the male and female abdomens become unattached from the ventral sterna so the male is able to deposit sperm, and the female is able to receive sperm and to flex the abdomen to aerate the eggs. A general linear model (GLM) was used to determine the size at which a male or female crab becomes behaviourally mature. This was estimated by the probability of having a movable abdomen at a given carapace width being greater or less than 0.5.

A positive or negative relationship between carapace width and all other measured variables using the allometric model $y = ax^b$ (Hartnoll, 1978; Simpson et al., 2016) allowed determination if the measured body part increased or decreased in growth proportionally to the carapace width. The morphometric measurements were then used to determine maturity level in terms of growth phases. Following a similar method to Simpson et al. (2016), a principal component analysis (PCA) was completed on all variables for both sexes.

Variables were then dropped in order to obtain clear subsets, using CW and AW for females, and CW, ChL and ChH in males. The chosen variables were suitable because carapace width is a standard measurement for crab size, while chelae length, height and abdomen width show changes in allometry in closely related crab species (Baeza et al., 2012). Following the PCAs, a hierarchical cluster analysis was used to further identify juveniles and mature individuals. The subsequent output of the clustering was then used to indicate the juvenile and mature individuals. Finally, a general linear model (GLM) was created using each variable against carapace width to model the resulting data, which then visually displayed the size of maturity in the form of a graph.

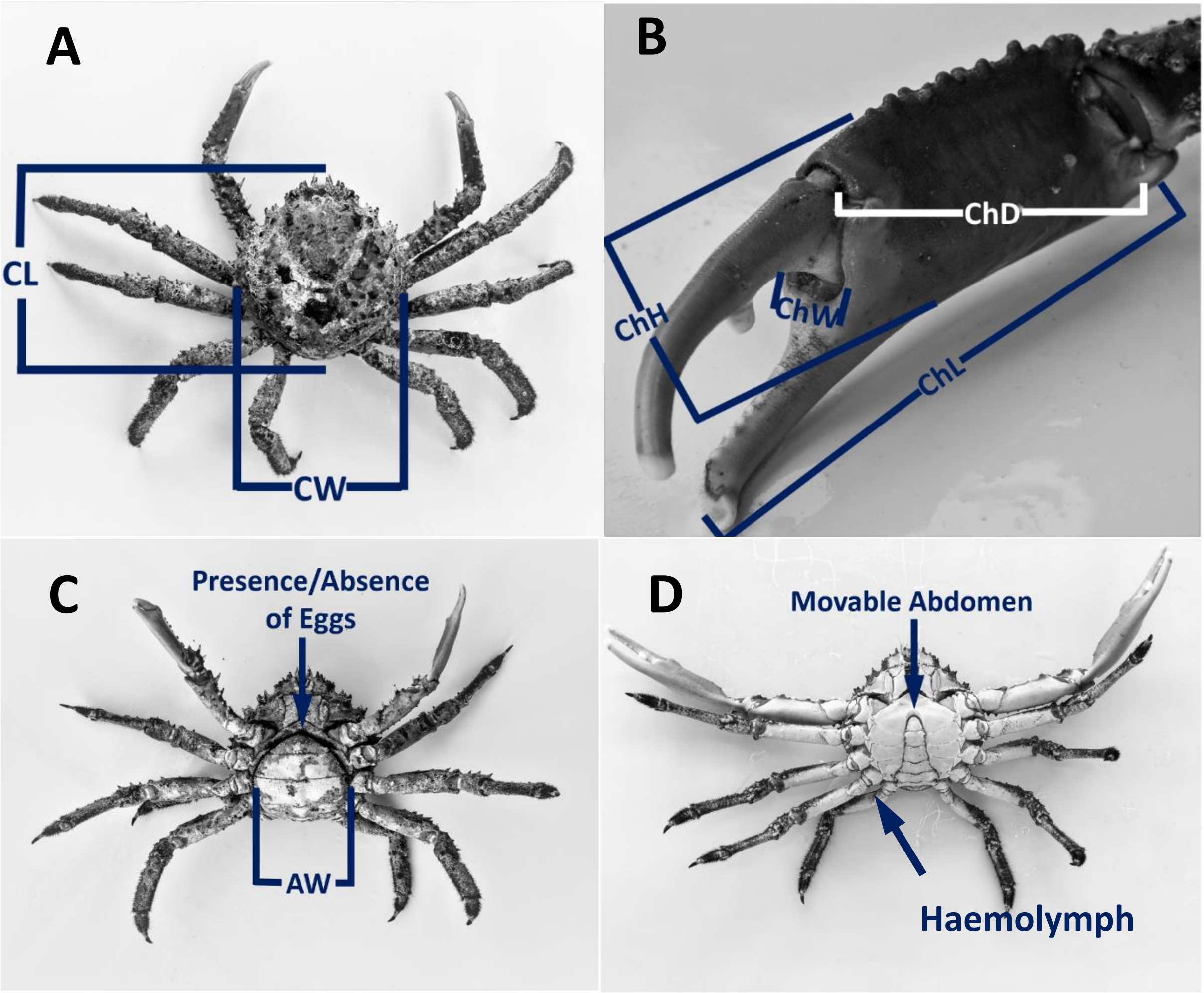

Figure 2.2. *Maguimithrax spinosissimus* morphometric measurements. (A) Carapace width (CW) and carapace length (CL). (B) Right chela measurements; chela length (ChL), chela height (ChH), chela width (ChW) and chela diagonal (ChD; the distance between the dactyl and the insertion point into the base of the propodus). (C) Abdomen width (AW) and examination for presence of eggs. (D) Examination for movable abdomen and arthrodial membrane where haemolymph was taken.

Haemolymph Sampling of *Maguimithrax spinosissimus*

Digital refractometers provide a rapid and non-invasive way to determine the physiological condition of crustaceans (Lorenzon et al., 2011). Low haemolymph protein levels may indicate trauma (Fotedar et al, 2002), stress (Chang 2005) or poor nutritional condition (Wang and McGaw, 2014). Haemolymph protein levels can be assessed using a Digital Pocket Refractometer, which takes three measurements: temperature compensated percent solids (Brix-TC), temperature compensated refractive index (TC-RI), and refractive index (RI). Brix-TC (hereafter referred to as BRIX) is a scale initially designed to report the dissolved sugar content of a liquid, and is based on the RI of the fluid. The RI, in turn, is determined by the amount of dissolved or suspended solutes within the fluid. Both the RI (Lorenzon et al., 2011; Oliver and MacDiarmid, 2001; Wang and McGaw, 2014) and BRIX (Bolton et al., 2009; Mendo et al., 2016;Simon et al., 2015a; Simon et al., 2015b) levels have been shown to correlate strongly with total haemolymph proteins in crustaceans. I chose to use BRIX, as it did not require transformation of the raw data and is commonly used in crustacean papers as a proxy for total haemolymph protein (Mendo et al., 2016; Simon et al., 2015a). One has to be careful with absolute values as there is an interaction with moult status. Immediately after moult, the levels are lowest and increase though intermoult. We avoided some of this by only using hard-shell intermoult crabs. Some late-stage intermoult crabs may have been present. The differences in intermoult crabs (Stage C) are likely to be less apparent than nutritional effects (Wang and McGaw, 2014)

Haemolymph was sampled using methods outlined by Wang and McGaw (2014). Briefly, a 0.3 mL sample of haemolymph was withdrawn using a 16 gauge needle and 1 mL syringe inserted into the arthrodial membrane at the base of the fourth walking leg (Figure 2.2). The serum protein concentration was measured using a Brix/RI-Chek Digital Pocket

Refractometer (Reichert Analytical Instruments, Depew, NY). After the refractometer was calibrated with distilled water, the sample was added to the well and the three measurements taken: BRIX, TC-RI, RI. The time between withdrawal of the sample and measuring did not exceed 60 seconds.

Migration/Homingof *Maguimithrax spinosissimus* on Coral Patch Reefs

Mark recapture experiments were carried out on a subset of spider crabs to determine whether they showed site fidelity or moved between patches. Many crustaceans undergo migrations which are linked to a life cycle change such as spawning or movement away from juvenile habitat (Penn et al., 2019; Shelley and Lovatelli, 2011). In addition, tag and release may also be used to estimate population size (Barnes et al., 2002; Robertson and Piper, 1991). Adult crabs (71 to 142 mm CW), were collected from Greencastle Blue Hole (n = 81) and tagged with a coded T-bar anchor Floy tag inserted into the posterior margin of the epimural suture allowed identification of individual animals. These tags have been shown to have high retention rates on other crab species (REF x 2). The crabs were then placed on a cluster of 9 coral patch reefs where spider crabs had been previously observed. The crabs were left for three weeks, following which the patch reefs were re-surveyed at night in order to recapture any marked individuals. The surrounding patch reefs and Greencastle Blue Hole were also surveyed for any crabs that may have migrated away or potentially returned to the Greencastle Blue Hole.

Meat Yield and Gastric Mill sampling of *Maguimithrax spinosissimus*

Five individual crabs, each with all limbs intact, were selected from each 10 mm size class (70 to 130 mm CW), three individuals larger than 130 mm CW were also used. At least two individuals from each sex were selected where possible. The sex, CW, and mass were recorded and crabs were then euthanized by submersion in iced seawater for one hour. The carapace was removed by cutting around epimural suture, the organs were carefully removed, and the remaining muscle and exoskeleton rinsed in fresh water. The gastric mill of each crab was dissected out from the foregut, and the labelled samples were frozen at -20°C for later analysis. The remaining exoskeleton and muscle were boiled for 8 minutes, following which the legs, claws and carapace were cracked open and the meat manually removed, similar to (Yomar-Hattori et al., 2006). The meat was weighed and expressed as a percentage of the total wet body mass measured prior to gastric extraction and boiling. The data were then expressed through a linear model, using crab meat yield as the response variable, and mass as the explanatory variable.

Gastric Mill analysis of *Maguimithrax spinosissimus*

The gastric mill samples were transported frozen back to Memorial University of Newfoundland for analysis. The gastric mills were used for aging the crabs using the methods outlined in Leland et al. (2011). The mesocardiac and zygocardiac ossicles were dissected from the gastric mill of the crab and rinsed with freshwater and then in 50% ethanol prior to embedding. The ossicles were placed in cylindrical moulds, which were pre-coated with a releasing agent, before a two-part cold-cure epoxy (Buehler EpoxyCure 2 Epoxy Resin and Epoxy Hardener) was mixed 4:1 (Resin:Hardener), then poured into the moulds. These were then left for 3 days to cure. After curing, the pucks were sectioned using a Buehler Isomet 1000 saw (Lake Bluff, IL, USA) and an IsoMet 15 LC diamond wafering blade. Sections were then polished using a Buehler MetaServ 250 grinder-polisher (Lake Bluff, IL, USA) before being mounted onto a glass slide, sectioned to 200µm, and photographed using a Zeiss AxioZoom V16 stereoscopic microscope (Oberkochen, Germany). Images were then digitally enhanced using Adobe Photoshop. Growth bands were counted from the basal to distal regions and were identified as paired light and dark areas in the endocuticle (Kilada and Ibrahim, 2016).

Statistical Analysis

Analyses were completed using RStudio (version 1.2.5033); packages used were ggplot2 (version 3.2.1), lme4 (version 1.1-21), lmerTest (version 0.9-37), car (Version 3.0-2), dplyr (version 0.8.3), knitr (version 1.23), lubridate (version 1.7.4), and FSA (version 0.8.25).

Results

Morphometric Measurements

Size Distributions and Sex Ratios.

Overall, males were significantly larger than females in CW (107.7 ± 1.48 vs 94.3 ± 0.87 mm) (Figure 2.3) and mass (710.8 ± 36.7 vs 430.9 ± 12.4 g, excluding Sweetings Pond) (Figure 2.4) (t-test: CW, t = -7.5173, *p* <0.001; mass, t = -6.5823, *p* < 0.001). Mass increased in proportion to CW and the relationship was significant (Figure 2.4). Due to issues with balances the mass for crabs collected from Sweetings Pond could not be measured accurately in the field. The overall ratio of males to females was 1:1.5. There were statistically significant differences between the carapace widths of females among the three sites (Two-Way ANOVA, F = 24.05, *p* < 0.001), however there was no statistically significant differences in male carapace widths among each of the three sites (Two-Way ANOVA, *F* = 2.461, *p* = 0.088) (Figure 2.5). The largest crabs in terms of carapace width were collected at the patch reefs (Figure 2.5); male crabs had a mean size of 112.3 ± 3.84 mm CW (size range: 62 – 155 mm) and mass of 760.4 ± 67.1 g (range: 106 – 1690 g), while females averaged 102.2 ± 2.34 mm CW (size range: 44 – 132 mm) and 509.2 ± 25.3 g (range: 48 – 1055 g); the male to female ratio was 1:1.14. Crabs from Greencastle Blue Hole were intermediate in carapace width (Figure 2.5); males had a mean carapace width of 109 ± 2.29 mm (size range: 72 – 142 mm) with a mass of 675.03 ± 40.4 (range: 182 – 1273 g), while females averaged a CW of 93.4 ± 0.93 mm (size range: 71 – 109 mm) and a mass of 383.03 ± 10.1 g (range: 133 – 607 g). The male to female ratio was 1:1.7. Crabs from Sweetings Pond had the smallest mean CW sizes (Figure 2.5); males measured 103.5 ± 1.43 mm (size range: 85 – 127 mm) and females at 87 ± 0.74 mm (size range: 72 – 101 mm). The male to female ratio was 1:1.3.

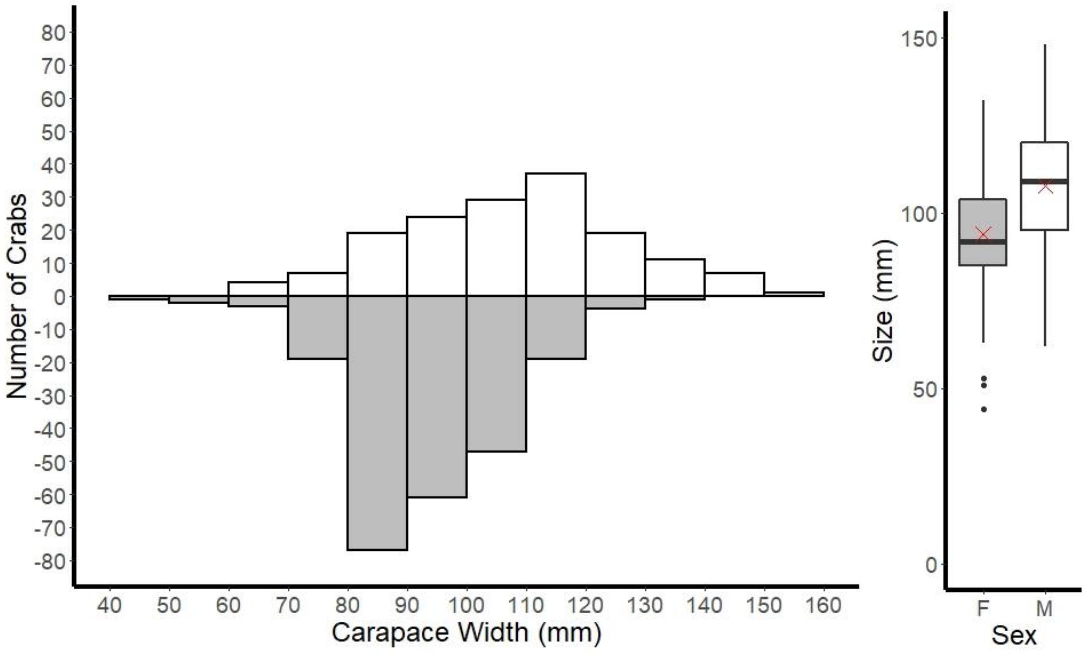

Figure 2.3. Overall size-frequency distributions of *Maguimithrax spinosissimus* (10 mm CW sizes) from all sites around Eleuthera (n = 392). Boxplots show the overall size distribution of CW from all sites. The boxes enclose data falling between the 1st and 3rd quartile and the bold horizontal lines represent the median, and mean size is represented by the X. The vertical lines indicate the 95% confidence intervals of the median. Data points falling outside these ranges are plotted individually. Males in white, females in grey.

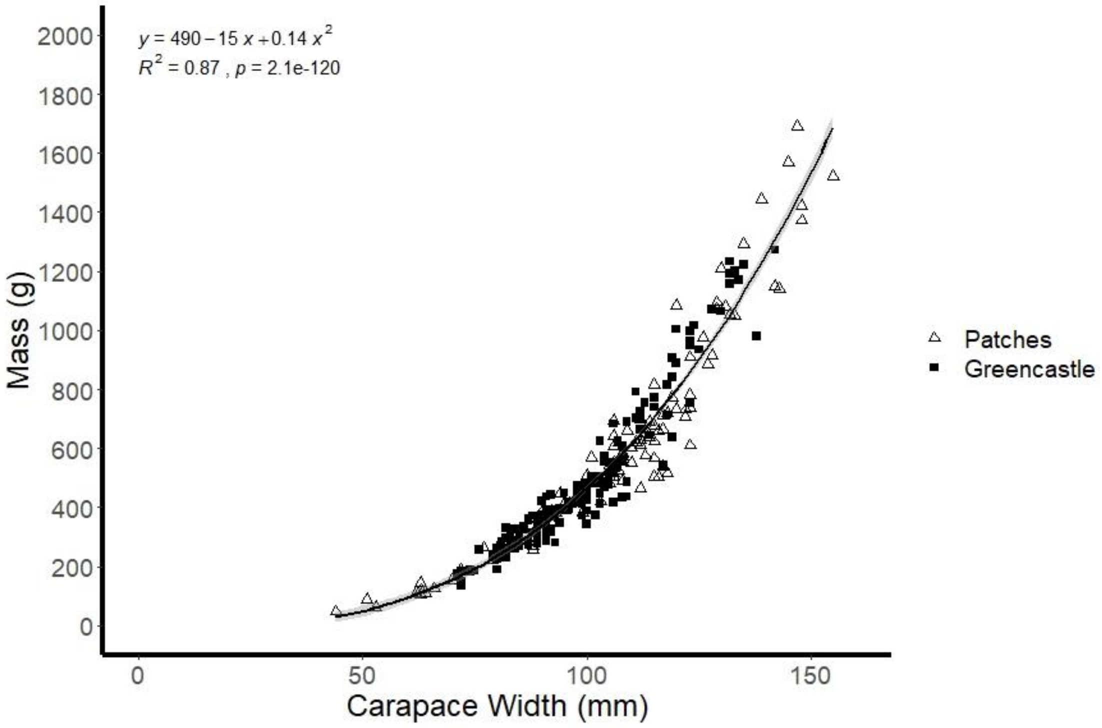

Figure 2.4. Regression analysis of the relationship between carapace width and mass of *Maguimithrax spinosissimus* from the patch reefs and Greencastle Blue Hole (n = 272). Shading represents the standard error. Accurate weights were not obtained from Sweetings Pond due to balance issues in the field.

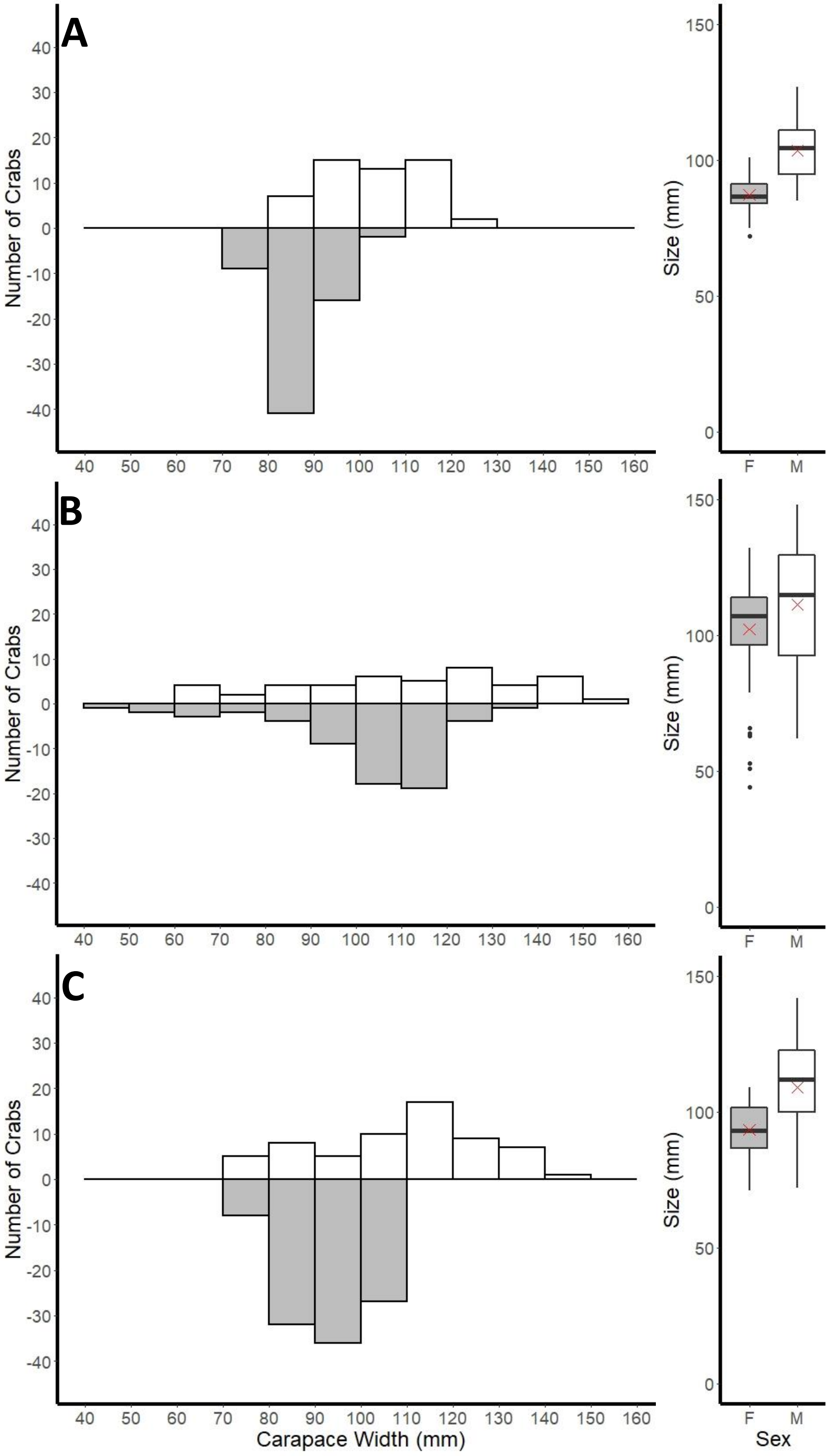
A
B
C
Number of Crabs
40
30
20
10
0
-10
-20
-30
-40
40 50 60 70 80 90 100 110 120 130 140 150 160
Carapace Width (mm)
Size (mm)
150
100
50
0
F
M
Sex

Figure 2.5. Size-frequency distributions of *Maguimithrax spinosissimus* (10 mm CW size classes) from each site around Eleuthera. Boxplots show the overall size distribution of CW from each site. The boxes enclose data falling between the 1st and 3rd quartile and the bold horizontal lines represent the median, and mean size is represented by the X. The vertical lines indicate the 95% confidence intervals of the median. Data points falling outside these ranges are plotted individually. Males in white, females in grey. (A) Sweetings Pond (n = 120). (B) The Patch Reefs (n = 107). (C) Greencastle Blue Hole (n = 165).

Size at Maturity.

Principal component analysis (PCA) using CW, ChL and ChH in male crabs indicated a presence of two growth phases. Hierarchical clustering allowed discernment of these phases which was then analysed by a GLM to ascertain morphological maturity for male crabs at 96.2 mm (confidence limit 96.0 – 96.3 mm) (Figure 2.6). PCAs between CW and AW in female crabs also indicated a presence of two growth phases. Hierarchical clustering allowed discernment of these phases and discriminant analysis assigned 98.06% of the crabs to the correct group. A GLM showed 50% of females reached morphological maturity at a CW of 72.3 mm (confidence limit 71.9 – 72.7 mm) (Figure 2.7). Females greater than 72 mm CW were found both with and without eggs; the smallest individual found bearing eggs was 72 mm CW, the largest individual with no egg clutch was 123 mm CW. Thus presence of eggs was not used as a factor in the analysis.

Abdomen flexibility and carapace width indicated 50% of males reached behavioural maturity at 80.1 mm (GLM, confidence limit 79.4 – 80.9 mm) (Figure 2.8). Female crabs reached behavioural maturity at a smaller size than males: 50% of females matured at 72.1 mm (GLM, confidence limit 71.8 – 72.4 mm) (Figure 2.9).

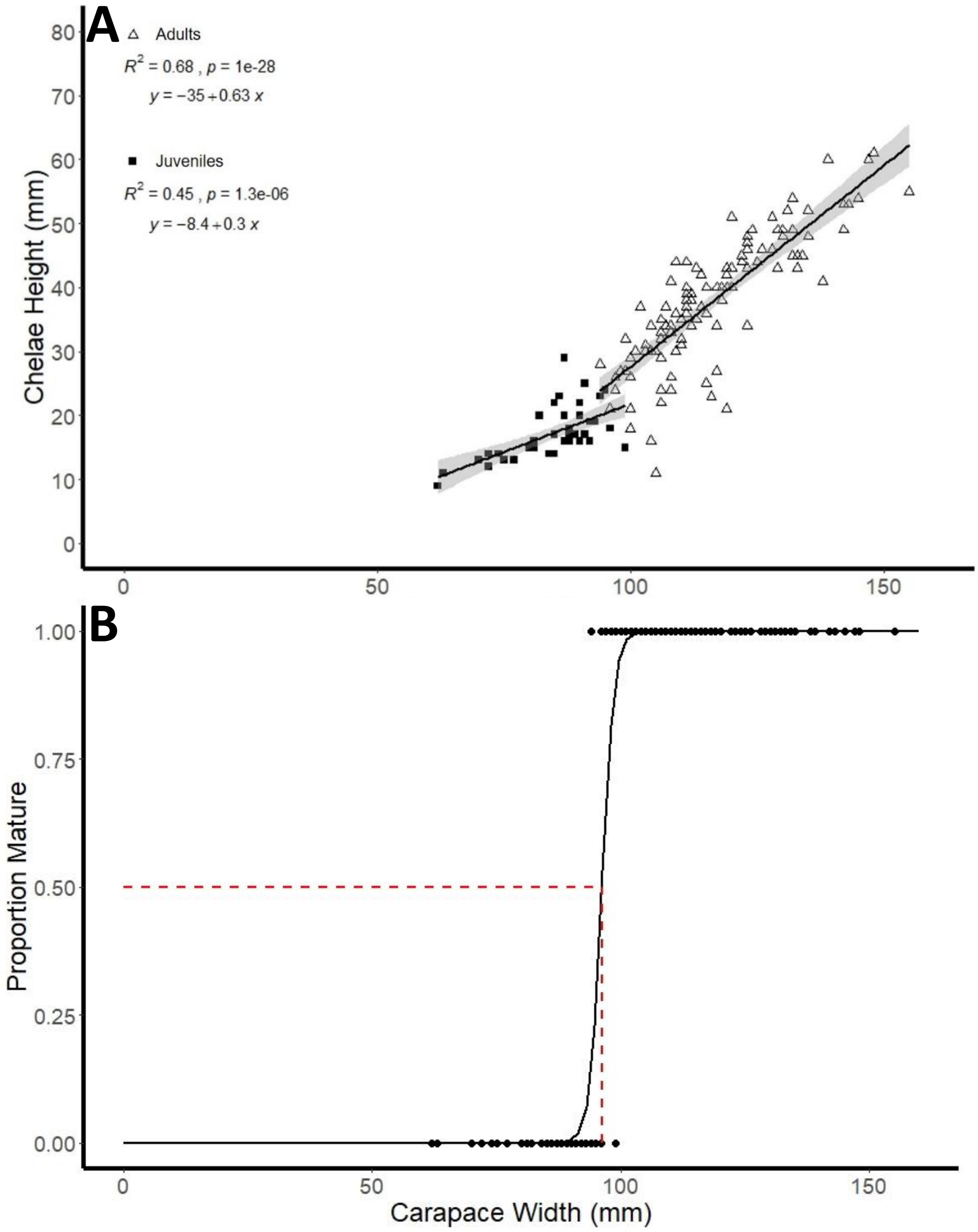

Figure 2.6. (A) Relationship between chelae height and carapace width for juvenile (n = 42) and adult (n = 111) male *M. spinosissimus* from Eleuthera. Shading represents the standard error. (B) Predicted size at morphological maturity for male (n = 153) *M. spinosissimus* using carapace width, chela length and chela height.

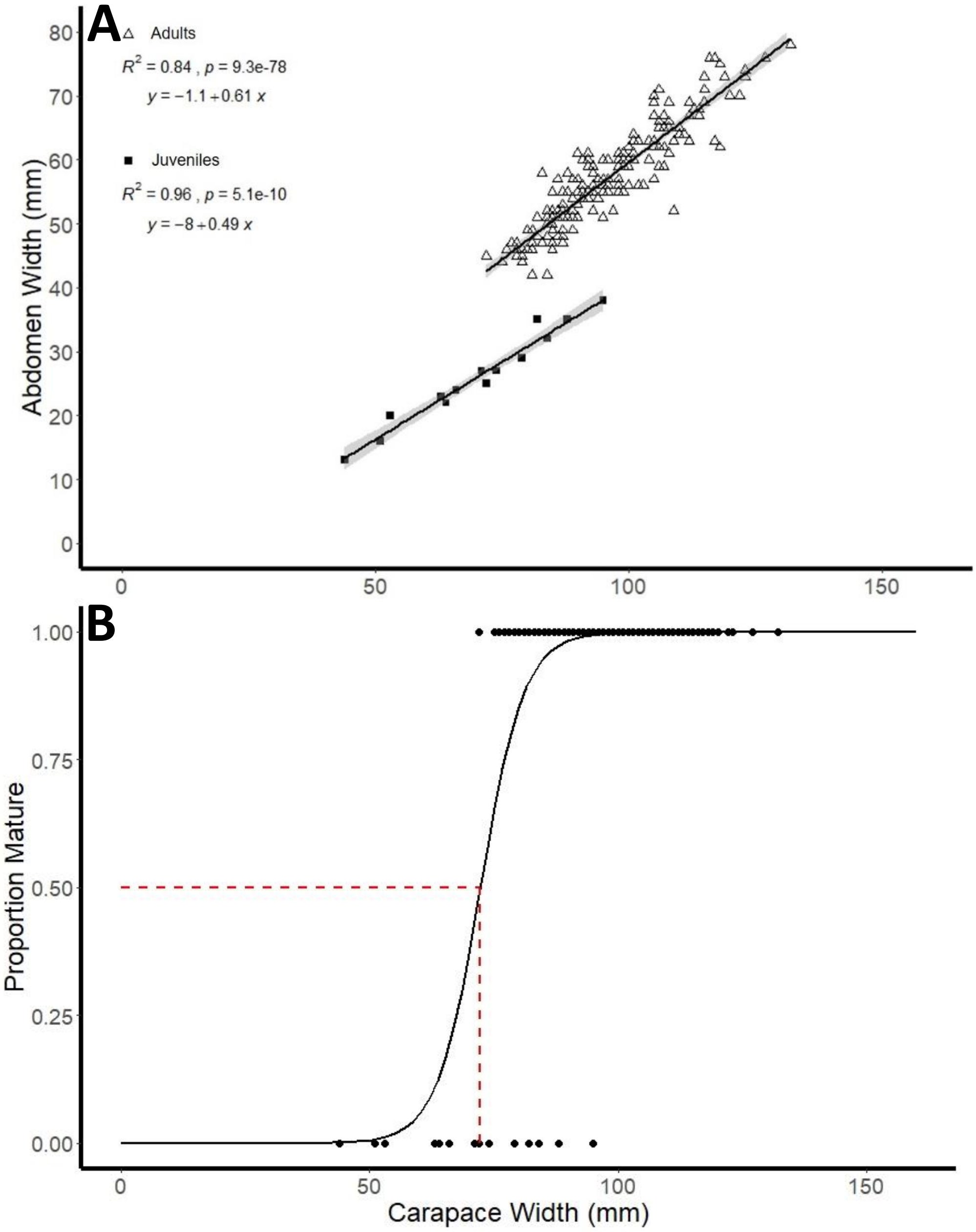

Figure 2.7. (A) Relationship between chelae height and carapace width for juvenile (n = 42) and adult (n = 111) male *M. spinosissimus* from Eleuthera. Shading represents the standard error. (B) Predicted size at morphological maturity for male (n = 153) *M. spinosissimus* using carapace width, chela length and chela height.

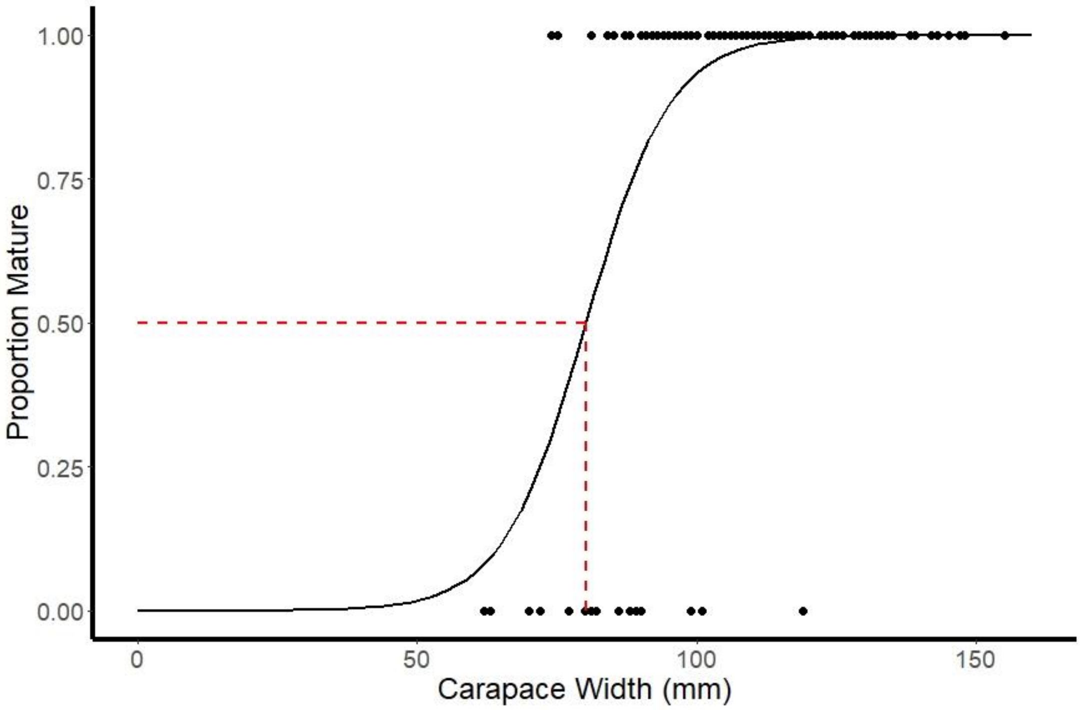

Figure 2.8. Predicted size at behavioural maturity for males from all locations (n = 153) for *Maguimithrax spinosissimus* using carapace width and abdomen flexibility.

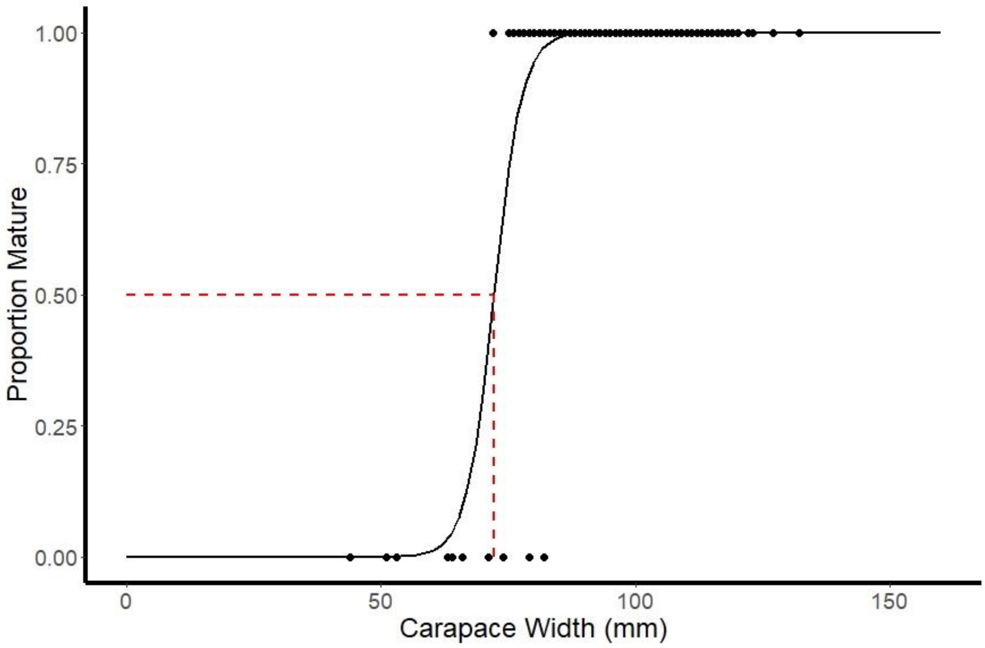

Figure 2.9. Predicted size at behavioural maturity for females from all locations (n = 206) for *Maguimithrax spinosissimus* using carapace width and abdomen flexibility.

Haemolymph Sampling of *Maguimithrax spinosissimus*

The BRIX levels were somewhat variable between the sexes, however they were not significantly different between males and females within each site (Tukey HSD; Greencastle, $p = 0.091$; Patches, $p = 0.74$, Sweetings, $p = 0.87$) (Figure 2.10). Male crabs from Greencastle Blue Hole had a mean BRIX of 7.12 ± 0.20 (BRIX range: 4.0 – 10.1), while females averaged 7.74 ± 0.16 (BRIX range: 3.4 – 13.2) (Figure 2.10). At the patch reefs, males had a mean BRIX of 7.26 ± 0.37 (BRIX range: 3.5 – 9.6), while females averaged 6.78 ± 0.19 (BRIX range: 4.4 – 9.3) (Figure 2.10). At Sweetings pond, males had a mean BRIX of 6.46 ± 0.15 (BRIX range: 4.2 – 8.3), while that of females was 7.17 ± 0.13 (BRIX range: 3.5 – 8.8) (Figure 2.10). Site and sex had a significant interaction with BRIX level (Two-way ANOVA; location, $p < 0.001$; sex, $p = 0.007$; location-by-sex, $p = 0.014$). Among locations, the BRIX level of crabs at the patch reefs and Sweetings Pond were significantly different to BRIX levels measured at Greencastle Blue Hole (Tukey HSD; Patches-Greencastle, $p = 0.017$; Sweetings-Greencastle, $p < 0.001$; Sweetings-Patches, $p = 0.89$; Figure 2.10). Subsequent linear models between the BRIX level, carapace width and site found the relationships at the patch reefs and Sweetings Pond were significant (Patches: $\text{BRIX} = 4.9 + 0.02\text{CW}$, $r^2 = 0.075$, $p = 0.016$; Sweetings: $\text{BRIX} = 10 - 0.037\text{CW}$, $r^2 = 0.14$, $p < 0.001$), while at the Greencastle Blue Hole was not (Greencastle: $\text{BRIX} = 6.3 + 0.012\text{CW}$, $r^2 = 0.013$, $p = 0.14$). However in each case the low r^2 value suggests the correlation between CW and BRIX was weak.

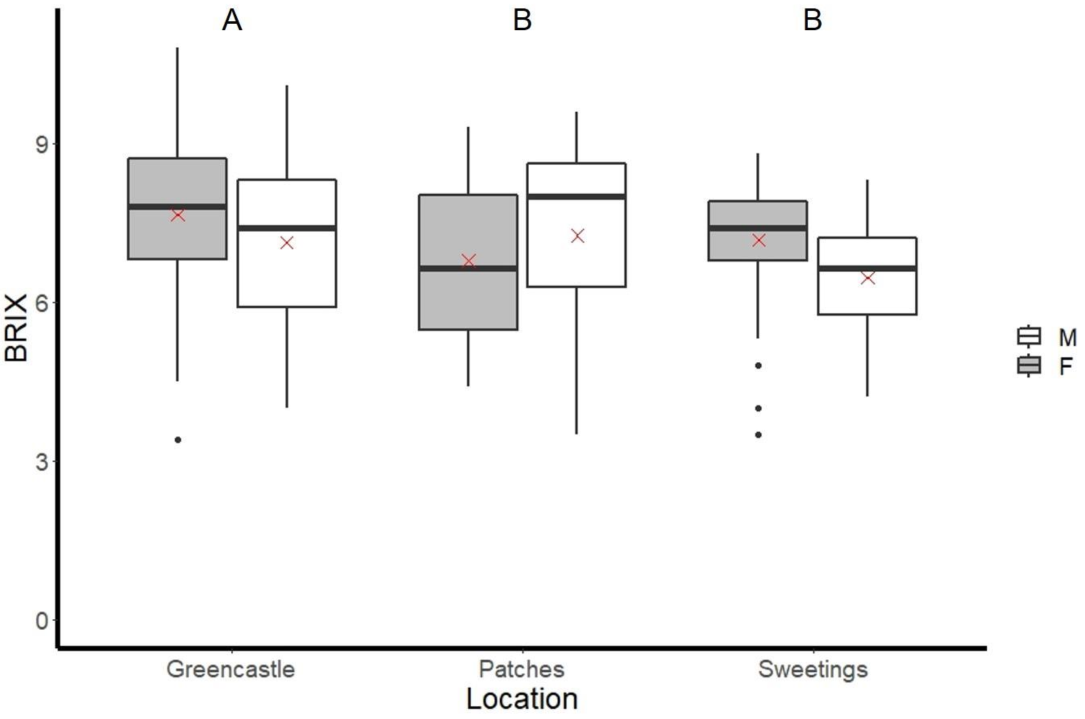

Figure 2.10. Boxplots show the BRIX levels from each site. The boxes enclose data falling between the 1st and 3rd quartile and the bold horizontal lines represent the median, and mean size is represented by the X. The vertical lines indicate the 95% confidence intervals of the median. Data points falling outside these ranges are plotted individually. Different letters above the bars indicate significant differences among sites.

Mark and Recapture of *Maguimithrax spinosissimus* on Coral Patch Reefs

Tag loss in other experimental trials was minimal, with no floy tag loss in crabs in the lab after two weeks, no tag loss in the enclosed cage trials (Chapter 3) after two to four weeks, and low (8 %) tag loss in the long term cage trials (Chapter 3) after four to six months. Tag retention during moult was not investigated. In support of this assumption other studies have shown up to 100% in moulting crustaceans (Stevens, 2002; van Montfrans et al., 1986). Mortality was dependant on tag location, with tags inserted into the dorsal musculature having the lowest incidence of mortality, while insertion into the basal leg musculature or body cavity was higher (Taylor and Hoenig, 1991; van Montfrans et al., 1986).

Of the 81 crabs released at 9 patch reefs, a total of 4 were recaptured after three weeks. These crabs were all females and were recaptured at their original release site: sites C2 (Crab 2), F4, and 112 (Figure 2.11, Table 2.1). No crabs were recaptured from patch reefs in a 500m radius from each release site two and three weeks post-release (green circles on figure), and none were found to have made their way back to the original collection site (Greencastle Blue Hole). Additionally, subsequent recreational harvest by members of CEI 3 months post-release resulted in no tagged individuals reported at the patch reefs. The Greencastle Blue Hole was not revisited by members of CEI after the initial recapture attempts. Due to these low recapture numbers, we were unable to successfully attempt an estimate of the population.

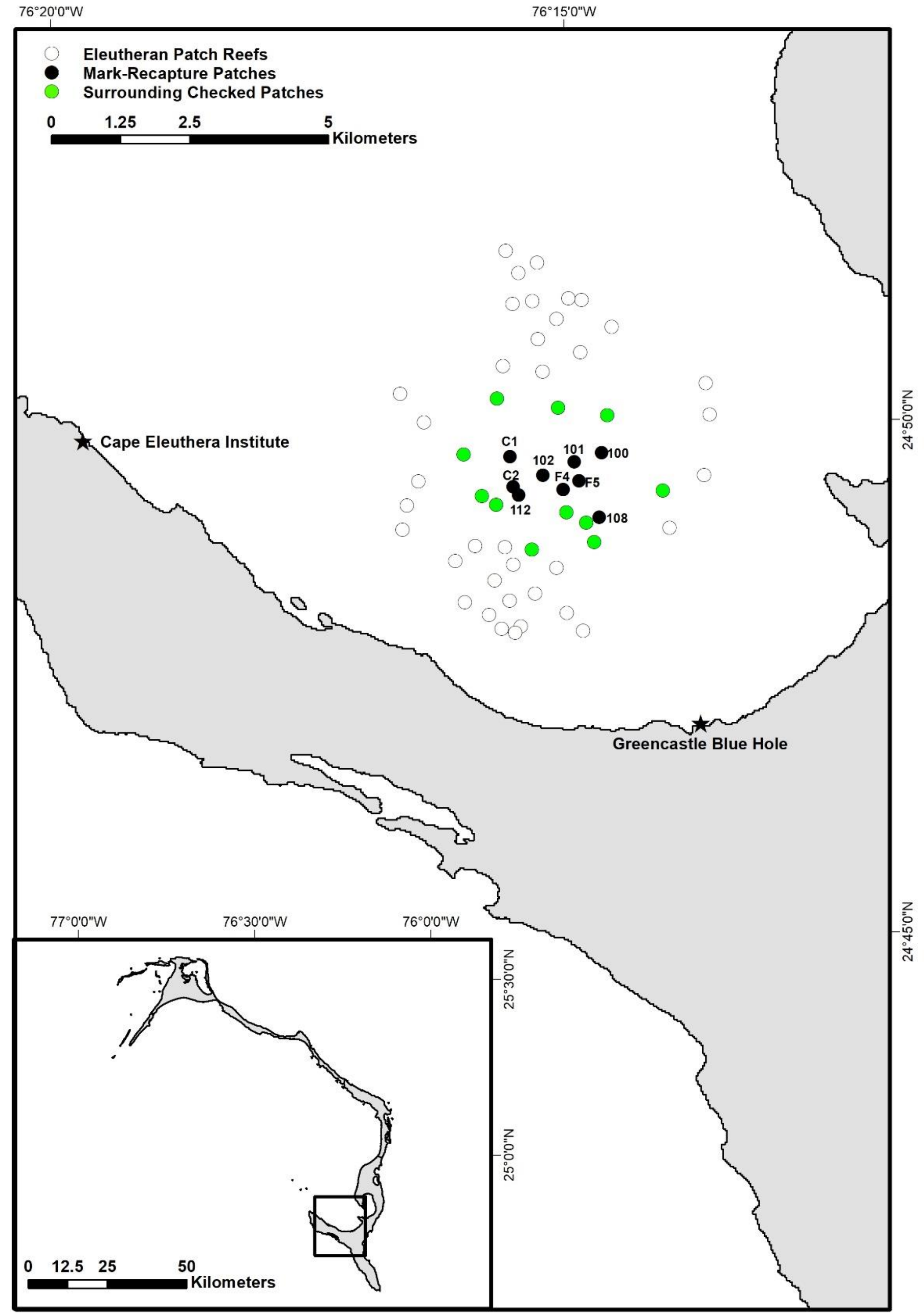

Figure 2.11. Patch reef locations in Rock Sound bight, Eleuthera. GPS data for patch reef locations provided by the Cape Eleuthera Institute. Black circles indicate patch reefs

used in the mark-recapture experiment, green circles indicate surrounding patch reefs checked for tagged crabs.

Table 2.1. Individual characteristics of crabs used in the mark-recapture trial, including release location and whether the crab was recaptured. Release location names are those used by CEI to identify individual patch reefs, except Crab 1 and Crab 2 reefs which were previously unnamed.

Tag Number	Collection Location	Release Location	Recaptured?	Sex	Mass	BRIX	Carapace Width
854	Greencastle Blue Hole	Crab 1		F	375	5.6	102
853	Greencastle Blue Hole	Crab 1		F	460	8.2	98
899	Greencastle Blue Hole	Crab 1		F	257	6.7	81
852	Greencastle Blue Hole	Crab 1		F	434	6.9	108
897	Greencastle Blue Hole	Crab 1		M	1192	6.6	132
900	Greencastle Blue Hole	Crab 1		M	330	9.1	82
858	Greencastle Blue Hole	Crab 1		F	261	7.2	82
857	Greencastle Blue Hole	Crab 1		M	713	8.8	118
859	Greencastle Blue Hole	Crab 2		M	1234	5.3	132
863	Greencastle Blue Hole	Crab 2		F	318	8.7	91
894	Greencastle Blue Hole	Crab 2	Y	F	373	7.8	90
895	Greencastle Blue Hole	Crab 2		M	414	7.8	103
890	Greencastle Blue Hole	Crab 2		F	314	5	88
860	Greencastle Blue Hole	Crab 2		M	665	5.9	112
862	Greencastle Blue Hole	Crab 2		F	240	5.5	79
861	Greencastle Blue Hole	Crab 2		F	482	8.1	102
893	Greencastle Blue Hole	Crab 2		F	486	4.8	109
883	Greencastle Blue Hole	Crab 2		M	1064	6.6	130
884	Greencastle Blue Hole	100		F	568	7.7	108
875	Greencastle Blue Hole	100		M	1157	6.5	132
889	Greencastle Blue Hole	100		F	337	6.6	86

872	Greencastle Blue Hole	100		M	951	5.6	123
874	Greencastle Blue Hole	100		F	395	7.8	96
885	Greencastle Blue Hole	100		M	490	5.5	102
864	Greencastle Blue Hole	100		F	347	7.6	94
882	Greencastle Blue Hole	100		F	287	8.8	84
869	Greencastle Blue Hole	100		M	755	6.4	113
871	Greencastle Blue Hole	100		F	368	4.8	92
868	Greencastle Blue Hole	101		M	702	5.9	111
916	Greencastle Blue Hole	101		M	406	9.4	96
831	Greencastle Blue Hole	101		M	186	7.4	75
913	Greencastle Blue Hole	101		F	366	7.3	89
912	Greencastle Blue Hole	101		M	1273	8.9	142
847	Greencastle Blue Hole	101		F	496	6.7	105
918	Greencastle Blue Hole	101		M	474	7.6	104
843	Greencastle Blue Hole	101		M	816	7.9	118
846	Greencastle Blue Hole	101		F	563	8.7	108
845	Greencastle Blue Hole	101		F	190	5.6	74
851	Greencastle Blue Hole	102		F	414	7.1	97
849	Greencastle Blue Hole	102		F	308	7.6	89
850	Greencastle Blue Hole	102		M	637	8.6	119
844	Greencastle Blue Hole	102		M	423	5.4	100
840	Greencastle Blue Hole	102		F	373	9.2	93
891	Greencastle Blue Hole	102		F	371	8.1	88
888	Greencastle Blue Hole	102		F	442	8.1	92
855	Greencastle Blue Hole	102		F	444	7.3	98
896	Greencastle Blue Hole	102		F	436	8.5	91
856	Greencastle Blue Hole	102		M	998	7.2	123
842	Greencastle Blue Hole	108		F	320	8.1	85
834	Greencastle Blue Hole	108		M	280	7.2	84
892	Greencastle Blue Hole	108		M	1004	7.9	120
881	Greencastle Blue Hole	108		F	290	7.4	84

880	Greencastle Blue Hole	108		F	473	7.9	98
879	Greencastle Blue Hole	108		M	690	7	109
878	Greencastle Blue Hole	108		M	626	5.7	103
877	Greencastle Blue Hole	108		F	355	7.4	87
828	Greencastle Blue Hole	108		F	374	7.6	93
827	Greencastle Blue Hole	108		F	417	6.3	106
867	Greencastle Blue Hole	F4		F	418	8.9	98
876	Greencastle Blue Hole	F4		F	390	8.1	91
866	Greencastle Blue Hole	F4		F	319	6.8	92
919	Greencastle Blue Hole	F4	Y	F	422	7.4	90
925	Greencastle Blue Hole	F4		M	963	6.2	123
870	Greencastle Blue Hole	F4	Y	F	503	8.8	102
853	Greencastle Blue Hole	F4		M	1223	8	135
921	Greencastle Blue Hole	F4		M	256	6.9	81
922	Greencastle Blue Hole	F4		M	1017	4.2	124
835	Greencastle Blue Hole	F4		F	576	8.7	104
829	Greencastle Blue Hole	F5		M	755	6.3	123
920	Greencastle Blue Hole	F5		F	362	9	87
832	Greencastle Blue Hole	F5		M	739	7.1	115
924	Greencastle Blue Hole	F5		M	477	8.6	100
923	Greencastle Blue Hole	F5		F	505	8	101
917	Greencastle Blue Hole	F5		F	174	4.7	71
915	Greencastle Blue Hole	F5		F	346	6.9	91
836	Greencastle Blue Hole	F5		F	518	6.9	106
837	Greencastle Blue Hole	F5		F	294	7.6	83
841	Greencastle Blue Hole	F5		F	449	6.2	95
950	Greencastle Blue Hole	112		F	345	7.8	90
914	Greencastle Blue Hole	112		F	297	6	82
838	Greencastle Blue Hole	112	Y	F	538	5.4	107

Meat Yield and Gastric Mills

Meat Yield.

Meat yield from males ranged between 6.39 to 21.2% of the wet mass of the crab, with a mean yield of 14.07 ± 1.07%. Yield from males increased almost linearly with CW (Figure 2.12). The meat yield from female crabs ranged between 5.95 and 16.78%, with a mean yield of 10.9 ± 0.71% of the wet mass of the crab. The yield from females increased linearly with CW (Figure 2.12). Yield increased proportionately with crab mass (Regression: Males, $t = 8.498$, $p < 0.01$, $r^2 = 0.836$; Females, $t = 5.626$, $p < 0.01$, $r^2 = 0.671$), in a similar curve to mass vs CW.

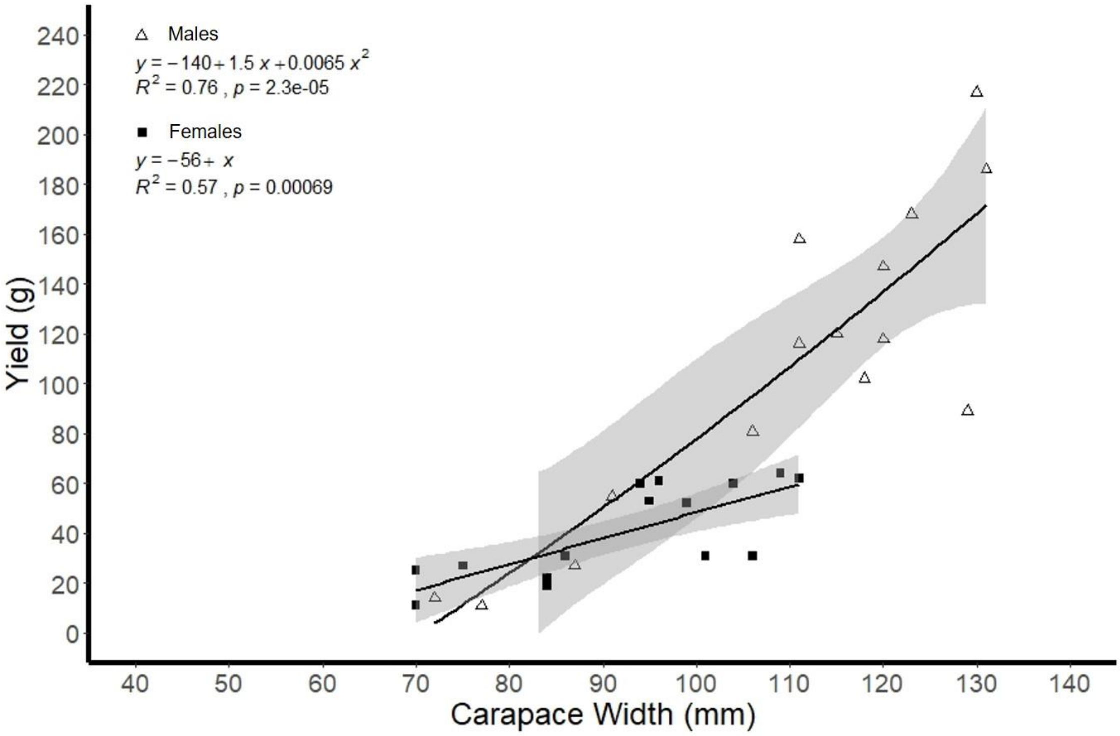

Figure 2.12. Regression analysis of the relationship between carapace width and meat yield of *Maguimithrax spinosissimus* (n = 31) collected from the patch reefs. Male regression is essentially linear, female regression is linear. Shading represents the standard error.

Gastric Mills

The gastric teeth of 31 crabs ranging between 70 and 148 mm CW were collected. The teeth were sectioned along the Y axis of the urocardiac ossicle and across the X axis of the zygocardiac ossicle (Figure 2.13), then polished to a thickness of 250 µm. Even in the largest crab sampled (Male, 148 mm CW), no growth rings were detected in the transverse cross sections of the urocardiac and zygocardiac gastric mill ossicles (Figure 2.14). Work continues on this aspect of the study.

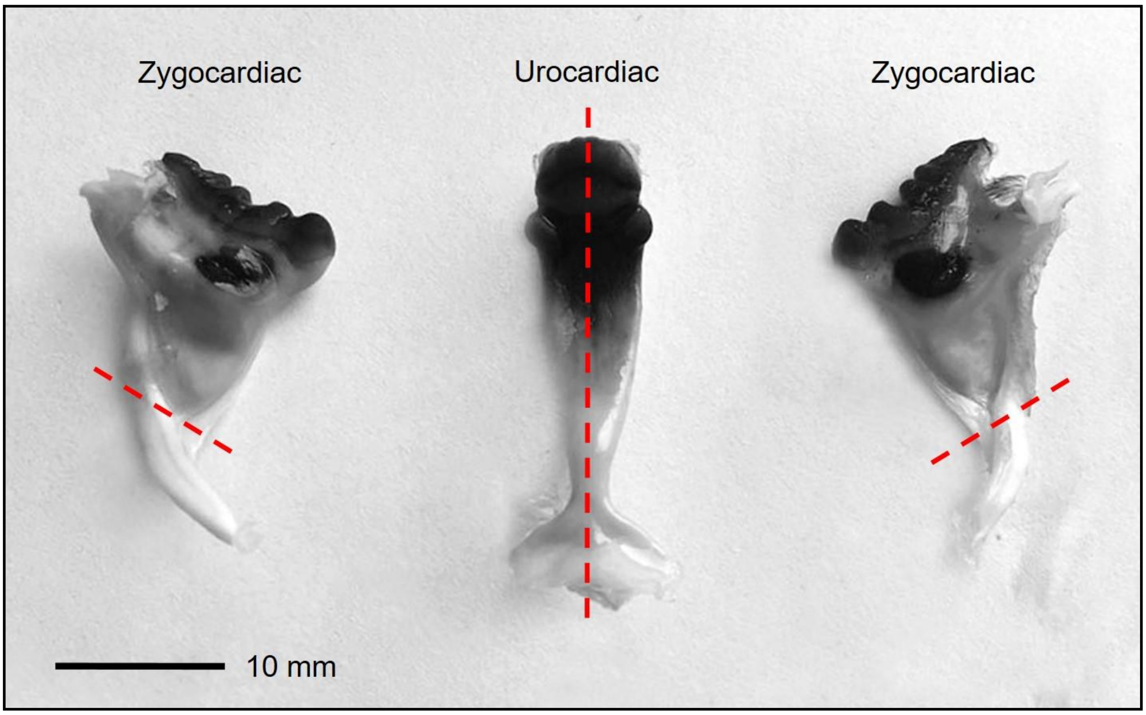

Figure 2.13. Dissected gastric mill ossicles of *M. spinosissimus*. The red dotted line indicates the cutting axis for the respective ossicle.

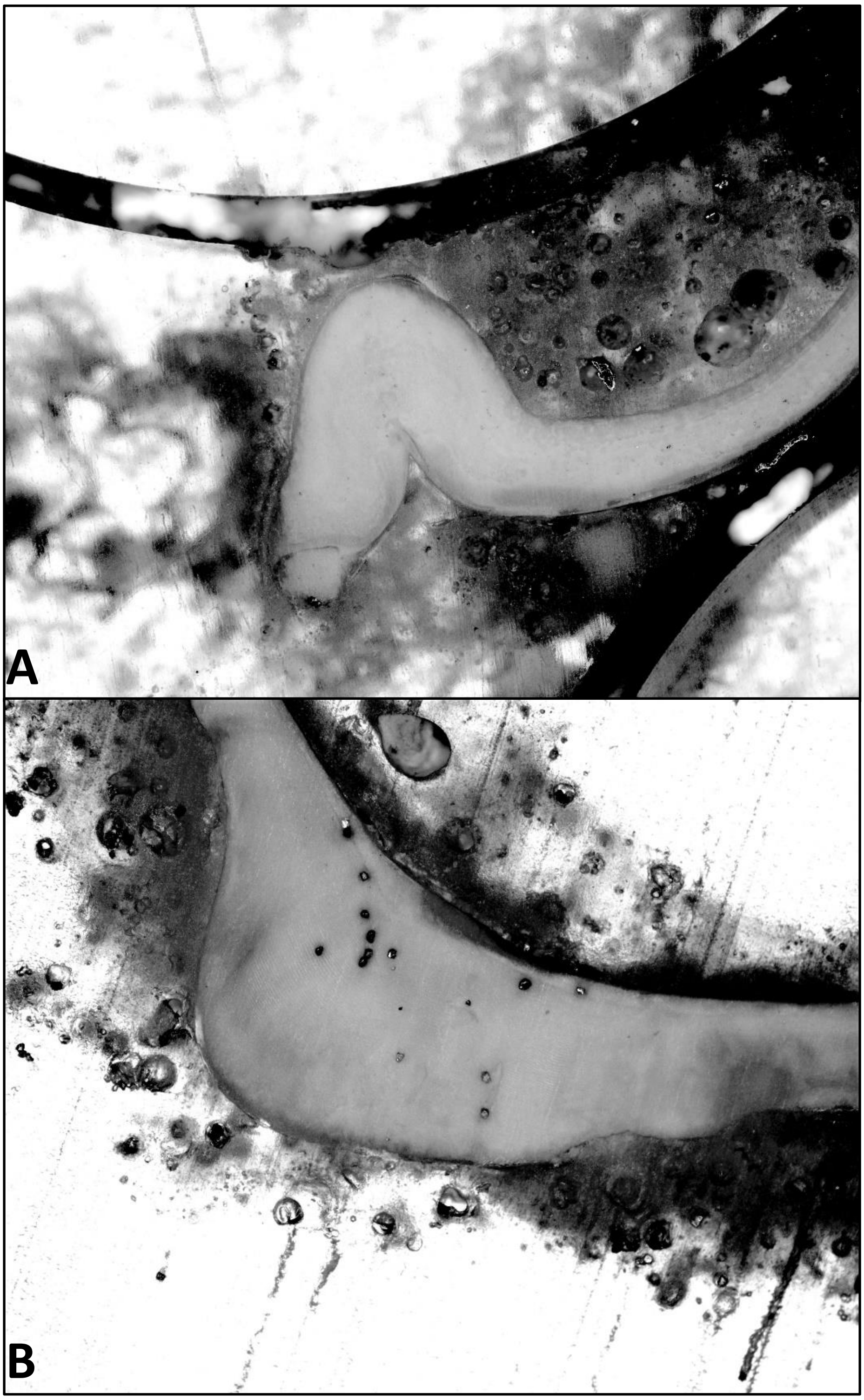

Figure 2.14. Examples of sections of the (A) zygocardiac and (B) urocardiac ossicles from an individual *M. spinosissimus* (male, 148 mm CW). Magnification: 56x.

Discussion

Morphometric Measurements

Carapace Distributions and Haemolymph

The mean sizes of male and female spider crabs collected in Eleuthera, The Bahamas fell in between those of populations surveyed in the Florida Keys (males, 65.4 mm; females 57.5 mm; Baeza et al., 2012) and Colombia (males, 129 mm; females, 115 mm; Campos et al., 2015). Temperature has a marked influence on growth as it is positively correlated with metabolic rate (Willmer et al., 2005) and influences protein synthesis (Whiteley et al., 1997), thus subsequently affecting growth rate. This likely declines at high temperatures. As the mean temperature is higher and variation lower in Colombia (mean 28.8 °C, 27.4 – 29.8 °C), compared with Key West (mean 26.2 °C, 22.7 – 30.7 °C) and Eleuthera (Dunmore Town, mean 26.4 °C, 23.4 – 29.7 °C; https://www.seatemperature.org/), temperature may have some influence on crab size through more sustained food intake, resulting in higher growth rates. However, differences such as population genetics and predation levels may also influence growth rates at each site regardless of whether the sites are neighbouring or distant (Hartnoll et al., 1993). It has also been suggested that the smaller sized *M. spinosissimus* in Florida may actually be a subspecies (Adey and Farrier, 1989; Baeza et al., 2019).

Local variation in crab size among sites surveyed in the present study could be linked to nutritional condition. Haemolymph BRIX levels are heavily influenced by food quality and intake (Wang and McGaw, 2014). Spider crabs collected from Sweetings Pond had the lowest BRIX levels (males: 6.46 ± 0.15, females: 7.17 ± 0.13), indicative of a lower nutritional condition. This may have occurred because of the limited variety of encrusting algae at the site, which largely consisted of mats of *Cladophora sp*. (Aronson and Harms, 1985). The invertebrate and fish fauna were also lower with regards to both diversity and number, likely limiting opportunistic grazing on sessile invertebrates or fish mortalities. In contrast, food sources at the Greencastle Blue Hole and the patch reefs did not appear to be limiting because there was a high amount of different types of turf algae at the depths where crabs were collected. Sweetings Pond also received significant local fishing pressure (O. O'Shea, personal communication, 2018), as the site was easily accessed and so this could account for the lack of larger crabs which were preferentially harvested, whereas there was no evidence of fishing at the other two sites.

Very few small crabs (< 50 mm CW) were found at any of the sites. These have also proven difficult to find in other studies (Baeza et al., 2012; Guzman and Tewfik, 2004), likely because smaller individuals are cryptic and cover themselves in algae (Adey and Farrier, 1989). Alternatively, differing habitat use between juveniles (< 50 mm CW), and sub-adults (50 – 80 mm CW) and adults (> 80 mm CW) may explain why the juveniles were difficult to find. Other crustaceans, such as the spiny lobster *Panulirus argus*, utilize nearshore habitats such as shallow sub-tropical lagoons as juveniles prior to migrating to offshore reefs (Butler et al., 1995; Davis and Dodrill, 1989). Both juvenile and adult blue crab *Callinectes sapidus* are found in estuarine environments, however juveniles utilize shallow seagrass beds while the adult stages are predominately found in deeper estuarine areas (Millikin and Williams, 1984). Long lived crustacean populations typically show a normal distribution curve of size-frequency (Hartnoll and Bryant, 1990), with larger multi-year cohorts making up the bulk of the crabs, whereas the smaller size classes are composed of a single recruitment event. Thus the lower abundance of smaller crabs (as well as very large individuals) found on Eleuthera might be expected as they are proportionally far less common.

The sex ratio in this study was skewed in favour of females at each site. Although there was some variance among the sites, this would be no more than random occurrence, especially as deviations from the "expected" 1:1 sex ratio are widespread in crustacea (Wenner, 1972). The variation in the present study potentially indicates population fluctuations from migration, differential habitat use, or mortality (Wenner, 1972). Hazlett and Rittschof (1975) showed significant negative correlation between crab density and movement among males, and among females, but not between males and females. It is therefore likely that patch reef size and the size of the Greencastle Blue Hole limits the number of home ranges available, as females tend towards one refuge, while males tend towards multiple refuge sites (Hazlett and Rittschof, 1975).

Size at Morphological and Behavioural Maturity

A number of different methods (e.g. PCA and LDA) have previously been used to determine size at morphological maturity: the hierarchical cluster analysis worked best for the present study, allowing determination of groups of mature and immature individuals based on chelae and carapace measurements. The size at morphological maturity of *M. spinosissimus* (males: 96.2, females: 72.3 mm) was larger than previously shown in the Florida Keys (males: 64.85, females: 58.77 mm, Baeza et al., 2012; males: 80 mm, Bohnsack, 1976), but smaller than that in Antigua (males: 105 mm, Adey and Farrier, 1989).

Behavioural maturity was easier to assess as there was only a small overlap between mature and immature individuals. The size at which behavioural maturity occurred around Eleuthera (males: 80.1, females: 72.1 mm) was again larger than in the Florida Keys (males: 45.2, females: 69.7 mm; Baeza et al., 2012). These differences suggest some populations are genetically distinct. The short larval stage of the spider crab (5 to 6 days) would reduce gene flow among populations (Adey and Farrier, 1989; Baeza et al., 2019), and ocean currents and deep waters surrounding many Caribbean islands may limit settlement in some locations. Further, temperature, growth rates and predation likely also influence the rate at which each respective population reaches maturity (Hartnoll et al., 1993; Whiteley et al., 1997).

The statistical tests indicated females reached morphological maturity (abdomen enlarged to hold an egg mass) prior to behavioural maturity (the abdomen releasing from the sternum). However the difference between morphological (72.3 mm) vs behavioural maturity (72.1 mm) was very small and biologically speaking both morphological and behavioural maturity are likely both reached during the same moult increment. This may help ensure that the pleopods and abdomen have the capacity to hold eggs prior to fertilisation and extrusion (Crawford and De Smidt, 1922). In contrast the males reached behavioural maturity prior to morphological maturity; whether or not the crabs are able to produce sperm at this stage remains to be determined. A more rapid attainment of behavioural maturity may allow smaller males an unconventional fertilization method as “sneakers” (Shuster, 2008), whereby smaller males invade larger males’ territories and mate with females. This has been recorded in the common spider crab *Libinia emarginata*, prior to becoming a territorial male after the pubertal moult (Laufer et al., 1994).

Although I attempted to determine whether both sexes were functionally reproductive at behavioural and morphologically maturity, the samples had deteriorated to a state where cell structure could not be discerned. Clearly, further analysis of the gonads is required. Although a macroscopic characterization of the female gonads post-extrusion has been developed (Adey and Farrier, 1989), including descriptions of development stages and visual colour aids, no work to date has been completed on gamete maturation within the ovaries or testes. Such findings will allow greater understanding of the reproductive biology of the crab, to specifically pinpoint gonadal maturity in relation to maturation characteristics (Sastry, 1983).

Meat Yield

Males crabs reached greater sizes overall, therefore the meat yield was greater from males. The meat yield was proportionate to body mass but was greater in morphologically mature males (compared to females of similar CW) due to larger limb and chelae sizes. Meat yield increased after the pubertal moult in males when chelae size increases; whereas female claws grow linearly and do not reach the large sizes found in males. This indicates that a male only harvest would be beneficial economically as overall yield from male crabs would be higher. The yield was comparable to other commercially harvested crab species such as *Callinectes sapidus* (10 to 14%) and *Scylla serrata* (21.9%), but lower than some deep sea crabs such as *Chionoecetes opilio* (30%) and *Paralithodes camtschatica* (18 – 25%) (Cited in: Vasconcelos and Braz, 2001) due to their differing morphologies. Nevertheless comparing between both individuals and species can be misleading due to the degree of mineralization in the exoskeleton, which can differ con- and allo-specifically (Harlioğlu and Holdich, 2001), however it does allow relative comparisons between species of various sizes which cannot be made when reporting muscle weight alone (Thompson et al., 2005).

Gastric Mill Analysis

Ageing of crabs via analysis of banding on the gastric mills (Kilada and Ibrahim, 2016; Kvalsund et al., 2015; Leland et al., 2011) was attempted, although I was able to cut teeth sections as thin as 250µm I was unable to detect any visible growth lines. It is possible that these sections were still too thick and if it was possible to reduce the thickness of the sectioned gastric mills to below 200µm (Leland et al., 2011) this may have helped determine whether this method can be used to age *M. spinosissimus*. It is also possible that because this species has rapid growth rates (Adey and Farrier, 1989) that differential seasonal growth rates (banding) may not be as obvious as those for crustaceans from temperate latitudes (Kilada and Ibrahim, 2016) . That being said, Leland et al. (2011) were able to detect growth lines in other sub-tropical species from areas with similar temperature variation to *M. spinosissimus*. Age determination in crustaceans using growth rings in the gastric teeth, is a fairly recent technique that has not been fully authenticated. For example, the band counts vary along the length of the ossicle, and the growth centre of the ossicle is species specific (Leland et al., 2011). At present, the bands are assumed to represent annual growth rings, however further studies are needed on captive crustaceans of a definitive age in order to provide verification (Kilada, pers comm). Additionally, recent evidence suggests that the ossicles are partly or fully shed into the stomach and lost during moult in some species (Sheridan et al., 2016; Sheridan and O'Connor, 2018). This reinforces the species specific verification needed for the possibility of gastric mill band counts in marine crustaceans.

Mark-Recapture of *Maguimithrax spinosissimus*

An attempt was made to recapture a subset of 81 tagged crabs on the patch reefs, but only four female crabs were recovered. All four were recovered from the patch reefs they were initially released on; two individuals were recaptured from the same patch reef. Recapture rates for decapod crustaceans are dependent on population size, migration, catchability, tag retention and mortality (Hyland et al., 1984; Le Vay et al., 2007; Miller, 1990). As such recapture rates can be quite variable, from 6.5% in *Scylla paramamosain* (Le Vay et al., 2007), 18.9% in *Scylla serrata* (Hyland et al., 1984), and upwards of 50% in *M.*

spinosissimus (Bohnsack, 1976) in the Florida Keys. The recapture rate in the present study was much lower than previous studies for this species (>50%; Bohnsack, 1976); this may be due to the translocation of individuals from the Greencastle Blue Hole to the patch reefs. Additionally, the area over which the mark-recapture survey was undertaken in the present study was much greater than that of Bohnsack (1976). Further, the low recovery rate in the present study was unlikely due to the highly cryptic nature of this species, as individual patch reefs were relatively small in size (average of 8 by 12 meters) and were thoroughly checked by 5 individual free divers repeatedly during a 20 minute roaming survey. This may indicate active migration at the patch reefs, this is in contrast to previous reports where crabs were indicated to have some form of home range, emerging from crevices during the night to forage, before returning to the same area (Hazlett and Rittschof, 1975). The surrounding patch reefs were surveyed for tagged individuals, but none were found. As we had translocated individuals, we hypothesised that the crabs may have migrated back to their original collection site (the Greencastle Blue Hole), however this was also surveyed, but none of the tagged individuals were found. The results from the locomotor activity experiment (chapter three) indicated that crabs moved between 70 and 130 meters during the night. If indeed the animals were migrating back to a home refuge, then it may have taken longer than the 3 weeks between release and further rechecks of crabs at the blue hole, given the distance between the blue hole and closest mark-recapture patch reef (4.4 km), may have been required.

Conclusions

Although the present study has provided useful data on population characteristics of spider crabs in Eleuthera, we still do not have enough data to complete a full assessment of the fishery potential. The population size is still unknown, however the present data may be helpful to estimate density data for the various habitats the crab is found in (patch reefs, anchialine ponds, blue holes), and comparing this to habitat maps to extrapolate the data across The Bahamas. Further work is needed to determine if any nursery grounds are present, which may be indicative of breeding success and recruitment. Crabs may move back to their home range or establish home ranges in new suitable habitat when translocated; further work is required in this area. In addition, we do not know the growth rate and longevity of this species (Penn et al., 2019). Adey and Farrier (1989) projected that “plate sized” male spider crabs (1000 g, 120 mm CW) could mature in around 360 days in captive culture in some regions. Beyond this short projection, longevity, age, and population structure remains unknown. If spider crabs grow this rapidly in the wild it still remains to be determined whether the pubertal moult is also the terminal moult, as is seen in other crab species (Hartnoll et al., 1993). If this terminal moult does occur, the lifespan of the crabs beyond this moult, mating success, and brood sizes during this time is required knowledge for fishery managers.

Spider crabs are difficult to catch in regular baited pots due to their herbivorous nature. Thus, collection by hand is a reliable method for harvesting these crabs from the wild. Collection on SCUBA for any species in The Bahamas is illegal unless under permit, so free diving to collect this species appears to be a sustainable approach to harvest. Further, aside from Sweetings Pond, very few spider crabs were found during the day, likely making this fishery a low priority for fishers.

Similar to a number of commercial crab species (Donaldson and Donaldson, 1992), a male only fishery would protect the reproductive potential of the stock, and depending on the minimum harvest size of the male crabs, allow males to mate at least once prior to harvest (Hankin et al., 1997). This brings into question what size should be allowed for harvest in The Bahamas? The minimum harvest size should be set to protect breeding stocks by being larger than the size at maturity, but also recognise acceptable sizes for market (Donaldson and Donaldson, 1992). The present study indicated that morphological maturity of males was reached at 96.2 mm CW, and behavioural maturity at 80.1 mm CW, thus minimum harvest size should be set above 96.2 mm. In Antigua males mature at 105 mm CW (Adey and Farrier, 1989), therefore to cover this potential variation minimum harvest size could be set at 110 mm CW, allowing males to mature and a significant portion to mate with females prior to harvest. However, further research is required to set this minimum size, as the continual year-round breeding and spawning of females may allow a lower minimum size.

Although at present knowledge required to develop a full-scale fishery may be limited, the crabs do show good potential for an aquaculture venture, especially with regard to removing biofouling on commercial fish cages (see Chapter 3 next). Small-scale local harvest may be beneficial for the development of hatcheries and grow out facilities for farmers. The selection of a local population is also important to reduce the risks and concerns from non-native species and to conserve population gene pools (Fetzner et al., 1997; Nguyen, 2015). These are essential considerations in initial set up and maintenance of aquaculture ventures, where wild harvest is required for broodstock development and management. Nevertheless, the future for the exploitation of the crab remains bright and the fishery potential for this species should be investigated further.

Chapter 3: The use of the Caribbean spider crab *Maguimithrax spinosissimus* for biofouling removal on marine aquaculture cages

Abstract

Biofouling is a significant issue for marine aquaculture pens and is conservatively estimated to contribute to 15% of production costs. With a global increase in the demand for sustainable aquaculture products a search for sustainable non-toxic alternatives to chemical treatment and manual removal of biofouling organisms, such as biological control, are becoming more sought after. To determine activity and feeding habits, trials in the lab on, Caribbean spider crabs (*Maguimithrax spinosissimus*) demonstrated nocturnal patterns of activity. They consumed between 3.3 and 4.16 % bodyweight (BW) of algae in 22 - 24°C water, and between 5.61 and 8.55 % BW in 26 - 26°C water. Although this species primarily herbivorous they also readily consumed whole fish (*Lutjanus apodus*). The spider crabs were placed on a heavily fouled, unused SeaStation 3000 cage offshore of Eleuthera, The Bahamas to determine their ability to remove fouling organisms. Large crabs (382 g – 1344 g) confined in mesh cages on the outside of the pen effectively removed between 40% (after two weeks), and 90% (after one month) of fouling organisms. Crabs were more effective at removing growth than manual diver scrubbing. Grazing by the crabs was non-discriminatory, with no significant change in the proportional makeup of epibionts at the end of the trial. The survival rates of crabs inside the cage varied between 50% and 55% during 3 to 6 month trials, with no significant decline in health status (blood protein levels). The Caribbean spider crab is a good candidate both economically and environmentally for controlling biofouling on aquaculture cages, could be used in multi-trophic aquaculture systems, and marketed as an environmentally friendly seafood alternative.

Introduction

In the past three decades, the aquaculture sector has increased rapidly as the world consumption of seafood has risen (Troell et al., 2009). This rapid increase has occurred because most wild fisheries are already fully exploited and are unable to meet the increasing demand for seafood (FAO, 2016). In 2014 over 50% of all seafood consumed by humans was produced from aquaculture (FAO, 2016). The rapid increase in the aquaculture sector has not been without problems. A significant issue that is prevalent in marine culture systems is biofouling: the accretion of organisms on submerged surfaces (De Nys and Guenther, 2009). The costs attributed to biofouling are conservatively estimated to be up to 15% of production (Adams et al., 2011; Lane and Willemsen, 2004). The impacts of biofouling vary based on the amount and type of fouling present, and can have negative effects on the structure, function, and health of the aquaculture facility.

In shellfish aquaculture, maintaining clean shells and ropes increases marketability of the final product and reduces costs associated with structural breakages and subsequent repairs. In finfish culture, fouling can compromise cage structure and mooring hardware (Swift et al., 2006), leading to cage deflection and deformation resulting in devastating effects such as cage collapse and the escape of fish (Jensen et al., 2010; Lader et al., 2008; Swift et al., 2006). Furthermore, fouling can decrease the flow of water (Gansel et al., 2012; Madin et al., 2010) by as much as 50% (Gormican, 1989), reducing oxygen availability for fish and concomitantly reducing removal of nitrogenous waste products from within the cage (Lader et al., 2008). Fouling organisms themselves can compete with the stock for space and food, reducing effective cage volumes (Aarsnes et al., 1990), and inhibiting growth of the farmed species (Adams et al., 2011). In addition, some fish diseases, (e.g., netpen liver disease) (Kent,

1990) and parasites (e.g., *Gilquinia squali, Cardicola forsteri*) (Cribb et al., 2011; Kent et al., 1991) can be attributed to the consumption of fouling organisms by the fish.

Commercial farming operations generally use a combination of three broad categories of control to mitigate the effects of biofouling on nets and cages. These include net changing and cleaning, chemical antifoulants, and biological controls (Fitridge et al., 2012). Net changing or cleaning frequency depends on latitude, season and mesh size, varying from between every eight days (Hodson and Burke, 1994) to once per year (Sutterlin and Merrill, 1978). Net changing is largely used to prevent damage from structural fatigue and deformation, but is labour intensive and expensive (De Nys and Guenther, 2009), and can also impact feeding regimes (Fitridge et al., 2012). Alternatively, *in situ* net cleaning can be completed by SCUBA divers using pressurised water hoses (Cronin et al., 1999) or automated using remotely operated vehicles (ROVs). *In situ* cleaning is expensive and can trigger larval release (Carl et al., 2011) or leave remnants of fouling organisms which regrow (Moss and Marsland, 1976). For example, breakdown of the hydroid *Ectopleura larynx* with power washers has been associated with reduced gill health of farmed salmon (Bloecher et al., 2018). Furthermore, *in situ* cleaning can damage nets, increasing numbers of loose filaments which create additional settlement locations for fouling species (Geffen, 1979) and release microplastics into the environment. While the fate of excess feed and faecal matter into the environment are reasonably well documented (Kutti, 2008; Torrissen et al., 2011), fouling material dispersal and deposition from net pen cleaning has not received as much attention, but could have similar impacts. These might include, but would not be limited to, excess benthic nutrient input and smothering of organisms, with the subsequent bacterial breakdown causing anoxic dead zones around the aquaculture operation (Bannister et al., 2016; Floerl et al., 2016; Reid et al., 2009).

Chemical antifoulants are also commonly used to deter larval settlement, and work by leaching a layer of biocide around the net (De Nys and Guenther, 2009). Copper-based treatments are frequently used because they are highly toxic to most marine organisms (Oliva et al., 2007). However they may also have negative effects on various non-target organisms such as macro- and micro-algae (Bond et al., 1999; Lim et al., 2006), fish (Mochida et al., 2006; Oliva et al., 2007), molluscs (Zhu et al., 1990), lobster (Chou et al., 2000) and urchins (Chou et al., 2003). All these organisms can be impacted by copper through bioaccumulation in sediment (Miller, 1998) and tissues (Chou et al., 2003, 2000; Zhu et al., 1990), and leeching through the water column (Brooks, 2000; Thomas and Brooks, 2010). In a number of developed countries, such as Norway and the European Union (Floerl et al., 2016; Sandberg and Olafsen, 2006), the introduction of hazardous chemicals directly into the environment is highly regulated, requiring registration of biocides under law or a regulatory agency (Thomas and Brooks, 2010). Although these chemicals are regulated in their use, the release of chemicals and materials from *in-situ* cleaning, e.g. from fragmentation during high-pressure cleaning, or the degradation of these materials over time is not as well regulated, potentially due to the lack of studies on the release of antifouling biocides (Thomas and Brooks, 2010).

There is a global move to find biocides that are both effective and 'eco-friendly' (Fitridge et al., 2012) which in turn would enhance public perceptions of aquaculture (Sandberg and Olafsen, 2006). Short term less-toxic alternatives include chemical treatments such as acids (e.g., acetic, silicic, formic and citric acids) (Denny, 2008; Guenther et al., 2011; LeBlanc et al., 2007; Piola et al., 2009) and bases (e.g., sodium hypochlorite (bleach)) (Denny, 2008). Such chemicals are used during times of heavy fouling and their impact on the environment considered to be minimal as nets and lines must be removed from the water during treatment. Acetic acid has been shown to remove between 55 – 100% of fouling species (Denny, 2008; Piola et al., 2009), while bleach successfully removed 75 – 100% of fouling organisms (Denny, 2008; Piola et al., 2009). In contrast to the use of short term less-toxic treatments, biofilms and coatings (de Nys and Ison, 2004; Huang et al., 2010; Qian et al., 2007) are impregnated into the mesh and generally used for longer term control. A novel experimental method by Da Gama (2001) involved the crude extraction of natural biofouling chemicals from three species of seaweed, with *Laurencia obtusa* showing some potential antifouling properties.

Finally, researchers have investigated the effectiveness of using fish (Kuwa, 1984; Kvenseth, 1996), sea cucumbers (Ahlgren, 1998), shrimps (Dumont et al., 2009), urchins (Lodeiros and García, 2004; Sterling et al., 2016; Zhanhui et al., 2014), gastropods (Enright et al., 1983) and crabs (Hidu et al., 1981; Ross et al., 2004) as biocontrol agents to remove organisms through naturally grazing on the netting. To date these have been largely small scale or experimental in nature (Fitridge et al., 2012). For example, urchins have been used on oyster, mussel and scallop farms (Lodeiros and García, 2004; Ross et al., 2004; Sterling et al., 2016; Zhanhui et al., 2014), but the use of animals to control growth on large commercial finfish operations has received much less attention. Constraints of using biological control mechanisms include concern about the polyculture of new species and the transfer of disease. In addition, grazing species often show a food preference which could lead to removal of competitors, allowing non-grazed species to flourish forming a successful monoculture on nets.

The Caribbean Spider Crab *Maguimithrax spinosissimus* (previously *Damithrax spinosissimus, Mithrax spinosissimus* (Hurtado-Alarcón et al., 2018; Klompmaker et al., 2015; Windsor and Felder, 2014)) hereafter the spider crab, is the largest brachyuran crab found in the Western Atlantic with sizes reaching over 3 kg and 170 mm carapace width (Winfree and Weinstein, 1989). The spider crab ranges from North Carolina, USA, through the Caribbean to Venezuela (Baeza et al., 2012). This species is a common nocturnal omnivore showing preference for fleshy macroalgae but also grazes on calcareous algae (Butler IV and Mojica, 2012), as well as consuming some animal material (Winfree and Weinstein, 1989). The per capita grazing rates have been shown to exceed most herbivorous fish in the Caribbean (Butler IV and Mojica, 2012). Because of these high grazing rates, Spadaro (2014) suggested using the spider crab for algal removal in coral reef restoration projects.

Given the large size, abundance and potential of this species as an effective grazer, the aims of this study were to assess the ability of the spider crab *Maguimithrax spinosissimus* as a biological control agent in removal of growth on commercial scale marine aquaculture cages in Eleuthera, The Bahamas. In order to test our hypothesis, we carried out: 1. A laboratory assessment of the feeding rates, foraging times, and the types of foods they would consume; 2.Investigated times for and the amount of removal of fouling on an aquaculture cage in comparison to manual cleaning of nets; and 3. Carried out longer term trials to determine survival and retention rates as well as indicators of overall health when the animals were retained inside the cage for several months.

Materials and Methods

Sampling Area and Measurement of *Maguimithrax spinosissimus*

The study was conducted at the Cape Eleuthera Institute (CEI) (24°49'46"N, 76°19'41"W), Eleuthera, The Bahamas. *M. spinosissimus* were collected from two locations: patch reefs northeast of CEI (GPS: 24°50'N, 76°14'W; depth range, 2.5 - 3.6 m) and a blue hole (GPS: 24°47'01"N, 76°13'39"W; maximum depth unknown, dive depth 15 m) northwest of the town of Greencastle (Figure 3.1). Crabs were collected at night by freediving at the patch reefs and SCUBA diving in the blue hole. The crabs were transported to the CEI wet lab in coolers within two hours of collection. The crabs were held at CEI in flow-through tanks (diameter = 1.5 m, depth = 0.7 m, filled to 50% of capacity), with ambient water and natural light cycles for a maximum of two weeks between January (20-22°C, 12:12 light:dark) and June (26-28°C, 14:10 L:D) prior to placement on the CEI offshore aquaculture cage. Cinder blocks and PVC pipes provided shelter for the crabs. Limestone rocks, covered in various algal species, were collected from the nearby intertidal shore and placed into the tank for feeding. These were changed daily and also acted as additional structure. Prior to their use in experiments the sex, mass (g), and carapace width (CW) in mm of the crabs were recorded, and any limb loss was noted. At the conclusion of experiments crabs were released back into the field.

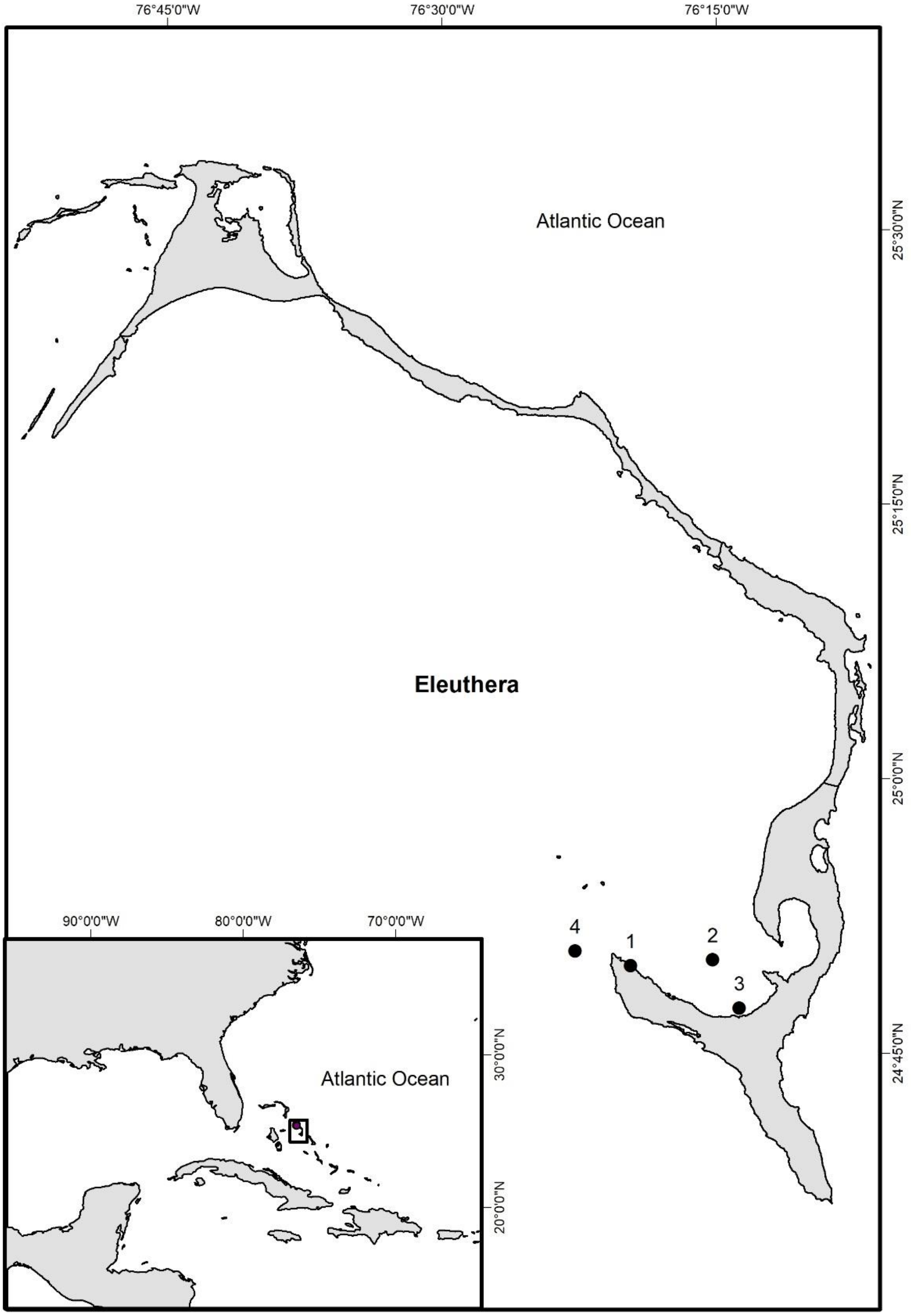

Figure 3.1. Eleuthera in relation to the southern United States of America. (1) The Cape Eleuthera Institute, (2) Coral Patch Reefs, (3) Greencastle Blue Hole, (4) SeaStation 3000 Aquaculture Cage.

Laboratory Experiments

Feeding Behaviour.

The food consumption rates of male and female spider crabs were assessed in the lab. Two ambient temperature ranges were selected: 22 - 24°C, and 26 - 28°C, representing mean water temperature ranges from December to May (Winter and Spring) and June to November (Summer and Fall) respectively. Crabs (22 – 24°C: n_{male} = 8, size = 235 – 1431 g; n_{female} = 6, size = 215 – 792 g; 26 - 28°C: n_{male} = 7, size = 206 – 866 g; n_{female} = 6, size = 301 – 709 g) were fasted for six days prior to being placed in separate flow through opaque plastic tanks (diameter = 0.8 m, depth = 0.4 m), each tank was supplied with an air stone that maintained oxygen levels above 90% saturation. Algae (*Laurencia sp.*) was collected from the intertidal area and patted dry using a paper towel to remove excess water. This species was used as it was previously shown the crabs grazed on it and it was readily available (Butler IV and Mojica, 2012; Francis et al., 2019). A pre-weighed amount (approximately 100 g wet weight) was then placed into each tank and the crab was left to feed for 24 hours. Alongside each trial, a control sample of algae or was placed in a tank to determine any potential change in wet weight of the algae over 24 hours. At the conclusion of the trial, the crabs were removed, and the remaining algae collected from the tank. This was again patted dry prior to being weighed. Total consumption (T_c) was determined as:

$$[\text{initial weight } (W_i) \text{ - final weight } (W_f) = T_c].$$

The final weight was corrected using the change in weight measured in algae in the control tanks. This mass was then converted to amount consumed as a percentage of wet body mass of each crab. The experiment was then repeated with separate crabs (n_{male} = 6 size = 215 – 850 g; n_{female} = 5, size = 322 – 512 g) at 22 - 24°C; these crabs were fed whole schoolmaster snapper (*Lutjanus apodus*; 75 – 150 g) to determine if they would potentially remove fish mortalities if maintained in an aquaculture cage.

The preceding experiments used crabs that had been fasted for six days; a separate experiment was carried out to determine if consumption rates changed over a time period of three days. Crabs (n_{male} = 3, size = 543 – 665 g; n_{female} = 3, size = 301 – 312 g) were fasted for six days prior to being monitored at the higher temperature range only. At the start of each day (08:00) a known mass of algae was introduced into the tank. The algae was removed after each 24 hour period and weighed to calculate consumption mass, prior to being replaced with fresh algae. The entire process was repeated for an additional two days.

Locomotor Activity and Feeding Frequency.

The locomotor activity and feeding frequency of crabs was assessed over a 48 hour period. Crabs (n = 10) were placed individually in raceway flow-through tanks measuring 3 m x 0.7 m x 0.5 m (L x W x D), with an ambient water temperature range of 22-24°C and a natural light cycle of 12:12 hours (day/night). The area was covered with a dark blue tarpaulin to avoid disturbance from surrounding activity. A PVC pipe measuring 300 x 150 mm (L x D) was placed at the outlet end of the tank and a small wire mesh cage filled with approximately 100 g of algae placed at the inlet end. A GoPro camera was used to record the location of the crab in each tank by taking a photo every 30 seconds. Insulation tape was placed on the bottom of the tank to indicated 10 cm intervals. Activity rates were calculated as the total distance moved each hour, while feeding time was determined by the amount of time the crab spent the vicinity (less than 25 cm) of the food cage.

Aquaculture Cage Trials

CEI has an offshore aquaculture cage (OceanSpar/InnovaSea SeaStation 3000, NETSystems Predator-X 1-inch mesh; spar height = 15.3m, diameter = 25 m; Figure 3.2) in South Eleuthera, The Bahamas (24°50'34"N 76°22'36"W; Figure 3.1). The cage was affixed at 27 m depth, with the top of the cage approximately 10 m below the surface. The aquaculture cage was previously used for the culture of cobia (*Rachycentron canadum*) however it had been unused for 5 years other than as a dive site. The cage was heavily fouled by various species owing to its lack of continued cleaning. Four different experiments were carried out at this site.

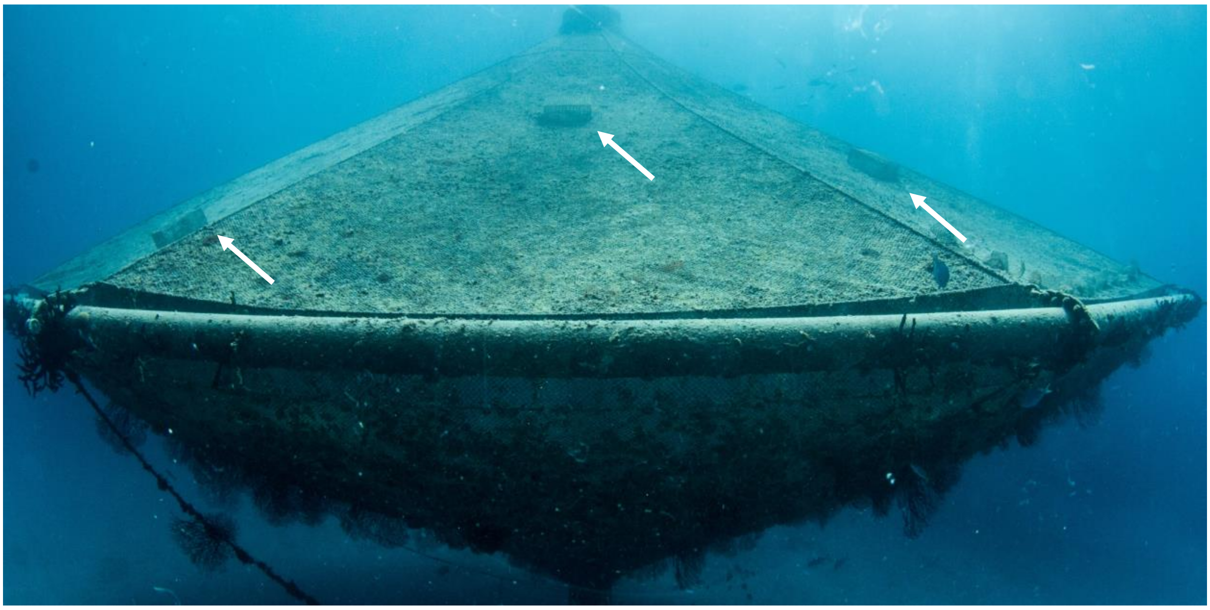

Figure 3.2. The Cape Eleuthera Institute’s SeaStation 300 Cage. Note the experimental crab feeding enclosures attached on the outside (arrows). Photo: Tom Carr.

In-cage Trials.

This experiment examined the long-term survival rates, growth potential and general condition (haemolymph protein levels) when the crabs were maintained in the cage for periods ranging from three to eight months. Prior to the placement of the crabs in the cage, a 0.3 mL sample of haemolymph was withdrawn into a 1 mL syringe by inserting a 16 gauge needle into the arthrodial membrane at the base of the fourth walking legs. The serum protein concentration was measured using a BRIX/RI-Chek Digital Pocket Refractometer (Reichert Analytical Instruments, Depew, NY). This measures the blood protein (haemolymph) concentration, the majority of which is made up of hemocyanin in crustacean haemolymph (Uglow 1969). Blood protein concentration can indicate physiological condition of crustaceans (Lorenzon et al, 2011): low levels may indicate trauma (Fotedar et al, 2002), stress (Chang 2005) or poor nutritional condition (Wang and McGaw 2014). After the refractometer was calibrated with distilled water, the sample was added to the well and three measurements taken: temperature compensated percent solids (BRIX-TC), temperature compensated refractive index (TC-RI), and refractive index (RI). The BRIX-TC value (hereafter referred to as BRIX) was used in the present study as a proxy for total blood haemolymph protein, because it could be measured rapidly and reliably with the meter (Bolton et al., 2009; Mendo et al., 2016; C Simon et al., 2015). The time between withdrawal of the sample and measuring did not exceed 60 seconds. Following the collection of the haemolymph sample a T-bar anchor Floy tag was inserted into the posterior margin of the epimural suture. Crabs were transported directly from the CEI wet lab to the offshore aquaculture cage, where SCUBA divers placed crabs into the cage. The zip opening was then closed and crabs were left *in-situ* for the trial period. This was repeated for three trial periods: March 2017 to May 2017 (n_{male} = 23, size = 353 - 1516 g; n_{female} = 28, size = 205 –

843 g); June 2017 to January 2018 (n_{male} = 13, size = 371 – 1447 g; n_{female} = 17, size = 367 – 1079 g); and January 2018 to June 2018 (n_{male} = 11, size = 236 – 1457 g; n_{female} = 35, size = 260 – 861). At the conclusion of each trial, crabs were collected from inside the cage and any dead animals or carapaces noted. Crabs were returned to the CEI wet lab and subsequently measured for size, mass, limb loss, and haemolymph samples were collected. The Floy tags were used to identify individual animals, or if tags were missing by matching carapace width, claw sizes, and limb loss, with pre-experiment individuals. Data were compared for individual crabs at the start and end of each experiment to determine any potential changes in parameters.

Crab Grazing and Biomass Trials.

The first series of experiments investigated the removal of fouling organisms on the offshore aquaculture cage by the grazing actions of the spider crab. Divers attached 10 experimental enclosures, created with 2.5 cm plastic coated wire mesh and measuring 0.6 x 0.6 x 0.2 m in height to the outside of the aquaculture cage. The experimental enclosures were bottomless and attached directly to the aquaculture cage using zip ties; this allowed the crabs direct access to the fouled aquaculture cage netting to feed. A photograph of the underlying cage netting was taken prior to the introduction of a crab of known size, sex, and weight; the enclosure was then securely fastened to the cage. Four separate trials (trial one, 20 days; trial two, 31 days; trial three, 16 days; trial four, 11 days) and one control trial (empty cage with no crab) were carried out between March – May 2017, and April – June 2018. A new cohort of crabs were introduced for each trial. At three to five day intervals following initial setup, divers would cut the zip ties along three edges, fold the enclosure back 90 degrees and photograph the netting, then re-secure the enclosure to the cage. On the final day of the trial, the cage netting was photographed, and the experimental enclosure moved to a new location. A control trial was carried out with no crabs in the enclosures. The change in net aperture (occlusion of mesh holes) was calculated by comparing time series images. Images were rotated and cropped to the size of the enclosure and individually thresholded and converted to binary using ImageJ 1.52d. Using the threshold tool, the binary images were then used to determine the percentage of black pixels in the image (P_b), representing the open spaces between the net, and the total number of pixels (P_t). Percent net aperture (PNA) was then calculated for both clean and fouled nettings (PNA_{clean} and PNA_{fouled}) following the equation in Guenther et al., (2010):

$$PNA = P_b / P_t \times 100$$

Percent net occlusion (PNO) was then calculated using the PNA values and following the equation from Braithwaite et al., (2007):

$$PNO = (1- [PNA_{fouled} / PNA_{clean}]) \times 100$$

Clean nets had a PNA_{clean} of 76.51, and an associated PNO of 0.

The species composition and percentage cover of each species was also assessed before and after feeding to determine if the crabs were selecting specific organisms. Ten quadrats measuring 0.5 x 0.5 m were randomly selected on fouled areas of the aquaculture cage, these represented the ungrazed areas. Divers collected all epibionts in each quadrat by scraping these areas of the net clean using a scalpel; the resultant falling debris was collected inside the cage by holding a fine mesh bag directly underneath the area. When the area was clean, the mesh bag was zipped closed then placed inside another mesh bag to ensure no biomass was lost. The bags were placed in a cooler of seawater and transported to the CEI wet lab. The samples were then identified to the nearest class and weighed. Each taxa was then expressed as percentage of total fouling biomass. Samples were also collected from the cage mesh after the crabs had grazed an area. The species richness and proportions were compared pre- and post-grazing to determine whether crabs selectively grazed some organisms while leaving others untouched.

Finally, the effectiveness of crabs as biofouling removers was compared to manual removal by divers. For this experiment, eight 0.3 x 0.3 m quadrats were photographed then scrubbed by divers using nylon scrubbing brushes to simulate diver cleaning. After one minute of scrubbing, the area was photographed again to calculate the PNA and PNO changes using the methods outlined above, and samples were taken of the remaining species.

Results

Laboratory Experiments

Feeding Behaviour.

The water temperature had a significant effect on the amount of algae consumed in the 24 hour feeding trial (Two-way ANOVA, F = 18.32, P < 0.001, Figure 3.3). Crabs in the 22 - 24°C temperature range consumed 3.91 ± 0.35 % BW, while crabs maintained in 26 - 28°C water consumed 6.97 ± 0.73 % BW. There was a significant interaction between sex and temperature (Two-way ANOVA, F = 6.139, P = 0.021) on the consumption of algae. Male and female crabs in 22 - 24°C water consumed 4.16 ± 0.51 and 3.3 ± 0.61 % BW respectively; these values were not significantly different from one another. In contrast, in the 26 - 28°C water, female crabs consumed significantly more (8.55 ± 1.08 % BW) algae than the males (5.61 ± 0.69 % BW) (Tukey HSD, *p* = 0.0389). No significant difference in consumption rates (t_{22} = 0.872, *p* = 0.395) were observed between crabs feeding on algae (mean consumption = 3.91 ± 0.38 % BW) or fish (mean consumption = 3.30 ± 0.61 % BW) in 22 - 24°C water (Figure 3.4).

The consumption rates of algae declined significantly between the first and third days of the three day feeding trial (Two-Way Repeated Measures ANOVA, F = 6.76, P = 0.0247, Figure 3.5). The amount eaten declined from 7.48 ± 1.41 % BW on day one, to the lowest levels of 4.37 ± 0.53 % BW on day three. (Figure 3.5). In this experimental trial there was no effect of sex on the amount of food consumed (Two-Way ANOVA, F = 2.985, P = 0.12).

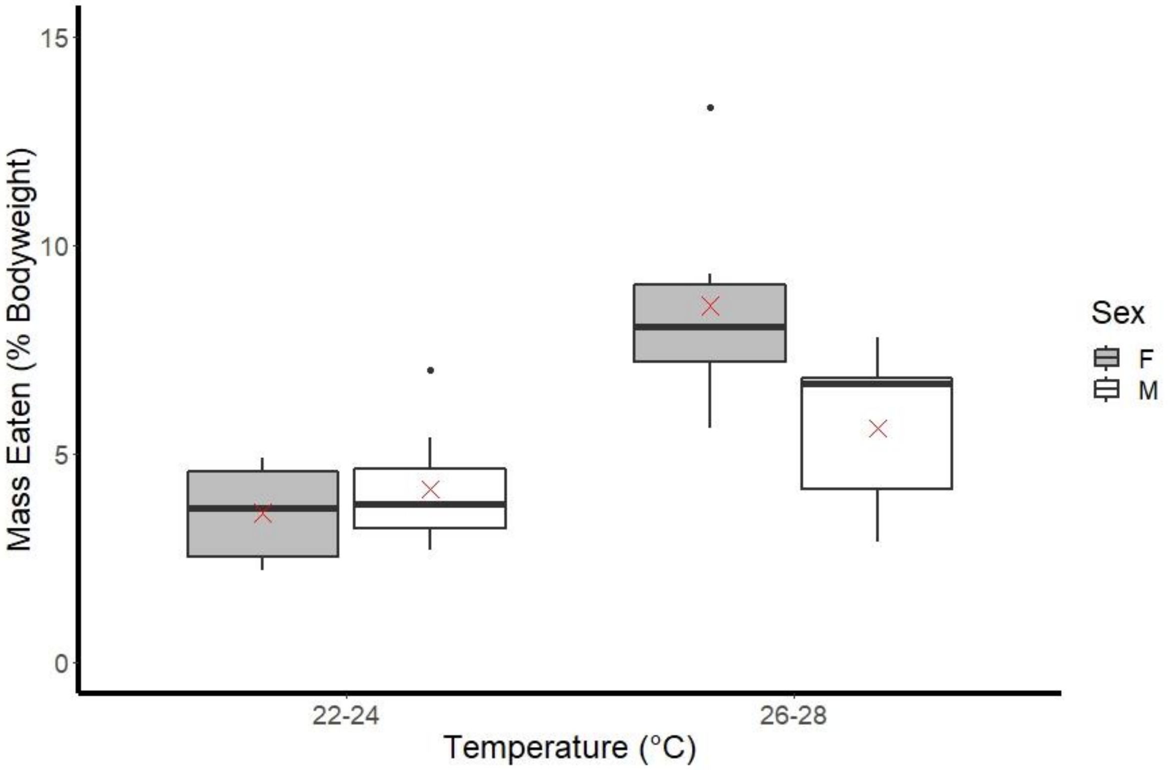

Figure 3.3. Consumption of seaweed in relation to body weight as a function of sex. Male (n = 8 and n = 7) and female (n = 6 and n = 6) *M. spinosissimus* in two temperature ranges, winter-spring 22 - 24 °C, and summer-fall 26 - 28 °C. The boxes enclose data falling between the 1st and 3rd quartile and the bold horizontal lines represent the median in each location, mean consumption represented by X. The vertical lines indicate the 95% confidence intervals of the median. Data points falling outside these ranges are plotted individually.

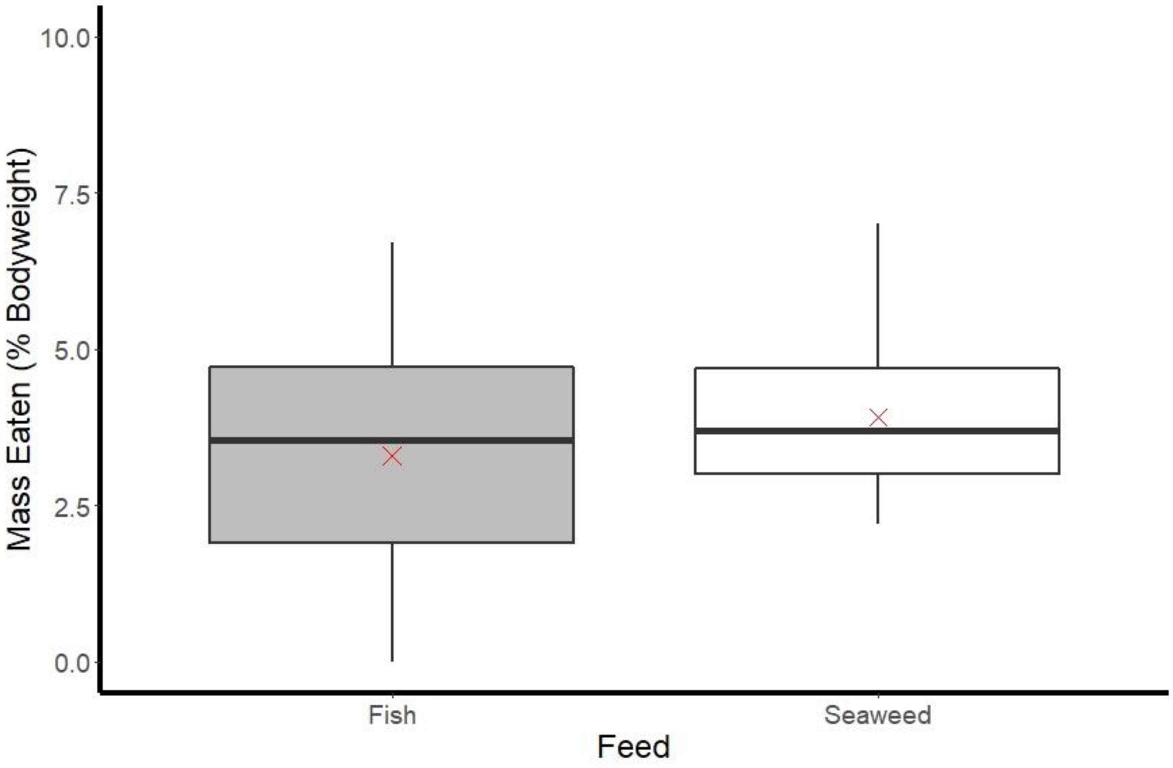

Figure 3.4. Consumption of fish (n = 12) and seaweed (n = 14) in relation to bodyweight by both sexes of *M. spinosissimus* during a 24 h period at 22 – 24 °C. The boxes enclose data falling between the 1st and 3rd quartile and the bold horizontal lines represent the median in each location, mean consumption represented by X. The vertical lines indicate the 95% confidence intervals of the median. Data points falling outside these ranges are plotted individually.

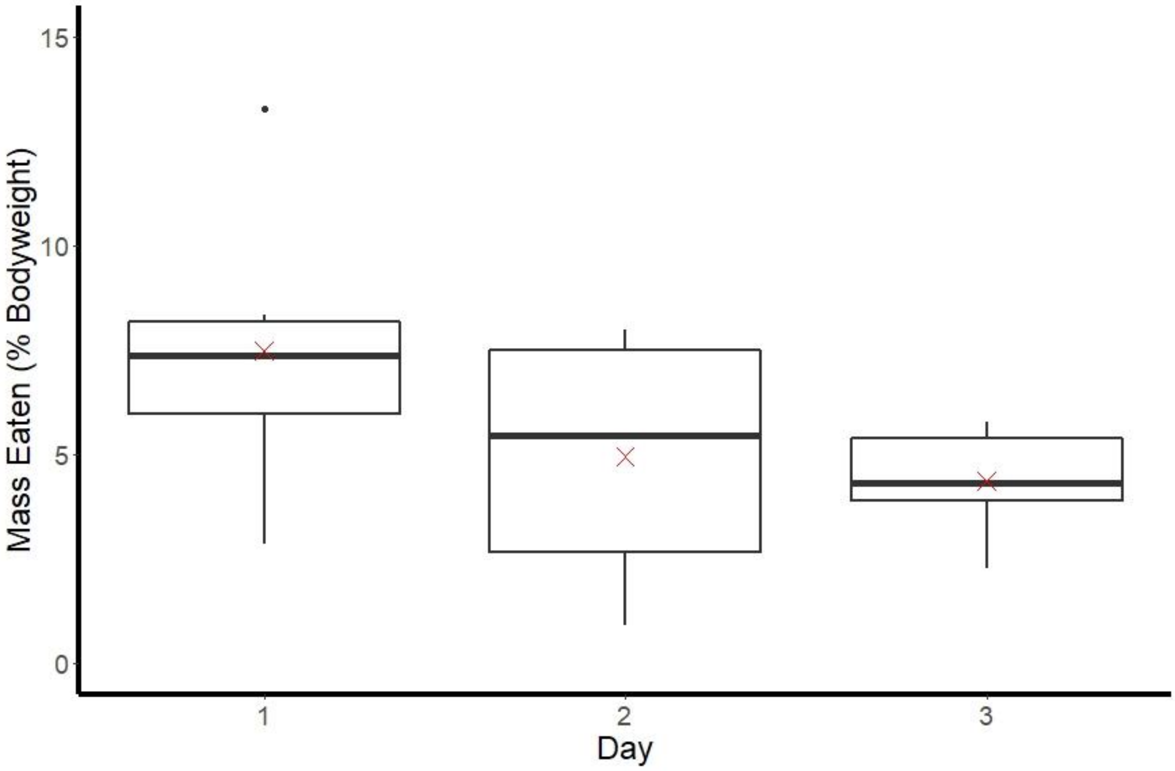

Figure 3.5. Daily consumption of seaweed in relation to bodyweight by *M. spinosissimus* (n = 6) over three consecutive days in the 22 - 24 °C range. The boxes enclose data falling between the 1st and 3rd quartile and the bold horizontal lines represent the median in each location, mean consumption represented by X. The vertical lines indicate the 95% confidence intervals of the median. Data points falling outside these ranges are plotted individually.

Activity Frequency.

The crabs exhibited a strong nocturnal pattern of activity. During daylight hours (hours 1-11, 23-35, and 47-48), crabs moved a mean distance of 0.84 ± 0.16 m per hour. There appeared to be a slight, insignificant increase in movement during the hour preceding sunset on both days (3.82 ± 1.21 m per hour). A significant and substantial increase in activity rates was reached during the hours of darkness (hours 12-22 and 36 - 46) (t-test, Day vs Night: t = -8.868, $p < 0.001$), with movement reduced but remaining above daylight levels after an initial peak (Figure 3.6). This peak movement was reached two to three hours after sunset, with respective distances moved of 19.65 ± 5.98 to 19.78 ± 4.77 m, with one individual crab travelling 101 m in an hour, while average night time movement was 10.0 ± 1.1 m. The crabs moved around the entire tank, pausing occasionally to forage on food. In general, crabs returned to a corner of the raceway or sought shelter in the PVC pipe at dawn.

Foraging activity also followed a nocturnal pattern. During daylight hours foraging was minimal. There was a significant and substantial increase in foraging activity during the hours of darkness (t-test, Day vs Night: t = -13.621, $p < 0.001$), with crabs foraging on average at night for 13.98 ± 0.85 minutes per hour (Figure 3.7). Peak foraging was reached three hours after sunset, with a mean of 20.5 ± 4.57 minutes of feeding activity, followed by a steady decline thereafter until dawn, at which time feeding had largely ceased.

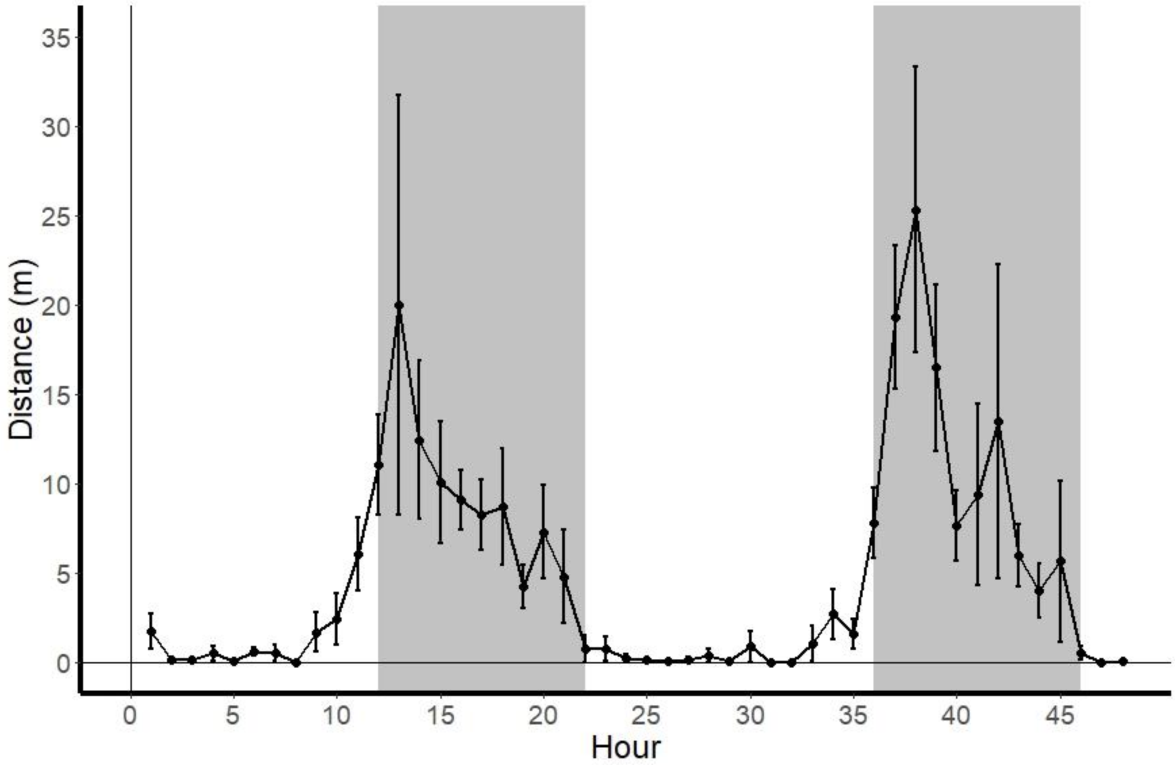

Figure 3.6. Mean hourly movement (± SEoM) of 10 *M. spinosissimus* during a 48 h period. Shaded areas represent the periods of darkness.

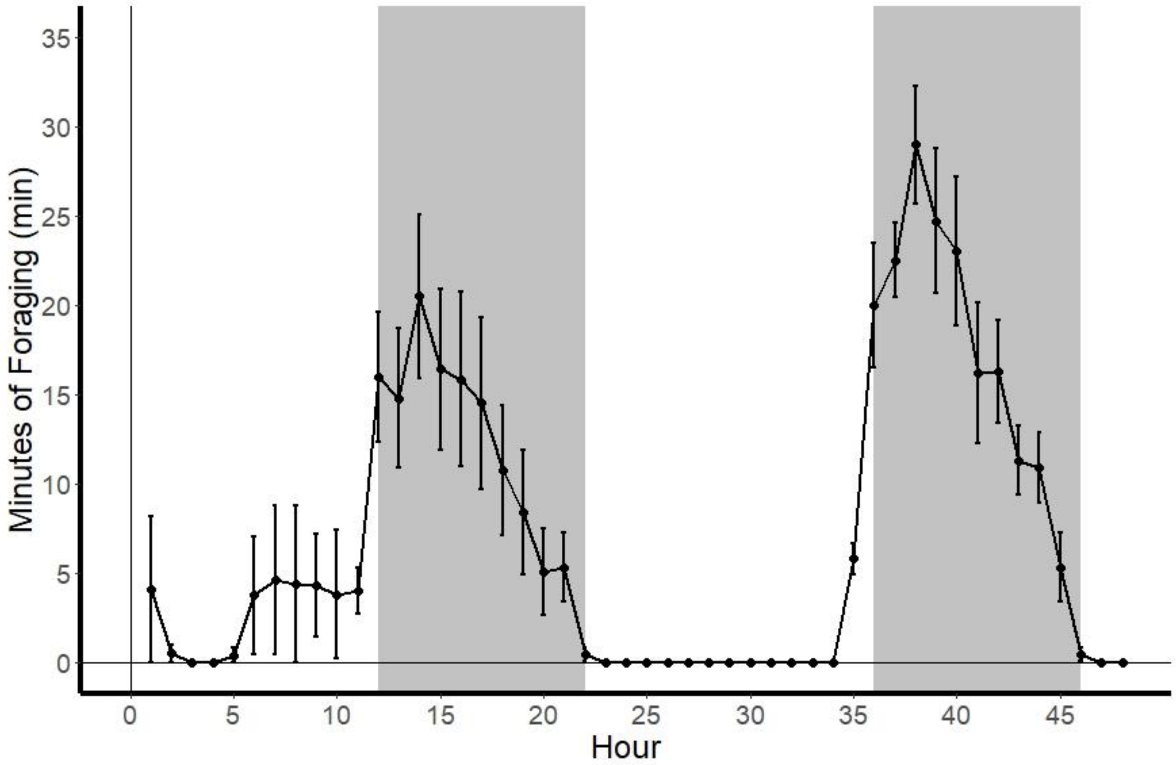

Figure 3.7. Mean hourly foraging time (± SEoM) of 10 *M. spinosissimus* over 48 hours in a flow through raceway at 22 – 24 °C. The shaded area represents the period of darkness.

Aquaculture Cage Trials

In-cage Trials.

For each of the three experiments when the crabs were left inside the aquaculture cage, 17 of 51 (March – May 2017), 10 of 30 (May 2017 – January 2018), and 14 of 46 (January 2018 – June 2018) crabs were retrieved from inside the cage. At the end of each trial the number of dead crabs found inside the cage (shells and bodies on the bottom of the cage) was 14, 10, and 12 respectively. This left 20, 10, and 20 crabs (in trials 1 – 3 respectively) unaccounted for.

There was no significant difference in carapace width or mass of crabs at the beginning and end of each trial (Table 3.1). The BRIX level showed no significant difference between the start and end of the first two trial periods (T-test, $df_{30} = -0.931$, $p = 0.359$; $t_{18} = 0.448$, $p = 0.659$), however there was a slight, but significant decline ($t_{26} = 2.714$, $p = 0.0116$) in the BRIX level during the third trial (Table 3.1). Overall the variance in BRIX levels appeared to stabilise throughout all trials (Figure 3.8); crabs with higher initial BRIX levels exhibited a reduction in BRIX, while in crabs with lower initial BRIX levels an overall increase was measured.

When crabs were retrieved from the cage, limb loss appeared relatively consistent throughout each of the trials. In trial one, 5 crabs had lost lost 1, 1, 1, 2, and 4 limbs. In trial two, 3 crabs lost 1, 1, and 3 limbs. In trial three, 4 crabs lost 1, 2, 2, and 3 limbs. During trial three, one crab showed limb bud emergence on 5 limbs, indicating it was nearing moult stage and regenerating limbs.

Table 3.1. Tracked data from in cage trials.

	March 2017	May 2017	May 2017	January 2018	January 2018	June 2018
Crabs In or Out	In	Out	In	Out	In	Out
n	51	17	30	10	46	14
Unaccounted	20		10		20	
Deaths	14		10		12	
n (Tracked)	17		10		14	
% Remaining	33.3		33.3		30.4	
BRIX	8.38 ± 0.22	8.51 ± 0.42	8.52 ± 0.29	8.47 ± 0.50	8.42 ± 0.21	7.19 ± 0.31
p-Value	0.359		0.659		**0.0116**	
Mass	656.8 ± 97.9 g	655.8 ± 95.1 g	630.1 ± 110 g	634.2 ± 107.5 g	596.9 ± 66.5 g	574.6 ± 71.1 g
p-Value	0.994		0.979		0.8202	
Carapace Width	113.5 ± 5.0	112.1 ± 6.89	112.1 ± 6.89	112.2 ± 6.87	106.5 ± 2.25	105 ± 4.3
p-value	0.869		0.991		0.708	
Limb Loss (total)	9		5		8	
No. of Crabs	5		3		4	
Limb Bud Presence (total)	0		0		5	
No. of Crabs	0		0		1	

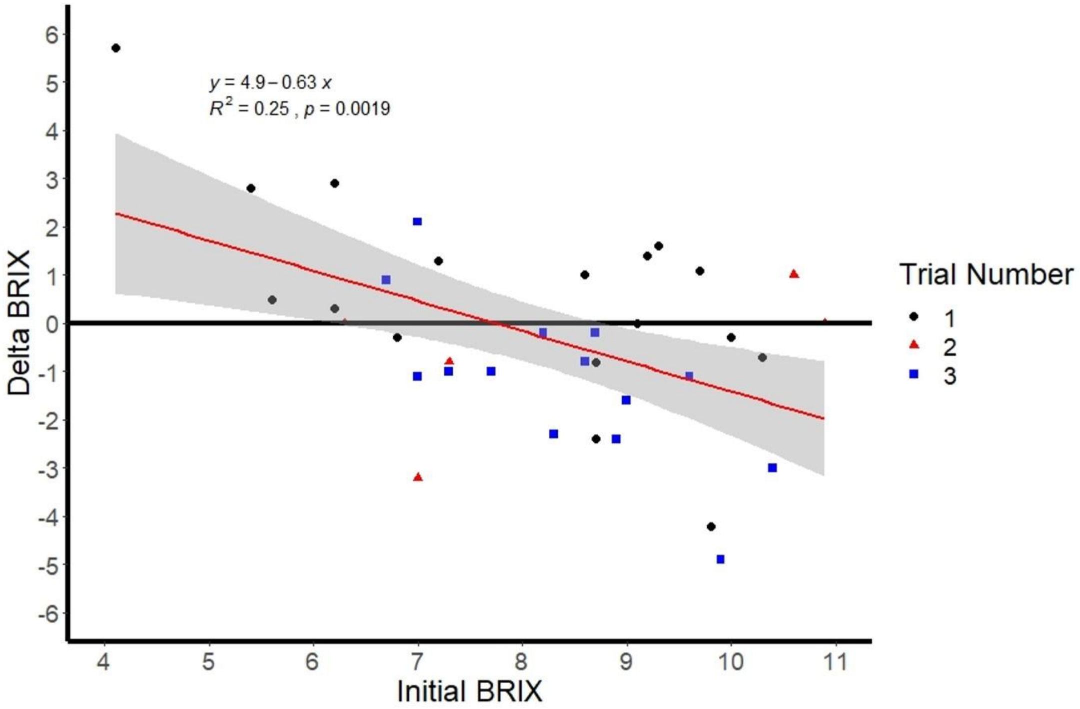

Figure 3.8. Change in BRIX levels over duration of each in cage trial. The points represent the starting BRIX levels of individual crabs and the change in BRIX level (Delta BRIX) during the respective trial (colour and shape). The solid black line represents no change in BRIX. Trial one lasted 3 months, trial two lasted 8 months, trial three lasted 5 months. The red line is the line of best fit for all trials. The black horizonal line represents no change in BRIX.

Confined Crab Grazing and Biomass Sampling.

Spider crab grazing activity visibly removed fouling organisms on the aquaculture cage (Figures 3.9, 3.10, 3.11). The longest trial lasting 31 days resulted in a noticeable removal of biofouling organisms on the net (One-Way Repeated Measures ANOVA: F = 187.3, $p < 0.001$) from 86.81 ± 3.28% at the start of the trial to final levels of 13.25 ± 2.61% net occlusion. The crabs reduced occlusion from 95.38 ± 2.60% to 57.55 ± 9.41% during the 20 day trial (One-Way Repeated Measures ANOVA: F = 14.46, $p < 0.001$), from 94.14 ± 2.92% to 76.59 ± 3.11% during the 16 day trial (One-Way Repeated Measures ANOVA: F = 15.09, $p = 0.003$), and from 82.91 ± 2.89% to 65.51 ± 1.60% during the 11 day trial (One-Way Repeated Measures ANOVA: F = 17.6, $p < 0.001$). This amounted to calculated reductions (using the pre-grazing biomass sampled weights) in the 60 cm x 60 cm experimental area from approximately 560 ± 20 g to 85 ± 15 g, 615 ± 15 g to 370 ± 60 g, 607 ± 19 g to 494 ± 20g and 535 ± 20 g to 420 ± 10 g of fouling for each trial, respectively. The control trial showed no significant change in net occlusion, varying between 89.04 ± 2.55% and 89.66 ± 3.30% net occlusion (T-Test: t = -0.154, $p = 0.88$).

In the trials lasting for 20 days or longer, crab grazing removed significantly higher amounts of epibionts than 1 minute of diver scrubbing (trial one: t = 1.058 $p = 0.317$; trial two: t = 14.57, $p < 0.001$). During the shorter trials there was no significant difference in the amount of biofouling removed when comparing crab grazing and diver scrubbing (trial three: t = -2.11, $p = 0.062$; trial four: t = 0.76, $p = 0.47$) (Figures 3.9 and 3.12).

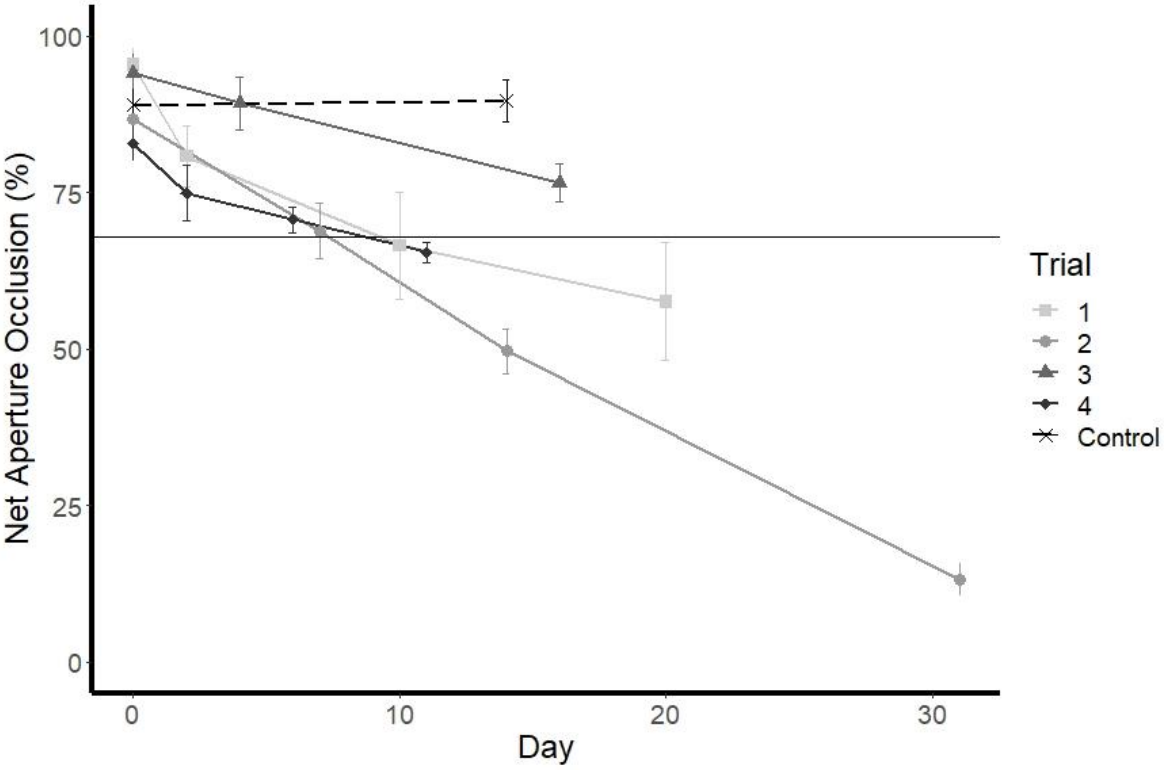

Figure 3.9. Mean net aperture occlusion (± SEoM) of a 60 cm x 60 cm area of the aquaculture cage when an individual crab was confined and allowed to graze on the biofouling. Four individual trials (n = 10 per trial) were carried out on different areas of the cage (2017 and 2018) using different individual crabs. The solid horizontal line indicates mean net aperture occlusion after one minute of diver scrubbing.

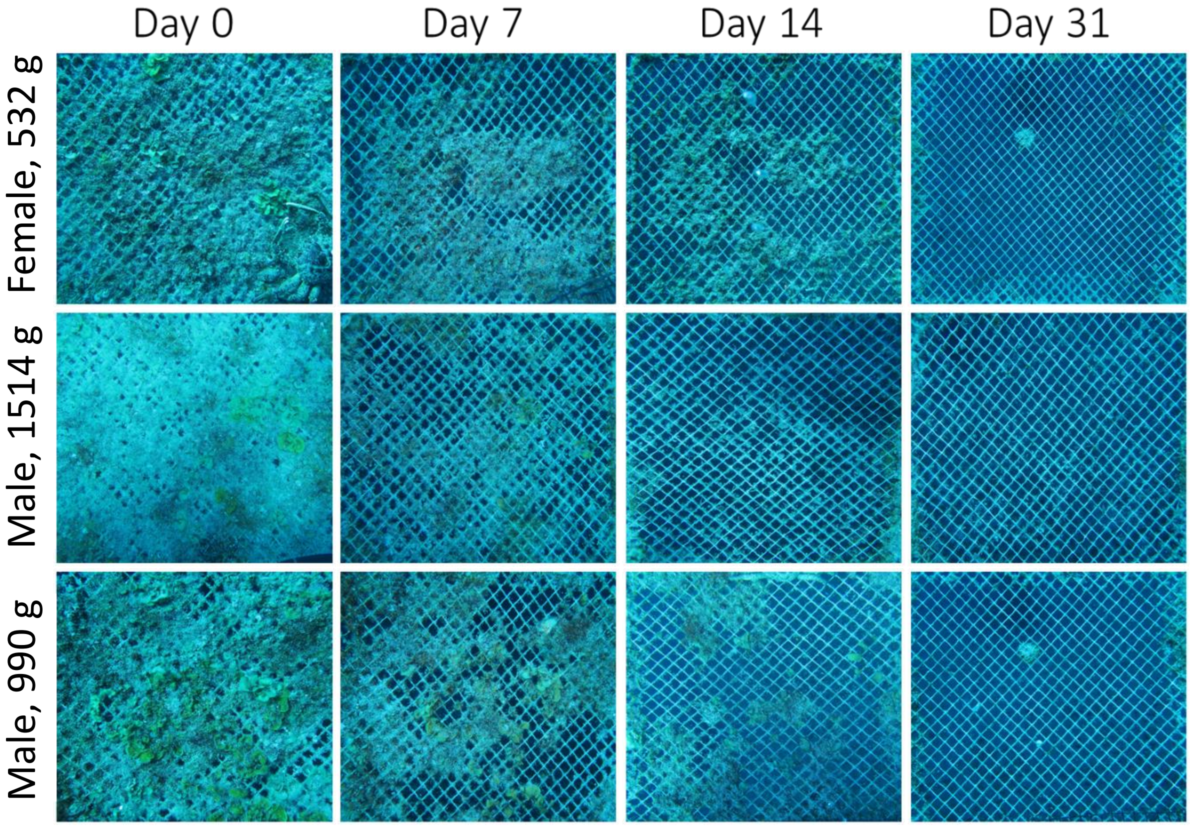

Figure 3.10. Examples of individual grazing removal by individual male and female *M. spinosissimus.* Photos were taken at day 0 and a crab then placed in the area and confined with a mesh enclosure. At regular intervals thereafter the enclosure and crab were removed for a photograph before being replaced. These images were used to calculate reduction in net occlusion

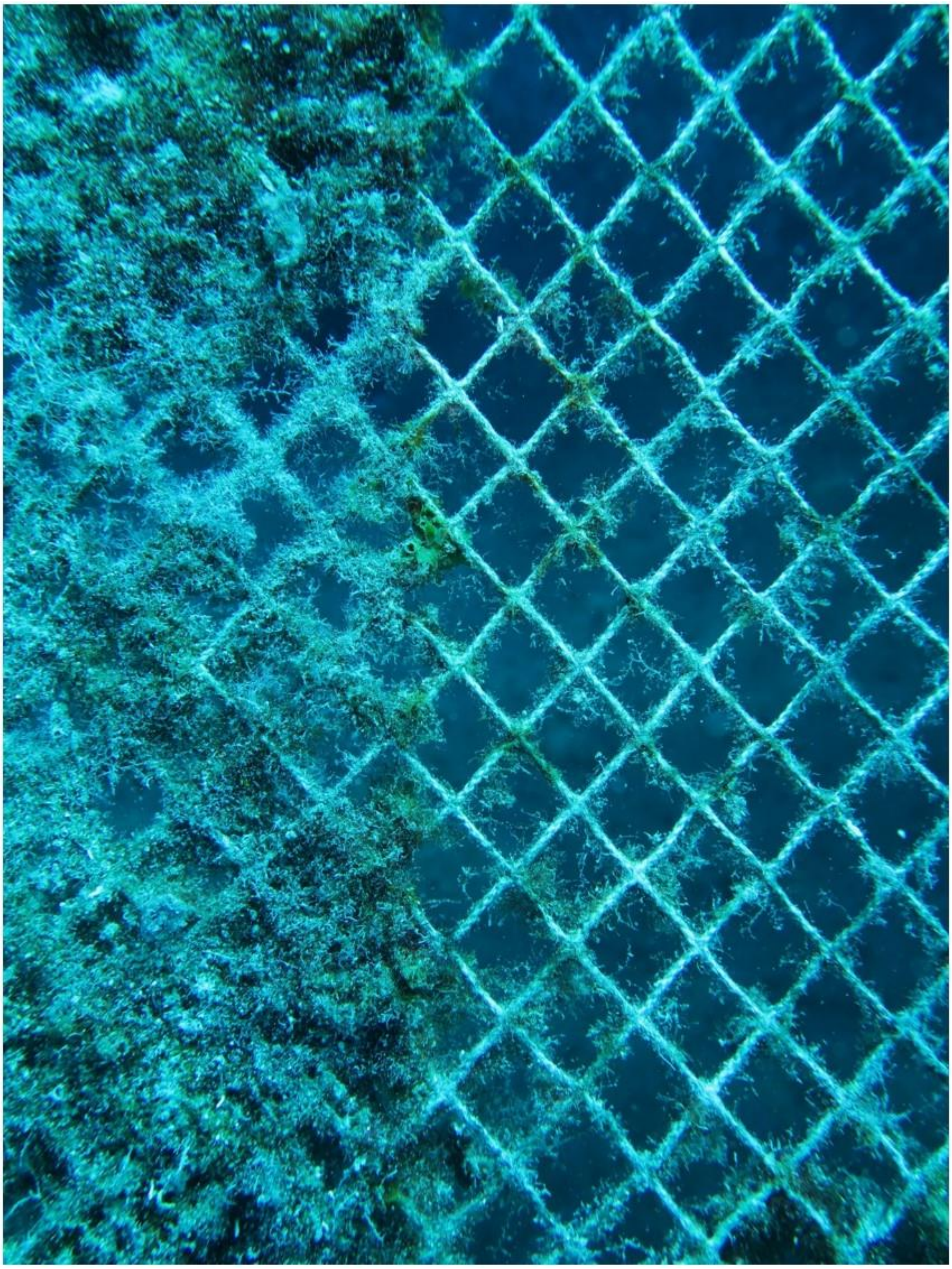

Figure 3.11. A close up photograph to allow comparison of an ungrazed area (left) and a grazed area (right) after 31 days along the border of a confined grazing cage. Note the reduced net aperture occlusion in the grazed area.

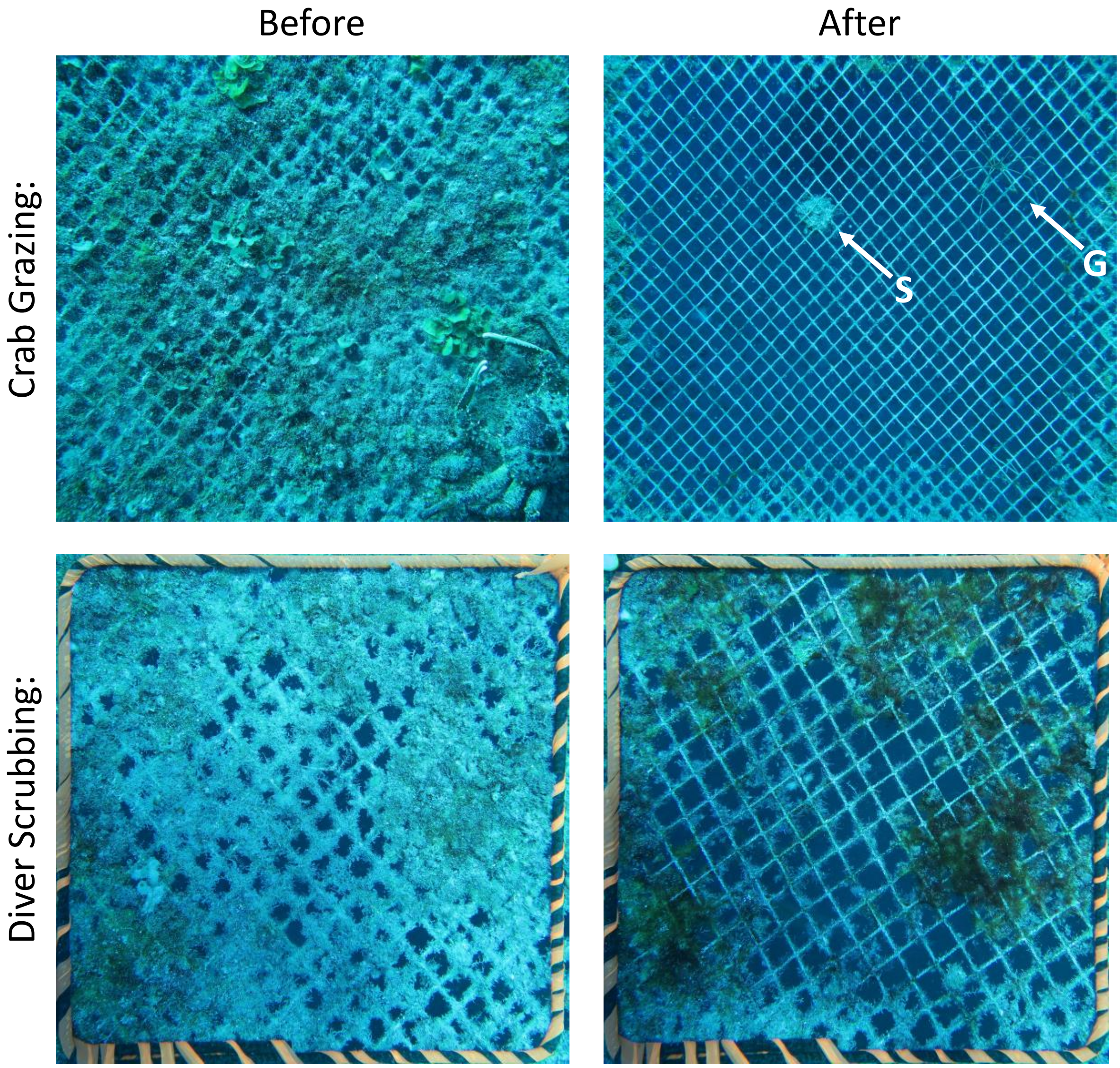

Figure 3.12. Comparison between individual crab grazing before and after 31 days (top row), and one minute of diver scrubbing with a nylon brush (bottom row). Note the Atlantic thorny oyster *Spondylus sp.*, indicated by arrow and (S) in the top right picture, which was unable to be removed by crab grazing, and the golden arrow crab *Stenorhynchus seticornis,* indicated by arrow and (G) in the top right picture, which were frequently found within the cages.

Investigation of the species richness of the epibionts on the cage showed that turf algae – thick, fast growing assemblages of multiple algal and cyanobacteria species (Littler et al., 2006; Steneck and Dethier, 1994; Vermeij et al., 2010) – dominated cage fouling, making up over 90 % of the biomass. The remaining assemblage consisted of brown algae (*Lobophora variegata*) making up around 2 %, motile animals (annelids, gastropods, and polychaetes) making up between 2 – 4 % of the total mass, and non-motile animals (corals, sponges, and molluscs) making up less than 1 % of the biomass. Following crab grazing there was found to be no significant difference (t-test; t = -1.33, *p* = 0.216) in the proportional makeup of turf algae, brown algae, and motile and non-motile animals on the cage (Table 3.2). The only organisms that were not effectively reduced were large (> 40 mm) encrusting bivalves (*Spondylus sp.*), and these were only found on 3 grazing quadrants on the cage.

Table 3.2. Biomass and makeup of 0.25 x 0.25 m quadrats of the aquaculture cage pre- (n = 10) and post- (n = 10) crab grazing.

Percentage values represent proportions of clades in the quadrats as the mean ± SEoM of the mass.

	Total Biomass	Motile Animals	Brown Algae	Turf Algae	Non-Motile Animals
Initial Sampling	286.5 ± 37.70 g	4.62 ± 0.59 %	2.32 ± 0.47 %	92.49 ± 1.08 %	0.57 ± 0.21 %
Final Sampling	74 ± 7.44 g	2.12 ± 0.47 %	1.54 ± 0.36 %	95.43 ± 0.46 %	0.91 ± 0.22 %

Discussion

Laboratory Experiments

Feeding Behaviour.

Food intake in crustaceans typically ranges between 2 – 4% of their body mass per sitting (Elner, 1980; Robertson et al., 2002; Simon, 2009; Simon and Jeffs, 2008; Wang et al., 2016). The mean consumption rate of spider crabs in the warmer water was approximately 7% per sitting, with some individuals consuming 9 – 15% of their body mass during a 24 hour period. Prior to the commencement of these one day feeding experiments, the crabs were starved for six days to ensure the gut was completely empty and that they would feed. Thus, the initial consumption rate was likely higher as crabs ate to satiation. When food consumption was tracked over three days there was a decline to mean levels of 4.3% of the body mass per day; this is similar to the 5% body mass per day previously reported for this species (Winfree and Weinstein, 1989), although still on the higher end of levels reported for most decapod species.

Herbivorous species often use a strategy of high food intake and short retention time to maximise energy utilization of lower quality food (Greenaway and Linton, 1995; Wolcott and O’Connor, 1992), this may explain the higher consumption rate in this species of crab. For example, in herbivorous crustacean larvae (Jones et al., 1997; Le Vay et al., 2001; Serrano Jr., 2012) and herbivorous land crabs (Linton and Greenaway, 2007) gut transit time is generally faster than omnivorous species. Additionally, the herbivorous crustaceans have lower assimilation efficiency compared to omnivorous and carnivorous species (Linton and Greenaway, 2007; Nordhaus, 2004), which would also support the idea that spider crabs need a higher food intake in order to gain enough energy.

In aquatic ectotherms metabolic rate is positively correlated with temperature (Kemp and Britz, 2008; Rayner and McGaw, 2019; Willmer et al., 2005; Woll et al., 2006), and a higher metabolic rate usually requires a higher food intake. Indeed, there was an overall higher feeding rate at the warmer water temperatures (26 - 28°C); however this was only statistically significant for female crabs. Maintenance energy costs of female giant fairy shrimp, *Branchinecta gigas*, are 11.3% higher than for male shrimp (Daborn, 1975), probably associated with the costs of egg production. Thus, the larger female spider crabs may have a higher energetic investment, and therefore higher food intake associated with higher fecundity (Baeza et al., 2015), in support of this 34% of crabs collected were berried.

In the present study, the spider crabs consumed both fish and seaweed during the respective feeding trials. Fish were used to determine if crabs could potentially remove mortalities from finfish aquaculture operations, while seaweed consumption rates were used to determine its potential to remove biofouling. Generally fish mortalities are removed daily from aquaculture cages through diving (Belle and Nash, 2008; Tucker et al., 2008) wherever possible. This allows tracking of mortalities and subsequent fish inventories. Carcasses are disposed of in landfills, incinerated, composted, or used for fertilizer, depending on region regulations (Tucker et al., 2008). In exposed, remote, or offshore sites the travel distances to sites or poor weather may limit mortality removal. The fact that the spider crabs did readily eat fish suggests that they could remove fish carcasses in an aquaculture operation. This may be an effective way to limit the potential spread of disease and ensure water quality is not comprised by decomposing stock. In turn it will supplement the nutrient intake of the spider crabs, which would likely improve their overall condition. Other crustaceans fed a varied, high quality diet (Castell and Budson, 1974; Hagerman, 1983; McLeese, 1972), exhibited higher feeding frequencies (Mente and Houlihan, 2002; Sánchez-

Paz et al., 2007; Stewart et al., 1972; Wang and McGaw, 2014), and this was associated with an increased wet mass and haemolymph protein levels, all indicative of a healthier, more robust animal (Wang et al., 2016). This may be important if the spider crabs were to be harvested and sold when the fish crop was ready for market.

Activity Frequency.

Movement and foraging increased during the night, consistent with previous studies confirming the species as a nocturnal forager (Baeza et al., 2012; Tunberg and Creswell, 1991; Wilber and Wilber, 1991; Winfree and Weinstein, 1989). While some individual crabs were highly mobile (moved up to 101 m in an hour), most of the crabs only moved between 70 and 130 meters in total, during the hours of darkness. *M. spinosissimus* may have a home range with the crabs emerging from cracks and crevices to forage nearby, before returning to their respective crevices (Hazlett and Rittschof, 1975). A small (81 individuals) mark-recapture trial was carried out and the spider crabs released on patch reefs (Chapter two). There was only a 5% recovery of the tagged crabs, which is much lower than a previous mark-recapture study for *M. spinosissimus* (>50%; Bohnsack, 1976). Recapture rates for decapod crustaceans are dependent on population size, migration, catchability, tag retention and mortality (Hyland et al., 1984; Le Vay et al., 2007; Miller, 1990). As such recapture rates can be quite variable, from 6.5% in *Scylla paramamosain* (Le Vay et al., 2007), 18.9% in *Scylla serrata* (Hyland et al., 1984) and over 50% in *M. spinosissimus* (Bohnsack, 1976). The low recovery rate in the present study was unlikely due to the highly cryptic nature of this species, as individual patch reefs were relatively small in size (average of 8 by 12 meters) and were thoroughly checked by 5 individual free divers repeatedly during a 20 minute roaming survey. Thus, it is more likely that crabs moved from the sites as they were initially translocated from the Greencastle Blue Hole, suggesting they may have attempted to return to their established home range.

Whilst movement distance was easy to measure in the experimental trials, differentiating between the actual ingestion of food and grooming activities (self-grooming and egg-grooming in females) was difficult to discern using a camera only. This experimental shortfall has also been noted previously for other species of crabs (Hold et al., 2015; Ramsay et al., 1997; Steen and Ski, 2014). Often the animals can merely be inspecting the food or passing over it without actually consuming anything (Rayner and McGaw, 2019). Thus, the foraging times in the present study were an estimate only, but the fact that the crabs were active in the vicinity of the food cage suggests that a significant portion of their activity is at least related to searching for food.

Aquaculture Cage Trials

In Cage Trials.

The three experimental trials where crabs were placed inside the aquaculture cage for extended periods returned 17 of 51, 10 of 30, and 14 of 46 crabs, with 14, 10, and 12 shells and tags retrieved from the bottom of the cage respectively. As there were no predators inside the aquapen, and the time period of our trials was not long enough for decomposition of the shells to occur, it was assumed the “unaccounted” crabs (20, 10, and 20) had escaped. Based on known-crab survivorship, survival was 55% in trial one, 50% in trial two, and 54% in trial three. A survey of the aquaculture cage prior to the commencement of the third trial revealed two feeding tube openings that the smaller crabs may have escaped through, these were sealed with mesh covers to prevent future escapes. Despite this, 20 crabs were still unaccounted for in the final trial. A detailed survey of the bottom of the cage was not carried out, and given the cage was not maintained for six years, and some areas were heavily fouled and overgrown, it is likely that there may have been additional holes or avenues for escape. A well-maintained commercial cage is unlikely to have these avenues of escape as regular net changing and cage maintenance would reduce the incidence of net damage that would allow for escape.

Even accounting for escapees, the survival of the crabs inside the cage was still lower than 75%. However, the survival rate of the crabs in the outside enclosures was over 80%. All crab mortalities on the outside of the cage occurred shortly after placement on the cage (less than five days), suggesting that stressors from prior lab confinement, handling, and emersion during transport were the most likely causes of death (Grant, 2003; Kruse et al., 1994; Urban, 2015). Aerial exposure is associated with increased blood ammonia, lactate, and urate levels (Barrento et al., 2010; Durand et al., 2000) from anaerobic metabolism (Spicer et al., 1990), as well as elevated glucose levels from increased handling stress (Barrento et al., 2010; Bergmann et al., 2001; Morris and Oliver, 1999; Paterson and Spanoghe, 1997; Speed et al., 2001; Spicer et al., 1990). Thus, the handling and transport of the spider crabs from the lab to the aquaculture site (60 minutes) was the likely cause of short term mortality.

While there was similar initial short term mortality inside the cage (also likely associated with handling and transport), regular inspection showed that mortalities occurred throughout the trial period. These mortalities were more likely associated with long term hypoxic exposure. Although we did not measure oxygen content inside and outside of the cage, when diving inside the cage there was little to no flow of water, in contrast on the outside the divers had to actively manoeuvre to maintain a working position in the current. The cage had not been cleaned for approximately 6 years and the extreme fouling level (97% occlusion) substantially reduced water flow and oxygen exchange (Fitridge et al., 2012), and the heavy fouling community itself would exacerbate the situation (Cronin et al., 1999). In support of this assumption, during the first trial, a large cubera snapper (*Lutjanus cyanopterus*) entered the cage when divers were putting crabs inside, but when revisiting the cage 5 days later had died, even though there was an abundance of prey in the aquapen.

While the handling stress and hypoxic exposure probably accounted for the short-term mortalities (less than 5 days), it is likely that the long term hypoxia also had some effect on the spider crabs. Decapod crustaceans react to chronic hypoxia by decreasing heart rate, along with a concomitant increase in cardiac output and ventilation rate (Burggren and McMahon, 1983; Butler et al., 1978; Taylor, 1982). While the decline in environmental oxygen levels can be offset by an increase in hemocyanin (blood pigment) levels and changes in its affinity, such physiological adjustments may be energetically costly. As such this chronic stress can lead to a reduction in feeding time, assimilation rates, and thus an overall decrease in the condition of the animal (McGaw, 2008).

The BRIX level is used as a health indicator and generally crustaceans that eat more and show more signs of vigour have a higher BRIX value and are deemed to be healthier and in better nutritional condition (Mendo et al., 2016; Simon et al., 2015). There was no change in BRIX levels in the first two trials and a slight but significant decline in BRIX levels in the final trial that ran for five months. However, earlier work showed that a decline in BRIX level of 1.3 was not a drastic decline that occurs during starvation or substantial deterioration (Wang et al., 2016; Wang and McGaw, 2014). It was also unrelated to changes that occur during moulting because none of the animals in the trials moulted (Wang and McGaw, 2014). Overall the crabs that were retrieved were of similar vigour to that at the start of the experiment, suggesting that crabs can gain enough nutrients by grazing on the epibionts growing on the cages.

A number of crabs lost limbs during their confinement in the aquaculture care. This limb loss likely occurred as a result of stress and autotomy during transport (Juanes and Smith, 1995). That being said, the limb loss in the re-captured crabs (29%) was similar to natural decapod crustacean populations (24% of population with injuries, Juanes and Smith, 1995), and lower than the incidence of limb loss in the surrounding population (39%, Zeinert Pers. Obs.). Crabs were frequently found aggregated at the top of the cage, either gripping the netting or the vertical spar whilst near other crabs. The aggregating behaviour of the spider crab indicated minimal aggressive behaviour toward conspecifics, as well as natural behaviour towards finding shelter. As juveniles, crabs are reported to be highly aggressive towards conspecifics (Wilber et al., 1992; Wilber and Wilber, 1991), but once mature show minimal aggression towards each other (Adey and Farrier, 1989; Tunberg and Creswell, 1988).

Confined Grab Grazing and Biomass Sampling.

Crab grazing activities successfully reduced biofouling in all trials. Crabs reduced percent net occlusion (PNO) by 18 - 37% in slightly over two weeks and by up to 74% in a month. The grazing method of the crabs and their ability to use the spoon shape chelae (Adey and Farrier, 1989; Coen, 1988) to “pinch” algae with their chela – allowed removal of fouling from both the inner and outer surfaces of the net. This is advantageous compared to species such as urchins which failed to remove fouling on the opposite side of the netting (Sterling et al., 2016). Under normal fouling conditions (rather than the extreme levels in the present study), the dexterous claws would be able to remove newly settling organisms so they would fail to establish. The divers noted the turf algae on the cage would peel off in large portions during biomass sampling, and the simple mechanical action of crabs walking over the netting would also dislodge material. Crabs in general are described as “messy feeders,” (Ahvenharju and Ruohonen, 2005; Barker and Gibson, 1977; McGaw and Penney, 2014) and thus the mechanical grazing activity (Winfree and Weinstein, 1989) likely contributed to some PNO reduction, rather than complete ingestion of all material. Using data from the lab feeding and the fouling level of the cage during the study, it was calculated that an average sized crab (539 g) it would take approximately 61 days for a crab to reduce fouling in a 1 m^2 area on the present aquaculture cage to 10% PNO. However one should be aware that this cage was not maintained and had not been in use for 6 years prior to the present study, and so although the above times may seen too long to be effect, one could assume that a well maintained commercial cage would not reach these levels to begin with.

One of the greatest concerns of using biological control animals is that selections of preferred prey will occur, leaving the uneaten organisms with no potential competitors. This could then result in a monoculture of a rapidly growing species that are potentially more difficult to remove or even harmful to stock (Fitridge et al., 2012; Ross et al., 2004). This did not appear to be the case here with *M. spinosissimus*, as there was no difference in the proportions of organisms left behind after grazing. Although *M. spinosissimus* has been classified as a herbivore, grazing on algal mats (Adey and Farrier, 1989; Bohnsack, 1976; Coen, 1988), there is also likely consumption of porifera, annelids, molluscs, or arthropods from within algae turfs (Wilber and Wilber, 1989), which have led other researchers to suggest its diet is more omnivorous (Guzman and Tewfik, 2004; Hazlett and Rittschof, 1975; Winfree and Weinstein, 1989). Indeed the feeding trials also showed this species will consume whole fish. Therefore, it is not surprising that the small motile and non-motile animals (porifera, cnidarians, gastropods, annelids, and polychaetes) within the turf algae on the cage were also removed by the grazing crabs. The only organisms that were not removed were large (4-6 cm) encrusted bivalves (*Spondylus sp.)*, however, such large bivalves can take up to 2.5 – 4 years to mature (Lodeiros et al., 2016) and in a maintained net the crabs would be able to graze and remove these before they became established.

The manual removal of growth by scrubbing by a diver reduced fouling by an average of 21.3%, this is similar to removal by commercial power washers on heavily fouled nets in both Norway (23%; Guenther et al., 2010) and Tasmania (15%; Hodson et al., 1997). This was likely single pass cleaning, at the industry standard speed of 0.3 m s^{-1} (Bloecher et al., 2019). Initial cost of the fouling removal equipment can be USD$1000 for power washers and USD$30,000 for simple disk washers (CRAB Project, 2007), and increases with the complexity of the machinery. On salmon farms most cleaning events are scheduled fortnightly, but during peak fouling season this can increase to every five days (Bannister et al., 2019). Thus, the equipment and time to remove fouling can make net cleaning an expensive requirement for farms.

Both diver scrubbing (this experiment) and commercial power washers in others left organisms on the netting, which can continue to grow (Moss and Marsland, 1976). In some cases these left over organisms increase the rate of colonization, such as in the hydroid *E. larynx*, where propagules are more abundant post-cleaning (Carl et al., 2011; Guenther et al., 2010). Both diver scrubbing and commercial scrubbers introduce organic wastes into the environment around the cage through removal of fouling and anti-fouling materials. This excess benthic nutrient input and subsequent bacterial breakdown may cause anoxic dead zones around the aquaculture operation (Bannister et al., 2016; Floerl et al., 2016; Reid et al., 2009). Another side effect of commercial scrubbers (Geffen, 1979) or pressure washers

(Bannister et al., 2019) are they can create loose filaments that increase sites for fouling attachment (Carl et al., 2011) and reduce tensile strength (Morte, 2018), while increasing the potential for anti-fouling coatings to be released into the environment. In the present study there was no evidence of net damage after spider crabs had fed.

Conclusions

Best Use of Crabs for Biofouling Removal in Aquaculture

The high survival rate of *M. spinosissimus* on the outside of the aquaculture cage, in addition to the significant removal of fouling, indicates the crabs have the potential to reduce and remove fouling on commercial farms. Cages such as the large SeaStations utilized in Panama (Welch et al., 2019) or other geodesic cages used in open ocean aquaculture are most likely to benefit from the biocontrol of the crabs. Access to the offshore locations of these farms is likely more influenced by inclement weather than inshore locations, thus cleaning and mortality removal may be delayed. The crabs show potential for use with Cobia or other finfish within these cages in the Caribbean region, because the crabs are large it is unlikely they would be targeted by fish, while their herbivorous nature would reduce negative interactions with fish. For best use in commercial aquaculture, transport to the sites for initial release needs to be rapid and low stress to reduce loss in terms of both mortality and limbs. As these crabs seek shelter in crevices during the day, there may be some need for artificial shelters to be spaced throughout the cage, such as those used by corkwing (*Crenilabrus melops*) and goldsinny wrasse (*Ctenolabrus rupestris*) (Deady et al., 1995). These may provide an additional benefit of encouraging the movement and enhancing the distribution of crabs within an aquaculture cage, ensuring larger sections of cage netting are grazed by crabs.

Finally, in addition to reducing biofouling on aquaculture pens, the crabs show great potential as an additional source of income as they look and taste like the Alaskan King Crab *Paralithodes camtschaticus* (Rubino and Stoffle, 1990). Their marketable potential as an environmentally friendly alternative to other seafood sets them apart from other invertebrate products. The potential problem of marketing these animals is the fact that the adults would need to be collected from the wild. That being said, a number of preliminary studies have suggested that the spider crab is a good candidate for aquaculture because it has a short non-feeding larval phase, with benthic settlement occurring within five to six days post-hatch (Brownell et al., 1977). The juvenile and adult stages primarily feed on algae, which reduces the need for more costly commercial feed (Rubino and Stoffle, 1990), and the final product may have high value. Nevertheless the time spent producing a marketable sized crab makes commercialization of this species challenging. Selectively breeding the crab could increase this potential further, increasing the growth rate of the crab to around 12 months to terminal moult, where the harvest sizes could reliably be over 1kg – a marketable size, especially as up to 20% of their body mass is meat, providing a good yield (Chapter 2).

Chapter 4: General Discussion and Conclusions

Summary

In this thesis, I investigated the population structure of the Caribbean spider crab *Maguimithrax spinosissimus* around Eleuthera, The Bahamas, and the potential of the crab for biofouling removal in commercial aquaculture in the Caribbean. Overall, this thesis showed that the Caribbean spider crab *Maguimithrax spinosissimus* has potential for biofouling removal in commercial aquaculture. Additionally the population may be robust enough to allow a small scale harvest for use as a biocontrol agent or possibly a small scale artisanal fishery.

Population structure and size at maturity around Eleuthera (Chapter 2)

There was a distinct sex related size difference in Caribbean spider crabs around Eleuthera. Males were most frequently found between 80 – 120 mm, with females slightly smaller at between 80 – 110 mm. Males were also heavier ($\bar{x}_{cw}$ = 107.7 mm, $\bar{x}_{mass}$ = 710.8 g) than females ($\bar{x}_{cw}$ = 94.3 mm, $\bar{x}_{mass}$ = 430.9 g), while females were found in greater numbers (n = 234) than males (n = 158). The haemolymph BRIX levels were used as an indicator of nutritional status, physiological condition and general health (C. Simon et al., 2015; Wang and McGaw, 2014). Mean BRIX levels for each site were relatively high for both males ($\bar{x}_{Greencastle}$ = 7.12, $\bar{x}_{Patches}$ = 7.26, $\bar{x}_{Sweetings}$ = 6.46) and females ($\bar{x}_{Greencastle}$ = 7.74, $\bar{x}_{Patches}$ = 6.78, $\bar{x}_{Sweetings}$ = 7.17) and the crabs showed obvious signs of vigour when handled. Total blood protein concentration can differ between species and as a function of life habits and environmental factors (Lorenzon et al., 2011; Wang and McGaw, 2014). This can make inter-specific comparisons difficult, however as each location showed normally distributed BRIX values and crabs were active when handled, this suggested the animals were healthy and gaining sufficient nutrients.

Both male and female spider crabs reached behavioural maturity at around 80 and 72 mm carapace width, respectively, while morphological maturity was reached at 96 and 72 mm. This indicated that females reached behavioural maturity (the abdomen releasing from the sternum) at the same time as morphological maturity (the abdomen is enlarged to hold an egg mass), this is similar to many brachyuran crabs (Gerhart and Bert, 2008; Gonzalez-Pisani et al., 2017). Males reached behavioural maturity prior to morphological maturity. Gonad samples were collected to determine if the crabs were able to produce sperm at this stage, however, when the samples were subsequently transported to, and analysed at Memorial University, they had deteriorated to a condition that cellular structures could not be differentiated. The gastric teeth were sectioned in order to determine the age, but produced inconclusive results as the sections were unable to be cut thin enough to show any growth bands: thus I was unable to determine the age at a particular size. The meat yield from the crabs ranged between 6 – 21 % of the mass of the crab; males yielded more meat due to their larger chelae size. An experienced crab meat cleaner or mechanical removal may yield more meat from the crab, but in general males would be better to harvest due to their larger overall size and available meat.

Feeding behaviour and potential biofouling removal on aquaculture cages (Chapter 3)

The spider crabs were nocturnal, and peak movement occurred two to three hours after sunset. They consumed between 3 and 8.5 % bodyweight of algae per day, dependant on water temperature and sex. Although often considered functionally herbivorous, the crabs consumed fish when it was provided, suggesting like most other decapods they are opportunistic omnivores. When placed in confined enclosures on a commercial scale aquaculture cage, the crabs reduced fouling by 40% after two weeks, and up to 90% after a month. This was more effective than manual scrubbing by divers. There was no evidence of discriminatory feeding: the crabs reduced the percentages of all encrusting species on the cage. Survival of the confined crabs on the outside of the cage was 80%, while survival rates in longer term trials with crabs (3 to 8 months) inside the cage ranged between 50 to 55%. There was no significant decline in the BRIX (blood protein) levels in the crabs retrieved from inside the cages, indicating that the animals were able to obtain sufficient nutrients. Short term mortalities were likely associated with handling stress and transport, while mortalities occurring after 5 days were thought to be associated with hypoxia in the cage, as extreme level of fouling restricted water flow. These results indicate the potential for this species to be used as a biological control agent for biofouling on commercial aquaculture cages.

Potential use of this data for the Caribbean region

Currently information of population dynamics of spider crabs in The Bahamas is still scant, however this study does suggest that the crabs are fairly common and reach large sizes. More data need to be collected to determine if they are plentiful enough to support a widespread fishery. A mark-recapture study may be able to estimate the population of the spider crabs in a given area, but given the low recapture rates it may be easier to estimate the abundance using density and habitat data, and estimate the number of males and females per m^2 of habitat. An additional mark-recapture without translocation may provide better insight into the movement behaviour and abundance of the crabs.

Fisheries

The density of individuals on a given reef appears to be limited by available refuges. Females tend to return to the same crevice daily, while males frequent multiple crevices (Hazlett and Rittschof, 1975). This was also supported by my current study, where only marked female crabs were recaptured. The smaller males may have been competitively excluded by larger males on the coral patch reefs (Ramsay et al., 1997). That being said, no individuals were recovered from surrounding patch reefs, indicating longer or more widespread migration may have occurred.

What does the data from my thesis and work of others suggest about a potential fishery for spider crabs? Spider crabs are difficult to catch in regular baited pots because they are primarily herbivorous and thus hand collection would be the obvious method of capture. Because collection on SCUBA is prohibited, a small scale artisanal fishery by free diving may be sustainable, as some refuges like the deeper blue holes could not be fished. The fact that few crabs were recaptured on the patch reefs during the mark-recapture study suggests that they may not have a home range, and that migration could replenish stocks, or that they are very cryptic and this may also protect from over harvest. However additional mark-recapture work is required to verify this, as the crabs were translocated in the present study. Nevertheless, the problem with setting a catch rate is that we still do not know the growth rate and longevity of this species (Penn et al., 2019). I was not able to accurately assess the age or the population structure, but Adey and Farrier (1989) projected that “plate sized” male crabs (1000 g, 120 mm CW) could mature in around 360 days in some regions. However, even if spider crabs do grow this rapidly it remains to be determined whether the crab’s pubertal moult is also the terminal moult, as is seen in other crab species (Hartnoll et al., 1993). If this terminal moult does occur, managers would need to know how many years they live after this moult and the mating success, brood size during this time.

Aquaculture

The work within this thesis displayed the potential of the Caribbean spider crab for commercial aquaculture in the Caribbean region, especially in regards to removing biofouling from open ocean cages. Geodesic style cages used in offshore open ocean aquaculture may be the most applicable for this technique, as access to these sites may be more influenced by inclement weather than inshore sites. However, this is not to say that inshore sites may not benefit, as the crabs may reduce the need for costly mechanical cleaning activities at multiple sites. The spider crab showed a number of advantages that suggests it would be an effective species to remove biofouling on aquaculture cages:

1. The biggest advantage is the non-selective grazing, which has been a problem in many other studies and the main problem with biocontrol in general (De Nys and Guenther, 2009; Fitridge et al., 2012). The crabs appeared to reduce the amount of all epibionts on the cage netting without creating an environment of inedible species, which would subsequently flourish without competition from other biofouling species.
2. Unlike animals such as urchins (Lodeiros and García, 2004; Sterling et al., 2016; Zhanhui et al., 2014) spider crabs can move freely and rapidly around the cage. This allows coverage of large areas, and their dexterous claws can reach and clean both sides of the cage netting.
3. The spider crabs have the ability to remove the farmed fish mortalities. This is beneficial because it may reduce labour costs associated with carcass removal,

and be especially beneficial at offshore sites where carcass removal may be difficult in bad weather.

4. The crab is a large species which may be too big for farmed fish inside the cage to predate. Likewise since the species appears to prefer encrusting algae it would not be expected to attack the fish stock. Both of these would minimize any deleterious interactions.
5. The reduction in mechanical cleaning, whether *in* or *ex situ*, would not only reduce expenses (De Nys and Guenther, 2009), but also chemicals, further reducing costs to the farm and any deleterious environmental impacts.
6. Future fouling rates may be lower as larval release may not be triggered by crab grazing, unlike that which occurs during underwater washing (Carl et al., 2011). Additionally, crabs appear to do no damage to the netting, which reduces the creation of loose filaments for settlement (Carl et al., 2011; Geffen, 1979), as hydroids such as *E. larynx* use these to securely fasten themselves to the netting, making future removal difficult.
7. Because the fouling material is consumed by the crabs, less biological matter would be directly deposited on the seabed compared to commercial power washing (which simply dislodges and kills the organisms). This would lessen benthic nutrient inputs and subsequent bacterial breakdown (Bannister et al., 2016; Floerl et al., 2016; Reid et al., 2009).
8. Crabs could be "fattened up" and also sold. After collection from the wild or placement from a hatchery, crabs could be grown using the epibionts on cage netting as feed, and once reaching a marketable size, sold themselves as a separate stock.

9. Sustainable green aquaculture is being embraced, and consumers would pay more for such a product. Thus, biological control mechanisms would further reduce the environmental impacts of commercial farms. In addition they would enhance the sustainability of aquaculture by harmonizing cleaning and antifouling technologies through cost-effective biofouling management and emission reduction of cleaning wastes and chemicals (Floerl et al., 2016).

Future work

The crabs have marketable potential, as they have good meat yield (15 % BW) and are reported to taste like the Alaska King Crab *Paralithodes camtschaticus* (Rubino and Stoffle, 1990). With little monetary input, the crab may increase profits to commercial fish farmers through two methods. First, the farmers could simply maintain the crab stock as cleaners, this would allow a reduction in mechanical or chemical cleaning costs. Second, a market could be developed and the crabs sold at the same time as the fish product. With the current high demand for similar seafood products such as lobster and molluscs, and the increasing demand for sustainably produced food, this appears plausible.

In terms of biofouling, full scale trials at a working farm are required to ensure the species has minimal negative interactions or effects on the main aquaculture species, while efficiently removing fouling from the aquaculture cage. One example may involve commercial cobia *Rachycentron canadum* farms in Panama, where the two species both occur naturally. Crabs could be collected from wild stocks or spawned from gravid females and grown out to the cage mesh size to limit escapees. Prior to their placement on the sea cages, lab based trials could first monitor interactions between the cobia and the spider crabs. If no excessive negative interactions are found, crabs may be placed inside aquapens to remove fouling. Subsequent monitoring of fouling on the cage and control cages could determine whether fouling growth is indeed limited by crab grazing in a commercial setting. Additional experiments could determine the optimum number of crabs per cage to prevent fouling growth and limit aggressive interactions, and also address the potential aggregation issue to ensure the entirety of the cage can be cleaned.

Aside from biofouling removal, the crabs show their own aquaculture potential, as they have short, non feeding larval stages, and can be rapidly grown to “plate size” (1000 g, 120 mm CW). The crabs have successfully been spawned and grown to maturity previously (Adey and Farrier, 1989; Creswell et al., 1989; Tunberg and Creswell, 1991, 1988; Wilber et al., 1992; Wilber and Wilber, 1991). Experimental trials carried out in the late 1980s focused on low economic farming techniques for this species (Adey and Farrier, 1989). This involved placing a gravid female into a wooden sea-cage, following the hatch, the resulting juveniles were transferred into cages with coarser mesh as they increased in size. However, these methods resulted in high mortality due to the presence of small predators in the juvenile’s cages, excessive wave action during moulting, and aggressive interactions of juveniles (Adey and Farrier, 1989). The aquaculture industry has increased in leaps and bounds since these preliminary experiments were carried out, and current intensive hatchery systems would be highly applicable to development of this species. Such hatchery systems, using shallow water tables, floating PVC pipes, and a constant supply of water, have been shown to reduce larval mortality (Creswell et al., 1989; Tunberg and Creswell, 1988). Juveniles could then be moved to a vertical farm using recirculating or flow through methods (Shelley and Lovatelli, 2011; Tavares et al., 2018). The outflow of water, high in waste nitrogen, could be utilized to grow turf algae, filtering the water and providing a source of food for the crabs which could be rotated into the tanks on small frames. This method could be used to produce both individual crabs for market, and crabs for biofouling removal.

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