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The Influence of Habitat Quality on the Community Structure, Distribution Pattern, Condition, and Growth of Coral Reef Fish: A Case Study of Grunts (Haemulidae) from Antigua B.W.I, A Small Island System

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UNIVERSITY OF MIAMI

THE INFLUENCE OF HABITAT QUALITY ON THE COMMUNITY STRUCTURE, DISTRIBUTION PATTERN, CONDITION, AND GROWTH OF CORAL REEF FISH: A CASE STUDY OF GRUNTS (HAEMULIDAE) FROM ANTIGUA B.W.I, A SMALL ISLAND SYSTEM

By

Sherry Lynette Constantine

A DISSERTATION

Submitted to the Faculty
of the University of Miami
in partial fulfillment of the requirements for
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A dissertation submitted in partial fulfillment of
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Structure, Distribution Pattern, Condition, and Growth
of Coral Reef Fish: A Case Study of Grunts
(Haemulidae) from Antigua B.W.I.,
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The goal of this research was to determine the relative quality of near shore marine areas by investigating their influence on Haemulidae community structure, distribution pattern, condition, and growth. Habitat was defined at the small spatial scale of individual habitat types such as seagrass beds, mangroves and coral reefs, and at the broader spatial scale of the interconnection of these individual habitat types within a mosaic (IHM). Ten spatial, biotic and abiotic parameters (percentage coverage of sand, mangroves, hard substrate, and seagrass, turbidity, pH, salinity, temperature, average depth, and predator density) were investigated. These environmental characteristics acted as proxies for the quality of IHMs. The major findings of the research were: (1) IHMs and discrete habitat types in tropical marine systems are not always equal in quality. Further, the highest quality IHMs/discrete habitat types have the critical resources whether spatial, abiotic or biotic, at the optimum levels needed by organisms to carry out their critical life functions; (2) IHMs of the highest quality contain all the discrete habitat types needed by organisms to carry out their life processes in a spatial arrangement that maximizes energy savings; (3) IHMs can be of high quality in the absence of one habitat type, if this habitat type is replaced by another that can take on its ecological role; and (4)

the percentage cover of hard substratum and seagrass, temperature, and predator density have a big impact on Haemulidae distribution pattern, community structure, condition and growth. In addition, this research highlighted some of many characteristics of benthic habitats such as type and configuration that should be included in the design of Marine Protected Areas for the effective management of fisheries resources. Effective Marine Protected Areas should have (1) large overall area with benthic habitat types of high quality; (2) spatial configurations with short distances (corridors) between habitat types; (3) spatial arrangements that place all individual habitat types in connection with all other habitat types so that energy expenditure in moving among habitat types is reduced; (4) habitats with high structural complexity; and (5) the inclusion of all the habitat types needed by focal organisms to carry out their life processes, or surrogate habitat types that can take on the role of ones that are absent.

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CHAPTER ONE

RESEARCH CHALLENGES IN UNDERSTANDING THE RELATIONSHIP BETWEEN HABITAY QUALITY AND THE COMMUNITY STRUCTURE, DISTRIBUTION PATTERN, CONDITION, AND GROWTH OF CORAL REEF FISH

Introduction to the Concept of Habitat

A habitat is “an area with a combination of resources (like food, shelter, water), and environmental conditions (temperature, precipitation, presence or absence of predators, and competitors) that promotes occupancy by individuals of a given species (or population) and allows those individuals to survive and reproduce” (Morrison et al. 2006). The exact terminology used to describe habitat types within marine coastal systems depends on the geographic location and the classification scheme being considered. Due to the benefits and challenges of the numerous habitat classification schemes available for use by ecologists there is no one that is universally accepted (Lund and Wilbur 2007). However, the majority of marine habitat classification schemes are defined down to the scale of an individual habitat type such as mangroves, soft bottoms (seagrass and bare sand), and hard substrate (nearshore and offshore coral reefs, reefal hard bars etc.) (Allee et al. 2000, Brown 2002, Madley 2002, Madden et al. 2005, Kutcher et al. 2005). Each of these habitats has specific spatial relationships to adjacent habitats. Marine organisms, particularly fish, have certain fundamental requirements of their habitats that must be fulfilled for them to meet their basic life processes of growth and reproduction. Habitats that satisfy those requirements can be considered essential fish habitats and have been defined by the US government as “the substrates and waters necessary for fish to spawn, breed, and feed or grow to maturity and include all the habitats used at any time during the life cycle of the organism" (Lindeman et al. 2000, Rosenberg et al. 2000). Thus, the definition and delineation of essential fish habitats begins first with the consideration of single habitat types, and then broadens its scope to include all areas contributing to the essential life processes of the organisms in question. The process of designating an area as an essential fish habitat considers both the ecological roles of fish species within the environment and their interactions with other components in the ecosystem (e.g. predator prey relationships and nutrient regeneration) (Hall et al. 1997, Rosenberg et al. 2000).

Marine habitats are not all equivalent in terms of their quality. Quality refers to the ability of a habitat to provide conditions appropriate for individual and population persistence. It can be viewed as a continuous variable such that habitats can range in quality form low to medium to high (Hall et al. 1997). When compared with other marginal environments, high quality habitats provide the conditions necessary for successful survival and reproduction of fish over long periods (Fretwell and Lucas 1970, Rosenzweig 1981, Able 1999, Werner 2002, Necaise et al. 2005, Morrison et al. 2006). Marginal habitats, on the other hand, are similar to high quality habitats in that they promote occupancy and support individuals. These benefits last for only short or intermittent periods of time, however, and the survival and reproduction rates of the individuals using these areas are low (Morrison et al. 2006). In trying to determine the quality of a habitat and how it accrues fitness benefits to the organisms using it, a number of habitat-specific factors must be considered (Table 1.1). In addition, it must be recognized that habitats do not exist in isolation of other habitats, and no one habitat type can provide all the essential requirements of the organisms using it. Therefore, in a similar manner to the definition of an essential fish habitat, the definition of a high quality habitat for a marine organism must include all the habitat types that occur in close association and work together to provide growth, condition, reproductive, and survival benefits to that organism. This combination of and connection among habitat types can be labeled as the “interconnected habitat mosaic” (IHM) (Sheaves 2005). The characteristics of the IHM can be considered a key determinant of the quality of marine systems. In addition to habitat specific factors of the IHM, the inherent abiotic characteristics (e.g. temperature, pH, salinity, and turbidity) within the IHM, also contribute to its quality.

The Interconnected Habitat Mosaic

The concept of the “interconnected habitat mosaic” (IHM) (Sheaves 2005) rests on the premise that marine organisms promote linkages between habitats in terms of energy flow and nutrient exchange due to their movements between these discrete areas to carry out their life functions (Ogden and Zieman 1977, Beck et al. 2001, Gillanders et al. 2003). Only recently has the linkages between adjacent habitats for coral reef associated fish species been elucidated (Nagelkerken at al. 2000a, 2000b, Adams and Ebersole 2002, Cochert de la Morinière et al. 2002, Dorenbosch et al. 2004, Mumby et al. 2004). These movements can occur at both long and short temporal scales. Short-duration temporal activities include daily feeding migrations (Hobson 1965, Ogden and Ehrlich 1977, McFarland et al. 1979, Helfman et al. 1982, Tulevech and Recksiek 1994, Beck et al. 2001, Beets et al. 2003, Cochert de la Morinière et al. 2003, Nagelkerken and van der Velde 2004a, 2004b), while longer temporal-scale activities include spawning migrations (Smith 1972, Zeller 1998, Claro & Lindeman 2003) and ontogenic habitat shifts

(Longhurst and Pauly 1987, Holland et al. 1993, Appledoorn et al. 1997, 2003, Lindeman et al. 2000, Meyer et al. 2000, Adams and Ebersole 2002). Habitat connectivity may be the outcome of pre-settlement and post-settlement mechanisms. Pre-settlement connectivity entails a combination of larval behavior such as swimming, chemical detection and performance, and oceanographic conditions such as current patterns, eddies and waves, which lead to inshore retention and off-shore advection of larvae (Roberts 1997, Cowen et al. 2000, Sponaugle et al. 2002, Mora and Sale 2002). Post-settlement activity entails physiological and biological changes in juveniles that settle in habitats that are different from adult habitats, and the subsequent movement into adult areas with ontogeny (Appeldoorn et al. 1997, Lindeman et al. 2000, Nagelkerken et al. 2000a, 2000b, Dahlgren and Eggleston 2000, Cochert de la Morinière et al. 20002).

The benefit of the IHM to the growth and survival of fish species depends on habitat-related factors, mosaic-related factors, and species-related factors (Table 1.1). Although the numerous characteristics that can be used to describe IHMs furnish each with its own unique properties, the potential benefits of each habitat within the IHM to the organisms that live and use them are comparable. Similar habitats perform equivalent roles across ecosystems such that seagrass beds within IHMs may have different spatial coverage, but still offer the same benefits; that of a nursery habitat that provides shelter against predators (Adams and Ebersole 2002, Parrish 1989) and an abundance of food (Odum and Heald 1972, Carr and Adams 1973, Ogden and Zieman 1977, Laegdsgaard and Johnson 2001). With this in mind, there should be an optimum configuration of habitats within IHMs that maximize growth rates and minimize energy expenditures and predation exposure. There are many ways to spatially arrange habitats within mosaics, however, any arrangement that minimizes the number of corridors and travel distances between feeding, resting and spawning areas will accrue growth and survival benefits to the organisms using them and thus, be of high quality (Figure 1.1).

The quality of an IHM is also influenced by the combination of abiotic environmental conditions (e.g. temperature, turbidity, pH, and salinity) present (Necaise et al. 2005). These abiotic factors are intrinsic characteristics of marine environments and have potentially tremendous effects on the growth and survival rates of organisms (Brett 1956, 1969, 1971, 1979, Elliot 1994, Jobling, 1994, Mommsen 1998, Wooton 1990) (Table 1.2). Temperature is the most critical variable in the physiological ecology of tropical marine organisms; however, other abiotic parameters such as turbidity, pH, and salinity play an important role (Livestad et al. 1980, Rosseland et al. 1980, Elliott 1994, Lambert et al. 1994, Jobling 1994, Woo and Kelly 1995, Dutil et al. 1997, Bash et al. 2001, Werner 2002, Sutherland and Meyer 2007). On a physiological level, an imbalance in the levels of any of these abiotic factors can cause modifications to the standard metabolic rate, total food intake and food conversion efficiency of fish (Gregory and Northcote 1993, Jobling 1994, Lambert et al. 1994, Woo and Kelly 1995, Buckel et al. 1995). On a behavioral and social level, imbalances in any of the abiotic environmental parameters may affect the distribution and movement (foraging efficiency and predator avoidance maneuvers) of juvenile and adult fishes (Malloy and Targett 1991, Gibson 1994) as they strive to stay within optimum parameter levels (Browder et al. 2002, Lugendo et al. 2007). Coral reef fish are particularly susceptible to localized changes in the abiotic conditions of their environments, because they generally remain near their “home” reefs, and usually undergo very low rates of large-scale movement (Springer and McErlean 1962, Moe 1966, Tulevech and Recksiek 1994, Kendall et al. 2003).

Habitat Quality Measures

Historically, ecologists have relied on the use of presence/absence and density estimates to measure habitat quality in terrestrial (e.g. wolves (Mladenoff and Sickley 1998), birds (Sherry and Holmes 1996), monkeys (Peres 1997), rodents (Dooley and Bowers 1998) and butterflies (Matter and Roland 2002)), and aquatic (e.g. dolphins (Fiedler and Reilly 1994), salmon (Lawson 1993), Caribbean spiny lobster (Lipcius et al. 1997), diatoms (Kutka and Richards 1996), coral reef fishes (Sutton 1985, Chapman and Kramer 1999, Shima and Osenberg 2003) and tunas (Bigelow et al. 2002)) organisms. Within the marine realm, this technique is suitable for fish because they respond to many physical and biological aspects of the habitat which in turn determines their diversity, distribution, and density (Öhman and Rajasuriya 1998). These estimates rest on the premise that the distribution of mobile organisms across an area can be interpreted in terms of their responses to habitat heterogeneity (Van Horne 1982), and can potentially be an accurate reflection of the underlying differences in quality among habitats (Bélanger and Rodríguez 2002). Considering that an IHM is a unit made up of different interacting parts of different quality, individuals will vary their distribution within each IHM so that they can exploit the highest quality resources (including food), while remaining within optimum levels of environmental parameters, and within acceptable levels of predation risk (Odum and Heald 1972, Werner and Gillian 1984, Jones 1991, Beck et al. 2001). Thus, it is expected that IHMs of high quality will support large populations of marine organisms at high densities. A comparison of the community patterns and distribution of fish between and within IHMs can reveal their relative quality. Overall, distribution and density estimates are useful community based parameters to contrast habitat quality between IHMs because data collection procedures are simple in concept, easy to carry out, can be used effectively over broad geographic scales, and are relatively cost effective.

Individual fish growth can be argued to be a better gauge of habitat quality than density estimates. First, because it is more sensitive to environmental perturbations and second, it is a better indicator of the success of a fish within its environment (Brett 1979, Elliot 1994, Jobling 1994, Mommsen 1998, Wooton 1990). Growth can be defined as an increase in the energy content of an organism's body as a result of food intake (Brett 1979, Jobling 1994) and is strongly associated with both biotic and abiotic characteristics of the environment (Brett 1979, Claro and García-Arteaga 2001). The quality of a habitat confers the benefits of enhanced growth and survival, and population persistence (Jobling 1994, Hall et al. 1997). At the level of the individual, fast growth offers a selective advantage over slower growing conspecifics, because it allows fish to quickly leave size classes that are vulnerable to predation, thereby reducing the probability of being eaten (Werner and Gillian 1984, Jones 1991, Werner 2002). At the population level, fast growth rates during early life stages have a great impact on fisheries productivity (Houde 1987). Ideally then, fish should preferentially choose habitats that allow for maximized growth, and fish growth is a powerful tool that can be used to investigate habitat quality in IHMs. It can be predicted that IHMs that contain high levels of high quality resources, and low predator numbers (which translates to a reduction in energy losses due to predator avoidance maneuvers) should support faster growth rates and bigger individuals. The growth indices that are commonly used in ecological studies are weight-at-length, condition and length-at-age measurements (Francis 1988, Schirripa and Burns 1997, Phelan et al. 2000, Crabtree et al. 2002, Choat et al. 2003, Le Pape et al. 2003), the determination of energy content of tissues (Sullivan and Smith 1982, Jobling 1994), and the ratio of RNA to DNA (Buckley and Bulow 1987, Buckley et al. 1999, Imsland et al. 2002, Smith and Buckley 2003, Tardif et al. 2005). All these methods can provide useful information on the relative quality of IHMs; however, the measurement of weight-at-length, condition and length-at-age are conceptually simple, cost effective methods, and were used in the research described below.

Research Design

The goal of the present research was to investigate the influence of habitat quality on the community structure, distribution pattern, condition, and growth rates of coral reef fish in tropical coastal marine systems. Tropical marine organisms simultaneously exploit a number of habitats including mangroves, seagrass beds, and coral reefs to carry out their life functions (Ogden and Zieman 1977, Appledoorn et al. 1997, Zeller 1998, Lindeman et al. 2000, Nagelkerken et al. 2000a, 2000b, Adams and Ebersole 2002, Cocheret de la Morinière et al. 2002, 2003, Dorenbosch et al. 2004, Nagelkerken and van der Velde 2004a, 2004b). The relative quality of these habitats, in terms of the benefits provided to the fish using them, can be determined by comparing their contributions to fish community structure, distribution pattern, condition, and growth rates (Rosenzweig 1981, Werner, 2002).

Data on the community structure and distribution pattern of one coral reef fish family, Haemulidae, was collected at four IHMs around a small tropical island. It was predicted that IHMs of high quality would have individuals with higher densities and biomass values of Haemulidae than IHMs of lower quality. These fish community parameters were estimated from data collected during underwater visual surveys. The underwater visual survey is a simple survey method that enabled censuses to be conducted at the four IHMs, a number of replications to be completed within each IHM (since it is a non-destructive technique), enabled the researcher to select specific species, required only one worker, was relatively rapid and inexpensive, and allowed comparisons to be made among IHMs (Fowler 1987, Bellwood and Alcala 1988). Data was also collected on growth rates and condition of individual fish. It was predicted that fish growth rates and condition would be related to habitat quality. Therefore, organisms in superior habitats would have, faster growth rates, individuals that are larger at a given age, and healthier fish. The growth measures employed were weight-at-length and age-at-length relationships, and mean daily growth rates. These growth indices were selected because they allowed direct determination of individual success, were sensitive to environmental perturbations, and were easily measured (Brett 1979, Jobling 1994, Mommsen 1998, Claro and García-Arteaga 2001, Le Pape et al. 2003).

To differentiate the major habitat types within each IHM, the classification scheme proposed by Madden et al. (2005) (Table 1.3 and Appendix I) was used as a guide. This habitat classification scheme was developed for estuaries, coasts and oceans in the United States. It is applicable to marine ecosystems in other countries, was consistent with regional, national and international standards (Madden et al. 2005), and attempted to combine the best elements of previous classification schemes that have been proposed for marine ecosystems (e.g. Cowardin et al. 1979, Dethier 1992, Greene et al. 1999, Allee et al. 2000, Madley 2002). It assisted with the delineation of habitat types within mosaics, such that differences between the mosaics could be diagrammatically represented, and then used during the survey effort to ensure that all component habitat types within mosaics were adequately surveyed.

In the design of this study, special attention was paid to the selection of both the study sites and the focal species. The sites selected had to meet the following minimum requirements: 1) be located in a tropical marine area; 2) have individual habitats types of approximately equal quality within mosaics; 3) have a number of contrasting IHMs; and 4) have IHMs that were far enough away from each other that the possibility of the study species migrating between these sites approximated zero (Table 1.4). It was imperative that individual habitat types within mosaics be of approximately equal quality so that realized differences in the habitat quality measures would reflect mosaic rather than individual habitat differences. Therefore, one tropical island was selected for this research and the assumption that each habitat type around this island was of equivalent quality was made. The selection of mosaics from different countries would mean that a large number of factors that need not be considered when only one country is used would have to be incorporated into analyses. This would make the analyses more complicated and less useful in detecting the factors contributing to the differences in habitat quality between mosaics.

The small Eastern Caribbean Island of Antigua and its surrounding marine habitats met the aforementioned criteria (Figure 1.2). This island is located in the Lesser

Antillean island chain between 17º 00' N and 17º 44' N and 61º 21' and 61º 55' W. It has a total land area of 280 km^2. Antigua and its sister island Barbuda sits on a shelf approximately 3,568 km^2 in area. The island has an intricate coastline which is deeply indented and fringed by nearshore and offshore coral reefs, shoals, rock islands, and sand bars (CCA 1991). The island is almost completely surrounded by coral reefs, 11% of the coastline is fringed by mangroves, and it has seagrass beds that cover large areas. Thus, there were a large number of suitable research areas that could be selected. This research was carried out at four sites around Antigua: Cades Reef (CAD) located on the southwest coast; around Guiana Island (GI) located on the northeast coast; the north coast from Boons Point to Shoal Point (JB); and Willoughby Bay (WILL) located on the southeast coast (Table 1.4 and Figure 1.2). Each site was carefully selected so that the design of its IHM differed from the others in terms of its spatial, physical, and biotic characteristics. As Figure A1.2 (Appendix I) illustrates, the four selected IHMs all have the same constituent habitats, however, the arrangement of habitat types within each IHM is unique.

Habitat is organism specific (Hall et al. 1997), such that the habitat of a bluefin tuna is not the same as that of a white grunt. Therefore, any study of IHMs must be tailored to a specific organism, family or guild that depends on that IHM to provide essential goods and services. The selected fish species had to meet the following minimum requirements: 1) perform daily migrations between constituent habitats of the interconnected habitat mosaics to carry out some critical life function; 2) undergo migrations of distances long enough to transverse habitat corridors within IHMs but not so long as to travel between IHMs; 3) at some point could be found in all of the habitats contained within the interconnected habitat mosaics; 4) exhibit significant growth rates during a life stage that could be easily measured; 5) have food requirements that could be easily met by researchers; and 6) is distinguishable from congeners in the field.

Individuals from the grunt (Haemulidae) family proved to be an ideal focal species for this research. Members of the grunt (Haemulidae) family have been implicated as important contributors to energy exchanges between coastal habitats (Ogden and Zieman 1977, Meyer and Schultz 1985, Hemminga et al. 1994, Duarte 2000). They are secondary consumers that belong to the feeding guild carnivores, and have diets composed of a large variety of invertebrates (mainly crustaceans, mollusks, polychaetes, and echinoderms) and fish (Claro and García-Arteaga 2001, Cocheret de la Morinière et al. 2003). They are typically nocturnal feeders that generally form large inactive schools at their daytime resting sites of coral reefs. At night, they migrate to seagrass beds and sand flats to feed (Hobson 1965, McFarland et al. 1979, Helfman et al. 1982, Rooker and Dennis 1991, Tulevech and Recksiek 1994, Burke 1995, Beets et al. 2003). For many years, fisheries biologists predicted the dispersal distance of juvenile grunts to range from tens to hundreds of meters (Ogden and Ehrlich 1977); however, Kendall et al. (2003) demonstrated that the likelihood of juvenile grunts being found at hard bottom sites in excess of 300 m from soft bottom was zero. Further, tagged adult *Haemulon plumieri* were used to confirm migrations of hundreds of meters between habitats (Tulevech and Recksiek 1994). Like many other tropical marine fish species, grunts are characterized by short life spans and relatively high growth rates, so much so that by the second year of life, 35-50% of maximum size can be reached (Claro and García-Arteaga, 2001, Potts and Manooch 2001, Murie and Parkyn 2005, Araújo and Martins 2007).

A number of studies completed to date, have relied on the use of single or two adjacent habitat types (Nagelkerken et al. 2000a, Nagelkerken and van der Velde 2004a, 2004b, Ogden and Zieman 1977), and not considered the implications of how all the habitats that are used by an organism to carry out its life functions, contribute to the growth and survival of that organism, and influences its distribution within the environment. In addition, few studies have attempted to study fishes from mangroves, seagrass beds, and shallow reefs simultaneously (Nagelkerken at al. 2000, Cocheret de la Morinière et al. 2002), and some studies used more than one methodology (e.g. underwater visual surveys and fish collection) to compare these habitats (Thayer et al. 1987, Acosta 1997). Further, even fewer studies have focused on studying the fish communities on Caribbean islands (most of them focus on the coasts of continents), and have attempted to investigate these communities in mangroves seagrass beds and coral reefs simultaneously (Nagelkerken at al. 2000a, Cocheret de la Morinière et al. 2002). This research aimed to extend the studies completed to date, by studying Haemulidae populations along a mangrove-seagrass-coral reef continuum, investigating contrasting IHMs around a small tropical island, and using the same sampling methodology in all habitat types.

Research Objectives

At present, no comprehensive studies have been undertaken that integrate a number of different measures to help determine the influence of habitat quality on the community structure, distribution pattern, growth, and condition of fish populations in tropical marine systems. Thus, the overarching aims of this research were to investigate habitat quality by determining how: (a) habitat variables in interconnected marine habitats affect Haemulidae community structure and distribution pattern; (b) habitat quality influences the growth and condition of *Haemulon plumieri* (Lacepède 1801); and (c) temperature as an indicator of habitat quality, influences the growth of juvenile *H. plumieri*.

The aim of Chapter 2 was to investigate IHM quality by using a number of spatial, abiotic, and biotic environmental characteristics (percentage coverage of sand, mangroves, hard substrate, and seagrass, turbidity, pH, salinity, temperature, average depth, and predator density) that acted as proxies for the quality of each IHM. The study assessed the community structure and distribution pattern of Haemulidae (density, length frequency distribution, biomass, and ratio of juveniles to adults) along an inshore-mid shore gradient. The study focused on three IHMs that had a mangrove-seagrass-coral reef continuum, and one other IHM that had no mangroves but large areas of seagrass and coral reef. The specific questions investigated were: 1) are there differences in the Haemulidae community structures and distribution patterns within IHMs; 2) are there differences in the environmental characteristics of IHMs; 3) is the distribution of Haemulidae across the IHMs related to the environmental variables investigated; 4) how is the distribution of Haemulidae related to those environmental variables; and 5) which IHM had the highest quality based on Haemulidae community structure and distribution patterns?

The aim of Chapter 3 was to compare the quality of three IHMs around Antigua using the parameters weight-at-length, condition, and length-at-age of *H. plumieri*, as proxies for the quality of these areas. The prediction here was that high quality IHMs would be inhabited by heavier *H. plumieri* at a particular length, longer *H. plumieri* at a particular age, and *H. plumieri* in better condition than lower quality IHMs. Thus, in terms of environmental and habitat characteristics, the highest quality IHMs would potentially have feeding (soft-bottom) habitats that cover large areas, short traveling distances between feeding and resting habitats (resulting in reduced energy expenditure during feeding migrations), and levels of abiotic parameters that support maximum growth and consumption rates and reduced metabolic rates.

The aim of Chapter 4 was to investigate experimentally, the influence of the abiotic environmental variable temperature on the growth rates of *H. plumieri*. More specifically, this study used the temperature regimes present in four different habitats (seagrass beds, mangroves, coral reefs, and an artificial jetty) as proxies for habitat quality, to determine how *H. plumieri* growth rates are affected by variations in habitat quality. Four different habitats were selected to ensure that there would be noticeable differences in the temperature regimes experienced by caged *H. plumieri*. The experiment was carried out in the field so that growth rates under somewhat natural conditions could be investigated. The questions addressed were: 1) are there differences in the mean daily temperatures experienced by *H. plumieri* caged in each habitat; 2) are there differences in the daily T_{max} - T_{min} experienced by the *H. plumieri* caged in each habitat; 3) are there differences in mean growth rates among the different habitats investigated; 4) is there a relationship between growth rates and mean daily temperatures experienced by the *H. plumieri*; and 5) is there a relationship between growth rates and daily T_{max} - T_{min} values experienced by *H. plumieri*?

In Chapter 5, the major conclusions of Chapters 2, 3 and 4 were discussed. This chapter highlighted the importance of habitat quality to the community structure, distribution pattern, condition, and growth of Haemulidae in Antigua, the Caribbean, and by extension tropical marine systems. In addition, it demonstrated how the results of the studies completed, can provide a better comprehension of the ecological interrelationships among mangroves, seagrass beds, and coral reefs, and how the knowledge of these relationships is crucial for the implementation of marine protected areas.

Table 1.1: Some of the habitat-related, mosaic-related, and species-related factors that influence the distribution, condition, and growth of fish in marine environments.

Habitat-Related Factors	**Mosaic-Related Factors**	**Species-Related Factors**
1. Protection from predators	1. Number of composite habitats	1. Home range size
2. Availability of food (spatial distribution and abundance)	2. Nature/Type of Composite Habitats	2. Physical ability to move between habitats and escape predators (physiological or morphological changes e.g. photon receptor sensitivity, development of gonads, development of swimming or navigation abilities)
3. Presence of predators	3. Aerial extent of each habitat	3. Importance of the services provided by different habitats to survival and reproduction
4. Distance from settlement areas	4. Distance separating habitats	4. Individual Size
5. Distance from spawning areas	5. Number of corridors between habitats	5. Ontogenetic changes in feeding strategy (e.g. from zoobenthivory to piscivory)
6. Seasonal changes or gradients in physical environmental factors (e.g. turbidity, temperature, salinity, depth)	6. Spatial arrangements of habitats	
	7. Presence of predators	

Table 1:2: The physiological effects on fish, of imbalances in the abiotic environmental parameters (temperature, turbidity, pH, and salinity).

Parameter	Effects	References
Temperature	Increased metabolic rate	Jobling 1994
	Reduced ingestion rate	
	Reduced growth potential	Malloy & Targett 1991
Turbidity	Impairs gill function Abrasion of gill tissue Respiratory impairment Osmoregulatory impairment	Bash et al. 2001, Sutherland & Meyer 2007
	Limits fish vision which can interfere with predator avoidance and foraging efficiency	Berg & Northcote 1985, Gregory & Northcote 1993, Vogel & Beauchamp 1999, Miner & Stein 1996, Merger et al. 2006
pH	Disturbance of the equilibrium between loss and active uptake of ions Decline in body Na^+ Cl^- content	Leivestad et al. 1980, Rask & Virtanen 1986, Vuorinen et al. 1990
	Recruitment failure (spawning failure, delayed spawning, fertilization difficulties, mortality of eggs or fry)	Rosseland et al. 1980, Vuorinen et al. 1992, Werner 2002
Salinity	Reduction in standard metabolic rate	Woo & Kelly 1995, Dutil et al. 1997
	Reduction in total food intake	Dendrinos & Thorpe 1985, Lambert et al. 1994, Buckel et al. 1995, Peterson-Curtis 1997
	Reduction in food conversion efficiency	Arunachalam & Reddy 1979, Lambert et al. 1994, Likongwe et al. 1996
	Balance of hormones involved in metabolism	Bluf & Payan 2001, Handeland et al. 2000

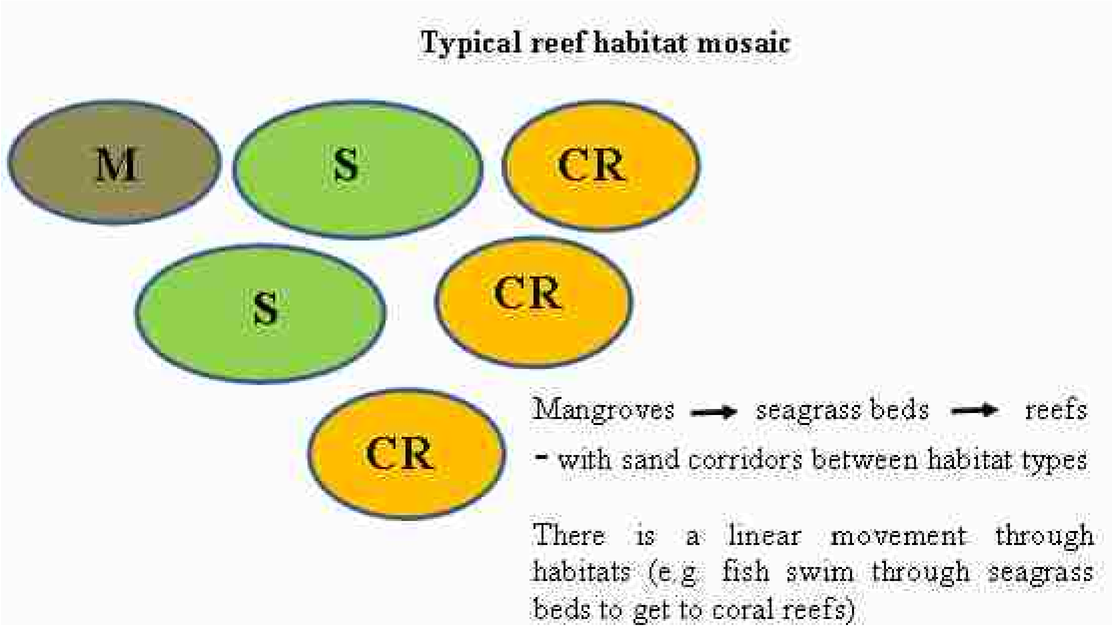
Table1.3: The Coastal and Marine Ecological Classification Standard (CMECS), developed by NatureServe, NOAA and other US national partners, for estuaries, coasts and oceans of North America (Madden et al. 2005). This scheme was used as a guide for classification of the constituent marine habitats in each IHM.

Level	Characteristics	Scale
1 - Regime	Differentiated by a combination of salinity, geomorphology and depth, and is organized into five categories: estuarine, freshwater-influenced marine, nearshore marine, neritic and oceanic	$10km^2$ to > $1,000km^2$
2 - Formation	Relatively large physical structures formed by water (currents) or substrate (islands)	$10,000m^2$ to $100km^2$
3 - Zone	Distinguishes between water column, littoral or sea bottom	$100m^2$ to $10,000km^2$
4 - Macrohabitat	Large physically complex structures that typically contain several habitats	$100m^2$ to $1,000m^2$
5 – Habitat	A specific combination of physical (i.e. grain size) and energy characteristics that create a suitable place for colonization or use by biota	$1m^2$ to $100m^2$
6 - Biotope	Identified by characteristic biology associated with a specific habitat	$1m^2$ to $100m^2$

Table 1.4: The constituent habitat types of the IHMs studied, and the approximate shortest distance (calculated from Google Earth) separating each IHM that would have to be transversed by Haemulidae, to undergo daily or seasonal migrations among IHMs. Cades Reef (CAD); Guiana Island (GI); Boons Point to Shoal Point (JB); Willoughby Bay (WILL)

IHM	**Location**	**Constituent Habitats**	**Shortest Distance between IHMS (km)**			
			CAD	**GI**	**JB**	**WILL**
CAD	Southwest	Mangroves, Seagrass, Coral Reefs	------	35.34	22.74	14.19
GI	Northeast	Mangroves, Seagrass, Coral Reefs		------	7.58	16.44
JB	North	Seagrass, Coral Reefs			------	27.14
WILL	Southeast	Mangroves, Seagrass, Coral Reefs				------

Figure 1.1: Two possible arrangements of habitat types within IHMs.

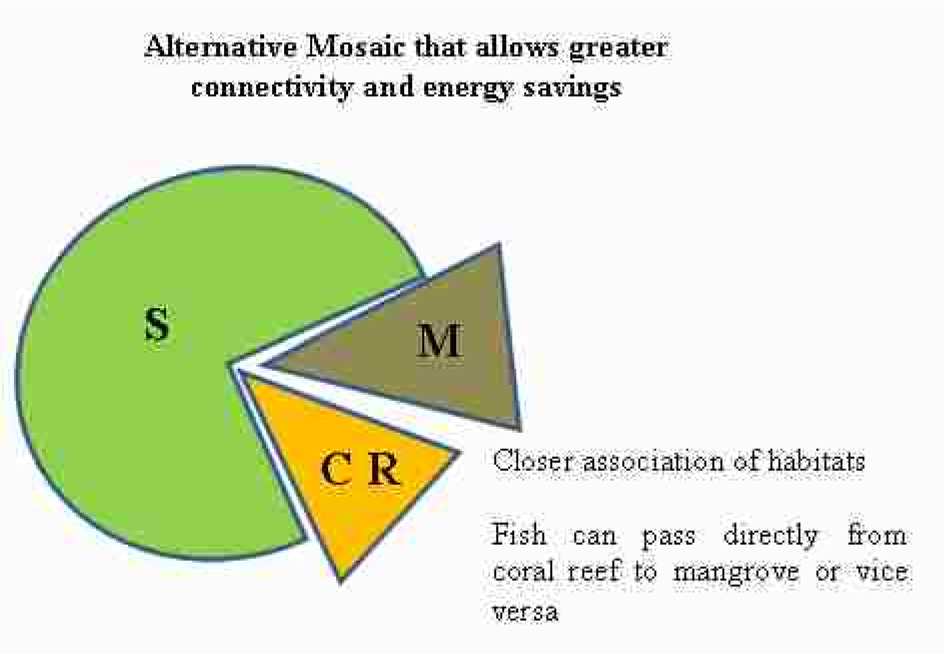


Typical reef habitat mosaic

Mangroves → seagrass beds → reefs

- with sand corridors between habitat types

There is a linear movement through habitats (e.g. fish swim through seagrass beds to get to coral reefs)

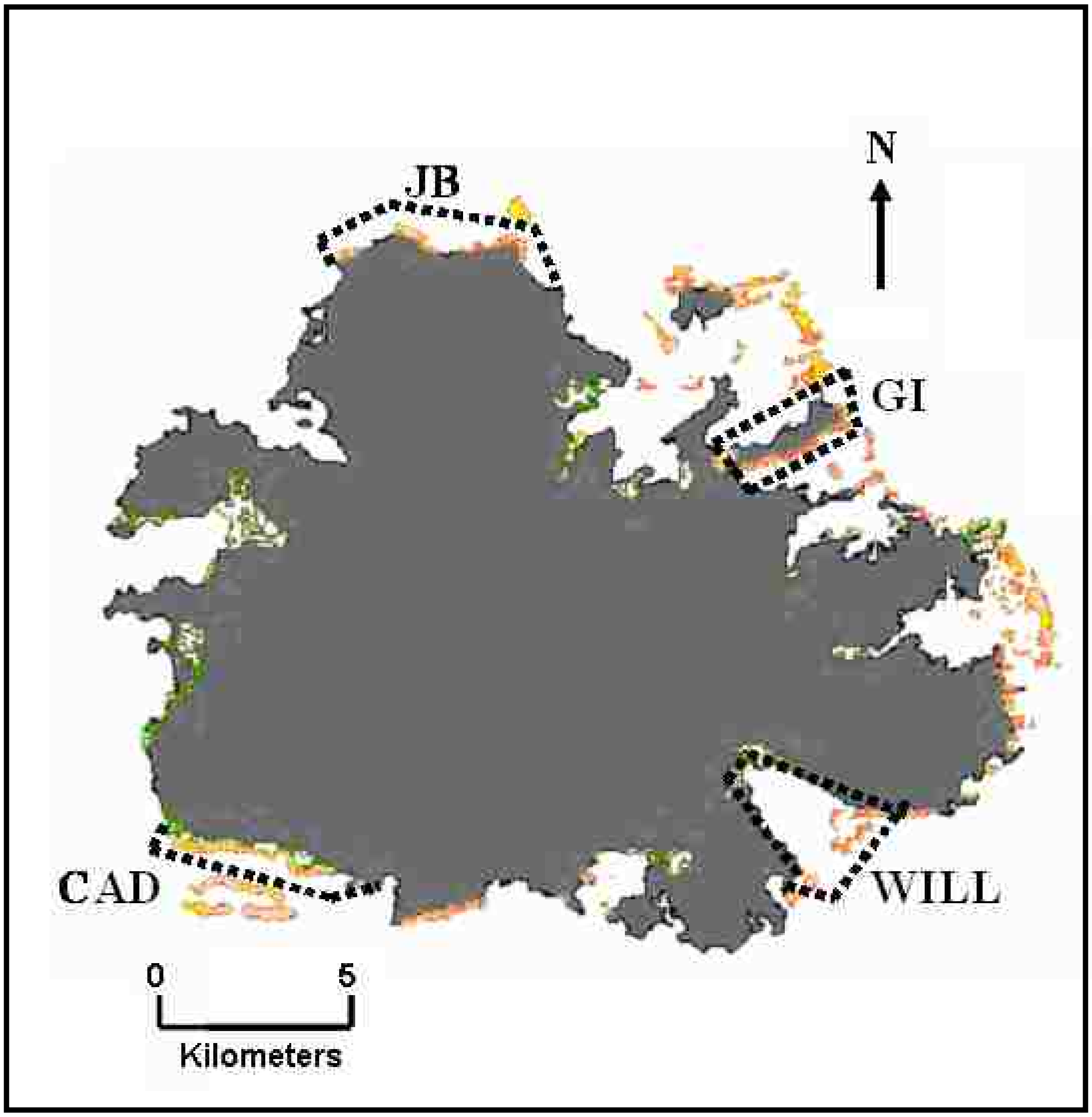


Alternative Mosaic that allows greater connectivity and energy savings

Closer association of habitats

Fish can pass directly from coral reef to mangrove or vice versa

Figure 1.2: Map of Antigua showing the four IHMs used in this study (Source: NCORE). Cades Reef (CAD); Guiana Island (GI); Boons Point to Shoal Point (JB); Willoughby Bay (WILL). Green areas represent mangroves and pink areas represent coral reefs.



CHAPTER TWO

INFLUENCE OF HABITAT QUALITY ON GRUNT (HAEMULIDAE) COMMUNITY STRUCTURE AND DISTRIBUTION PATTERN

Background

The habitat of an organism is the area that provides the resources necessary for survival, which include migration and dispersal corridors (Hall et al. 1997). Shallow-water tropical marine fishes do not remain in the same benthic habitats throughout their entire life cycles (Werner and Gillian 1984, McNamara and Houston 1986, Ludwig and Rowe 1990). In fact, most fish species do not even stay in one habitat for extended periods of time because of home range expansion with ontogeny, the need to migrate to search for food and mates, and the need to avoid predators (McFarland et al. 1979, Quinn and Ogden 1984, Helfman et al. 1982, Helfman 1993, Warner 1995, Appledroon et al. 1997, 2003, Dahlgren and Eggleston 2000, Beck et al. 2001, Beets et al. 2003, Claro & Lindeman 2003, Gillanders et al. 2003). During migrations, fishes often cross several benthic habitat types. Such movement is commonly observed in small tropical island systems, where limited coastal shelf areas comprise a combination of benthic habitat types. Consequently, in these systems it is highly unlikely that the habitat type where a fish is observed is its exclusive habitat providing all the resources critical for growth and survival. In addition, the distribution of reef-fish among habitats may be related either to ecological interactions, such as differential survival among habitats as a result of inter and intra-specific competition and predation (Hixon 1991, Roberts 1996), or to behavioral responses to preferred habitat based on resource availability (Jones 1991) and the need to reproduce (Robertson 1991). The movement of organisms between habitats provides growth, reproductive and survival benefits to migrating individuals, and it also benefits the entire ecosystem by translocating nutrients and energy (Ogden and Zieman 1977, Meyer and Schultz 1985, Hemminga et al. 1994, Duarte 2000). Such connectivity among habitats because of movement of organisms has been described and documented by a number of authors (McFarland et al. 1979, Quinn and Ogden 1984, Helfman et al. 1982, Helfman 1993, Appledroon et al. 1997, 2003, Beck et al. 2001, Beets et al. 2003, Claro & Lindeman 2003, Gillanders et al. 2003).

Interconnected habitat mosaics (IHM) (Sheaves 2005) are defined by the inter-relatedness of the discrete benthic habitats that exchange energy and matter on tidal, daily, and seasonal cycles. These systems may contain varying combinations of habitat types including a continuum of mangroves-seagrass-coral reefs. They are robust ecological systems that provide growth, reproductive and survival benefits to the organisms that use them (Sheaves 2005). The benefits are related to the inherent characteristics of IHMs and the focal species because habitat is organism-specific (Hall et al. 1997). Therefore, any study of IHMs must be tailored to a specific organism, family, or guild that depends on that IHM to provide essential goods and services. Further, because of variation in IHM characteristics, they are not all of equal quality. Quality refers to the ability of an IHM to provide conditions appropriate for individual and population persistence. It can be viewed as a continuous variable such that IHMs can range in quality from low to medium to high (Hall et al. 1997).

Many marine-based ecological studies have assessed the relationship between habitat quality and fish community characteristics such as density and biomass estimates, but results have been mixed. So much so that the amount of variation in a species' density or biomass explained by habitat quality has ranged from comparatively high to relatively little (Ault and Johnson 1998, Jones and Syms 1998, Holbrook et al. 2000, 2002a, 2002b). One of the drawbacks of many of these studies is that they have relied on the use of single or two adjacent habitat types (Nagelkerken et al. 2000a, Nagelkerken and van der Velde 2004, Ogden and Zieman 1977) and not considered the implications of how all the habitats that are used by an organism contribute to its growth, survival and distribution. Few studies have attempted to study fishes from mangroves, seagrass, and shallow reefs simultaneously (Nagelkerken at al. 2000a, Cocheret de la Morinière et al. 2002), and some studies have used multiple methodologies (e.g. underwater visual surveys and fish collection) to compare these habitats (Thayer et al. 1987, Acosta 1997). Even fewer studies have focused on studying the fish communities of Caribbean islands (most of them focus on continental coasts), and have attempted to investigate these communities along a mangroves-seagrass-coral reef continuum (Nagelkerken at al. 2000a, 2000b, Cocheret de la Morinière et al. 2002). This study aimed to extend the studies completed to date by investigating the influence of habitat quality in varying habitat combinations along a mangroves-seagrass-coral reef continuum on Haemulidae community structure and distribution pattern.

Haemulidae have been implicated as one of the major families contributing to the interconnection of marine habitats (Appeldoorn et al. 1997, 2003, Lindeman et al. 2000, Nagelkerken 2000a and 2000b, Recksiek et al. 2001, Cocheret de la Moriniére et al. 2002). Their movements include daily forage migrations, predator avoidance maneuvers, ontogenic habitat shifts, migrations onto reefs during the day for shelter, and habitat relocations to remain within optimum levels of critical abiotic parameters (Hobson 1968, McFarland et al. 1979, Helfman et al. 1982, Rooker and Dennis 1991, Tulevech and Recksiek 1994, Burke 1995, Beets et al. 2003). Their dispersal capabilities are less than 300 meters for juveniles (Kendall et al. 2003), and hundreds of meters for adults (Tulevech and Recksiek 1994). In order for an IHM to be of good quality for Haemulidae it should potentially have the following spatial, abiotic and biotic characteristics: spatial - large seagrass and/or mangrove areas (juvenile and feeding habitats) adjacent to large areas of hard substratum (resting habitat), with ideally, less than 300 m traveling distance between them; abiotic - optimum levels of key abiotic parameters such as temperature regimes, turbidity, pH and salinity; and biotic – low densities of predators (Appeldoorn 1993, 2003, Tulevech and Recksiek 1994, Lindeman et al. 1998, Nagelkerken et al. 2000a and 2000b Cocheret de la Moriniére et al. 2002, Kendall et al. 2003, Nagelkerken and van der Velde 2004a, 2004b). If these environmental criteria are met, IHMs of high quality should have larger energy and nutrient fluxes with 1) more fish species and individuals; 2) greater fish densities; 3) larger fish; 4) and more biomass, than lower quality systems.

The aim of this study was to investigate IHM quality by using a number of spatial, abiotic, and biotic environmental characteristics (percentage coverage of sand, mangroves, hard substrate, and seagrass, turbidity, pH, salinity, temperature, average depth, and predator density) that might contribute to the quality of each IHM. The study assessed the community structure and distribution pattern of Haemulidae (density, length-frequency distribution, biomass, and ratio of juveniles to adults) along an inshore to mid-shore gradient. The study focused on three IHMs that had a mangrove-seagrass-coral reef continuum, and one other IHM that had no mangroves but large areas of seagrass and coral reef. The specific questions investigated were: 1) are there differences in the Haemulidae community structures and distribution pattern within the IHMs; 2) are there differences in the environmental characteristics of the IHMs; 3) is the distribution of Haemulidae across the IHMs related to the environmental variables investigated; 4) how is the distribution of Haemulidae related to those environmental variables; and 5) which IHM had the highest quality based on Haemulidae community structure and distribution pattern?

Methodology

Study Sites

The study was carried out on the Eastern Caribbean Island of Antigua. This island is located in the Lesser Antillean island chain between 17º 00' N and 17º 44' N and 61º 21' and 61º 55' W (Figure 2.1). It is almost completely surrounded by nearshore and offshore coral reefs, shoals, rock islands and sand bars (CCA 1991). In addition, mangroves border 11% of the coastline and seagrass beds cover much of the near-shore area. The four focal sites around Antigua selected for their unique IHMs were Cades Reef (CAD), located on the southwest coast; around Guiana Island (GI), located on the northeast coast; the north coast from Boons Point to Shoal Point (JB); and Willoughby Bay (WILL) located on the southeast coast (Figure 1.2).

Haemulidae Community Data Collection

During the first sampling season, preliminary visual surveys were conducted at the four IHMs using replicate 100 x 2 m transects. The coefficient of variation of

Haemulidae density during these surveys was used to determine a final transect length such that the length chosen was a compromise between optimal transect length and optimal sample size. Transects of 30 x 2 m were chosen as the basic sampling unit. The benefit of this transect size was that 1) it covered an area of 60 m^2, 2) it was amenable for use in the three habitat types (mangroves, seagrass and coral reefs), and 3) it required less time to complete than the long (100 x 2 m) transects, allowing more areas to be sampled within a given time span.

A stratified sampling procedure was applied to investigate the distribution of Haemulidae within the selected IHMs. Habitat maps generated from Google Earth (www.googleearth.com) and hard-copy sectional topographic maps of Antigua (Government of the United Kingdom Directorate of Overseas Surveys 1980) were used together with site visits to characterize of the four IHMs based on their location and spatial extent of major constituent habitat types (mangroves, seagrass beds, hard substratum). Appendix I provides an in-depth description of the habitats at the four IHMs. 100 transects, 50 in the wet season and 50 in the dry season per IHM were selected as an a priori number that would adequately cover each IHM. The number of transects per habitat type for each IHM was determined based on the total number of transects that were to be completed and with the goal of ensuring that all habitat types were equally sampled based on the relative spatial coverage of each major habitat type present.

The species identity, abundance, and total length (cm) of all Haemulidae individuals observed along 30 x 2 m transects were recorded on underwater paper while carrying out the "belt transect" methodology of Rooker and Dennis (1991). Transects were laid out haphazardly within each habitat type (mangrove, seagrass, coral reefs) within each IHM. Fish counts were started 5 – 10 minutes after the measuring tape had been laid along the bottom, and all surveys were conducted by the same observer between 900 and 1700 hours to minimize problems of low light. Prior to the censuses, length estimation was practiced on objects of known length lying on the sea bottom until size estimates were accurate to within 1 cm (slight modification of Bell et al. 1985). In addition, underwater slates for data recording were marked with a ruler for guidance in size estimation (Bellwood and Alcala 1988). Previous assays were performed to calibrate number of individuals estimated by using counting techniques for shorebirds (Haig 2004), and this method was used where groups of more than 50 Haemulidae occurred in a school. Approximately 400 transects (50 at each IHM for each season, except 49 at WILL during the dry season) were completed during consecutive dry and wet seasons (April to June and August to November respectively).

IHM Environmental Characteristics Data Collection

Benthic Habitat Data

After the grunt data were recorded, a second transect swim was completed to collect data on the substrate life-form characteristics along each transect. Benthic habitat variables were recorded every 1 m along each transect, which resulted in 30 observations for each transect. The categories of habitat variables recorded are listed in Table 2.1 (after Lindeman 1997). Based on these data, the percentage coverage of each habitat category (seagrass, mangrove (prop root), coral reef and sand) was determined.

Abiotic Data

The average depth of each transect was determined by measuring the depth at the shallowest and deepest parts of each transect and taking a mean of the values. Temperature was recorded during transect swims and water samples were collected and analyzed in the laboratory for pH, salinity and turbidity.

Predator Density Data

Data on the density of all fish species (entire community composition) was estimated at the four IHMs using a similar methodology as was described above for the Haemulidae community. During transect swims, rocks and crevices were searched for cryptic fish and a mid-water count was completed for fish swimming above the substrate. Fish species were grouped into the following logarithmic-based abundance categories: 1- a single individual was observed, 2 – between 2 and 10 individuals observed, 3 – between 11 and 100 individuals observed and 4 – over 100 individuals observed (Schmitt et al. 2002). From the fish community data, a list of potential Haemulidae predators was determined by compiling data from Claro and García-Arteaga (2001) on the food preferences of all fish seen during transect swims, and then selecting only those fish species that were noted to be predators of eggs, larvae and fish. Appendix II contains a complete list of the fish community seen at the IHMs in Antigua along with species' relative densities, food preferences, and trophic categories.

Data Analysis

Haemulidae Community Data

Heamulidae community parameters density (individuals per 60 m^2), length frequency distribution of individuals, biomass (g $60m^{-2}$), and ratio of juveniles to adults were compared among IHMs (sites), seasons, and species (the four dominant Haemulidae species *H. sciurus, H. flavolineatum, H. chrysargyreum* and *H. plumieri,* which represented more than 90% of the total number of individuals observed at the IHMs). For length frequency distribution comparisons, Haemulidae were placed in 5 cm length classes (Faunce et al. 2002, Schmitt et al. 2002). Biomass was calculated based on literature values of length-weight relationships of Haemulidae from around the region (Table 2.2). The observed lengths of grunts in the field were recorded as total length (cm) while the length-weight relationships from the literature were in fork lengths (cm), so the appropriate conversions were made. The conversion factors (Table 2.2) were calculated from fork and total length data of grunts caught by subsistence fishermen in Antigua (Chapter 3 of this research). The Haemulidae adult and juvenile stages were determined as the size at which the individual reaches sexual maturity based on values obtained from the literature. The female size at sexual maturity was always smaller than that of males in the literature, so the female value was used because the sex of the observed fish was unknown. The numbers of juveniles observed at each transect was divided by the number of adults observed to produce juvenile to adult ratios. This gave the number of juveniles observed for every adult observed along each transect. The density, length frequency distribution, biomass, and ratio of juvenile to adult were compared between sites, seasons, and for the four main Haemulidae species using the three-way ANOVAs or

Kruskal- Wallis tests after the data were tested for normality and homogeneity of variance, and data transformations completed. If there were significant differences between IHMs post-hoc multiple comparison tests were performed to determine the IHMs contributing to differences (Zar 1996). When Kruskal-Wallis analyses were completed, the post-hoc test used was Dunn's test. The benefits of this test were that it enabled multiple pair-wise comparisons among samples and could be used with unequal sample sizes (SigmaStat 3.5 manual). All analyses were done in SigmaStat 3.5 and Systat 12.0.

IHM Environmental Characteristics

The environmental data (% cover of seagrass, mangroves, coral reef, and sand, and pH, turbidity, salinity, temperature, average depth, and density of predators) were compared among IHMs using the one-way ANOVAs or Kruskal-Walis test after the data were tested for normality and homogeneity of variance, and data transformations completed. If the data could not be normalized or made homoscedastic by transformation, Kruskal-Walis tests were performed. If there were significant differences between IHMs post-hoc multiple comparisons tests were performed to determine the IHMs contributing to the differences (Zar 1996).

IHM Characteristics and Haemulidae Density Comparisons

A Pearson correlation analysis was conducted on the environmental data to test for significant correlations among variables. In cases where this occurred among pairs of variables, only one of the two variables was retained for further analyses. Haemulidae density [log (x +1)] and the corresponding environmental characteristics (percentage cover of seagrass, mangroves, hard substratum and sand (arcsin √p transformed) (Zar 1996), and pH, turbidity, salinity, temperature, average depth and density of predators (log (x + 1) transformed) (Zar 1996)) collected for each transect at each IHM, plus the relationships among them, were analyzed through a Canonical Correspondence Analysis (CCA) (ter Braak and Verdonschat 1995, McCune and Grace 2002). CCA was selected as the ordination technique because: 1) it is considered to be a powerful multivariate technique that is useful to elucidate the relationship between species assemblages and their environment; 2) it can be used to visualize the different habitat preferences (niches) of taxa via an ordination diagram; 3) it can be used to rank environmental variables in importance; 4) it takes advantage of species abundance often being a unimodal function of the environmental variables; 5) it uses linear combinations of environmental variables to explain optimally the species variables; and 6) it is suitable for use when the data have positive values but contain many zeros, as was the case with the Haemulidae abundances (ter Braak and Verdonschat 1995, McCune and Grace 2002). Haemulidae density was the community parameter used in the CCA because it was equivalent to abundance. In addition, the density values were probably more accurate than the biomass values, because the biomass values were estimated based on length-weight relationships obtained from the literature. A Spearman ranked correlation analysis using the BIO-ENV routine in Primer was used to analyze the correlation between the environmental IHM characteristics and Haemulidae densities (Clarke and Warwick 2001). For the fish data the input for the BIO-ENV procedure was the similarity matrix of standardized, transformed density data (fish similarity matrix).

Results

Haemulidae Community Patterns

At CAD, GI, JB and WILL, 6 species of grunt (*H. flavolineatum, H. sciurus, H. chrysargyreum, H. plumieri, H. aurolineatum and H. parra*) were observed during the dry and wet seasons. At CAD and JB one additional species, porkfish (*Anisotremus virginicus*) was observed during both seasons. The mean densities 60 m^{-2} of Haemulidae by IHM from greatest to lowest were WILL, JB, GI and CAD (Figure 2.2a). The results of density comparisons among IHMs using a Kruskal-Wallis test indicated a significant difference between the IHMs ($H_{0.05, 3} = 11.73$, $P = 0.008$). CAD and JB, and CAD and WILL were found to be significantly different from one another (Table 2.3). Seasonal comparisons of density (Figure 2.2b) indicated that there was no significant difference among IHMs during the dry season ($H_{0.05, 3} = 1.36$, $P = 0.72$), but during the wet season there was a significant difference ($H_{0.05, 3} = 20.78$, $P < 0.001$) between CAD and JB and CAD and WILL (Table 2.3). Comparisons of Haemulidae density among IHMs by species (Figure 2.2c) indicated for *H. sciurus* ($H_{0.05, 3} = 4.01$, $P = 0.26$) and *H. flavolineatum* ($H_{0.05, 3} = 6.60$, $P = 0.09$) there were no significant differences among IHMs. For *H. chrysargyreum* ($H_{0.05, 3} = 15.23$, $P = 0.002$) and *H. plumieri* ($H_{0.05, 3} = 12.33$, $P = 0.006$) there were significant differences among IHMs (Table 2.3). For *H. plumieri*, significant differences in densities occurred between CAD and GI.

The mean lengths of Haemulidae by IHM from greatest to lowest were WILL, CAD, JB, GI (Figure 2.3a). The results of length frequency distribution comparisons among IHMs indicated that there was no significant difference among IHMs ($H_{0.05, 3} = 0.74$, $P = 0.87$). Seasonal comparisons of length frequencies (Figures 2.3 b, c, d, e) indicated that there was no significant difference among IHMs during the dry or wet seasons ($H_{0.05,\,3} = 3.57$, $P = 0.31$ and $H_{0.05,\,3} = 1.67$, $P = 0.64$ respectively). Comparisons of length frequencies among IHMs by species indicated for *H. flavolineatum* ($H_{0.05,\,3} = 2.73$, $P = 0.44$) and *H. chrysargyreum* ($H_{0.05,\,3} = 2.19$, $P = 0.53$) there were no significant differences among IHMs. For *H. sciurus* ($H_{0.05,\,3} = 13.69$, $P = 0.003$) and *H. plumieri* ($H_{0.05,\,3} = 9.98$, $P = 0.02$) there were significant differences among IHMs (Table 2.3).

The mean biomass 60 m^{-2} of Haemulidae by IHM from greatest to lowest was WILL, JB, CAD, GI (Figure 2.4a). The results of the biomass comparisons among IHMs indicated that there were no significant differences among IHMs ($H_{0.05,\,3} = 7.95$, $P = 0.05$) (Table 2.3). Seasonal biomass comparisons (Figure 2.4b) indicated no significant difference among IHMs during the dry season ($H_{0.05,\,3} = 3.23$, $P = 0.36$), but during the wet season there was a significant difference ($H_{0.05,\,3} = 16.67$, $P < 0.001$), between CAD and JB (Table 2.3). Comparisons of biomass for the four dominant Haemulidae species among IHMs (Figure 2.4c) indicated for *H. sciurus* ($H_{0.05,\,3} = 1.00$, $P = 0.80$) and *H. flavolineatum* ($H_{0.05,\,3} = 4.08$, $P = 0.25$) there were no significant differences among IHMs. For *H. chrysargyreum* ($H_{0.05,\,3} = 12.14$, $P = 0.007$) and *H. plumieri* ($H_{0.05,\,3} = 12.28$, $P = 0.006$) there were significant differences among IHMs (Table 2.3).

For *H. flavolineatum*, *H. chrysargyreum* and *H. plumieri*, over 95% of the individuals observed at the four IHMs were juveniles. For *H. sciurus*, approximately 68% of the individuals seen at CAD were juveniles and over 86% were juveniles at GI, JB and WILL. The Haemulidae juvenile to adult ratios by IHM from greatest to lowest were WILL, CAD, GI and JB (Figure 2.5a). The results of juvenile to adult ratio comparisons among IHMs indicated that there was a significant difference among IHMs ($H_{0.05,\,3} =$

30.82, $P < 0.001$). Dunn's post-hoc tests confirmed significant differences between CAD and GI, CAD and JB, and GI and WILL (Table 2.3). Seasonal comparisons (Figure 2.5b) indicated a significant difference among IHMs during both seasons (dry season $H_{0.05,\,3}$ = 22.04, P = 0.001; wet season $H_{0.05,\,3}$ = 14.51, P = 0.002). During the dry season there were significant differences between CAD and GI, GI and WILL, and JB and WILL and during the wet season between CAD and GI (Table 2.3). Comparisons of juvenile to adult ratios for the four dominant Haemulidae species among IHMs (Figure 2.5c) indicated for *H. plumieri* ($H_{0.05,\,3}$ = 7.56, P = 0.056) there was no significant difference among IHMs. For *H. sciurus* ($H_{0.05,\,3}$ = 12.09, P = 0.007), *H. flavolineatum* ($H_{0.05,\,3}$ = 20.33, $P < 0.001$) and *H. chrysargyreum* ($H_{0.05,\,3}$ = 16.86, $P < 0.001$) there were significant differences among IHMs (Table 2.3). Dunn's post-hoc tests indicated significant differences between CAD and JB for *H. sciurus*, GI and CAD, GI and WILL and GI and JB for *H. flavolineatum*, and CAD and JB for *H. chrysargyreum*.

IHM Environmental Characteristics

<u>Benthic Habitat Data</u>

For the environmental characteristic percent coverage of sand, there were significant differences among some of the IHMs (H = 18.99, $P< 0.001$) (Tables 2.4 and 2.6). Significant differences were found between CAD and GI, JB and GI, WILL and CAD and WILL and JB. JB was not included in the analyses for the percent coverage of mangroves because there were no mangroves at that site. There were significant differences in the percent coverage of mangroves among the IHMs ($H_{0.05,\,3}$ = 10.89, P = 0.012) (Table 2.6). For the percent coverage of hard substratum, there were significant differences between all the IHMs ($H_{0.05,\ 3} = 91.06$, $P < 0.001$) except between JB and WILL. For percent coverage of seagrass ($H_{0.05,\ 3} = 84.82$, $P < 0.001$), the only two IHMs not significantly different from one another were WILL and JB.

Abiotic Data

For the turbidity values the only two IHMs significantly different from each other ($H_{0.05,\ 3} = 8.25$, $P = 0.041$) based on the results of the Kruskal-Wallis test were CAD and WILL. All IHMs ($H_{0.05,\ 3} = 213.36$, $P < 0.001$), except CAD and WILL, were significantly different from each for pH. For both salinity $H_{0.05,\ 3} = 60.53$, $P < 0.001$) and temperature ($H_{0.05,\ 3} = 50.70$, $P < 0.001$) some IHMs were significantly different from one another (Table 2.6). For salinity and temperature, GI and CAD, and JB and WILL were the only IHMs not significantly different from each other. There were significant differences in depth among the IHMs ($H_{0.05,\ 3} = 45.77$, $P < 0.001$). CAD and WILL, and GI and JB were the only pair-wise comparisons found to not be significantly different from one another for depth.

Predator Density Data

Kruskal-Wallis tests indicated significant differences in predator densities among IHMs ($H_{0.05,\ 3} = 105.64$, $P < 0.001$) (Tables 2.5 and 2.6). Post-hoc tests indicated significant differences among all IHMs.

IHM Characteristics and Haemulidae Density Comparisons

Percentage cover of hard substratum and percentage cover of seagrass were collinear ($r^2 = -0.93$) (Table 2.7) suggesting that areas with more hard substratum cover had less seagrass cover. This caused multicollinearity problems so the percentage of seagrass cover was excluded from further analyses. The CCA ordinations highlighted the relationships between: IHMs (transects at each IHM) and Haemulidae species (Figure 2.6a); environmental variables and Haemulidae species (Figure 2.6b); and environmental variables and IHMs (transects at each IHM) (Figure 2.6c). The species and site ordination indicated that *H. sciurus*, *H. plumieri* and *H. flavolineatum* had the greatest densities at the IHMs. The large distances separating *H. parra*, *H. aurolineatum* and *A. virginicus* markers from the site markers indicated their low abundances at all IHMs. *H. sciurus* appeared to have higher densities at JB than at the other IHMs. *H. flavolineatum* had higher densities at JB, GI and WILL than at CAD. *H. plumieri* had higher densities at WILL than at the other IHMs. Further, one transect at JB had a higher density of *H. plumieri*, *H. flavolineatum*, *H. sciurus* and *H. parra* than any other transect. The nearness of *H. plumieri* and *H. flavolineatum* (closer than any two other species on the ordination diagram) indicated the similarity of their distributions across transects. *H. flavolineatum* and *H. sciurus* also had quite similar distributions. The marker for *H. aurolineatum* was located very far away from any other species marker suggesting the dissimilarity of this species density from that of the other Haemulidae species.

The three most important environmental variables, listed in order of importance, were percentage cover of hard substrate, temperature, and predator density (Figure 2.6c). Transects with high percentage cover of hard substratum, temperature, and predator density had low percentage cover of sand and mangroves and low turbidity and salinity. In addition, the percentage cover of hard substrate, temperature, and predator density varied more among transects than the other variables. CAD had the largest number of transects with high values of these environmental parameters while GI had the lowest number of transects. *H. chrysargyreum*, *H. sciurus*, *A. virginicus* and *H. parra* occurred at higher percentage cover of hard substrate, temperature and predator densities than the other Haemulidae species. *H. flavolineatum*, *H. plumieri* and *H. aurolineatum* occurred at low values of these environmental variables but at high percentage cover of sand and mangroves, and high turbidity and salinity values.

Similar to the results of the CCA analysis, the Spearman correlation coefficients showed that the percentage cover of hard substrate, temperature, and predator density ($\rho_s = 0.66$) grouped the transect data in a manner consistent with the Haemulidae density patterns. These three IHM environmental characteristics occurred in all of the top 10 combinations of the environmental variables that best explained the Haemulidae distribution pattern ($\rho_s = 0.66 - 0.45$). Although the percentage cover of seagrass was removed from the CCA and Spearman correlation analyses because it was collinear with the percentage cover of hard substrate, it can be inferred that it may have also been important in influencing Haemulidae density distributions.

Discussion

Haemulidae were observed at all dominant habitat types (mangroves, seagrass beds and hard substratum) within the IHMs studied. This distribution was similar to that observed in other studies on Haemulidae that have documented the presence of adults and juveniles in all major benthic marine habitats (Hobson 1965, Ogden and Ehrlich 1977, McFarland et al. 1979, Helfman et al. 1982, Rooker and Dennis 1991, Appledoorn et al. 1997, Kendall et al. 2003, Beets et al. 2003). There were no significant differences in Haemulidae length frequency distributions and biomass values among any of the IHMs.

There were significant differences in densities, however, between CAD and JB and CAD and WILL. Density values were highest at WILL, then JB and lowest CAD. The significant differences in densities between CAD and JB and CAD and WILL may be the result of either post-settlement processes or larval supply. A large number of scientists believe that post-settlement processes including amount, type and distribution of habitat (Ebersole 1985, Eggleston 1995, Tolimieri 1995, Tupper and Boutilier 1997), predation (Hixon and Beets 1989, 1993, Hixon 1991, Beukers and Jones 1997, Eggleston et al. 1997, Steele 1997a), competition (Smith and Tyler 1972), or a combination of these and other post-settlement factors (Shulman et al. 1983, Shulman 1985a, Shulman and Ogden 1987, Steele 1997b) are the main determinants of coral reef fish density.

Post-settlement factors such as the amount of hard substrate available and the distance between hard substrate and seagrass areas may explain the differences in densities observed at CAD and JB, and CAD and WILL. Notable here is that all underwater visual surveys were conducted during the day at times when Haemulidae normally are resting on coral reefs and other hard bottoms because of the shelter these habitats provide against predators (Hobson 1965, McFarland et al. 1979, Helfman et al. 1982, Rooker and Dennis 1991, Tulevech and Recksiek 1994, Burke 1995, Beets et al. 2003). In addition, Haemulidae normally are found on hard substrate in close proximity to seagrass (feeding) areas, thereby reducing feeding migration travel time and the amount of time exposed to predators during those migrations (Nagelkerken and van der Velde 2004a and 2004b). Review of the characteristics of each IHM (Tables 2.2 and 2.3), however, suggests that neither percentage cover of hard substrate nor distance between seagrass and substrate help to explain the observed density patterns at the two IHMs. First, not only was there much more hard-substrate cover at CAD (64.7% of the area) than at JB (20.1% of the area), or WILL (21.9% of the area), the percentage coverage of hard substrate was significantly different between these IHMs. Secondly, the distance between feeding (seagrass) and resting (hard bottom) habitats were approximately the same for all three IHMs (< 10 m).

Some scientists believe that larval supply and settlement are the primary factors influencing fish density/abundance, and that reef fish populations do not reach resource-defined carrying capacities because larval supply is insufficient (Doherty 1982, 1983, Sale et al 1984, Victor 1983, 1986, Abrams 1984, Doherty and Fowler 1994, Sale 1982). A review of Figures 2.3d and 2.3b highlights that there were more juveniles at JB than at CAD. In addition Figures 2.3e and 2.3b highlights that there were more juveniles at WILL than at CAD. Thus, it is possible that the differences in densities between these IHMs were related to larval supply and settlement, and by extension the amount of suitable juvenile habitat present. At CAD, the juvenile habitat covered only 34.6% of the area but at JB it covered approximately 71.9% of the area, and at WILL 60.7% of the area.

The results of the CCA analysis and the Spearman correlation analyses demonstrated that the percentage cover of hard substrate and seagrass, temperature, and density of predators may be the most important factors that influenced Haemulidae density distributions at the IHMs investigated in this study. These data suggest that a combination of both larval supply and settlement, and post-settlement factors may be responsible for the observed Haemulidae density patterns at the IHMs. The influence of the percentage of hard substrate and predator densities may act together to determine Haemulidae densities.

Haemulidae densities were highest at WILL and lowest at CAD. In contrast, WILL had the highest density of predators and CAD the second lowest (GI had the lowest). One of the major differences between these two IHMs in terms of environmental characteristics was the structural complexity. First, WILL was a large bay that had numerous isolated coral heads, small rock formations, patches of algal plain, and patch reefs distributed throughout large areas of seagrass and sandy areas. These microhabitats added a large amount of structural complexity to WILL. Second, WILL had an area of mangroves at the landward curve of the bay and extensive high relief reef development close to the mouth of the bay (see Appendix I and Figure1.2). CAD on the other hand, had an extensive area of hard substrate, but much of this area was composed of low-relief coral heads, coral formations, coral rubble, gorgonians, and sponges. The high structural complexity of WILL potentially provided a large number of predator refuges to the Haemulidae populations using this IHM (Hixon 1991). Beukers and Jones (1997) suggested that adult abundances of coral reef fish were strongly influenced by the densities of different predators and the attributes of the habitats such as the availability of refuges from predators. Further, in the presence of predators, prey has been observed to use the most complex habitats (Stein and Magnuson 1976, Shulman 1984) because they diminish encounters between predators and their prey (Anderson 1984, Christensen and Persson 1993). Therefore, the impact of predation may be reduced in habitats with a high abundance of refuges (Crowder and Cooper 1982, Werner et al. 1983, Menge and Sutherland 1987, Hixon and Menge 1990).

The large number of patch reefs and coral rubble areas located within the seagrass and sandy areas at WILL provided large areas of resting habitat for Haemulidae. These microhabitats allowed the fish resting within them access to food sources in the surrounding habitats. Kerrigan (1994) showed that food availability might be as important as shelter in determining fish densities. Much more of the area of WILL (72.3 %) was covered by seagrass and sand than CAD (26.7%) suggesting higher food availability at WILL than at CAD. In fishes such as Haemulidae that suffer size-dependent mortality, patch reefs and coral rubble surrounded by habitats that provide large amounts of food are most attractive to individuals of all sizes (Shulman 1985b) because of the reduction in exposure time during feeding migrations.

Temperature is important in influencing fish distribution pattern because fish modify their positions to remain within optimum temperature ranges (Brett 1956, 1979, Wooton 1990, Elliot 1994, Jobling 1994, Mommsen 1998). Parker (1990) did not observe *H. plumieri* during one winter off the coast of North Carolina when temperatures dropped below average. He assumed that the fish migrated to avoid the unusually cold winter. The result of a number of studies completed to date (Phelan et al. 2000, Atrill and Michael 2002, Le Pape et al. 2003, Chapter 4 of this dissertation) have highlighted how small changes in the temperature regimes experienced by fish can have large consequences for growth rates and population persistence. Thus, fish will modify their position to stay within optimum parameter ranges. Mean temperature values which were highest at JB and WILL, were not significantly different from each other. Mean temperature values which were lowest at CAD and GI, were not significantly different from each other. In addition, WILL and JB had higher mean density, biomass and total lengths values than either CAD or GI.

The presence of critical habitat for different sizes of fish may play a role in determining fish distribution pattern at the IHMs. Appeldoorn et al. (1997) proposed that the size distribution patterns of Haemulidae across a shelf are influenced by the distribution of critical habitat for distinct ontogenetic stages. Juvenile Haemulidae habitat is shallow-water near seagrass beds, and that of adults is the area from inshore reefs to the shelf edge (Appeldoorn et al. 1997). WILL and JB had similar high values for Haemulidae mean density, biomass and total lengths (which were the highest of the IHMs). These sites also had the largest area of juvenile habitat, although not adult habitat. This might explain why there were so many more juveniles at JB and WILL than at the other two IHMs. In opposition to the Appledoorn et al. (1997) study, Kendall et al. (2003) found that adult *H. flavolineatum* were no more likely to be found at lagoon sites (seagrass beds and mangroves) than offshore at deeper sites (coral reefs) as had been reported by other studies (Ogden and Erlich 1977, Appeldoorn et al. 1997). GI had the highest ratio of juveniles to adults but the lowest area of adult habitat and in many instances juveniles and adults co-occurred in the same habitats.

There are two distinct seasons in Antigua: a dry season that extends from January to July and a wet season that extends from August to November (CCA 1991). The considerable variation in the amount of precipitation between these two seasons has implications for nearshore fish communities and fish distribution patterns. Fish populations show transient fluctuations caused by seasonal variability in food sources and abiotic environmental factors (Magnan et al. 2002). During the wet season, runoff from the land into nearshore waters maintains nutrient concentrations at high level, which greatly enhance aquatic productivity. Sierra et al. in Claro and García-Arteaga (2001) found that abundant and long-lasting runoff after heavy rainfall in September 1979 provoked a plankton bloom in the coastal areas of Cuba that lasted more than 6 months and contributed to high fisheries productivity. During the dry season there were no significant differences in density, length frequency distribution and biomass values among the IHMs. During the wet season, however, there were significant differences between CAD and JB for both density and biomass values. During the wet season, CAD had higher density and biomass values than JB, but the opposite was true during the dry season. In addition, the differences in the wet season were more pronounced than the differences in the dry season. These data suggest differences in food and nutrient availability during the two seasons at these two IHMs. Lugendo et al. (2007) found that environmental variables and fish community structure remained relatively constant for most of the year, but that marked changes were seen during the rainy period. They found significant variations in fish community variables (density, biomass, and species richness) during the rainy season. Mangroves covered 8.6% of CAD, while JB had no mangrove areas. The presence of mangroves at CAD might have contributed to enhanced levels of nutrients and dissolved and particulate organic matter (Ogden and Gladfelter 1983) that could have caused enhanced fisheries productivity at CAD during the wet season.

For juvenile to adult ratios (number of juveniles observed for each adult) during the dry season, GI had larger values than any of the other IHMs, and WILL had the lowest. Pair-wise comparisons showed that GI was significantly different from WILL. In the wet season however, the ratio of WILL surpassed that of GI, with WILL having the highest ratio overall. A number of studies have demonstrated the influence of physical conditions that vary because of seasonal changes in freshwater input, on the abundance of juvenile fish (Cyrus and Blaber 1987, Barletta et al. 2000, Barletta et al. 2003, 2005). Fish vary their use of marine habitats during different seasons of the year such that areas of high primary productivity are used more than low productivity areas (Lugendo et al. 2007). In the tropics, this usually occurs during the warm, wet season, which results in spatial variation in the densities and recruitment of fish (Robertson and Duke 1987) and changes in fish community structure (Robertson and Duke 1990). At GI, the mangrove areas surrounded a small island (Guiana Island), which does not receive much rainfall during the year. There is no freshwater input into GI other than rain. WILL experiences high rainfall values (Environment Division of Antigua and Barbuda 2005) and the mangrove stand at that IHM borders agricultural farms. It is inferred that those farms possibly contribute to higher nutrient loads in near-shore waters. Therefore, high rainfall and agricultural runoff may help explain why there were more juveniles at WILL than at GI during the wet season.

One additional factor structuring Haemulidae populations around Antigua that was not included in these analyses but may have had major implications for the results of this study was the level of fishing pressure at each IHM (Appeldoorn and Lindeman 1985, Jennings and Polunin 1997, Kendall et al. 2003). It was not possible to accurately ascertain the number of persons fishing at each IHM because there were undocumented recreational fishers at each IHM. Based on interviews with commercial fishers around Antigua and information from the Antigua Fisheries Division, however, JB faced the lowest level of fishing pressure of the four IHMs. In fact, for the duration of this study I did not find any commercial fishers engaged in fishing at JB, although I found several fishers that specifically targeted Haemulidae, in particular *H. plumieri,* at the other IHMs.

Table 2.8 indicates that based on the Haemulidae community structure and distribution pattern investigated, WILL had higher quality than the other IHMs. A number of environmental factors were measured that could serve as proxies for habitat quality. The four that were found to be most important were percentage cover of hard substratum and seagrass, temperature, and predator density. There are a large number of additional environmental factors that influence habitat quality, however, such as the proximity of adult and juvenile habitats to spawning areas, density-dependent control of fish distribution, inter- and intra-specific competition between individuals for resources, ocean currents and hydrology, and anthropogenic influences (Sutton 1985, Richmond 1993, Jennings and Polunin 1997, Chapman and Kramer 1999, Friedlander et al. 2003, Shima and Osenberg 2003, William et al. 2006). The environmental factors that I examined were selected based on the system under consideration: a small tropical island with limited shelf area, and a need to limit the variables to those that captured the differences among habitats. Overall, this study highlighted that the community structure and distribution of Haemulidae populations around Antigua was probably not governed by a single dominant process, but rather, by many processes acting simultaneously. Habitat quality - a reflection of all those processes - is a major ecological factor determining the community structure and distribution of Haemulidae species within benthic habitat types along the coastlines of small islands such as Antigua. The knowledge of the influence of habitat quality on fish community structure and distribution pattern has implications for understanding fisheries productivity and for implementation of protective measures for the habitats upon which fishery resources depend.

Table 2.1: Description of how benthic habitat components were characterized within IHMs (modified version of Lindeman 1997).

Habitat Category	Description of natural habitat types	Code
Mangroves & Coastal Trees	Red mangrove (*Rhizophora mangle*) roots	MR
Grasses & Algae	*Thalassia* (tall wide blades)	GT
	Syringodium (tall thin blades)	GS
	Halodule (short, thin blades)	GH
	Mixed (two or more intergrown grass species)	GM
	Algae – attached (*Halimeda, Caulerpa*, many others)	AA
	Detached Macrophyte piles, benthic (e.g. wrack)	DM
	Detached drift macrophytes (incl. *Sargassum*, grasses)	DD
Sediments (Bare bottom)	Sediments – Fine (e.g. mud)	SF
	Sediments – Coarse (e.g. sand)	SC
Hard subtratum	Exposed Hardbottom (e.g. *Anastasia* bedrock)	EH
	Live hard Corals	CL
	Corals – Gorgonians	CG
	Corals – Coral rubble	CR
	Invertebrate – Miscellaneous (e.g. *Diadema*)	IM
	Invertebrate – Sponges	IS

Table 2.2: Length-weight relationships (FL cm) and conversion factors used in biomass analyses of the Haemulidae species. a and b are constants derived from the equation $W = aL^b$. Conversion factors (CF) calculated from TL (cm) and FL (cm) for Haemulidae caught in Antigua by commercial fishermen.

Grunt Species	a	b	n	Site	Reference	CF	n
H. sciurus	0.022	3.00	138	St. Croix	Bohnsack & Harper 1988	1.12	165
H. flavolineatum	0.021	3.00	232	St. Croix	Bohnsack & Harper 1988	1.13	64
H. chrysargyreum	0.014	3.08	17	Jamaica	Gaut & Munro 1983	1.13	5
H. plumieri	0.013	3.13	2,787	Antigua	This study	1.14	2,787

Table 2.3: Results of Dunn's post-hoc multiple comparison test (Q-values) and Cohen's d (effect size - *italicized*) comparing Haemulidae densities 60 m^{-2}, length frequency distributions, biomass 60 m^{-2}, and ratio of juveniles to adults among IHMs. In cases where no significant differences occurred, no post-hoc tests were performed so no data are reported in the table. * indicates where there was a significant difference, $P < 0.05$. Cohen's d was calculated as the difference between means divided by the pooled standard deviation. Cohen's d is positive if the mean difference is in the predicted direction. Cohen's d values do not always follow the test-statistic values because of the extremely patchy nature of *Haemulon* spp and high variances in community parameter estimates.

	CAD x GI	**CAD x JB**	**CAD x WILL**	**GI x JB**	**GI x WILL**	**WILL x JB**
Densities 60 m^{-2}						
Site Comparisons	2.49	2.79*	2.87*	0.84	0.69	0.31
	-0.12	*-0.01*	*-0.12*	*-0.02*	*-0.05*	*0.02*
Wet Season	2.30	4.03*	2.68*	1.73	0.39	1.33
	-0.07	*-0.16*	*-0.17*	*-0.13*	*-0.13*	*-0.00*
Dry Season	---	---	---	---	---	---
	-0.20	*0.12*	*-0.05*	*0.28*	*0.11*	*0.11*
H. sciurus	---	---	---	---	---	---
	0.00	*-0.12*	*-0.07*	*-0.12*	*-0.07*	-0.03
H. flavolineatum	---	---	---	---	---	---
	-0.39	*-0.21*	*-0.17*	*-0.02*	*0.11*	*-0.09*
H. chrysargyreum	1.35	0.83	1.19	2.18	2.53	0.35
	-0.13	*-0.28*	*-0.16*	*-0.20*	*-0.16*	*0.12*
H. plumieri	2.98*	2.00	2.51	0.99	0.47	0.52
	0.08	*0.06*	*-0.08*	*-0.02*	*-0.17*	*0.15*
Length Frequency						
Site Comparisons	---	---	---	---	---	---
	-0.17	*-0.23*	*-0.37*	*-0.04*	*-0.11*	*0.07*
Wet Season	---	---	---	---	---	---
	-0.10	*-0.30*	*-0.42*	*-0.21*	*-0.28*	*0.02*
Dry Season	---	---	---	---	---	---
	-0.23	*0.21*	*-0.08*	*0.31*	*0.17*	*0.25*
H. sciurus	2.72*	2.59	0.080	0.13	2.64	2.51
	0.03	*-0.31*	*-0.03*	*-0.30*	*-0.25*	*-0.08*
H. flavolineatum	---	---	---	---	---	---
	-0.43	*-0.51*	*-0.43*	*-0.04*	*0.17*	*-0.22*
H. chrysargyreum	---	---	---	---	---	---
	-0.41	*-0.65*	*-0.77*	*-0.51*	*-0.74*	*0.61*
H. plumieri	1.96	1.71	0.68	0.25	2.64	2.39
	0.17	*0.12*	*-0.18*	*-0.05*	*-0.35*	*0.31*
Biomass 60 m^{-2}						
Site Comparisons	1.7	2.15	2.18	0.45	0.48	0.04
	0.00	*-0.07*	*-0.13*	*-0.07*	*-0.13*	*0.05*
Wet Season	1.89	3.64*	2.17	1.75	0.27	1.47
	-0.03	*-0.20*	*-0.20*	*-0.19*	*-0.19*	*-0.01*
Dry Season	---	---	---	---	---	---
	0.03	*0.31*	*-0.05*	*0.28*	*-0.06*	*0.17*
H. sciurus	---	---	---	---	---	---
	0.09	*0.12*	*0.11*	*0.03*	*0.02*	*0.02*
H. flavolineatum	---	---	---	---	---	---
	-0.18	*-0.19*	*-0.13*	*-0.13*	*-0.05*	*-0.07*

H. chrysargyreum	1.35	0.58	0.94	1.94	2.29	0.36
	-0.01	*-0.18*	*-0.17*	*-0.16*	*-0.17*	*0.15*
H. plumieri	2.75*	1.96	2.97*	0.79	0.036	0.83
	0.20	*0.09*	*-0.20*	*-0.09*	*-0.30*	*0.25*
Ratio of juveniles to adults						
Site Comparisons	4.72*	2.74	0.38	2.19	4.59*	2.50
	-0.19	*0.03*	*-0.09*	*0.27*	*0.04*	*0.11*
Wet Season	3.75*	1.79	1.72	2.34	2.12	0.03
	-0.08	*0.06*	*-0.15*	*0.19*	*-0.11*	*0.19*
Dry Season	2.89*	2.20	1.07	0.66	4.11*	3.37*
	-0.36	*0.05*	*0.13*	*0.41*	*0.45*	*-0.14*
H. sciurus	0.64	3.17*	0.95	2.55	0.35	2.07
	0.17	*0.03*	*0.05*	*-0.32*	*-0.16*	*-0.04*
H. flavolineatum	3.83*	0.62	0.21	3.32*	3.67*	0.42
	-0.50	*-0.17*	*-0.15*	*0.38*	*0.23*	*0.06*
H. chrysargyreum	2.61	3.79*	1.77	0.13	1.51	2.47
	-0.92	*-0.96*	*-0.24*	*0.70*	*-0.17*	*0.23*
H. plumieri	---	---	---	---	---	---
	0.20	*0.23*	*0.21*	*0.09*	*0.03*	*0.06*

Table 2.4: Summary of the spatial characteristics of each IHM. These data were complied from habitat maps generated from Google Earth (www.googleearth.com), hard-copy sectional topographic maps of Antigua (Government of the United Kingdom Directorate of Overseas Surveys 1980), and site visits including benthic substratum data collected during visual surveys.

	SITES			
Characteristic	**CAD**	**GI**	**JB**	**WILL**
Location	Southwest	Northeast	North	Southeast
Number of Habitat Types	4	4	3	4
Approximate Total Area (m^2)	3,312,500	3,031,250	2,215,000	4,098,125
% Cover of seagrass	26	42.5	71.9	54.9
% Cover of mangroves	8.6	16.9	0	5.8
% Cover of hardbottom	64.7	13.2	20.1	21.9
% Cover of soft substrate	0.7	27.4	8	17.4
Average distance between seagrass and coral reefs (m)	< 10	< 10	< 10	< 10
Average distance between seagrass and mangroves (m)	> 100	< 10	-----	< 10
Average distance between coral reefs and mangroves (m)	< 100	> 100	-----	> 2,000

Table 2.5: Summary of the abiotic and biotic characteristics of each IHM. For each parameter the mean ± SD is presented. For pH the range is given rather than a mean value. All data were collected during underwater visual surveys.

	SITES			
Characteristic	**CAD**	**GI**	**JB**	**WILL**
		Physical Variables		
Turbidity (NTU)	1.19 ± 1.02	0.87 ± 0.47	1.09 ± 1.01	0.80 ± 0.60
pH	7.94 – 8.70	7.31 – 8.21	6.83 – 8.42	7.93 – 8.74
Salinity (ppt)	35.57 ± 0.86	35.88 ± 0.75	35.01 ± 1.37	34.87 ± 1.78
Temperature (^{0}C)	28.92 ± 1.37	28.69 ± 1.11	29.68 ± 0.61	29.70 ± 1.31
Average Depth (m)	2.83 ± 1.45	2.03 ± 1.13	1.83 ± 0.90	2.76 ± 1.63
		Biotic Variables		
Relative Predator Density	0.28 ± 0.14	0.24 ± 0.12	0.32 ± 0.13	0.35 ± 0.16

Table 2.6: Results of the Dunn's post-hoc multiple comparison test (Q-values) and Cohen's d (effect size - *italicized*) to determine which IHMs were significantly different from each other for pair-wise comparisons of environmental parameters. In cases where no significant differences occurred, no post-hoc tests were performed so no data are reported in the table. * indicates where there was a significant difference P < 0.05). Cohen's d was calculated as the difference between means divided by the pooled standard deviation. Cohen's d is positive if the mean difference is in the predicted direction.

	CAD x GI	CAD x JB	CAD x WILL	GI x JB	GI x WILL	WILL x JB
% Sand	3.47*	0.44	3.42*	3.04*	2.42	3.03*
	-1.55	*-0.02*	*1.36*	*-1.29*	*0.22*	*1.04*
% Mangroves	0.51	----	0.86	---	0.36	---
	0.24		*0.00*		*0.21*	
% Hard bottom	3.92*	4.87*	3.07*	8.79*	6.97*	1.79
	0.66	*0.81*	*0.51*	*-1.48*	*-1.18*	*-0.32*
% Seagrass	4.85*	3.18*	3.21*	8.04*	7.05*	0.97
	-0.92	*0.40*	*0.69*	*1.47*	*1.16*	*0.30*
Turbidity	0.94	1.14	2.82*	0.19	1.88	1.68
	0.39	*0.09*	*0.46*	*-0.28*	*0.14*	*-0.35*
pH	12.98*	7.14*	1.26	5.84*	11.69*	5.86
	---	---	---	---	---	---
Salinity	1.95	3.89*	4.75*	5.83*	6.69*	0.87
	-0.38	*0.49*	*0.50*	*0.79*	*0.74*	*-0.09*
Temperature	1.68	3.77*	3.52*	5.45*	5.19*	0.25
	0.19	*-0.72*	*-0.58*	*-1.11*	*-0.83*	*0.02*
Depth	4.71*	5.60*	0.91	0.89	3.80*	4.68*
	0.62	*0.83*	*0.05*	*0.19*	*-0.52*	*0.70*
Predator Density	3.00*	3.56*	6.55*	6.56*	9.54*	2.99*
	0.29	*-0.31*	*-0.49*	*-0.62*	*-0.77*	*0.21*

Table 2.7: Correlation coefficients among the environmental variables used in the CCA analysis. Only the correlation between hardbottom and seagrass was significant so seagrass was removed from further analyses to prevent the problems of multicolinearity. * indicates where there was a significant difference (P < 0.05). The codes in the table area: MAN- % cover of mangroves; HAR - % cover of hard substratum; SAN - % cover of sand pH – pH; TUR – turbidity; SAL – salinity; TEM – temperature; DEP - average depth; and PRED - density of predators)

	SAND	**MAN**	**HAR**	**SEA**	**TURB**	**PH**	**SAL**	**TEMP**	**DEP**	**PRED**
SAND	---	-0.10	-0.35	0.08	-0.01	0.05	0.09	-0.23	0.16	-0.08
MAN	-0.10	---	-0.37	0.18	0.32	0.07	0.11	-0.27	-0.13	-0.02
HAR	-0.35	-0.37	---	-0.93*	-0.13	0.12	-0.11	0.31	0.20	0.28
SEA	0.08	0.18	-0.93*	---	0.06	-0.17	0.06	-0.20	-0.26	-0.28
TURB	-0.01	0.32	-0.13	0.06	---	-0.06	0.29	-0.23	0.07	-0.05
PH	0.05	0.07	0.12	-0.17	-0.06	---	-0.27	0.19	0.07	0.13
SAL	0.09	0.11	-0.11	0.06	0.29	-0.27	---	-0.42	0.13	-0.10
TEMP	-0.23	-0.27	0.31	-0.19	-0.23	0.19	-0.42	---	-0.09	0.08
DEPTH	0.16	-0.13	0.20	-0.26	0.07	0.07	0.13	-0.09	---	0.05
PRED	-0.08	-0.02	0.28	-0.28	-0.05	0.13	-0.10	0.08	0.05	---

Table 2.8: Checklist of Haemulidae community structure and distribution parameters and how they compared for each IHM. The table allows easy comparisons of habitat quality among the four IHMs based on these parameters. X indicates which IHM had the highest mean value of the factor.

Factor	**CAD**	**GI**	**JB**	**WILL**
Mean Density				
IHM				X
Dry Season		X		
Wet Season			X	
H. sciurus			X	
H. flavolineatum			X	
H. chrysargyreum				X
H. plumieri				X
Mean Length				
IHM				X
Dry Season		X		
Wet Season				X
H. sciurus				X
H. flavolineatum			X	
H. chrysargyreum				X
H. plumieri				X
Mean Biomass				
IHM				X
Dry Season				X
Wet Season			X	
H. sciurus	X			
H. flavolineatum			X	
H. chrysargyreum				X
H. plumieri				X
Mean A:J Ratio				
IHM				X
Dry Season		X		
Wet Season				X
H. sciurus	X			
H. flavolineatum		X		
H. chrysargyreum				X
H. plumieri	X			
TOTAL	**3**	**4**	**6**	**15**

Figure 2.1: Map of Antigua showing its location within the eastern Caribbean island chain.

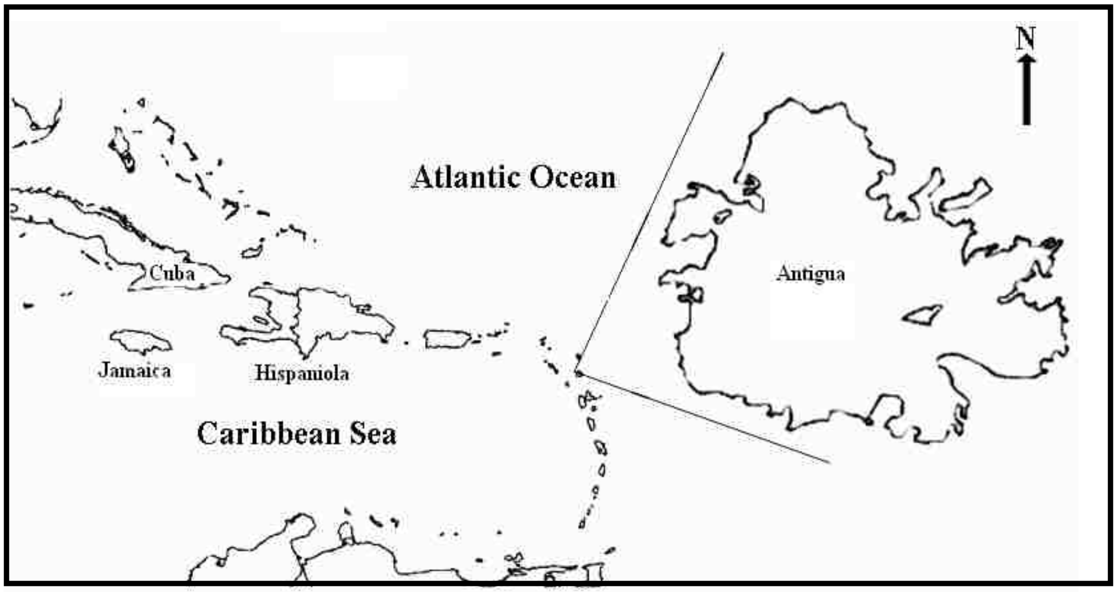


Figure 2.2a: Density 60 m^{-2} values for the four IHMs. The error bars represent one standard deviation.

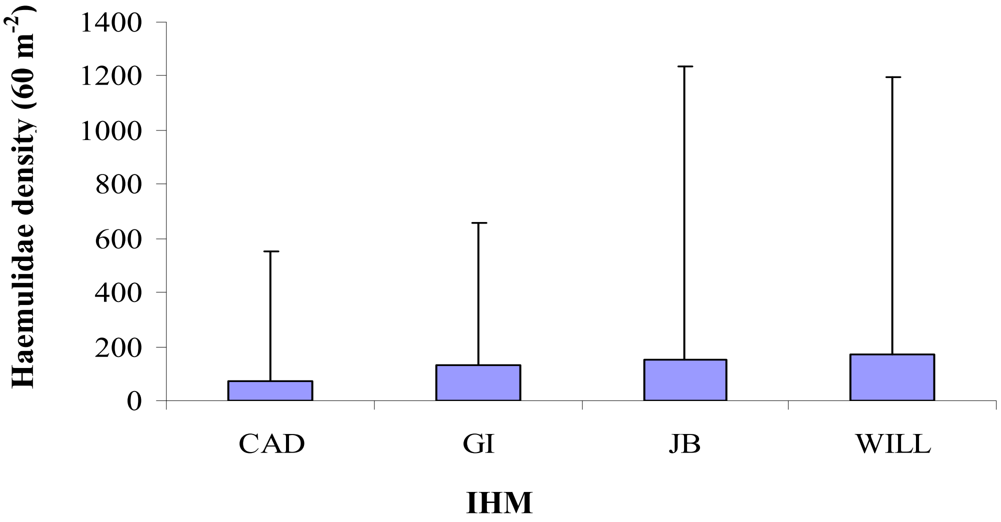


Figure 2.2b: Density 60 m^{-2} values for the two seasons at the four IHMs. The error bars represent one standard deviation.

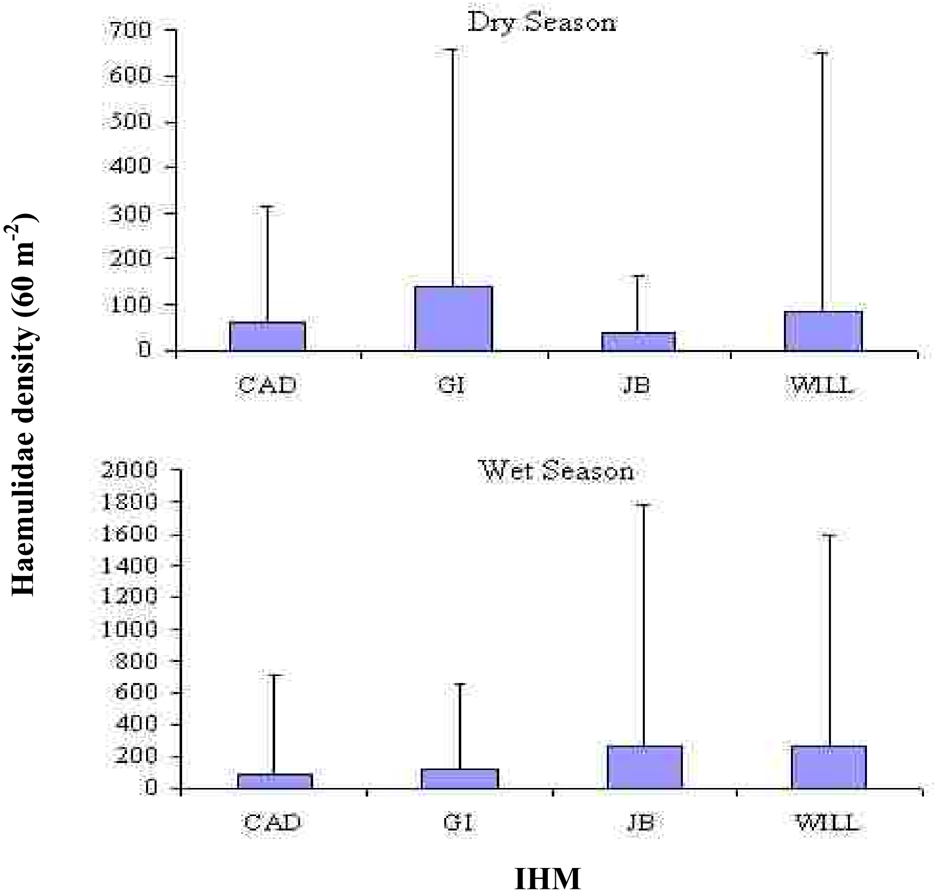


Figure 2.2c: Density 60 m^{-2} values by species for the four IHMs. The error bars represent one standard deviation.

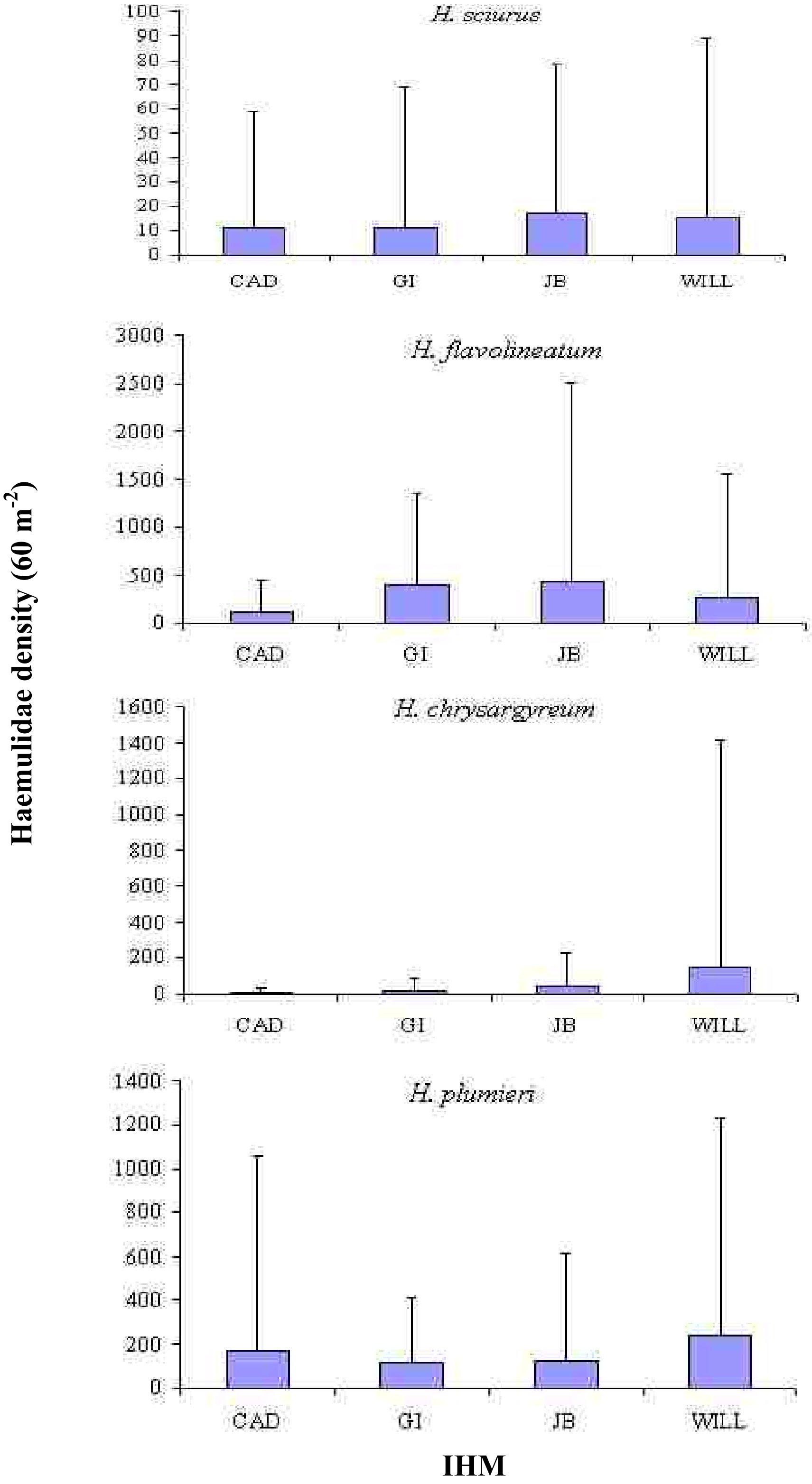


Figure 2.3a: Length frequency distributions using total lengths (TL cm) for the four most abundant Haemulidae species (*H. sciurus*, *H. flavolineatum*, *H. chrysargyreum* and *H. plumieri*) observed at the four IHMs CAD, GI, JB and WILL.

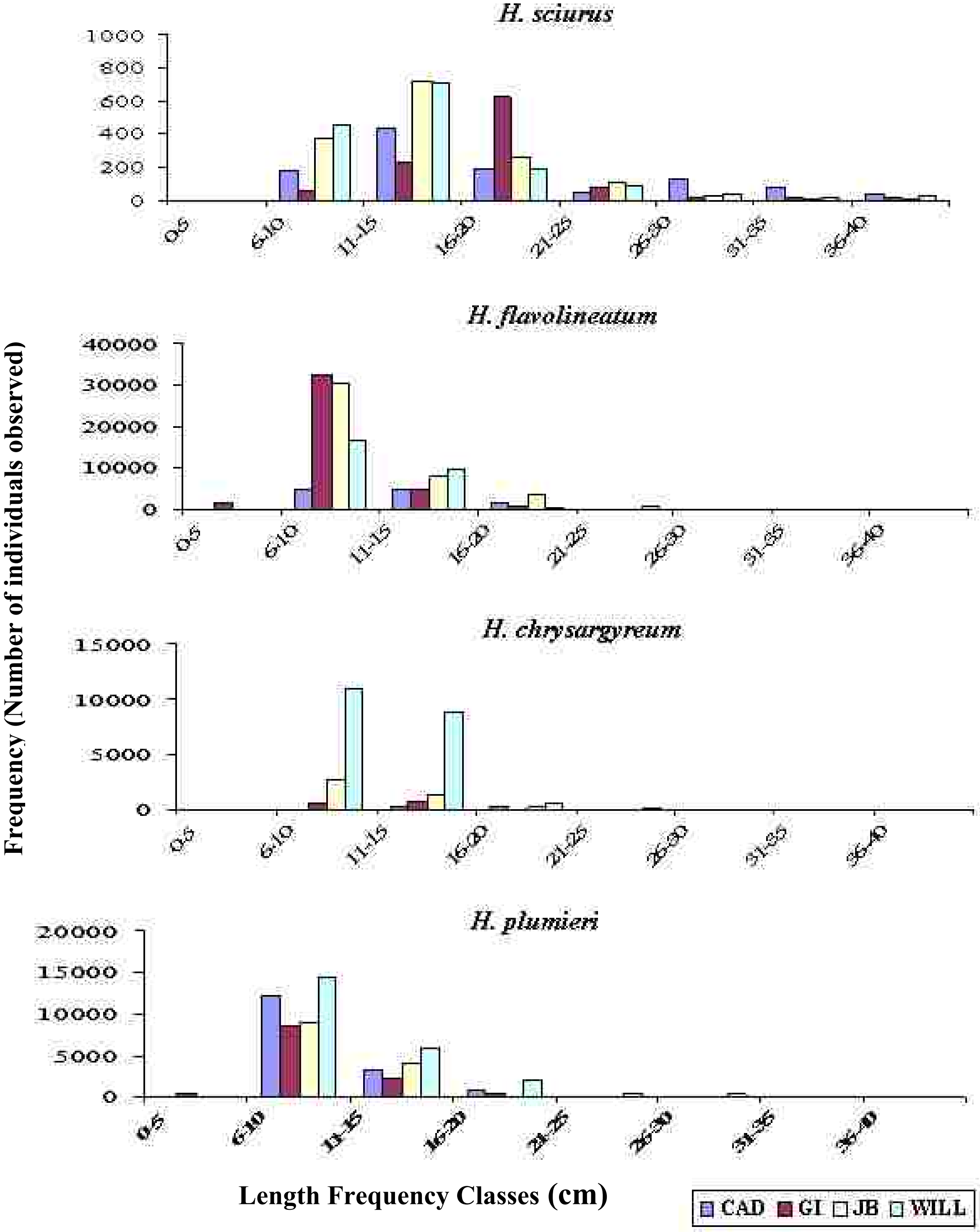


Figure 2.3b: Length frequency distributions for the four most important Haemulidae species observed during visual surveys at CAD during the wet and dry seasons. TL_{max} values from Froese and Pauly (2007).

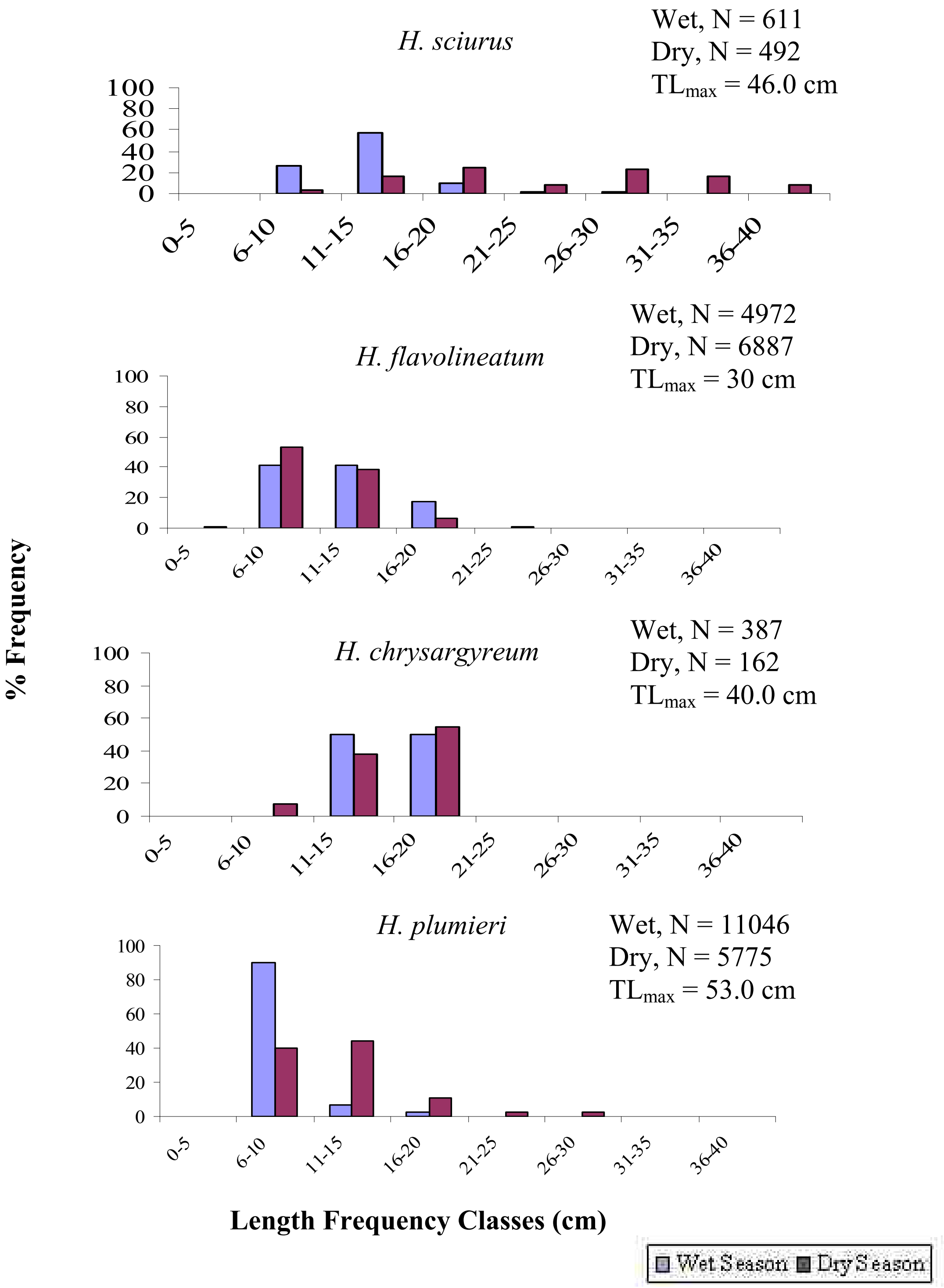


Figure 2.3c: Length frequency distributions for the four most important Haemulidae species observed during visual surveys at GI during the wet and dry seasons. TL_{max} values from Froese and Pauly (2007).

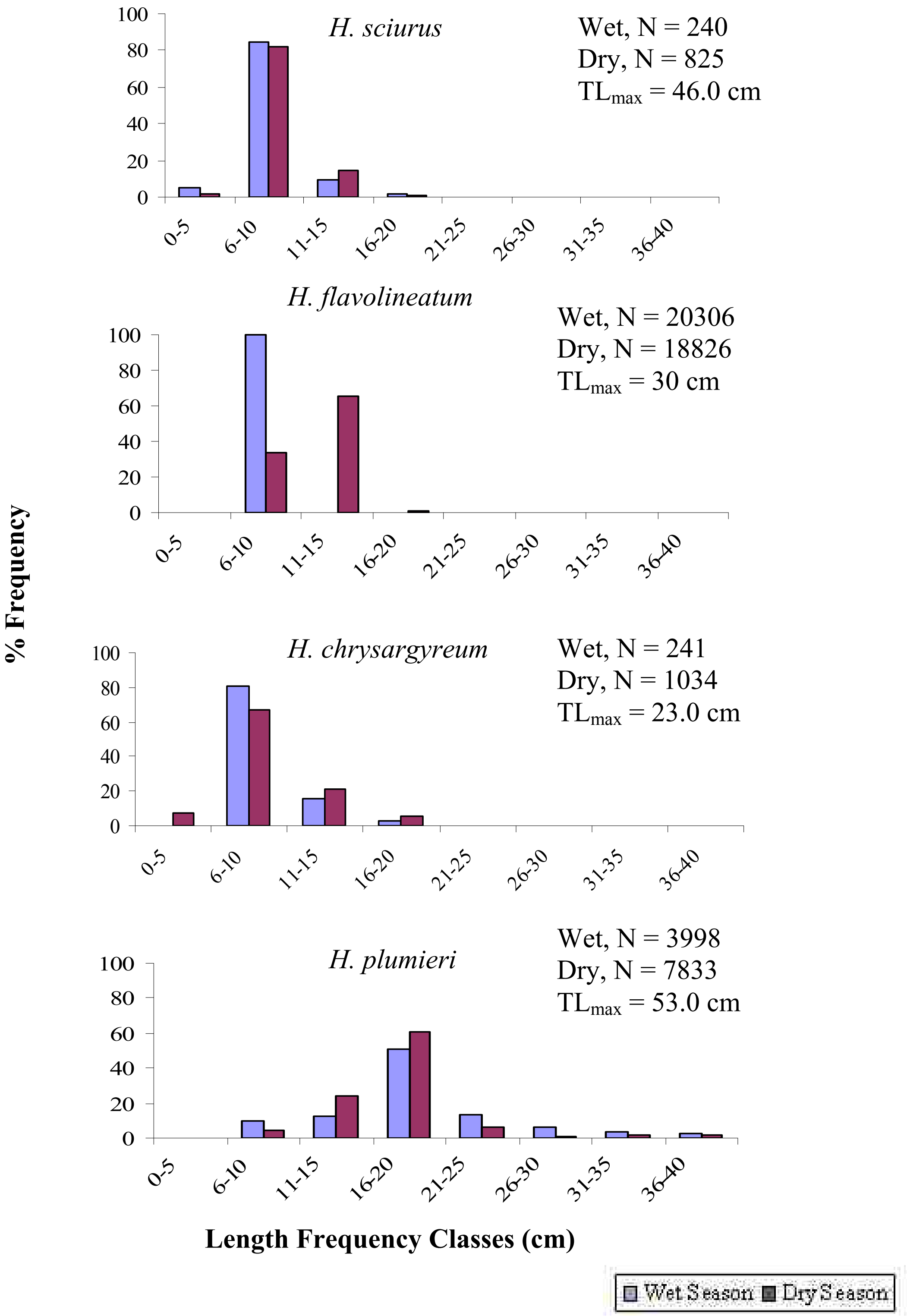


Figure 2.3d: Length frequency distributions for the four most important Haemulidae species observed during visual surveys at JB during the wet and dry seasons. TL_{max} values from Froese and Pauly (2007).

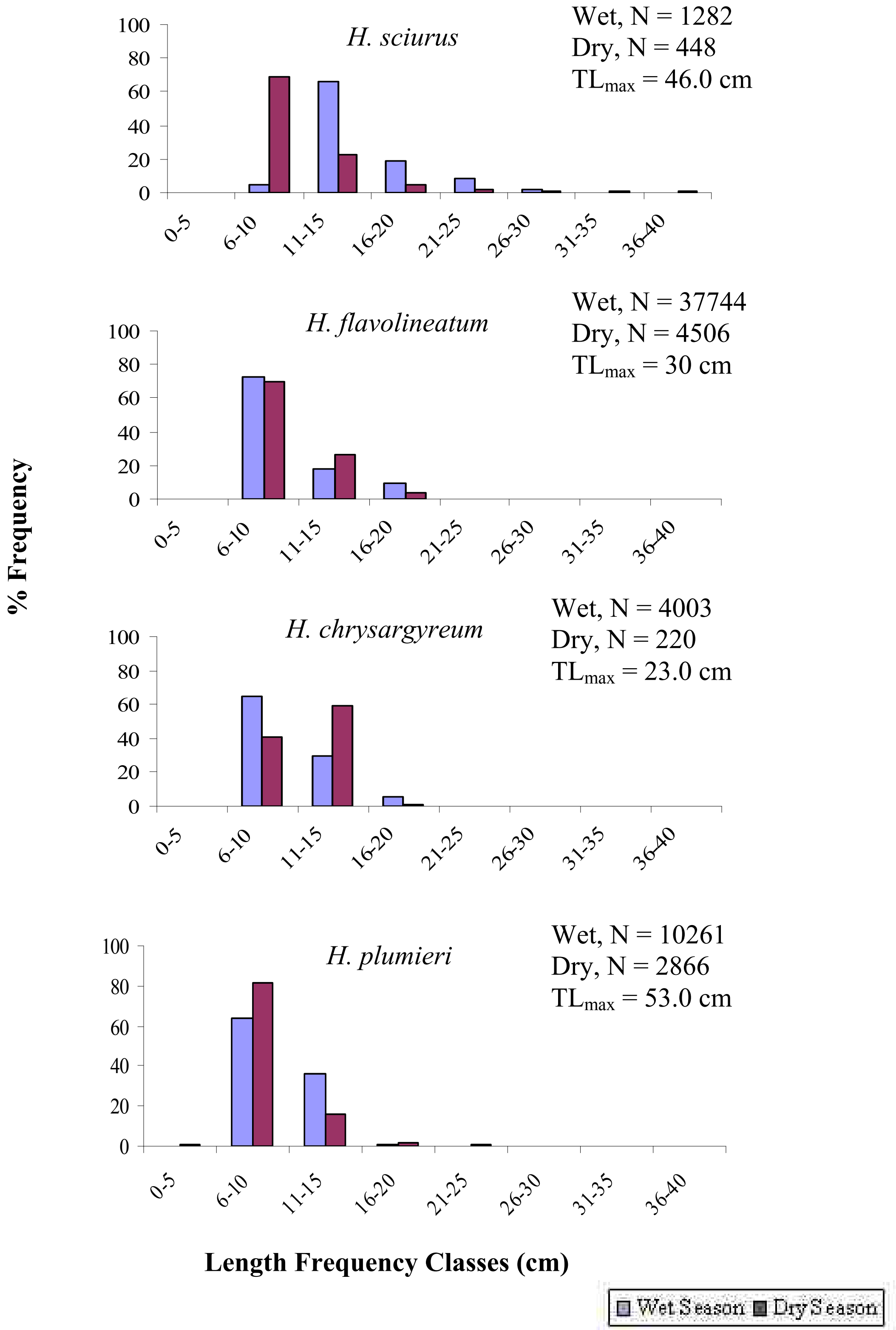


Figure 2.3e: Length frequency distributions for the four most important Haemulidae species observed during visual surveys at WILL during the wet and dry seasons. TL_{max} values from Froese and Pauly (2007).

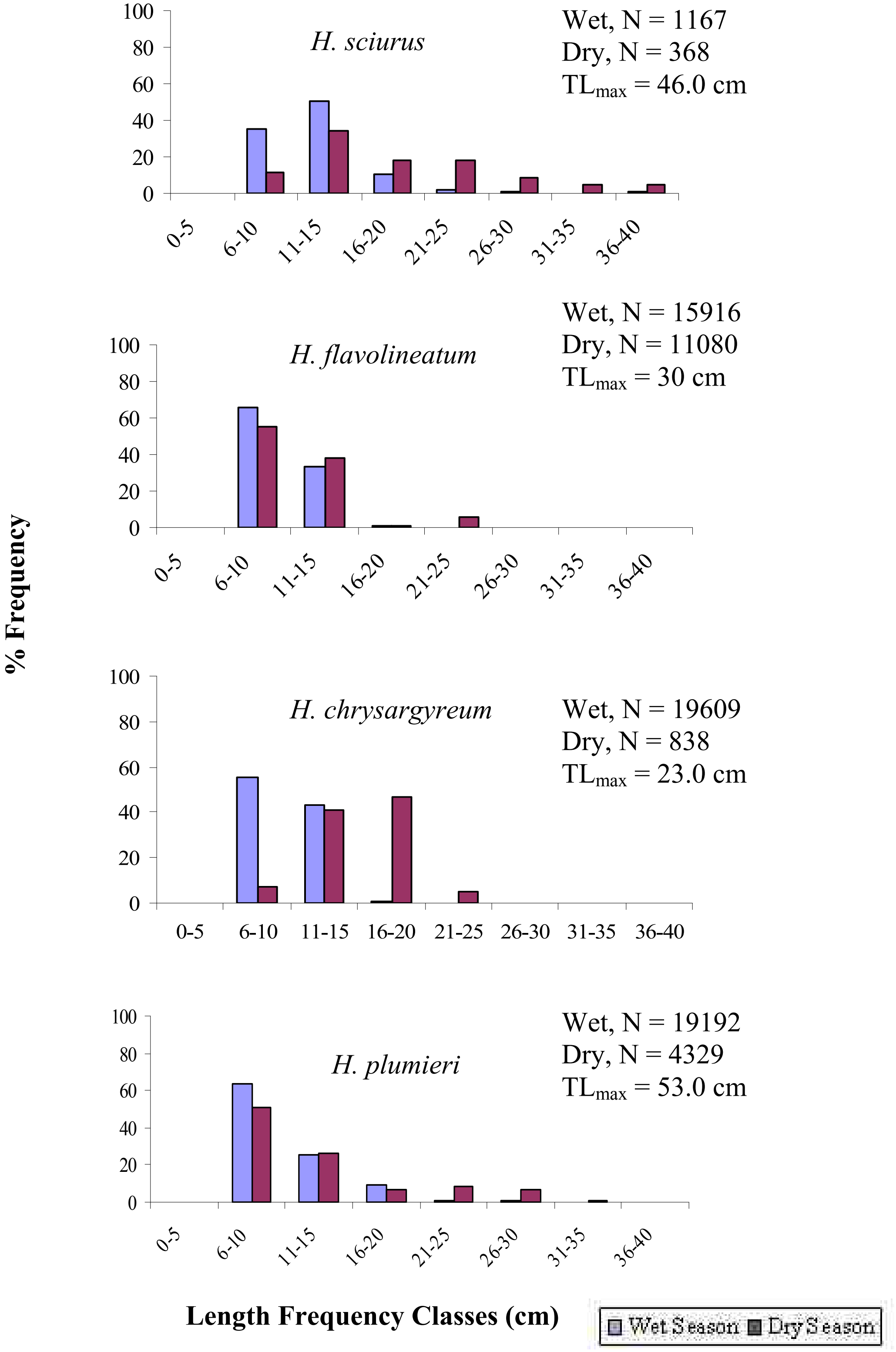


Figure 2.4a: Biomass 60 m^{-2} values for the four IHMs. The error bars represent one standard deviation.

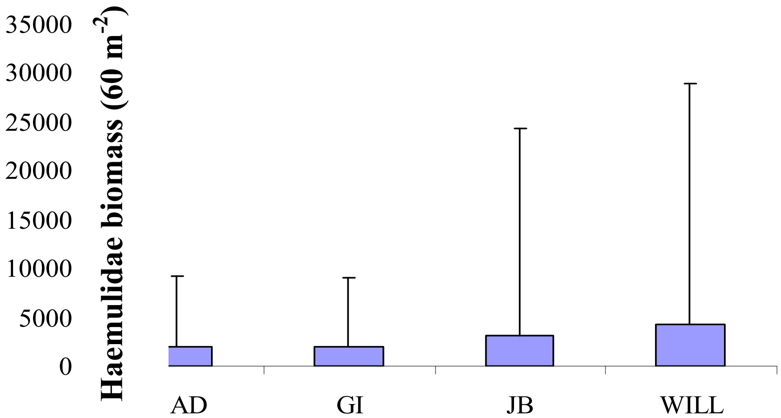


Figure 2.4b: Biomass 60 m^{-2} values for the two seasons at the four IHMs. The error bars represent one standard deviation.

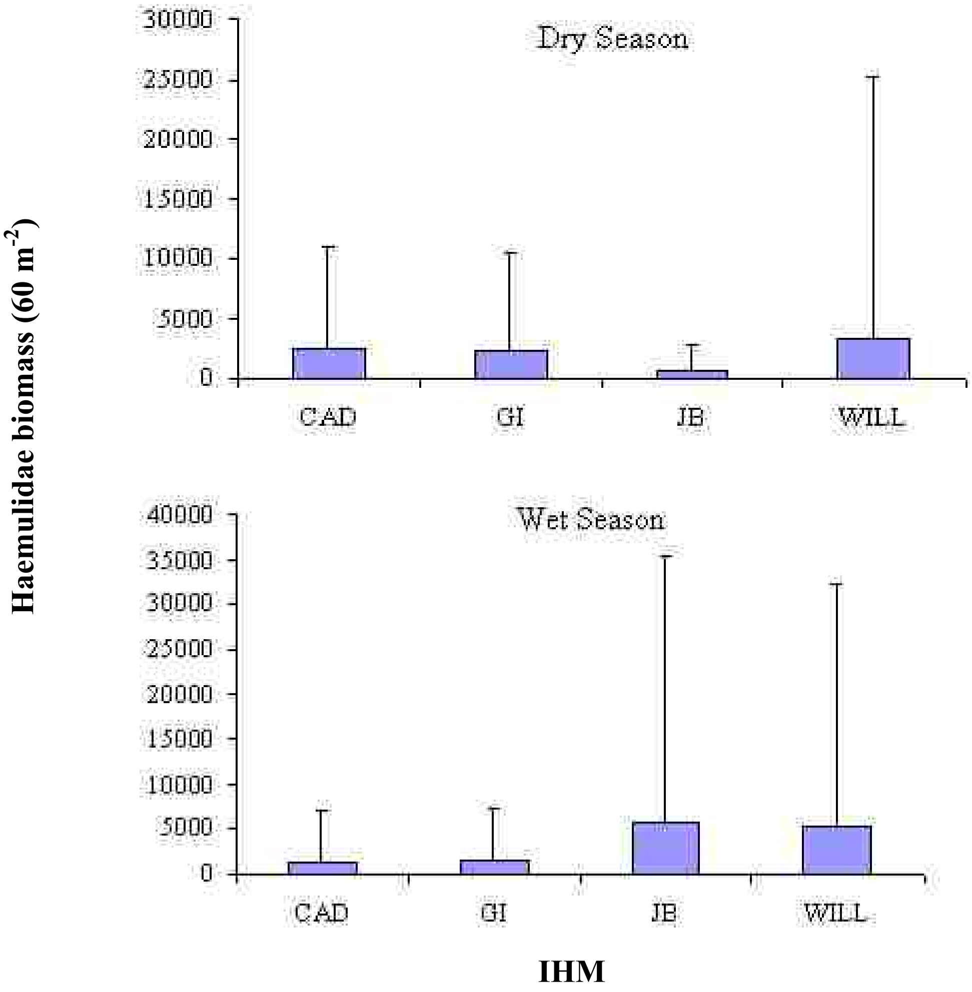


Figure 2.4c: Biomass 60 m^{-2} values by species for the four IHMs. The error bars represent one standard deviation.

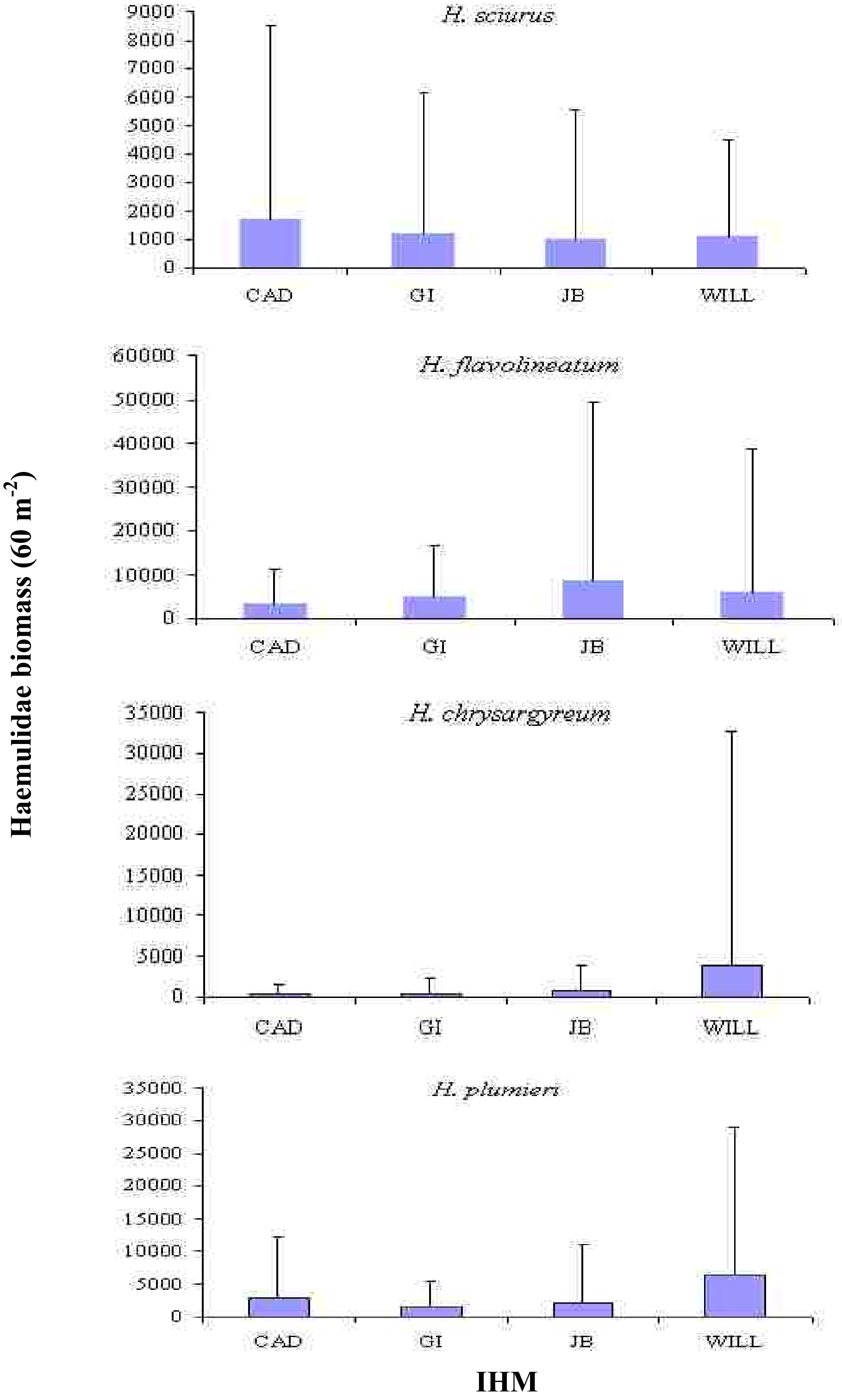


Figure 2.5a: Juvenile to adult ratios for the four IHMs. The error bars represent one standard deviation.

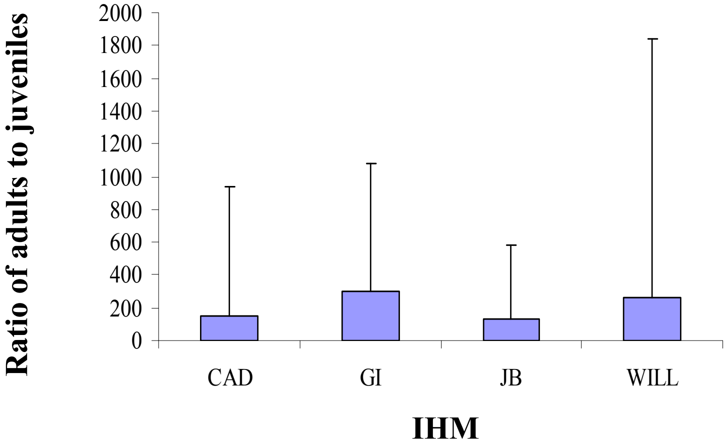


Figure 2.5b: Juvenile to adult ratios (for every adult how many juveniles are observed) for the two seasons at the four IHMs. The error bars represent one standard deviation.

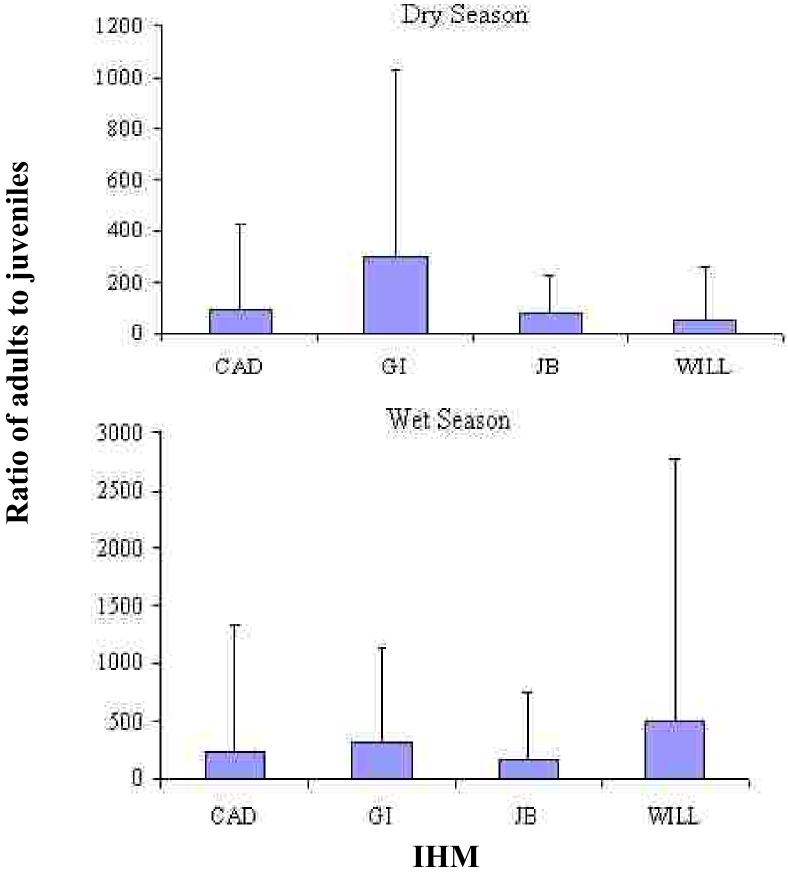


Figure 2.5c: Juvenile to adult ratios by species for the four IHMs. The error bars represent one standard deviation.

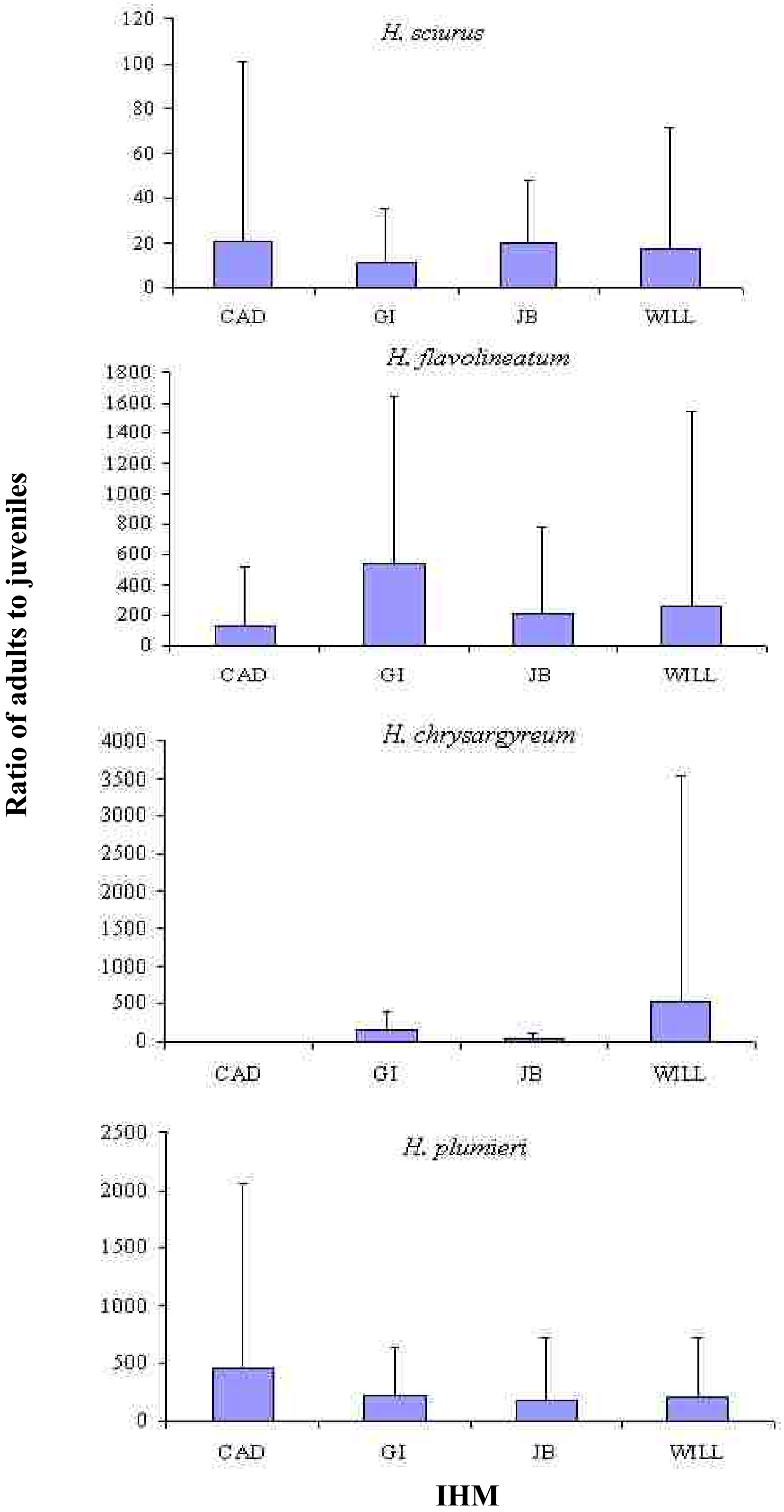
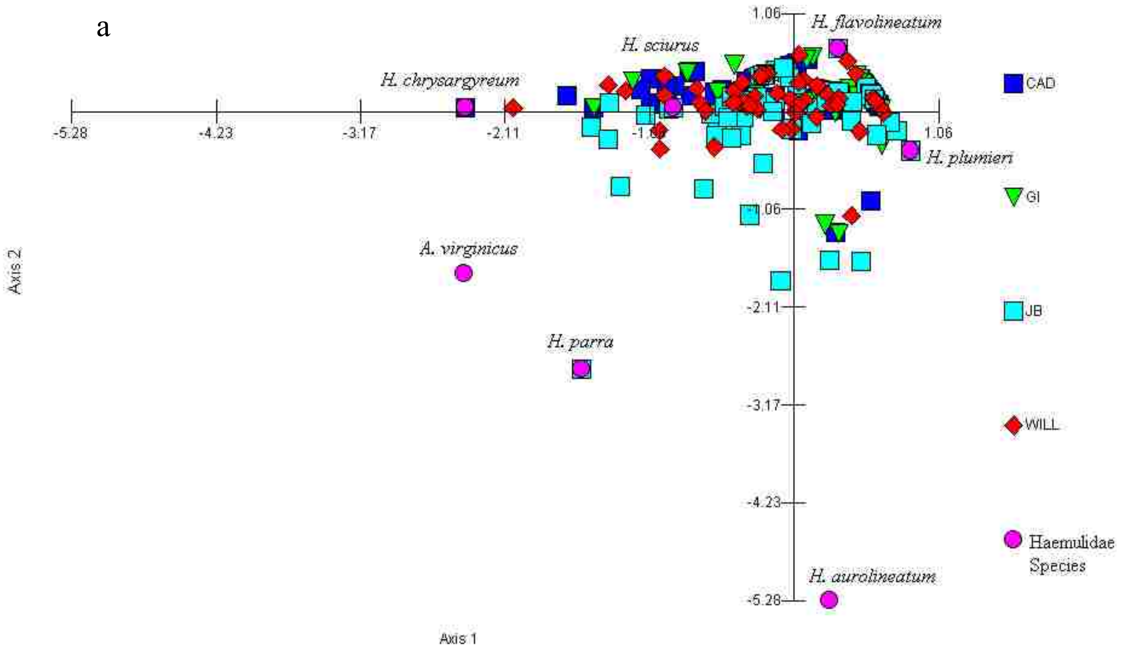
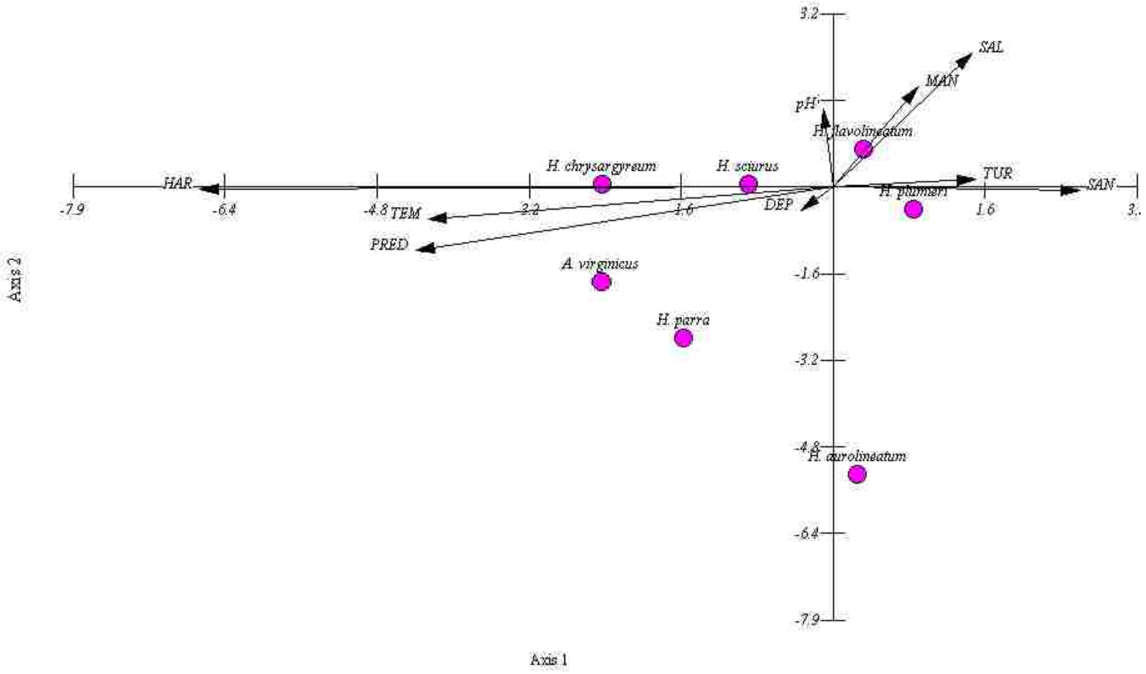


Figure 2.6a, b, c: Site-conditional biplot for the four IHMs based on a canonical correspondence analysis of the Haemulidae density data displaying 78% of variance in the weighted averages and class totals of species with respect to environmental variables. LC scores were used. Quantitative environmental variables are indicated by arrows in Figures b and c. The scale marks along the axes apply to the quantitative environmental variables. The codes represent the environmental variables as follows: MAN- % cover of mangroves; HAR - % cover of hard substratum; SAN - % cover of sand pH – pH; TUR – turbidity; SAL – salinity; TEM – temperature; DEP - average depth; and PRED - density of predators. Figure a presents species in relation to transects. Site names are omitted to reduce clutter in the diagram. Figure b presents the Haemulidae species in relation to the environmental variables. Species are weighted averages of site scores. Figure c presents transects in relation to environmental variables.

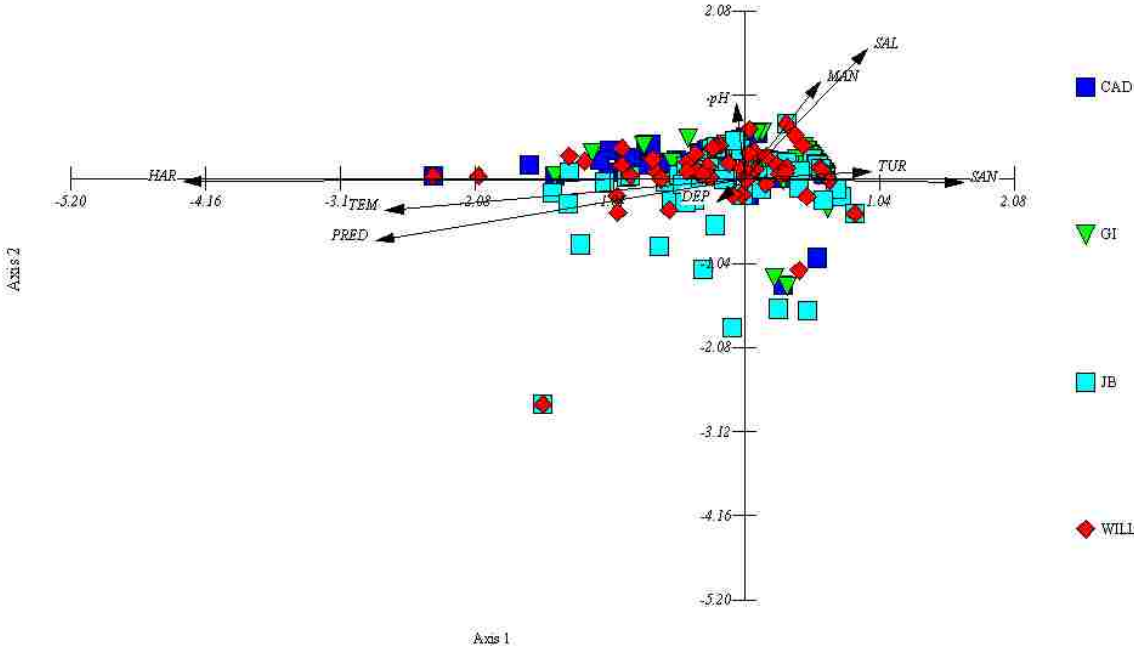
a



b


3.2
SAL
MAN
pH
H. flavolineatum
H. chrysargyreum
H. sciurus
TUR
HAR
SAN
H. plumieri
DEP
-7.9
-6.4
-4.8
TEM
-3.2
-1.6
1.6
3.
PRED
A. virginicus
-1.6
H. parra
-3.2
-4.8
H. aurolineatum
-6.4
-7.9
Axis 2
Axis 1

c


2.08
SAL
MAN
pH
CAD
TUR
HAR
SAN
-5.20
-4.16
-3.1
TEM
-2.08
-1.04
DEP
1.04
2.08
PRED
GI
-1.04
-2.08
JB
-3.12
-4.16
WILL
-5.20
Axis 2
Axis 1

CHAPTER THREE

INFLUENCE OF HABITAT QUALITY ON THE GROWTH AND CONDITION OF WHITE GRUNT (*HAEMULON PLUMIERI*)

Background

High quality habitats accrue fitness benefits in terms of growth and survival to the organisms using them (Rosenfeld and Boss 2001, Railsback et al. 2003). These high quality habitats are rich in food sources, offer refuge from predators and suitable spawning substrate, and have the right combination of environmental conditions that promote fast fish growth. These conditions allow individuals to outgrow the early life history stages that make them more vulnerable to predation and environmental stress (Werner et al. 1983, Houde 1987, Werner 2002). In previous chapters (Chapters 1 and 2) the concept of "habitat" for coastal fishes was expanded to include the mosaic of specific habitat types used by fish during their lifecycles to spawn, breed, feed and grow, and was given the synonym the interconnected habitat mosaic (IHM). This chapter will use the same terminology (IHM) to describe the interconnected habitats that influence the growth rates and condition of white grunt, *Haemulon plumieri* (Lacepède 1801).

The demography of fish populations, in particular individual fish growth, is influenced by a number of factors including environmental variables such as temperature, salinity, dissolved oxygen concentration and food supply (Brett 1979, Jobling 1994, Mommsen 1998, Wootton 1990) and anthropogenic influences such as the level of fishing pressure (Russ 1991, Roberts 1995, Halpern and Warner 2002). Haemulidae generally remain near their "home" reefs and usually undertake few large-scale movements (Springer and McErlean 1962, Moe 1966, Tulevech and Recksiek 1994, Kendall et al. 2003). As a result, Haemulidae may be very susceptible to localized changes in the quality of the environment in which they reside. Differences in the environmental conditions present in an area have notable influences on Haemulidae growth rates and condition and thus, differences in growth and condition of Haemulidae populations may indicate the relative quality of the habitats in which the populations reside. Murie and Parkyn (2005) suggested that the growth of the Haemulidae species *H. plumieri* might be modulated on a relatively small geographic scale. Thus, it is predicted that small differences in quality among IHMs that are geographically close to each other may be expressed as differences in the growth and condition of Haemulidae populations that live in these areas. Further, IHMs with the optimum levels of environmental and habitat characteristics that promote Haemulidae growth can potentially support fishes with greater growth rates and condition as compared to lower quality IHMs. These differences may be apparent even at the small geographic scale of the IHMs studied on the small Caribbean island of Antigua.

Growth, which is generally determined by measuring body length and weight and the age associated with these measurements (Claro and García-Arteaga 2001), can be defined as an increase in body length, condition and tissue energy concentration of fish (Bolger and Connolly 1988) and continues throughout the lifespan of fish. Indices like weight-length relationships, condition and growth rates, can be used to gauge the quality of IHMs. These indices provide an indication of the amount and quality of food available in the IHM for ingestion, assimilation and transformation into body mass and the ease of acquiring these resources by the individuals residing and feeding in these areas (Claro and García-Arteaga 2001). Reduction in consumption (the result of reduced food availability), or an increase in metabolic rates (the result of perturbations in abiotic environmental factors and/or increases in predator avoidance maneuvers) leaves less energy available for deposition of body tissues and thus may indicate an IHM of low quality. Weight-at-length, condition and length-at-age data are measures of the "well-being" or fitness of a fish. These indices assume that heavier fish for a given length or longer fish at a given age are in better condition or are healthier than their counterparts (Bolger and Connolly 1988, Jones et al. 1999, Sutton et al. 2000). Therefore, fish growth parameters, age structure, maximum longevity and condition factors can be used as proxies for the quality of IHMs.

H. plumieri, which was the focal species of this research, is a reef-associated species that attains maximum lengths of approximately 50.0 cm (Froese and Pauly, 2007). In Antigua and the wider Caribbean, it is a functionally dominant species in marine ecosystems and makes up a large percentage of the catches of subsistence near-shore reef fishermen (Appeldoorn and Lindeman 1985). The diet of *H. plumieri* is composed of a large variety of invertebrates (mainly crustaceans, mollusks, polychaetes, and echinoderms) and fish (Claro and García-Arteaga 2001, Cocheret de la Morinière et al. 2003). In addition, *H. plumieri* are typically nocturnal feeders that migrate from their daytime resting sites of coral reefs into seagrass beds and sand flats to feed at night (Hobson 1965, McFarland et al. 1979, Helfman et al. 1982, Rooker and Dennis 1991, Tulevech and Recksiek 1994, Burke 1995, Beets et al. 2003). Generally, *H. plumieri* are restricted to mangroves, seagrass beds and coral reefs that are situated within a few hundred meters of each other, and do not undertake substantial movements or seasonal migrations (Springer and McErlean 1962, Moe 1966, Tulevech and Recksiek 1994, Kendall et al. 2003).

The objective of this study was to compare the quality of three IHMs around Antigua using the parameters weight-at-length, condition and length-at-age for *H. plumieri* as proxies for the quality of these areas. The prediction here was that high quality IHMs would be inhabited by heavier *H. plumieri* at a particular length, longer *H. plumieri* at a particular age and *H. plumieri* in better condition than lower quality IHMs. Thus, in terms of environmental and habitat characteristics, the highest quality IHMs would potentially have feeding (soft-bottom) habitats that cover large areas, short traveling distances between feeding and resting habitats (resulting in reduced energy expenditure during feeding migrations) and levels of abiotic parameters that support maximum growth and consumption rates and reduced metabolic rates.

Methodology

Fish Collections

H. plumieri were caught monthly from June 2006 to December 2007 (Table 3.1) using three different fishing techniques at the three selected IHMs around the small Eastern Caribbean island of Antigua. These IHMs were all unique (see Chapters 1 and 2 and Appendix I) and were located on the southwestern coast at Cades (CAD), on the north eastern coast around Guiana Island (GI), and on the southeastern coast Willoughby Bay (WILL) of Antigua (Figure 1.2). To ensure that the parameters estimated in this study were true reflections of the entire fish populations at the IHMs studied, two types of sampling were conducted; fishery-dependent sampling (large individuals from commercial catches) and fishery-independent sampling (juveniles not trapped in fishermen's gear but caught using seine nets). *H. plumieri* that measured greater than 170 mm total length were caught by commercial fishermen using square and arrowhead fish traps of dimensions 1.37 m (length) by 0.46 m (width) by 0.97 m (height) and mesh size 1⅝". The fish traps were set on sand or seagrass beds in close proximity to coral reefs, in waters 1 to 30 meters deep. These traps were un-baited and were hauled at approximately one-week intervals. Gill nets 20 m long and 4 m wide with 2½" and 3" mesh were also used to catch adult *H. plumieri*. These nets were set over coral heads and hard bottoms; areas used by *H. plumieri* during the day for resting. Generally, gill nets were soaked for an average of 2 hours before retrieving but the total fishing time depended on the number of fish caught, and could last anywhere from 2 to 6 hours. *H. plumieri* that measured less than 170 mm total length were caught with seine nets (fishery-independent sampling). These nets were 3.3 m wide and 33.3 m long with mesh dimensions of 1.27 cm. They were set over seagrass beds and sandy areas. All captured *H. plumieri* were placed on ice until processing.

Fish and Otolith Processing

Each fish was uniquely numbered, and using a measuring board, the total length (TL) and fork length (FL) were measured to the nearest 0.1 cm. Fish weight was recorded to the nearest 0.1 gram using an electronic balance. In addition, data on the area of capture and date of capture were recorded for each individual. The two sagittal otoliths were extracted from the head of a sub-sample of the landed fish, rinsed in water to remove surrounding tissues and stored dry in labeled coin envelopes until they were sectioned. The left sagitta was preferably used for age estimation; however, if it was broken, lost or destroyed the right was used. For age analysis, three transverse (dorsoventral) sections were taken from each otolith using a low speed saw. One section was made on either side of the core, and the other encompassed the core. Sections were mounted on glass slides with thermal cement. Without knowledge of fish size, capture site or capture date, and using a compound microscope equipped with transmitted light, annuli were counted on each otolith section at 40x magnification. Annuli in sections viewed under transmitted light appear as opaque black rings (opaque zone) against an otherwise translucent background (translucent zone) (Murie and Parkyn 2005). Ages were assigned based on the number of opaque zones. Two readers independently counted the zones on each otolith section. The results of the two readings were compared and if there was a discrepancy in the counts between readers, the section was re-examined and independently aged by each reader a second time. An age was assigned only after three out of the four ages agreed. If ages did not agree, the otolith was discarded and not included in analyses. All *H. plumieri* were assigned an age based on the international birth date of January 1st (Chilton and Beamish 1982). This was necessary so that *H. plumieri* collected throughout the year could be correctly assigned to the appropriate age class based on the year of their birth. The periodicity in the opaque zone formation in sagittal otoliths (marginal increments) was assumed to be annual (Potts and Manooch 2001, Murie and Parkyn 2005, Araújo and Martins 2007).

Data Analyses

To determine if there were significant differences between frequency distributions of fish total length (cm) and weight (g) data among IHMs, the data were tested for normality and homogeneity of variances and the appropriate data transformations were performed, and either parametric (one-way ANOVA) or non-parametric (Kruskal-Wallis) tests were performed. If there were significant differences among IHMs, post-hoc multiple comparisons tests were performed to determine the IHMs contributing the most to these differences (Zar 1996). The relationship between the length and weight (i.e., "plumpness") of white grunt was described by the relationship:

$$\text{Log } 10\ W = \log 10\ a + b \log 10\ L \qquad \text{Equation 3.1}$$

where W = total wet weight in *g*; L = maximum total length in mm; a = the y-axis intercept of the regression; and b = the slope of the regression. This was then transformed into the power function:

$$W = aL^b \qquad \text{Le Cren (1951)} \qquad \text{Equation 3.2}$$

Differences in the log10 (weight) against log10 (total length) relationships among areas were tested using analysis of covariance (ANCOVA) (Zar 1996, Snedecor and Cochran 1989, Godinho 1997, Murie and Parkyn 2005). *H. plumieri* condition using the age combined data for each IHM was compared among IHMs using the Fulton condition factor (Safran 1992, Godinho 1997, Jones et al. 1999):

$$K = W / L^3 \qquad \text{Equation 3.3}$$

where K = Fulton condition factor, W= weight (g), L = total length (cm). The condition factors from each IHM were compared using a one-way ANOVA or a Kruskal-Wallis test after the data were tested for normality and equality of variances and transformed where appropriate, and post-hoc tests were used to determine where significant differences occurred.

Age and growth data of white grunt from the three IHMs were modeled by fitting the von Bertalanffy (Ricker, 1975) growth curve to the length-at-age data using regression procedures. The form of the von Bertalanffy growth curve for length-at-age was:

$$L_t = L_\infty \left[1 - e^{-K(t-t0)}\right] \qquad \text{Equation 3.4}$$

where L_t = total length at time t (age); L_∞ = asymptotic length; K = Brody growth coefficient which expressed the curvature of the growth function (Ricker 1975); and t_0 = theoretical age when length would be 0. To determine if the von Bertalanffy model gave a good fit to the length-at-age data, the curves were overlain on the actual length-at-age data for each IHM individually. If the model did not produce a good fit to the data, a number of data transformations were attempted including the non-transformed variables, the log transformed variables, the square root transformed variables, and the square root of the log transformed variables for the dependent variable total length (cm) and the independent variable age. The age data was recoded by adding 1 to all ages so that the transformations could be completed on fish 0 years old. A best-subset linear regression procedure was completed on the data for all the IHMs combined and the data transformation producing the highest coefficient of determination was selected. The intercepts and the slopes of the regression lines on the transformed data were then compared among IHMs to determine if there were significant differences in length-at-age data.

A combined age-length key was constructed for *H. plumieri* collected at the three sites in Antigua. Age-length data were grouped into 25-mm length classes. This age-length key was used to assign ages to the *H. plumieri* collected at each IHM for weight-length relationship comparisons, but not used for ageing via otolith analysis. The age distribution among IHMs was then compared for these landed fish using one-way ANOVAs or non-parametric Kruskal-Wallis tests on the transformed data where appropriate, after the data were tested for homogeneity of variances and normality.

Results

To compare weight-at-length relationships and condition of *H. Plumieri* among IHMs, 2,787 fish were caught at the three IHMs: 2,047 were caught on the southwestern coast (CAD); 369 on the northeastern coast (GI); and 371 on the southeastern coast (WILL) of Antigua (Tables 3.1 and 3.2 and Figure 3.1). The Kruskal-Wallis tests indicated a significant difference for both the total length ($H_{0.05,\,2} = 195.71$, $P < 0.001$) and total weight ($H_{0.05,\,2} = 169.34$, $P < 0.001$) among IHMs. Dunn's post-hoc multiple comparison test indicated that all the sites were significantly different from each other for both length and weight analyses (Table 3.3). The relationship between total body weight (W) and total length (TL, cm) (Figure 3.2) was:

CAD $W = 1.01 \times 10^{-2} (TL)^{3.09}$ ($r^2 = 0.94$, n = 2,047 $P < 0.001$)

GI $W = 2.16 \times 10^{-2} (TL)^{2.87}$ ($r^2 = 0.88$, n = 369 $P < 0.001$)

WILL $W = 9.66 \times 10^{-3} (TL)^{3.13}$ ($r^2 = 0.98$, n = 371 $P < 0.001$)

The results of the ANCOVA analysis indicated a significant difference among slopes ($F_{0.05,\ 2781}$ = 96.98, $P<0.001$) and among elevations ($F_{0.05,\ 2783}$ = 14.58, $P<0.001$) of the weight-at-length relationships.

The comparison of the Fulton condition factors among the IHMs for the combined age data showed that GI had the fish in the best condition ($14.29 \times 10^{-3} \pm 2.06 \times 10^{-3}$), followed by WILL ($14.14 \times 10^{-3} \pm 2.11 \times 10^{-3}$) and finally CAD ($13.68 \times 10^{-3} \pm 2.05 \times 10^{-3}$). The Kruskal-Wallis test performed to compare the condition factors among the IHMs indicated a significant difference among IHMs ($H_{0.05,\ 2}$ = 10.79, P = 0.005). Dunn's multiple comparison test revealed that CAD and WILL were significantly different from each other (Q = 2.52, $P < 0.05$, Cohen's d = 0.22), CAD and GI were significantly different from each other (Q = 2.47, $P < 0.05$, Cohen's d = 0.14) but GI and WILL were not significantly different from each other (Q = 0.040, $P > 0.05$, Cohen's d = 0.074).

To compare von Bertalanffy growth curves among the IHMs, 635 otoliths were sectioned from *H. plumieri* landed in Antigua. Six hundred and twenty-nine (99 %) of the otoliths were assigned ages based on the agreement between the readings of the primary and secondary reader (all ageing disagreements were ± 1 year difference). Of this number, 224 otoliths were from fish caught at CAD, 310 from fish caught at GI and 95 from fish caught at WILL (Figure 3.3). These individuals were all assigned ages between 0 to 15 years. Between these two extremes there was generally an even spread of ages for all IHMs. For CAD, 3 years was the most common age, 4 years the most common at GI and a tie between 2 and 3 years at WILL (Figure 3.3). At CAD there were no 13 year-old fish in the samples and for WILL there were no 13, 14 or 15 year-old fish in the samples (Figure 3.3). The von Bertalanffy growth curves (Figure 3.4) for the three sites were:

CAD	$L_t = 27.1\ [1\text{-}e^{-0.46(t-0.20)}]$
GI	$L_t = 26.7\ [1\text{-}e^{-0.33(t-0.10)}]$
WILL	$L_t = 26.9\ [1\text{-}e^{-0.51(t-0.20)}]$
ALL (IHMS combined)	$L_t = 28.1\ [1\text{-}e^{-0.42(t-0.30)}]$

As figure 3.4 illustrates, the individual von Bertalanffy growth curves for the different IHMS did not give a good fit to the data, especially for fish 0 – 3 years old. A best-subset linear regression procedure, using a number of different data transformations, suggested that for data from all sites combined, the highest coefficient of determination ($R^2 = 0.61$) was given by a simple combination of log transformed total length data against the square root of the log of (age +1) transformed data. A comparison of the intercepts and slopes of the regression lines for the three sites using the transformed data indicated that CAD and GI did not differ in slopes ($P = 0.8584$) (Figure 3.5). These data were then combined and the slopes and elevations of the regressions were tested against WILL. Both the intercept and slope of this combined data were significantly different from that of WILL (slope – $F_{0.05,\,623} = 6.20$, $P = 0.002$; elevation – $F_{0.05,\,625} = 9.04$, $P = 0.0001$). Further, young fish at WILL were smaller on average than those from CAD and GI (Figure 3.5).

The age-length key for the combined IHM age data is presented as Table 3.5. The age distribution of the catches from each IHM showed that GI had the oldest fish in the catches 7 ± 4 years, CAD the second oldest 6 ± 4 years and WILL the youngest 4 ± 3 years. The age of the catches from the different IHMs were significantly different from each other ($H_{0.05,\,2} = 162.28$, $P < 0.001$) and the post-hoc tests showed all IHMs were different from each other (CAD – GI $Q = 6.03$, $P < 0.05$, Cohen's $d = 0.25$; CAD – WILL

Q = 9.62, $P < 0.05$, Cohen's d = 0.57; and GI - WILL Q = 12.03, $P < 0.05$, Cohen's d = 0.85).

Discussion

The results of this study, which compared habitat quality at three contrasting IHMs around Antigua, indicated that GI had the highest quality and CAD the lowest quality. Generally, the habitat qualities of GI and WILL were much more similar to each other than either was to CAD. Growth and condition of *H. plumieri* were used as proxies to gauge the quality of each of these IHMs, because these indices are greatly influenced by the abiotic, biotic and anthropogenic-related conditions present within habitats (Brett 1979, Jobling 1994, Mommsen 1998, Wootton 1990, Russ 1991, Roberts 1995, Halpern and Warner 2002, Murie and Parkyn 2005). Thus, growth and condition can indicate the inherent quality of one IHM relative to another based on the inherent environmental characteristics of the IHMs.

The weight-at-length relationship for each IHM revealed that GI had the greatest relationship followed by WILL and then CAD, and that these weight-at-length relationships for the three IHMs were significantly different from each other. Thus, at any chosen length, *H. plumieri* from GI were on average heavier than individuals from CAD or WILL. This result suggests that GI was a higher quality IHM than CAD and that both GI and WILL were of higher quality than CAD. Further, these results suggest the presence of habitat and environmental differences at the small geographic scale of these IHMs that may be influencing the weight-at-length relationships of the *H. plumieri* populations utilizing these IHMs. The same tendency was found in a study by Murie and

Parkyn (2005), in which they suggested that the growth of *H. plumieri* may be controlled on a relatively small geographic scale of less than 100 km. The results of their study showed that *H. plumieri* in the north-central area of the west coast of Florida were consistently larger than fish from the central area of the west coast of Florida, even though there was a distance of only about 70 km separating these two sampling regions. The results of the Muire and Parkyn study are similar to the results of the present study for Antigua and highlight the susceptibility of *H. plumieri* populations to growth differences due to small-scale variation in habitat quality among areas separated by small geographic distances.

H. plumieri condition was greatest at GI, followed by WILL and then CAD. In addition, the condition of the *H. plumieri* at CAD was significantly different from the fish at GI and WILL but the condition of the *H. plumieri* at GI and WILL were not significantly different from each other. Condition factors give an indication of the health of a fish and how well it is doing in its environment (Bolger and Connolly 1988). Studies have shown that variations in fish condition primarily reflect extrinsic conditions such as; food availability, suitability of the environment and seasonal changes in environmental parameters (Le Cren 1951, Godhino 1997, Lambert and Dutil 1997a 1997b, Williams 2000, Yaragina and Marshall 2000). Therefore, the results of this study indicate that, in terms of environmental conditions, which are shown to have a direct impact on the health of fish, GI was the IHM with the best habitat quality followed by WILL. CAD was the IHM of the lowest quality. Similar studies into the influence of environmental characteristics on fish condition (Grecay and Targett 1996, Perry et al. 1996, Rätz and Lloret 2003) have shown that different stocks or populations of fish display different levels of condition related to the environmental characteristics of their habitats, including spatial differences in food availability and temperature.

A comparison of the distribution of ages within the populations and the mean age of fish caught at the IHMs highlights the differences in underlying habitat quality among the three sites. At both CAD and GI, the oldest fish caught were 15 years old, while the oldest fish caught at WILL were only 12 years old. In addition, the mean age of fish within the catches was highest at GI and lowest at WILL. These results further reinforce the fact that GI appeared to be the IHM of highest quality.

Potentially, the IHM characteristics having the biggest influence on *H. plumieri* growth and condition were 1) the availability of food in each IHM, as indicated by the amount of soft-bottom habitat available, 2) the proximity of soft-bottom feeding habitats to hard-cover resting habitats and juvenile habitats, and 3) the abiotic regime present in each IHM that may have had an influence on consumption and metabolic rates. Estimates of the precise amount of food available to *H. plumieri* may be critically important in the elucidation of habitat quality because the expression of growth rates in terms of tissue deposition, and fish condition rest heavily on the amount of food consumed and the efficiency by which this food is used (Rosenfeld and Boss 2001, Railsback et al. 2003). In 2001, Claro and García-Arteaga showed that growth rates in mutton snappers on the northwest coast of Cuba were lower than on the southwest coast during the first three years of life, and then faster in subsequent years. They proposed that this difference might be related to the relative extent of habitat available for juveniles and for adults. The preferred habitat for juveniles (seagrass beds) is more extensive in the southwest of Cuba, resulting in larger size-at-age in southwest than northwest individuals. However, the area of adult habitat (shelf-border reef and patch reefs) is similar in both regions, resulting in higher amounts of food available per adult individual in the northwest as opposed to the southwest. Specifically for the three IHMs studied in Antigua, both GI and WILL had much larger areas of soft-habitat than CAD. At GI, 69.9 % of the total area was covered by feeding areas and 72.3% at WILL however; only 34.6% of CAD was covered by feeding areas (Table 2.4).

Studies around the Caribbean have illustrated the importance of seagrass and other soft-bottom habitats as the primary source of food for both juvenile grunts residing in mangrove areas, and larger adult and sub-adult individuals that rest on hard-bottom areas during the day (Collette and Talbot 1972, Helfman et al. 1982, Quinn and Ogden 1984, Nagelkerken et al. 2000a, 2000b, Cocheret de la Morinière et al. 2003, Nagelkerken and van der Velde 2004a, 2004b). In terms of the proximity of soft-bottom feeding habitats to hardcover resting habitats and juvenile habitats, all three IHMs had approximately the same distance between these habitats (less than 10 meters separating them) (Table 2.4). Conversely, the average distance between seagrass and mangroves was much lager for CAD than for GI or WILL (less than 10 m at GI and WILL, and greater than 100 meters at CAD). Thus, if a large proportion of the juvenile *H. plumieri* at the three IHMs use mangrove areas as their primary juvenile habitat, the individuals at CAD would expend larger amounts of energy during their daily feeding migrations than either juveniles at GI or WILL, thus leaving less energy available for somatic growth. More importantly though, at both GI and WILL, seagrass and mangroves habitats were in direct connection with each other allowing the migration of juvenile grunts into the seagrass beds to feed unobstructed. At CAD however, the larger of the two mangroves stands at this IHM was separated from the seaward seagrass beds and coral communities by a ridge of coral rubble that was inundated only at high tide. Thus, at low tide, the mangroves and their accompanying biological communities were separated from the other habitats by this coral rubble ridge. This obstruction of the regular movement of juvenile grunts from mangroves to seagrass beds may have big implications for the growth of fish at CAD because regular feeding migration routes may be blocked with the falling tide.

The length-at age data for the three IHMs indicated that young fish at WILL were on average smaller than young fish at either CAD or GI. For older individuals however, there were no apparent differences among the IHMs. This is an interesting and unexpected result since the other growth and condition factors investigated indicated that the quality of WILL was slightly lower than that of GI but higher than that of CAD. It is possible that the smaller size of young fish at WILL maybe related to competition among these juveniles for food and space. Density comparisons among IHMs based on underwater visual survey data (Chapter 2) indicated that WILL had the highest density of all Heamulidae species combined and of *H. plumieri* by itself. In addition, for the community structure and distribution pattern parameters (density, length-frequency distribution, biomass, and ratio of juveniles to adults) measured in Chapter 2, WILL was the IHM with the highest overall quality. WILL was also the IHM with the highest structural complexity. This high structural complexity at WILL potentially provided a large number of predator refuges. Studies have shown that habitat heterogeneity can modify the outcome of biological interactions such as competition and predation (Coen et al. 1981, Danielson 1991). Competition and predation can influence the structure of ecological communities by increasing mortality rates, which results in altered densities and age structures. Predation and competition can also alter fish growth rates (Beukers and Jones 1997). Although habitat complexity reduces the impacts of predation by providing refuges against predators (Werner et al. 1983, Menge and Sutherland 1987, Hixon and Menge 1990), it also increases competitive interactions because more individuals survive to use the available resources. Thus, the high structural complexity of WILL may have caused reduced predator impacts, but enhanced competition among juvenile *H. plumieri* and other Haemulidae species because of enhanced survival of juveniles and new recruits. It is important to note here that reef associated species such as *H. plumieri* have relatively high growth rates, so much so, that by the second year of life, 35-50% of maximum size can be attained (Claro and García-Arteaga, 2001, Potts and Manooch 2001, Muire and Parkyn 2005, Araújo and Martins 2007). Therefore, small changes in food consumption may result in significant differences in length-at-age for young fishes. Studies such as stomach content analysis and experiments aimed at investigating competitive interactions may help clarify whether the juveniles at WILL do actually consume less food on average than those at CAD or GI. The lack of significant length-at-age differences among IHMs for the older sized fish may be related to the combined influence of the area of adult habitat and the amount of feeding habitat available, along with post-settlement processes not investigated here.

For some of the abiotic parameters tested (see Chapter 2) there were significant differences among IHMs (Table 2.6). These differences may have great implications for fish growth and condition. Three of the abiotic characteristics of the IHMs potentially having the greatest influence on fish growth and condition were turbidity, salinity and temperature. Turbidity can negatively affect fish growth and condition by limiting fish vision, thereby interfering with social behavior (Berg and Northcote 1985), foraging efficiency (Gregory and Northcote 1993, Vogel and Beauchamp 1999) and predator avoidance maneuvers (Miner and Stein 1996, Meager et al. 2006). Turbidity was significantly different between CAD and WILL (Chapter 2). The effect of salinity is expressed in the modification of the standard metabolic rate (Woo and Kelly 1995, Dutil et al. 1997), total food intake (Dendrinos and Thorpe 1985, Lambert et al. 1994, Buckel et al. 1995, Peterson-Curtis 1997), food conversion efficiency (Arunachalam and Reddy 1979, Lambert et al. 1994, Likongwe et al. 1996) and the balance of hormones involved in metabolism (Bluf and Payan 2001, Handeland et al. 2000). Salinity was significantly different between CAD and WILL and GI and WILL (Chapter 2). Temperature influences the rates of ingestion and metabolism (Malloy and Targett 1991, Jobling 1994) and modifies the influence of all the other abiotic variables. Temperature was significantly different between CAD and WILL and GI and WILL (Chapter 2). Small-scale variations in these abiotic characteristics among the IHMs may partially explain the differences seen in *H. plumieri* growth and condition.

Overall, the results of this study indicate that GI was the IHM of the highest quality based on the growth and condition of *H. plumieri*; indices which were used as proxies for habitat quality. GI had the *H. plumieri* populations with the highest weight-at-length relationships and in the best condition. The extensive feeding areas, the proximity of soft-bottom feeding habitats to hard cover resting habitats and juvenile habitats, and the abiotic regime present at GI may have acted together to make this an IHM of higher quality than WILL or CAD.

Table 3.1 Summary table of the number of individuals, mean total length (cm) ± SD, and mean weight (g) ± SD of *H. plumieri* caught monthly at each IHM during June 2006 to December 2007. Cades Reef (CAD) located on the southwest coast; around Guiana Island (GI) located on the northeast coast; on the north coast from Boons Point to Shoal Point (JB); and Willoughby Bay (WILL) located on the southeast coast of Antigua.

Month	**CAD**			**GI**			**WILL**		
	# of Fish	**Mean TL (cm)**	**Mean Weight (g)**	**# of Fish**	**Mean TL (cm)**	**Mean Weight (g)**	**# of Fish**	**Mean TL (cm)**	**Mean Weight (g)**
Jan	192	25.3 ± 1.8	236.3 ± 51.6	55	25.3 ± 0.5	236.9 ± 35.1	73	20.8 ± 0.4	128.7 ± 25.7
Feb	22	23.2 ± 5.4	191.6 ± 134.3	35	26.6 ± 0.3	290.3 ± 41.4	49	22.2 ± 0.4	156.4 ± 18.5
Mar	406	22.0 ± 1.6	151.1 ± 35.7	11	27.4 ± 0.1	295.8 ± 34.3	6	23.0 ± 0.2	174.2 ± 21.3
Apr	387	23.2 ± 2.4	159.5 ± 73.5	6	27.8 ± 0.4	332.7 ± 31.2	5	24.3 ±0.3	204.4 ± 19.8
May	207	23.3 ± 2.8	171.5 ± 60.5	14	28.3 ± 0.2	314.6 ± 44.2	4	24.7 ± 0.4	222.3 ± 20.0
Jun	154	22.8 ± 2.2	176.7 ± 53.8	31	29.3 ± 0.5	338.2 ± 45.2	5	23.5 ± 0.4	188.2 ± 21.7
Jul	109	10.7 ± 2.7	21.2 ± 47.2	8	30.8 ± 0.7	366.8 ± 31.8	52	24.0 ± 0.8	202.7 ± 33.4
Aug	162	27 .0 ± 3.1	312.7 ± 80.1	123	21.6 ± 2.0	147 ± 35.4	11	26.6 ± 0.7	278.6 ± 29.2
Sep	326	24.7 ± 3.0	216.3 ± 70.9	64	23.9 ± 0.4	193.0 ± 28.1	123	14.4 ± 4.5	54.4 ± 44.5
Oct	60	24.1 ± 2.5	203.8 ± 71.3	4	33.0 ± 1.1	426.8 ± 23.2	11	17.1 ± 4.1	83.5 ± 42.5
Nov	8	25.1 ± 3.0	237.5 ± 89.6	7	23.9 ± 0.5	192.3 ± 35.4	11	26.3 ± 0.8	259.8 ± 36.7
Dec	14	28.0 ± 2.5	344.0 ± 83.9	11	22.1 ± 1.1	145.6 ± 28.1	16	26.5 ± 0.9	263.1 ± 56.1

Table 3.2: Summary of the total number of fish caught at each IHM, the range of total and fork lengths (cm) and the range of weights (g) of *H. plumieri* used for weight-at-length and condition analyses.

IHM	Number of Individuals	Range of FL (cm)	Range of TL (cm)	Range of weight (g)
CAD	2047	7.0 – 29.4	7.8 – 33.3	8.0 - 453.0
GI	369	10.8 – 29.0	12.3 – 34.6	31.0 – 460.0
WILL	371	7.5 – 26.2	8.5 – 29.5	8.0 – 409.0

Table 3.3: Dunn's pair-wise multiple comparison test results and effect sizes for total length (cm) and weight (g) comparisons between the three IHMs CAD, GI and WILL. The values on the top part of the table represent the total length comparisons and the values on the bottom of the table highlighted in grey represent the weight comparisons. The values in the table are Q-values, and the effect size values (Cohen's d values) are italicized. The level of significance is P < 0.05.

	CAD	GI	WILL
CAD	------	6.51	11.24
		0.41	*0.65*
GI	7.56	------	13.63
	0.43		*1.06*
WILL	9.31	12.96	------
	0.55	*1.01*	

Table 3.4: von Bertalanffy parameters (± 1 SE) fitted to total length (TL)-at-age data for *H. plumieri* from the three IHMS in Antigua.

IHM	L_∞ (cm)	K	t_0 (years)	n	Range of ages (years
CAD	27.1 (7.26)	0.46 (0.16)	- 0.42	224	1 – 12 and 14-15
GI	26.7 (3.50)	0.61 (0.12)	- 0.33	310	1-15
WILL	26.9 (5.46)	0.51 (0.24)	- 0.38	95	1-12
ALL	28.1 (5.47)	0.42 (0.35)	- 0.08	629	1-15

Table 3.5: Age-length key of *H. plumieri* from the combined data of the three IHMs. Only one key was produced because the von Bertalanffy growth equations were not significantly different from each other. The table shows the number of fish in 25-mm length (TL) categories as a function of age.

TL (mm)	**N**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**
75-99	1	1															
100-124	18	18															
125-149	10	8	2														
150-174	10	0	6	3	1												
175-199	46	4	7	13	12	8	2										
200-224	148	3	14	28	39	26	23	12	3								
225-249	197		7	20	27	34	31	43	25	8	2						
250-274	114			8	32	14	13	15	12	7	6	3	1	1	2		
275-299	69			2	11	9	3	6	10	7	1	4	7	4	3	1	3
300-324	13						2	3	1	2	1	1				2	1
325-349	1																1
Total	**629**	**34**	**36**	**74**	**122**	**91**	**74**	**79**	**51**	**24**	**10**	**8**	**8**	**5**	**5**	**3**	**5**

Figure 3.1: Size frequency distribution of *H. plumieri* caught at the three IHMs Cades Bay (CAD), Guiana Island (GI) and Willoughby Bay (WILL). Total lengths are in 1 cm intervals.

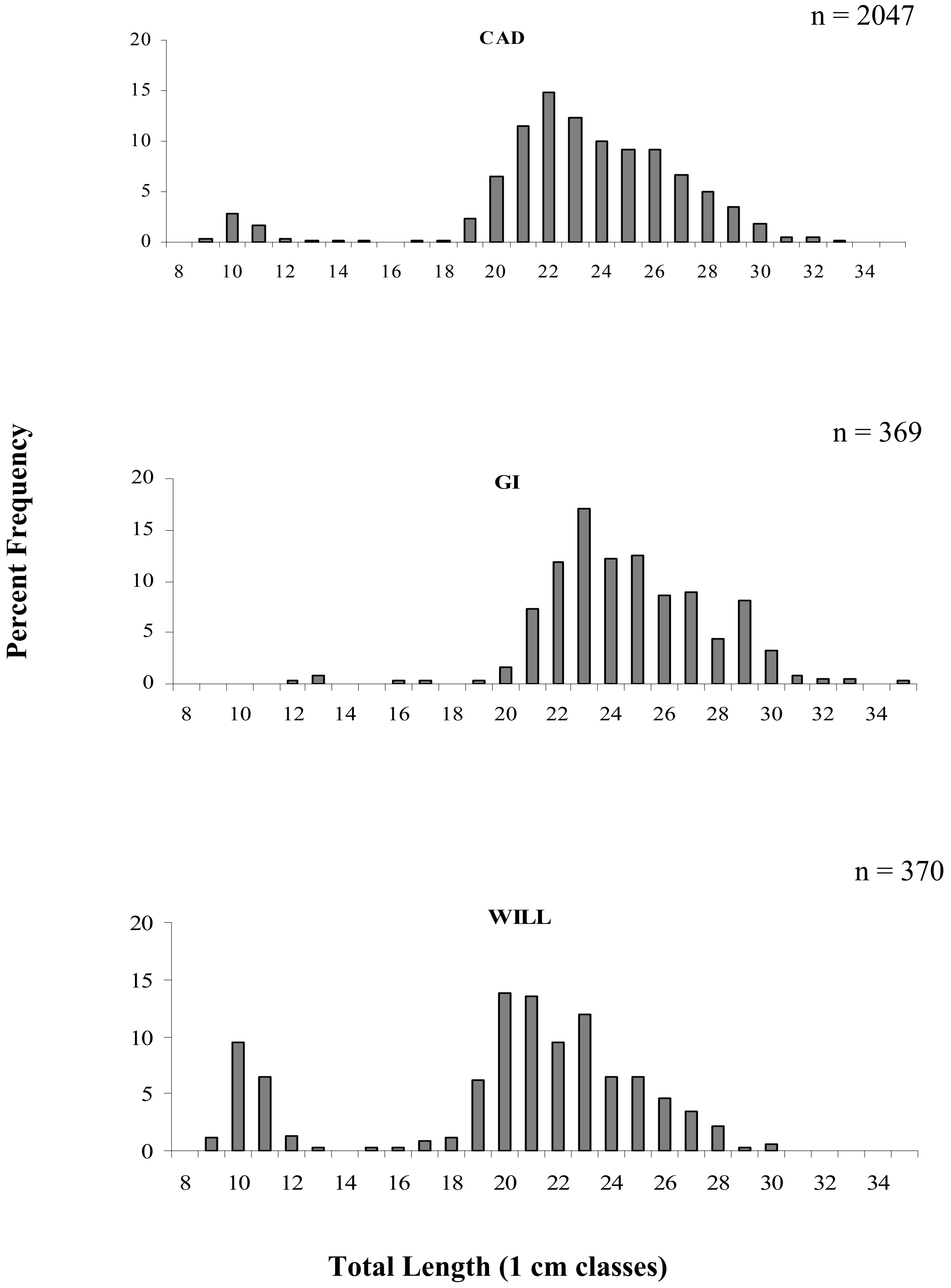


Figure 3.2: Total body length as a function of total body weight for grunts caught at the three IHMs.

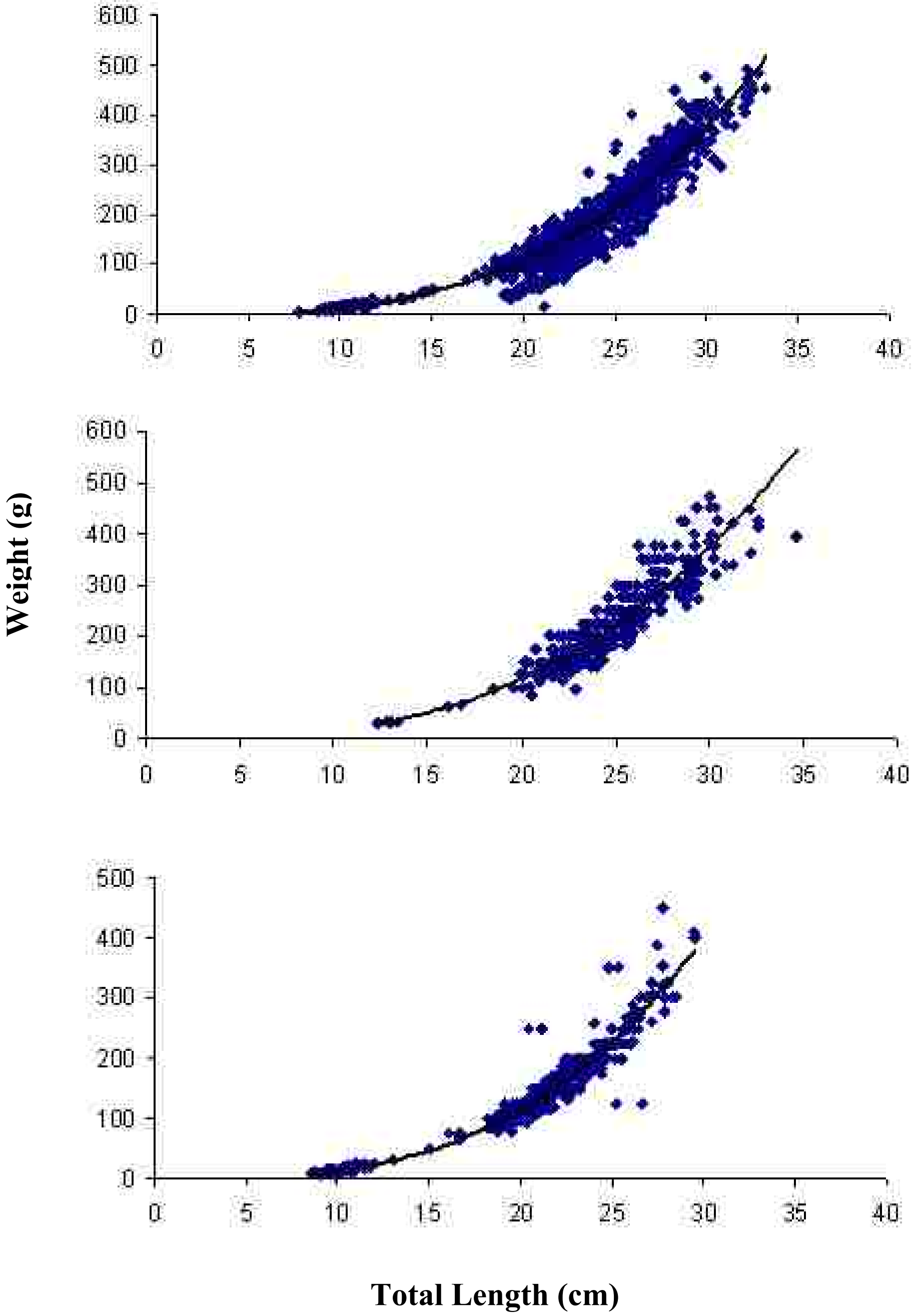


Figure 3.3: Age frequency distribution of *H. plumieri* caught at the three IHMs.

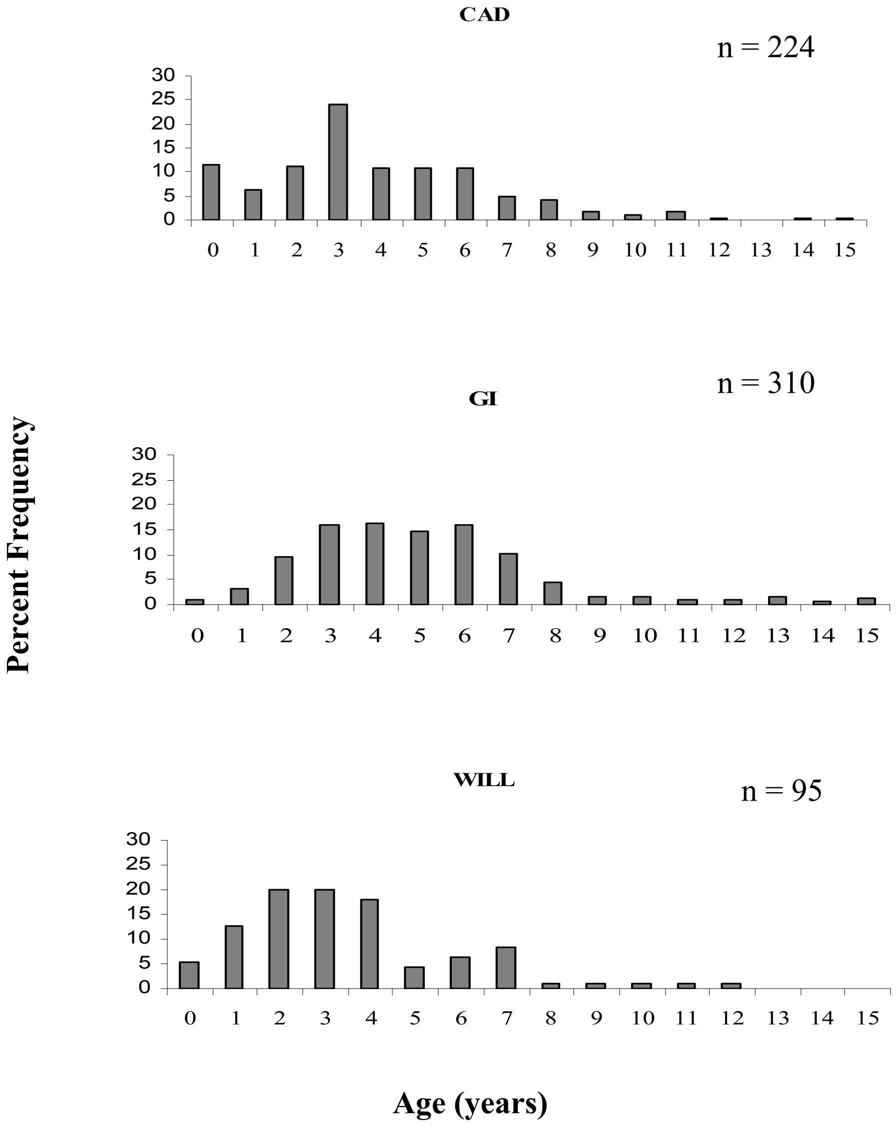


Figure 3.4: von Bertalanffy growth curves fitted to total length as a function of age for *H. plumieri* caught at the three IHMs around Antigua.

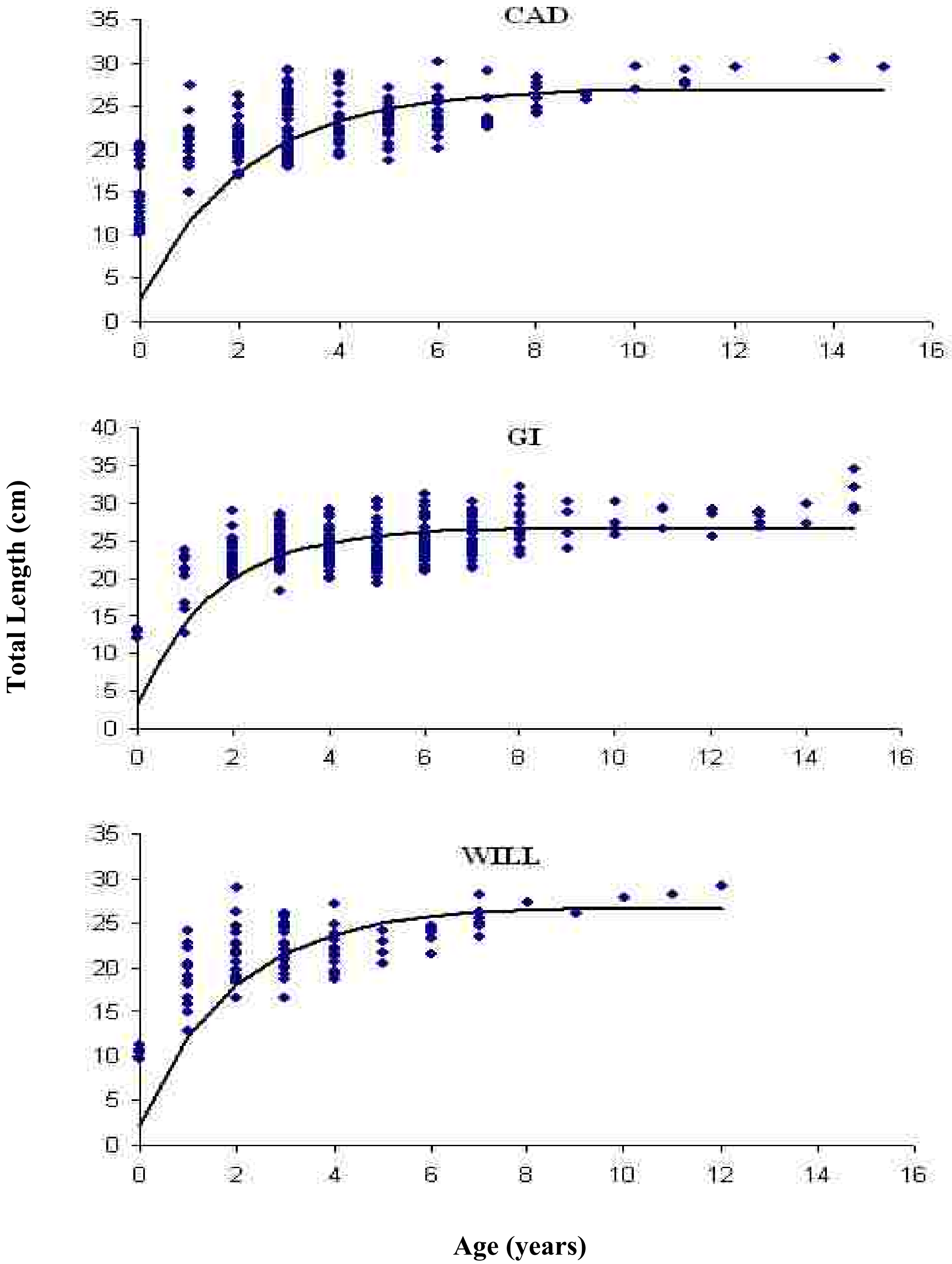
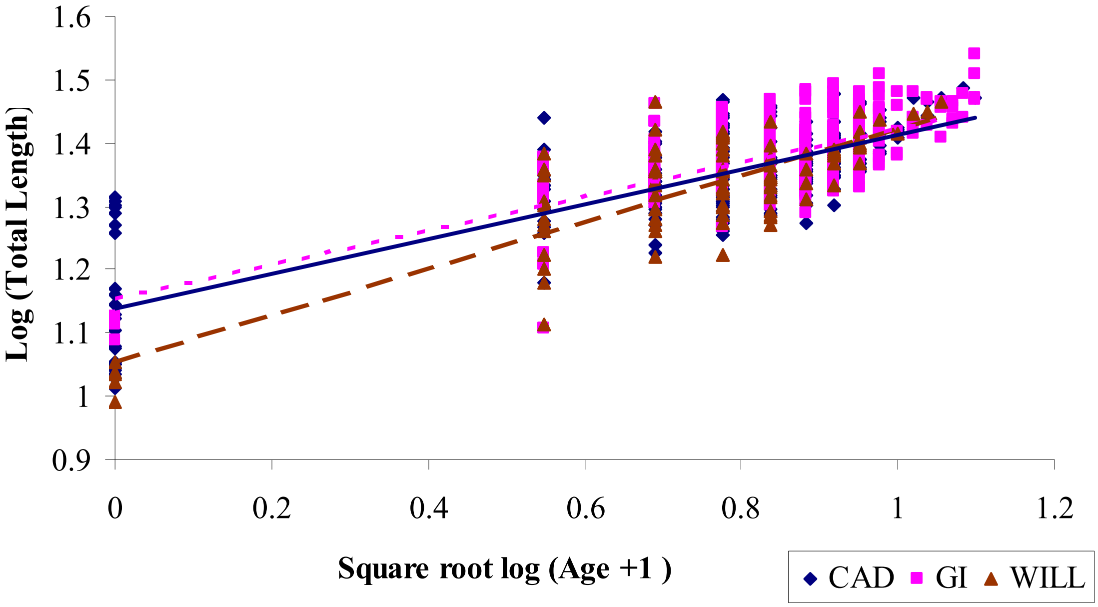


Figure 3.5: Linear regression of square root log transformed age + 1 data against log transformed total length data for *H. plumieri* from the three IHMs around Antigua.



CHAPTER FOUR

TEMPERATURE AS AN INDICATOR OF HABTAT QUALITY: AN EXPERIMENTAL APPROACH USING THE GROWTH OF WHITE GRUNT (*HAEMULON PLUMIERI*)

Background

Marine habitats are not all equivalent in quality. High quality habitats provide the conditions necessary for successful growth, survival and reproduction of fish over long periods (Able 1999, Werner 2002, Necaise et al. 2005, Morrison et al. 2006). High quality habitats are rich in food sources, offer refuge from predators and suitable spawning substrate, and have the right combination of environmental conditions to promote fast fish growth so that individuals can outgrow the early life history stages that make them more vulnerable to predation and environmental stress (Werner et al. 1983, Houde 1987, Werner 2002). There likely is an optimum suite of environmental parameters the levels and rate of change of which influence attainment of maximum fish growth rates in tropical marine areas. For these exogenous parameters, fish normally have a narrow preference limit rather than a fixed value. When outside their optimum range or when changes in these parameters occur too rapidly, the physiological systems of fish can be stressed, resulting in increases in the diversion of energy to maintain internal physiological state, with subsequent decreases in growth rates, and possibly death. Short-term exposure to these environmental stressors is not normally lethal, but they do negatively effect feeding and growth (Brett 1979, Jobling 1994, Mommsen 1998, Wootton 1990).

Fish growth is an excellent gauge of habitat quality because it is sensitive to environmental perturbations and is a good indicator of the success of a fish within its environment. Growth can be defined as an increase in the energy content of an organism’s body as a result of food intake (Brett 1979, Jobling 1994), and it is strongly associated with the abiotic and biotic characteristics of the environment (Brett 1979, Claro and García-Arteaga 2001). Environmental variables including temperature, salinity, dissolved oxygen concentration, and food supply have profound influences on fish growth (Brett 1979, Jobling 1994, Mommsen 1998, Wootton 1990). Coral reef fish are particularly susceptible to localized changes in the abiotic parameters. Therefore, they are sensitive to the quality of the environments where they reside because they generally remain near their “home” reefs and seldom exhibit long-distance movements (Springer and McErlean 1962, Moe 1966, Tulevech and Recksiek 1994, Kendall et al. 2003).

Temperature is one of the critical variables in the physiological ecology of fish (Elliott 1994, Jobling 1994, Werner 2002). Fish are poikilotherms (Brett 1956) whose growth rates are influenced by their ambient water temperature (Jobling 1994, Elliot 1994) such that any changes in the environment greatly affect their rates of ingestion and metabolism (Jobling 1994) and ultimately their growth potential (Malloy and Targett 1991). In the wild, fish have the option to move among habitats to stay within optimum temperature ranges (Mommsen 1998), but that makes ecological studies difficult, because it is impossible to directly determine and measure the ambient temperature regimes having the greatest influence on the growth rates of free ranging fish. Le Pape et al. (2003) suggested that in investigations of the influence of habitat quality on the growth of fish, it is necessary to use a more sensitive and less integrative method, such as caging experiments, which better respond to environmental perturbations. Further, an integrative indicator of growth, such as size, which represents intrinsic habitat quality, should also be used. Several studies that have employed fish cages and enclosures to evaluate the influence of habitat quality on juvenile fishes (Sogard 1992, Guidon and Miller 1995, Duffy-Anderson and Able 1999, Able et al. 1999) have been able to demonstrate the effects of environmental characteristics, including temperature, on growth rates. Therefore, to ensure that the growth rates attained in this study were directly related to the temperature regimes experienced by fish, cages were used.

Manipulations of environmental parameters including temperature, lead to increases in growth rates and are well documented in aquaculture and laboratory-based energetic studies. These research studies usually involve the manipulation of a single environmental variable under otherwise constant conditions (Malloy and Targett 1991, 1994, Taylor and Miller 2001) because it is extremely difficult to carry out investigations manipulating several variables at one time. Laboratory experiments, however, have limited application in field ecological studies because the ecological success of wild stocks is influenced by a number of interacting environmental characteristics. In addition, it is impossible to accurately model the natural environments of fish in the laboratory (Jobling 1994). Thus, ecological studies on fishes require new approaches, such as in situ experiments, to examine fish growth rates. In situ experiments have the advantage of allowing the investigation of energy partitioning and growth rates in wild populations of fish with slight modifications to the conditions fish will usually experience in nature.

White grunt, *Haemulon plumieri* (Lacepède 1801), is a reef associated species with relatively high growth rates, so much so, that by the second year of life, 35-50% of maximum size can be attained (Claro and García-Arteaga, 2001, Potts and Manooch 2001, Muire and Parkyn 2005, Araújo and Martins 2007, Chapter 3 of this research). In

Antigua and the wider Caribbean, it is a functionally dominant species in marine ecosystems, and makes up a large percent of the catches of subsistence near-shore reef fishermen (Appeldoorn and Lindeman 1985). The diet of *H. plumieri* comprises a large variety of invertebrates (mainly crustaceans, mollusks, polychaetes, and echinoderms) and fish (Claro and García-Arteaga 2001, Cocheret de la Morinière et al. 2003). In the wild, *H. plumieri* can be found in all near-shore naturally occurring marine and artificial habitats (seagrass beds, mangroves, coral reefs, artificial jetties) (Appeldoorn et al. 1997, Collette and Talbot 1972, Helfman et al. 1982, Quinn and Ogden 1984, Nagelkerken et al. 2000a and 2000b, Cocheret de la Morinière et al. 2003, Nagelkerken and van der Velde 2004a, 2004b)

The aim of this study was to investigate experimentally the influence of the abiotic environmental variable temperature on the growth rates of *H. plumieri*. More specifically, this study used the temperature regimes present in four different habitats (seagrass beds, mangroves, coral reefs and an artificial jetty) as proxies for habitat quality to determine how *H. plumieri* growth rates are affected by variations in habitat quality. Four different habitats were selected to ensure that there would be noticeable differences in the temperature regimes experienced by caged *H. plumieri*. The experiment was carried out in the field so that growth rates under somewhat natural conditions could be investigated. The questions addressed were: 1) are there differences in the mean daily temperatures experienced by the *H. plumieri* caged in each habitat; 2) are there differences in the daily T_{max} - T_{min} experienced by the *H. plumieri* caged in each habitat; 3) are there differences in mean growth rates among the different habitats investigated; 4) is there a relationship between growth rates and mean daily temperatures experienced by the *H. plumieri*; and 5) is there a relationship between growth rates and daily T_{max} - T_{min} values experienced by *H. plumieri*?

Methodology

Fish Collection and Handling

The study was carried out in four different habitats along the northeastern coastline of Antigua (Figure 4.1). *H. plumieri* that measured between 70 mm and 140 mm total length were used in the study because they were juveniles (Stages 1 and 2) based on the life-history stages of *H. plumieri* proposed by Appeldoorn et al. (1997)), suggesting that they were not yet sequestering energy towards the maturation of reproductive structures, and that they were still actively growing (Claro and García-Arteaga, 2001, Potts and Manooch 2001, Muire and Parkyn, 2005, Araújo and Martins 2007, Chapter 3 of this research). To ascertain energy allocation to somatic development as opposed to gonad development, the gonads of a number of *H. plumieri* of similar sizes to cage residents were investigated and all were found to be immature. In addition, all surviving fish dissected at the end of the experiment were found to be immature.

Modified Antillean fish traps of dimensions 1.33 m by 1 m by 0.5 m, and ½" mesh zinc wire, baited with conch and fish, were used to catch juvenile *H. plumieri*. The traps were left in place for 24 hours before collection. Juvenile fish of the desired species in good condition (based on their swimming ability) were selected and placed in holding bins containing circulating seawater until processing. The total length of each fish was measured to the nearest mm, the fish was tagged between the pterygiophores of the dorsal fin with numbered FLOY spaghetti tags (for individual identification) and then the fish was placed in a holding bin to assess its condition. All fish displaying good swimming ability were placed in growth cages or released back into the natural environment. Approximately 25 juvenile *H. plumieri* were randomly assigned to each growth cage. The dimensions of the growth cages were similar to those of the modified Antillean traps used to capture the juvenile *H. plumieri* (dimensions 1.33 m by 1 m by 0.5 m, and ½" mesh zinc wire). The cages had a trap door that allowed food to be placed inside, and the fish to be removed. The cages were not placed flat on the substrate, but were elevated on legs such that the base of each cage was approximately 1 m above the level of the substrate.

Two growth cages were positioned in each of the four focal habitats; mangroves, seagrass, coral reef and an artificial habitat (a rock jetty). The cages were placed right next to each other in each habitat. In the seagrass habitat, the cages were placed 35 meters from the high tide mark and in water 1.3 meters deep at high tide. This habitat was vegetated by T*halassia testudinum* and a number of algae species including the calcareous algae *Halimeda* spp. The cages under the jetty were placed 48 m from the high tide mark, in water 1.8 m deep at high tide. The benthic substrate in this area was a combination of sand and mud. The cages in the mangroves were placed 30m from the seaward edge of the mangroves in water 1.4 m deep at high tide. The substrate in this area was composed mainly of sandy mud covered by seagrass and algae (not as dense as in the seagrass habitat). The cages at the coral reefs were placed 50 meters from the shoreline in water 1.9 m deep at high tide. All cages remained completely submerged at low tide. The outsides of the cages were scrubbed every other day with a metal brush to remove any algae that had started to grow on them and to maintain water flow. The daily food rations for each cage resident were estimated at 80-110% of its body weight. The feeding diet consisted solely of fish, 99% of which was Mozambique tilapia (*Oreochromis mossambicus*). At three different time periods, total length measurements were taken of each surviving individual in the growth cages. The experiment was conducted for 110 days from June to October 2007.

To investigate the influence of the cages on fish growth rates, 95 *H. plumieri* were exposed to the same treatment as the caged individuals (measurement and tagging) but were released back into their natural environment at the same jetty where one of the growth cages was placed. These individuals represented the control for the experiment. The tagged and released fish were re-trapped using the modified Antillean fish traps that were set daily for the duration of the experiment. Once caught, the total length of each recaptured individual was measured to the nearest mm and the tag number noted. The fish was then released.

The temperature of the waters surrounding the growth cages were measured at 2 hour intervals using HOBO Temps (digital recording thermometers) for the duration of the experiment. One HOBO Temp was connected to the two cages in each habitat via plastic straps. The HOBO Temps were attached to the cages at the start of the experiment and were retrieved upon completion of the experiment. The salinity, pH and turbidity of the waters surrounding the growth cages were measured at each feeding for the duration of the experiment to determine if there were differences among the habitats.

Data Analysis

The mean daily growth rate of each fish in mm per day was calculated using the following formula:

$$(L_2\text{-}L_1/t_2\text{-}t_1) \qquad \text{Equation 4.1}$$

where L_2 is the total length in mm at the time of measurement, L_1 is the initial total length in mm, and t_2-t_1 is the number of days between measurements. To avoid pseudoreplication, the individual fish growth rates from each cage were pooled to give a single mean daily growth rate for each cage in the habitats. A student's t-test was completed to determine if there were significant differences in pooled mean daily growth rates of individuals between the cages in each habitat. If no significant differences existed, the mean growth data for the two cages were pooled in subsequent analyses. One-way ANOVAs or Kruskal-Wallis tests were used to compare mean daily growth rates among habitats and the tagged and released (control) individuals after the data were tested for normality and equality of variances. Data transformations, log (x + 1) were performed on the mean daily growth data as necessary.

The temperature regimes experienced by the *H. plumieri* in the growth cages were estimated from the HOBO Temp data by: 1) calculating the mean daily temperature experienced by the *H. plumieri* in each cage and 2) calculating the daily T_{max} - T_{min} values for each day that there were live fish in the cages in each habitat. Appropriate one-way ANOVAs or Kruskal-Wallis tests were used to compare the mean temperature and daily T_{max} - T_{min} data among the habitats after the data were tested for normality and equality of variances, and after the appropriate data transformations were performed. A Pearson correlation analysis was used to determine if there was a linear association between mean daily temperature and daily T_{max} - T_{min} values. Least-squares linear regression was used to determine if there was a significant relationship between growth rates and mean daily temperature of each habitat, and growth rates and the daily T_{max}-T_{min} values in each habitat. one-way ANOVAs or Kruskal-Wallis tests were applied to the salinity, pH and turbidity data to test if there were significant differences among the habitats after the data were tested for normality and equality of variances, and the appropriate data transformations (log (x + 1)) completed.

Results

The total number of *H. plumieri* tagged and released (the control for the experiment) was 95. Of that number, 50.5% (48) were recaptured at least once during the course of the experiment, 9.5% were recaptured twice, 10.5% were recaptured three times, 1.1% was recaptured four times and 1.1% recaptured five times (Figure 4.2). The last recapture was made on day 67 of the 110 day-long experiment.

There was no significant difference between the mean growth rates of the fish held in the cages in any of the four habitat types: jetty ($t_4 = 1.83$, $P = 0.07$, Cohen’s $d = 0.57$); seagrass ($t_3 = 0.01$, $P = 0.99$, Cohen’s $d = 0.004$); mangroves ($t_4 = 0.45$, $P = 0.66$, Cohen’s $d = 0.15$); and coral reef ($t_3 = 0.31$, $P = 0.76$, Cohen’s $d = 0.15$). The mean daily growth rates (mm/day) for the caged individuals and control group ± SD were: mangrove 0.4 ± 0.2; seagrass 0.3 ± 0.2; control group 0.3 ± 0.2; jetty 0.2 ± 0.0; and coral reef 0.2 ± 0.0 (Figure 4.3). Approximate monthly growth rates (cm/month) for each habitat, based on the daily growth rates (mm/day) were 1.2 cm per month in the mangrove habitat, 0.9 cm per month in the seagrass habitat, 0.9 cm per month for the control group, 0.6 cm per month in the jetty habitat and 0.6 cm per month in the coral reef habitat. There was no significant difference in mean growth rates among the habitats and the control group ($H_{0.05, 4} = 4.99$, $P = 0.29$) based upon a Kruskal-Wallis test.

Figure 4.4 presents the temperature raw data for the different habitat types during the course of the experiment. The mean temperature values of the different habitats ± SD were: jetty 29.12 ± 0.75; seagrass 29.00 ± 0.69; mangroves 28.97 ± 0.61; and coral reef 29.97 ± 0.78 (Figure 4.5). The Kruskal-Wallis test ($H_{0.05, 3} = 1218.02$, $P < 0.001$) indicated a significant difference among some habitats. The results of the post-hoc test indicated no significant difference in mean temperatures between the seagrass and mangrove habitats, but significant differences in the mean temperature data between the jetty and coral reef, mangroves and coral reef, seagrass and coral reef, jetty and seagrass, and jetty and mangrove habitats (Table 4.1). The daily T_{max} - T_{min} values ± SD for the four different habitat types were: jetty 1.74 ± 0.57; seagrass 1.56 ± 0.44; mangroves 1.26 ± 0.42 and coral reef 1.74 ± 0.60. Figure 4.6 shows the frequency distribution of the daily T_{max} - T_{min} values for each habitat. A Kruskal-Wallis test indicated a significant difference in the daily T_{max} - T_{min} values among habitats ($H_{0.05, 3} = 54.73$, $P \leq 0.001$), and the post-hoc test confirmed a significant difference between the mangrove and jetty, mangrove and coral reef and mangrove and seagrass values (Table 4.2).

The results of the Pearson correlation indicated that for each habitat type there was a very small relationship between mean daily temperature and daily T_{max} - T_{min} values experienced by the *H. plumieri* (jetty $r = 0.030$; seagrass $r = 0.050$; mangrove $r = -0.15$; coral reef $r = 0.032$) (Figure 4.7). Linear least-squares regression indicated that there was no significant relationship between mean daily temperature and growth rate for juvenile *H. plumieri* ($F_{0.05,\ 3} = 3.79$, $P = 0.19$, $r^2 = 0.65$); however, there was a significant relationship between the growth rates and daily T_{max} - T_{min} values ($F_{0.05,\ 3} = 16.56$, $P < 0.05$, $r^2 = 0.89$). There was no significant difference in turbidity, pH or salinity values among the habitats (turbidity $H_{0.05,\ 3} = 2.30$, $P = 0.51$; pH $H_{0.05,\ 3} = 6.90$, $P = 0.075$; salinity $H_{0.05,\ 3} = 3.72$, $P = 0.29$) Figures 4.8, 4.9, 4.10, respectively).

Discussion

Growth rates, which were easily measured by a change in length over time, were used to compare habitat quality among four habitats. The temperature regimes (specifically mean daily temperature and the daily T_{max} - T_{min}) of each habitat were used as one aspect of habitat quality. The results showed that the *H. plumieri* in the mangrove habitat grew on average 1.2 cm per month, those in the seagrass habitat 0.9 cm per month, the control group 0.9 cm per month, the jetty 0.6 cm per month and the coral reef 0.6 cm per month. Based on the results of Chapter 3 of this dissertation, which analyzed the growth rates of wild *H. plumieri* in Antigua, the juvenile *H. plumieri* used in this study were between 0 and 1 years old. Brothers and McFarland (1981) investigated the early growth of *H. flavolineatum* to 100 days and found that those fish grew to a size of 4 cm over the first 100 days, averaging growth of 1.2 cm per month. Saksena and Richards (1975) obtained similar results (1.6 cm per month) rearing *H. plumieri* for the first 40 days of their lives. These *H. plumieri* were reared at a mean temperature of 26.4 ^{0}C and were fed continuously. These results are comparable to the results of our study for the mangrove habitat; however, we obtained lower growth rates for the other habitats. From the results of Chapter 3 of this research, wild *H. plumieri* grew approximately 0.6 cm (TL

– total length) per month during their first year of life; growth rates comparable to that obtained in the jetty and coral reef habitats. The growth rates obtained for wild *H. plumieri* populations in Antigua were smaller than those obtained in this study because the wild fish had to expend energy on swimming to search for their own food and to mount predator avoidance maneuvers. On the other hand, our study individuals were protected against predators and were fed to satiation so were able to allocate all their excess energy to growth. Other studies around the region on the growth of *H. plumieri* between the ages 1 and 2 years using back-calculated length values, have documented growth rates of approximately 0.5 cm (FL – fork length) per month for north-central Cuba (Claro and García-Arteaga 2001), approximately 0.4 cm (FL) per month for southwest Cuba (Claro and García-Arteaga 2001), and approximately 0.7 cm (TL) per month for North and South Carolina (Manooch 1976). Noteworthy here, is that the fish in these studies had to expend energy that could have been put towards growth on searching for food and predator avoidance maneuvers. In addition, the growth rates of fish slow down as they get older (Murie and Parkyn 2005, Araújo and Martins 2007) which means that the growth rates of the fish from around the region (between 1 and 2 years old) would potentially be lower than those for the fish used in this study (between 0 and 1 year old) based of their ages.

Cages were used to eliminate the dispersal of the juvenile *H. plumieri*, and for the experiments to be conducted in a controllable environment (Planes and Lecaillon 2001) such that the influence of the temperature regimes being experienced by the fish on their growth rates could be determined. It was recognized that there were a number of artifacts caused by the use of cages that could have influenced the growth rates attained (Connell

1997, Fernandes et al. 1999, Phelan et al. 2000, Englund and Cooper 2003, Como et al. 2006) and so a control group (tagged and released individuals), was used to facilitate the investigation of the influence of the cages on *H. plumieri* mean daily growth rates. The caged individuals had the benefit of a readily available abundant food source and the protection from predation. Because of their confinement, however, they had to face the challenge of not being able to undergo their daily feeding migrations. In addition, they had to endure variations in temperature regimes. The control group faced many more challenges because they had to search for their own food and were more susceptible to predators because of the colored spaghetti tags, which made them more conspicuous and potentially affected their swimming ability. Their food acquisition issues were somewhat catered for because they were released into an area used by fishermen to clean their catch, which also served as a nursery habitat for numerous fish species (as indicated by the large schools of appropriately sized fry that were always present in the area). Therefore, they had a bountiful supply of readily available food. The mean daily growth rate of the tagged and released *H. plumieri* (control group) was 0.3 mm per day which was similar to the growth rates of the individuals caged in the same habitat (0.3 mm per day) suggesting that there was no apparent negative effect of the cages on *H. plumieri* growth rates. Other caging studies completed by Sogard (1992), Duffy-Anderson and Able (1999), Able et al. (1999) found that cage confinement did not alter the growth rates of winter flounder or tautog relative to wild populations.

Temperature was the abiotic environmental characteristic of choice because it dictates the lethal limits of a fish's life, controls the development, feeding, metabolic, growth and reproductive rates of fish, influences the distribution of fish so that they remain within optimum parameter ranges, and modifies the action of most other biotic and abiotic environmental parameters (Brett 1956, 1971, 1979, Jobling 1994, Wootton 1990, Browder et al. 2002, Werner 2002). Further, fish are ectotherms, whose internal temperatures match the ambient temperature of their immediate environment. Studies of fish growth at different temperatures have shown that fish may live for extended periods and attain maximum growth rates if they are reared at a certain range or zone of temperature (usually spanning a few degrees), but outside this range growth rates slow down (Brett 1956, 1979, Elliot 1994, Jobling 1994, Sylvester 1973).

It was critical to investigate the effects of changes in the mean daily temperature because within the normal thermal range of a fish, changes in the mean daily temperatures experienced have well-documented effects on the rates of many physiological process and can thus ultimately influence growth rates (Sanford 2002). Phelan et al. (2000) conducted a study on estuarine and habitat-related differences in growth rates of young-of-the year winter flounder (*Pseudopleuronectes americanus*) and tautog (*Tautoga onitis*) in three northeastern US estuaries and were able to show that temperature changes do influence growth rates. In addition, Le Pape et al. (2003) showed that the size of juvenile sole after two summers of life had a positive linear relation to seawater temperature. Attrill and Michael (2002) showed that temperature was important in determining juvenile fish growth in estuaries for commercially important marine groups such as flatfish gadoids, clupeids, bass, gobies eels, smelt, pogge and Nilsson's pipefish. The action of temperature is such that when food is unlimited, increases in temperature lead to increases in growth rates up to a maximum. As temperature continues to increase beyond the optimum, however, there is an abrupt decline in ingestion rates, metabolic rate increases, growth rate decreases and further increases in temperature lead to mortality (Brett 1956, 1971, 1979, Jobling 1994, Mommsen 1998, Wootton 1990). Our results indicate significant differences in the mean daily temperature between the coral reef and all other habitats and the jetty and all other habitats. The lowest mean daily temperature values were experienced in the mangrove habitat and the highest in the coral reef habitat. There was however, no significant relationship between mean daily temperature and mean daily growth rates of *H. plumieri* based on Kruskal-Wallis tests. This lack of a significant relationship may be because fish have the ability to shift their tolerance of high and low temperatures within short spaces of time. Laboratory investigations into the thermal tolerance of fish have demonstrated their ability to shift their tolerance of temperature ranges based on their previously experienced conditions such that a fish acclimated at a higher temperature is better able to withstand increases in temperatures (Brett 1956, 1971, 1979, Brown and Feldmeth 1971, Jobling 1994). For many fish species, the time needed to acclimate to higher temperatures is less than 24 hours at temperatures above 20^0C (Jobling 1994). Therefore, it is possible *H. plumieri* were able to quickly adapt to the mean daily temperatures they experienced in the cages with no significant impact on growth rates.

Daily fluctuations in temperature also influence fish growth rates. Fish counteract excessive temperature fluctuations in a short space of time with physiological mechanisms. These physiological mechanisms, which are aimed at maintaining a consistent internal environment, have energetic costs and thus, affect growth. As temperature fluctuations occur in the environment, the extra energy available for growth is used for physiological compensatory mechanisms at both the molecular and cellular level (Hochachka and Somero 2002) such that the more extreme the fluctuations the more energy needed to maintain a constant internal environment. For daily T_{max} - $T_{min,}$ significant differences were obtained between the jetty and mangrove habitat and the mangrove and coral reef habitat. Further, there was a significant relationship between growth rates and the T_{max} - T_{min} values of the habitats. The mangrove habitat had the lowest T_{max} - T_{min} values and the highest growth rates, while both the coral reef and jetty habitats had the highest T_{max} - T_{min} values and the lowest growth rates. This means that *H. plumieri* growth is potentially negatively affected by large fluctuations in daily temperatures. A study completed by Sylvester (1973) may help explain these findings. He showed that juvenile *H. flavolineatum* acclimated at 27 ^{0}C showed a median critical thermal maximum of 36 ^{0}C. Further, the resistance to lethal temperatures was greater with slowly increasing temperature rather than with an abrupt change indicating that some degree of physiological adjustment occurred with the gradual temperature change which was not possible with abrupt transfer.

The lack of significant correlation between the mean daily temperature and daily T_{max} - T_{min} values experienced by the *H. plumieri* in each habitat indicates that the days with large fluctuations in T_{max} - T_{min} were not the same days with high mean daily temperatures. This explains the lack of a significant relationship between mean daily temperature and growth rates but a significant relationship between mean daily growth rates and daily T_{max} - T_{min} values. In the natural environment, the daily fluctuations in temperature appear to be more important in influencing fish growth rates than the mean temperatures experienced by fish.

It can be argued that this experiment was not ideal because there were potentially a number of confounding factors that may have influenced the growth rates attained in the different habitats that were unrelated to the temperature regimes experienced by the fish. In defense of this work, the main objective was to investigate under field conditions how temperature regimes influence fish growth rates. Considering that this experiment was completed in situ, there were a number of abiotic characteristics of the habitats studied such as salinity, turbidity, and pH that could have potentially influenced the observed *H. plumieri* growth rates. The influence of these parameters can be somewhat ruled out however, because they were tested and were found not to differ significantly among the habitats investigated. This study also suffered from only investigating four different temperature regimes. In the natural environment it is extremely difficult to find temperature regimes that are significantly different from each other unless it is in areas where outfalls heat up seawater. Thus, improvements to this study would be to select more sites for cage placement, increase replication of cages at each site, and complete the study over the course of 1 year or longer to allow for the possibility of more variations in temperature regimes.

Overall, this field study allowed for a more realistic determination of the influence of differing temperature regimes on fish growth rates than laboratory experiments, because it is very difficult to model, ecologically meaningful daily temperature fluctuations simultaneously with changing mean daily temperature values in the laboratory. This study demonstrated under natural conditions, and in the presence of abundant food supplies, how differing temperature regimes influence juvenile *H. plumieri* growth rates.

Table 4.1: The results of Dunn's multiple comparison post-hoc tests comparing mean temperature (^{0}C) values among the four focal habitats. The Q-values at α-level 0.05 are reported, along with the values of Cohen's d (italicized). * indicates cases where there is a significant difference between habitats.

	Jetty	Mangrove	Coral Reef	Seagrass
Jetty	----	4.07* *0.22*	25.71* *1.11*	3.10* *0.17*
Mangrove		----	29.78* *1.42*	0.97 *0.046*
Coral Reef			----	28.82* *1.32*

Table 4.2: The results of Dunn's multiple comparison post-hoc tests comparing T_{max}-T_{min} values among the four focal habitats. The Q-values at α-level 0.05 are reported, along with the values of Cohen's d (italicized). * indicates cases where there is a significant difference between habitats.

	Jetty	Mangrove	Coral Reef	Seagrass
Jetty	----	6.41* *0.96*	0.10 *0*	2.38 *0.35*
Mangrove		----	6.30* *0.93*	4.02* *0.7*
Coral Reef			----	2.28 *0.34*

Figure 4.1: Map of Antigua showing the general area where the growth cages were positioned

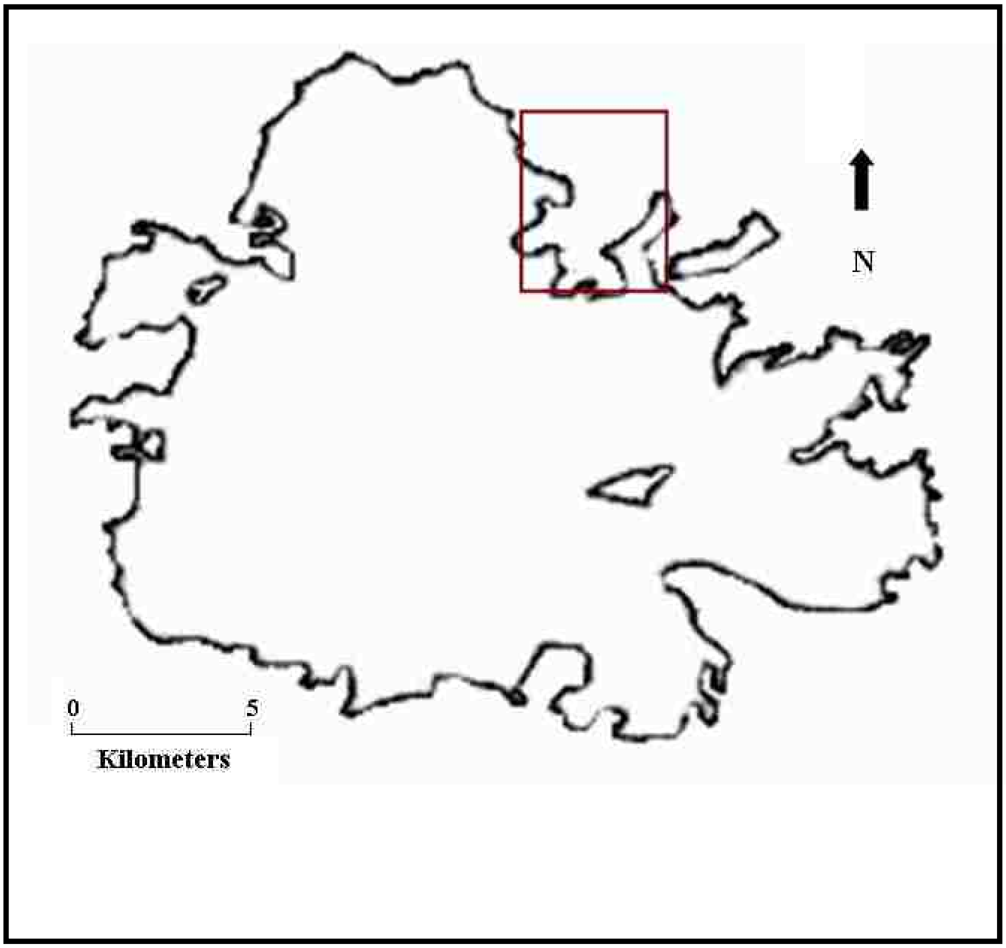


Figure 4.2: The distribution of the number of times each tagged and released juvenile *H. plumieri* was recaptured during the course of the experiment.

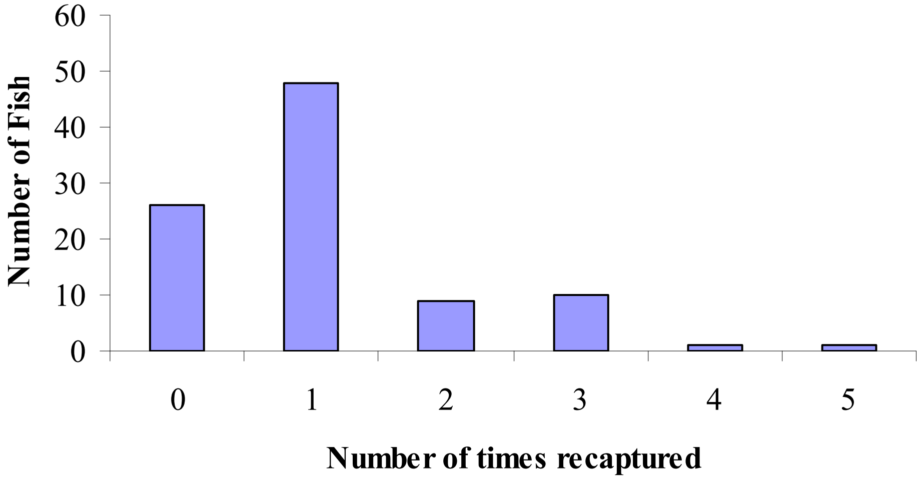


Figure 4.3: The mean daily growth rates in mm/day of the juvenile *H. plumieri* caged in the four focal habitat types (jetty, mangroves, seagrass, and coral reefs) and the tagged and released (control) individuals. The bars represent the upper and lower 95% confidence limits.

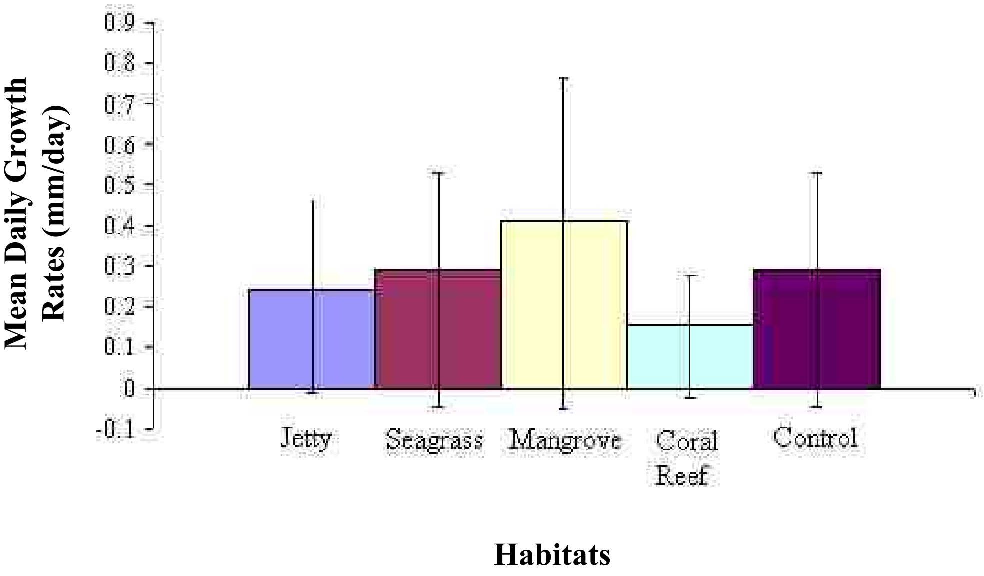


Figure 4.4 Temperature data for the four different habitats.

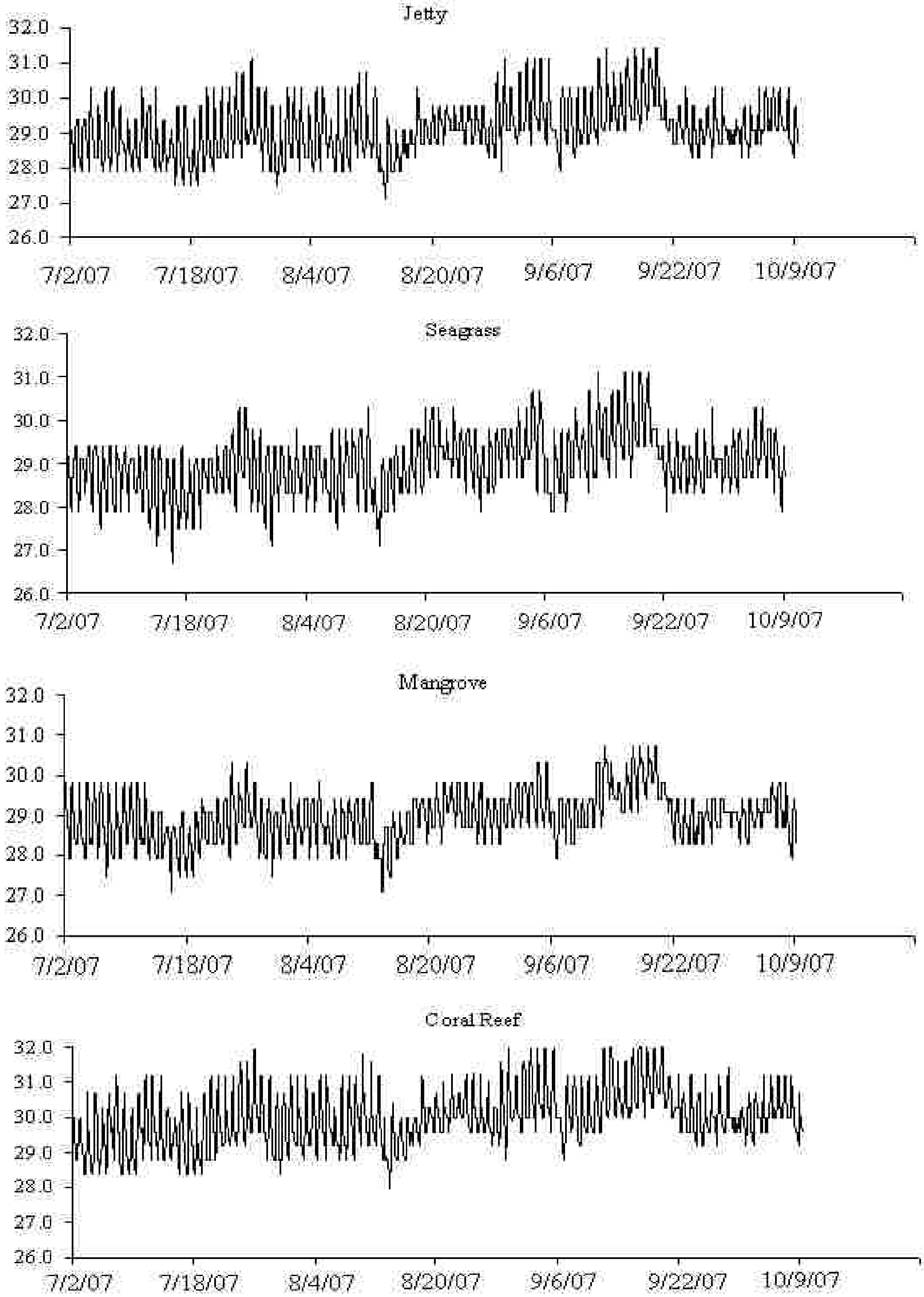


Figure 4.5 Box plot showing the temperature values measured in ^{0}C for each of the four focal habitats used in the experiment. Each box represents the upper and lower quartiles of the dataset, and the horizontal line within each box represents the median value. Whiskers represent the greatest and smallest non-outlier values, and black dots beyond the whiskers represent outlier values.

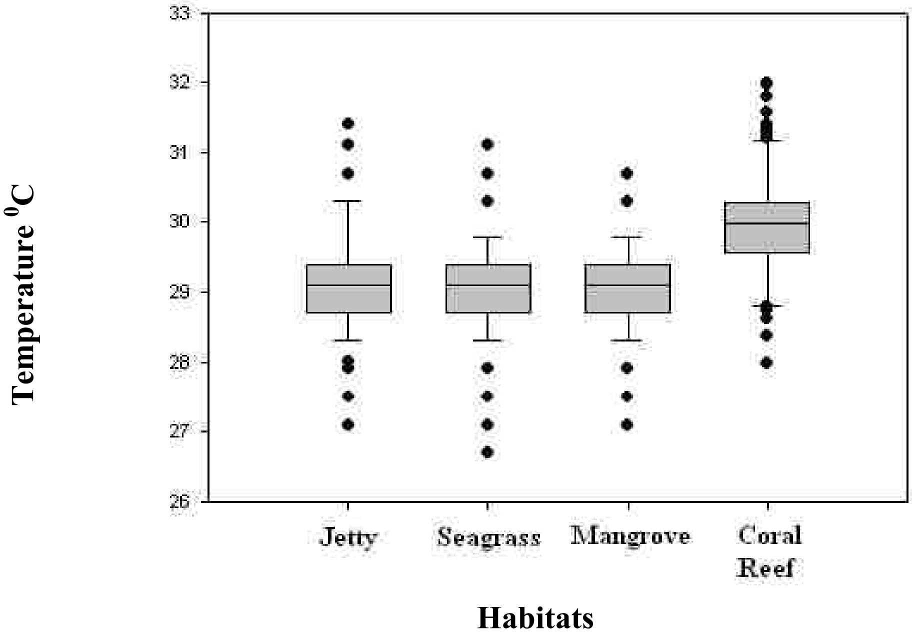


Figure 4.6 Frequency distribution of T_{max} - T_{mix} for the 4 different habitats used in this study

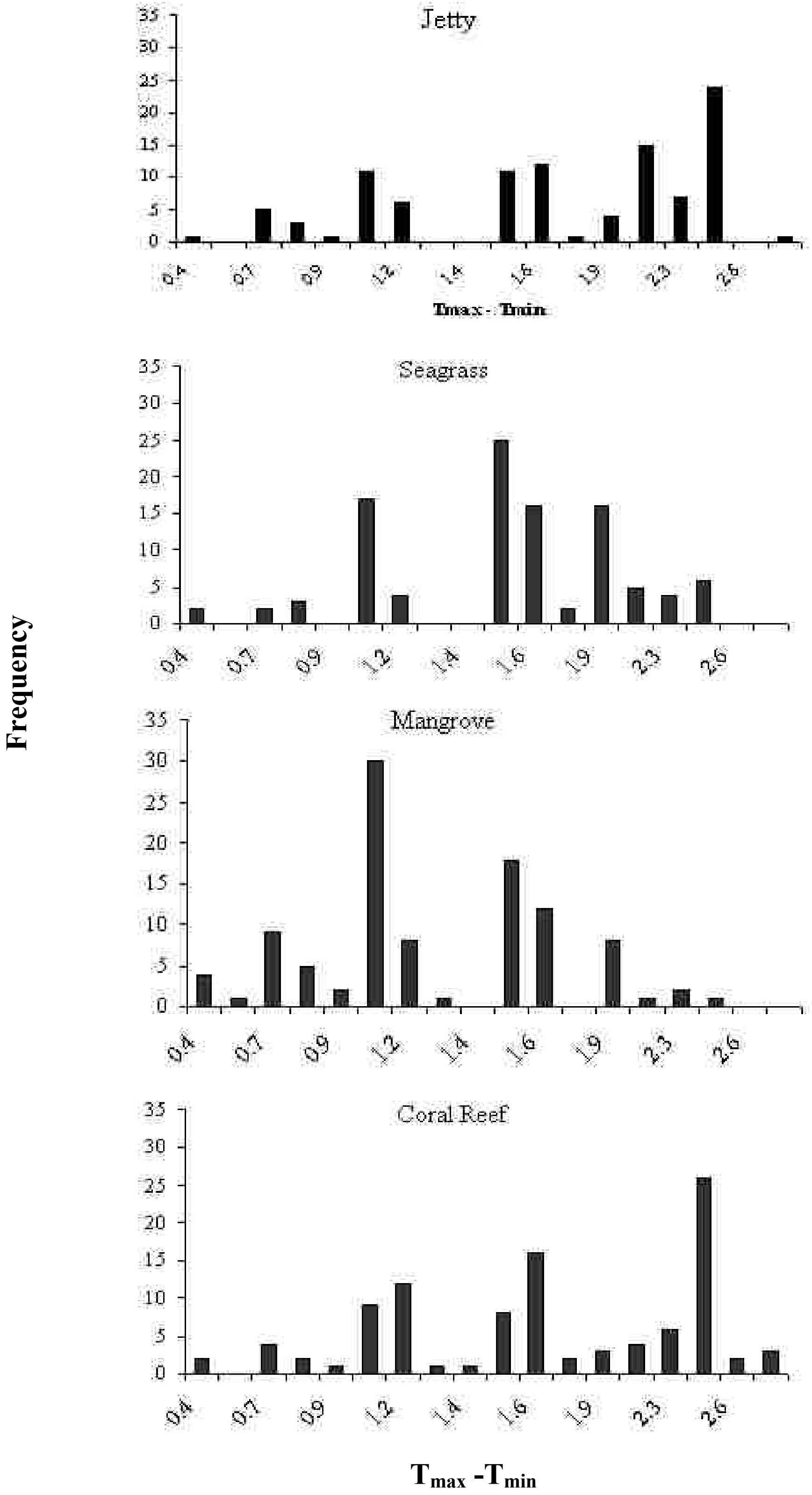


Figure 4.7 Comparison of the mean daily temperatures in 0C to the daily T_{max} - T_{mix} values for the four habitats.

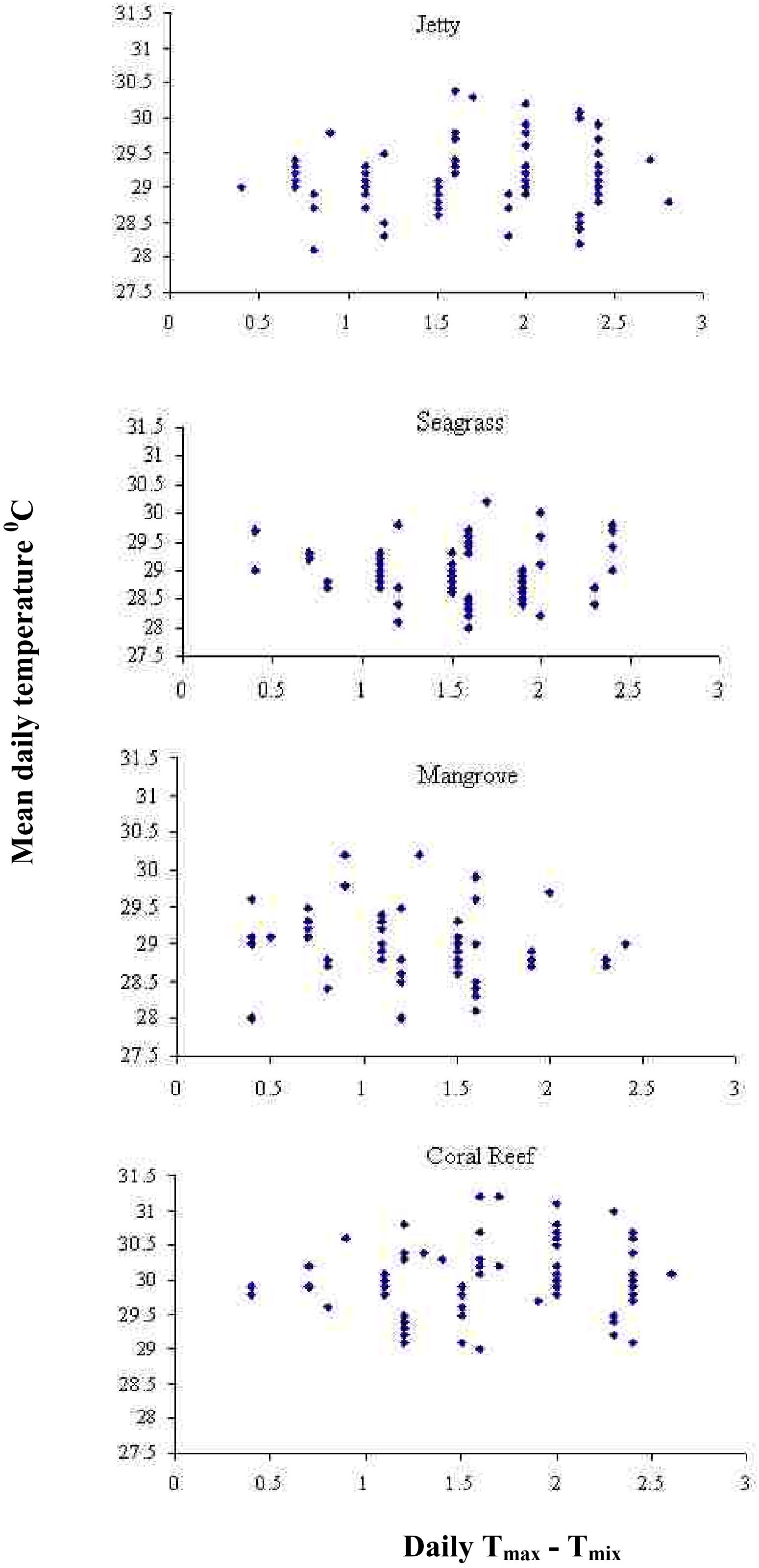


Figure 4.8: Box plot showing the turbidity values measured in NTUs (Nephelometric Turbidity Units) for each of the four focal habitats used in the experiment.

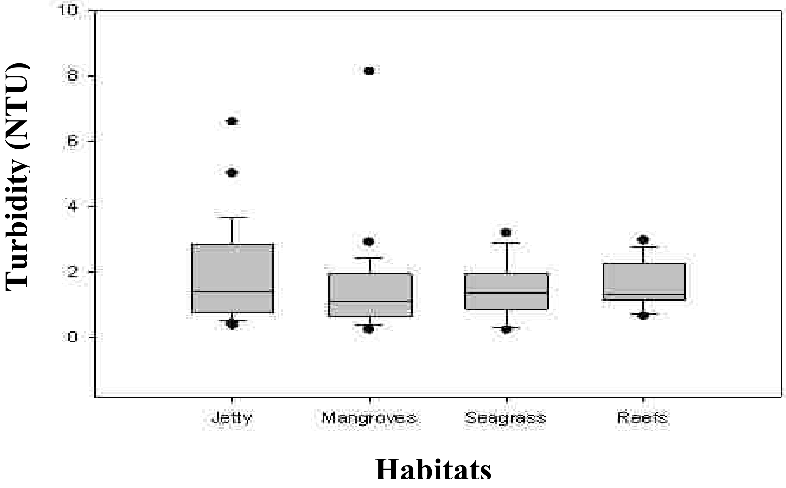


Figure 4.9: Box plot showing the pH values for each of the four focal habitats used in the experiment.

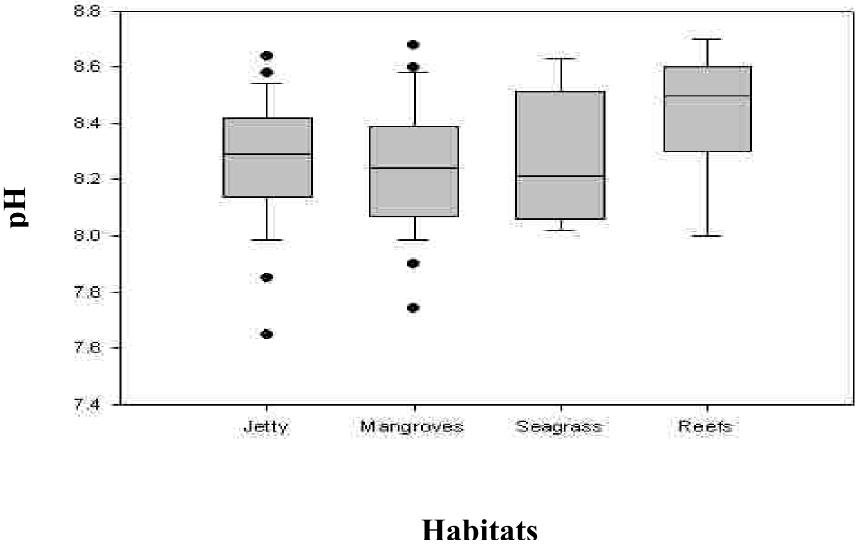
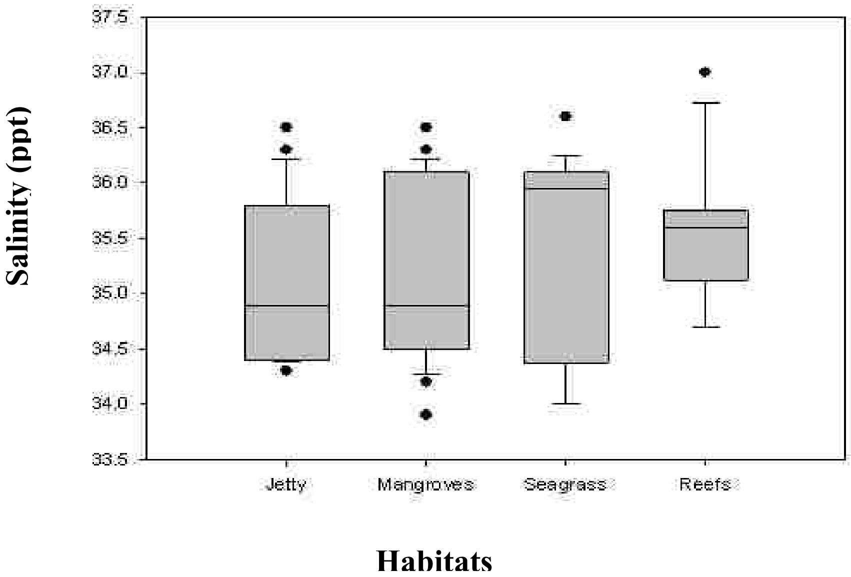


Figure 4.10: Box plot showing the salinity values measured in parts per thousand (ppt) for each of the four focal habitats used in the experiment.



CHAPTER FIVE

IMPORTANCE OF HABITAT QUALITY IN THE ECOLOGY, CONSERVATION AND MANAGEMENT OF CORAL REEF FISHES

Background

The goal of this research was to determine the relative quality of different near shore marine areas by investigating their influence on Haemulidae community structure, distribution pattern, condition and growth. Habitat was defined at the small spatial scale of individual habitat types such as seagrass beds, mangroves and coral reefs, and at the broader spatial scale of the interconnection of these individual habitat types within a mosaic (IHM). Ten spatial, biotic and abiotic parameters (percentage coverage of sand, mangroves, hard substrate, and seagrass, turbidity, pH, salinity, temperature, average depth, and predator density) were investigated. These environmental characteristics acted as proxies for the quality of IHMs. It was recognized that there are a large number of additional factors that contribute to environmental quality such as the proximity of adult and juvenile habitats to spawning and settlement areas, density dependent control of fish distribution, inter- and intra-specific competition between individuals for resources, the influence of ocean currents and hydrology, and anthropogenic influences (Sutton 1985, Richmond 1993, Chapman and Kramer 1999, Friedlander et al. 2003, Shima and Osenberg 2003, William et al. 2006). However, the factors investigated were selected based on the system under consideration, which was a small tropical island with limited shelf area. Also, there was the need to try to limit the variables to a subset that captured much of the variability among IHMs and had the biggest influence on the Haemulidae characteristics measured. This chapter presents the major findings of this research, the implications of these findings to the ecology management and conservation of coral reef populations in tropical marine systems, and recommendations for the design of similar investigations into habitat quality.

Major Research Findings

1. <u>IHMs and discrete habitat types in tropical marine systems are not always equal in quality.</u>

The research demonstrated that IHMs and discrete habitat types in tropical marine areas are not of equal quality and therefore, differ in their contribution to the community structure, distribution pattern, condition, and growth of marine organisms. The highest quality IHMs/discrete habitat types have the critical resources whether spatial, abiotic or biotic, at the optimum levels needed by organisms to carry out their critical life functions. Differences in the quality among IHMs result in significant intra-species differences in: density, length frequency distributions, biomass, ratios of adults to juveniles (Chapter 2), weight-at-length relationships, condition, and length-at-age relationships (Chapter 3). Differences in quality among discrete habitat types can be determined from the investigation of specific environmental characteristics such as temperature regimes (Chapter 4) that have a notable influence on fish growth rates.

2. IHMs of the highest quality contain all the discrete habitat types needed by organisms to carry out their critical life processes in a spatial arrangement that maximizes energy savings.

Overall, WILL was found to be the IHM of highest quality. GI, had the highest weight-at-length relationships and condition (Chapter 3); however, for only weight-at-length and length-at-age data for young fish was this relationship significantly different from WILL. This suggested that for the growth and condition parameters measured, GI and WILL were not very different in terms of quality. For the Haemulidae community structure and distribution pattern (Chapter 2), however, WILL was a much higher quality IHM than any of the other IHMs. Taking all these factors into consideration, WILL was the IHM of highest overall quality. WILL had the all the habitat types needed by Haemulidae to carry out their life functions, the greatest structural complexity (that potentially provide a large amount of refuge holes against predators), large amounts of nutrient input as a result of run-off from the land (that caused enhanced primary productivity in its waters), and large amounts of resting habitats with easy access to food sources in surrounding habitats.

3. IHMs can be of high quality in the absence of one habitat type, if this habitat type is replaced by another that can take on its ecological role.

For the Haemulidae community structure and distribution pattern investigated, JB was the second highest in quality after WILL (Chapter 2). This IHM had no mangroves but the largest area of seagrass. In tropical marine areas these two habitat types act as nurseries for juvenile fish such as Haemulidae (Parrish 1989, Beck 2001, Nagelkerken et al. 2000b, 2001, Cocheret de la Morinière et al. 2002, 2003). Therefore, it appears that at

JB, the seagrass beds adequately fulfilled the nursery role and so the absence of mangroves did not have a severe negative impact on the quality of this IHM.

4. Percentage cover of hard substratum and seagrass, temperature, and predator density were the environmental characteristics investigated that had the biggest impact on Haemulidae distribution pattern, community structure, condition and growth.

Percentage cover of hard substratum and seagrass, temperature, and predator density were all highly correlated to Haemulidae density values (Chapter 2) and thus, significant determinants of IHM quality. In addition, the temperature regimes present including the daily T_{max}-T_{min} values were good proxies for habitat quality, because they had a big influence on fish growth rates (Chapter 4). The influence of the percent cover of hard substratum and predator density probably acted together to determine habitat quality, since increased habitat complexity translates to an increase in the number of available prey refuges.

Ecological, Conservation and Management Implications

In a heterogeneous environment, it is necessary to understand how the quality of habitats influences the distribution, movement, growth and condition of fishes if their populations are to be effectively managed (Irlandi and Crawford 1997). Spatially heterogeneous environments of high quality support large biomasses, and high species and genetic diversity because there is a greater range of resources available for partitioning among many species (Koeing et al. 2000). More fundamentally though, high quality heterogeneous environments provide a wide range of benthic substrates, and the levels of the biotic and abiotic parameters that are needed by fish for successful spawning, recruitment and settlement, and maximum development and growth rates, and minimum mortality rates (Luckhurst & Luckhurst 1978, Bell & Galzin 1984, Sale et al. 1984, Sweatman 1985). Because degradation of habitat quality can greatly impact the viability of fish populations, the maintenance of habitat quality must be incorporated into fisheries management plans.

Traditionally, fisheries management did not take into account the influence of habitat quality on fish abundance, diversity, biomass, condition, and growth rates. However, it is becoming accepted that any effective management scenario must be ecosystem-oriented incorporating both the preservation of biodiversity, and the maintenance of the ecosystem structure and function upon which this biodiversity depends (Koenig et al. 2002). In an ecosystem-based approach, the emphasis is given to protecting the habitat within a larger regional context such as large marine ecosystems (Sherman and Duda 1999) such as IHMs, and biogeochemical provinces (Longhurst 1998). In keeping with the need for a more ecosystem-based approach, in 1996 the US government enacted the Magnuson-Stevens Fishery Management and Conservation Act. This act highlighted the need for the incorporation of ecosystem preservation into sustainable fishery production. The act mandated that habitat be at the center of fisheries management (Koenig et al. 2000). It defined habitat as “the substrates and waters necessary for fish to spawn, breed and feed or grow to maturity” (Lindeman et al. 2000, Rosenberg et al. 2000) and is highly applicable because most fish species use many different habitats to carry out lifecycle processes.

The influence of habitat types where fish are not normally observed on their growth, condition, reproduction, and survival also dictated that the definition of habitat be broadened. The growth, survival, and reproductive benefits fish gain from their environment is potentially the consequence of or influenced by events occurring in different habitat types within the environment (Sheaves 2005). Further, the need to move among multiple habitat types means that the influence of a controlling factor that only operates in one habitat type during a limited time period can be propagated throughout an entire system of interconnected habitats (Sheaves 2005). Thus, the use of multiple habitat types makes fish especially vulnerable to adverse effects of habitat modification. The degradation of any one of the constituent habitats within a mosaic can negatively influence species across the whole mosaic (Matheson and Gilmore 1995). Therefore, by broadening the definition of habitat to include all the habitat types that influence fish growth, condition, and reproduction, the viability of fish populations can potentially be enhanced.

To be effective, management tools for fish must then ensure that all the habitat types used by mobile marine organisms are protected and maintained at high quality. In addition to protecting habitat quality and species diversity, effective management measures must ensure that large enough numbers of individuals needed for the persistence of focal species are protected over the long-term. Therefore, fishery managers must use ecological tools such as minimum viability analyses (MVA) in the design of management initiatives. A MVA allows the determination of the minimum size of a fish population that constitutes a viable population (Boyce 1992) and thus, be the target of conservation efforts. MVAs are a subset of the mathematical models that make up population viability analyses (PVAs). PVAs enable the assessment of population health and the factors that impact the survival and persistence of species (Boyce 1992, Akçakaya et al. 1999, Morris et al. 1999). The benefit of PVAs is that they can be used when data are sparse, which is usually the case for exploited fish populations, identifies the key life stages or processes that should be the focus of recovery and conservation efforts, and can incorporate information about environmental variation (for example variation in habitat quality, rainfall, temperature, and duration of the growing season) that directly or indirectly affect the target population and place it at risk (Morris et al. 1999). For any proposed management options for coral reef fishes to be effective over the long term, they must then focus around species diversity, habitat quality, and the numbers of individuals within each species that constitute a viable population.

Marine protected areas (MPAs) are important tools for the conservation and management of coral reef fishery resources (Lubchenco et al. 2003, Gell and Roberts 2003). If designed properly, MPAs can protect both viable sizes of diverse fish populations, and the habitats upon which these fishes depend (Lubchenco et al. 2003) and therefore, are arguably the most effective management tool for exploited fish populations. This research highlighted some of many characteristics of benthic habitats such as type and configuration that must be included in the design of MPAs for the effective management of fisheries resources. Effective MPAs should have 1) large overall area with benthic habitat types of high quality; 2) spatial configurations with short distances (corridors) between habitat types; 3) spatial arrangements that place all individual habitat types in connection with all other habitat types so that energy expenditure in moving among habitat types is reduced; 4) habitats with high structural complexity (e.g. WILL); and 5) the inclusion of all the habitat types needed by focal organisms to carry out their life processes, or surrogate habitat types that can take on the role of ones that are absent.

Recommendations for Future Studies into Habitat Quality

During the design phase of any ecological study a number factors have to be considered. Presented here is a short review of some of the research issues that were dealt with during the design of these habitat quality studies. It is intended to serve as a guide to other researchers planning studies investigating habitat quality.

1. The selection of study species and sites for habitat quality investigations must comply with some minimum criteria.

Habitat is organism specific (Hall et al. 1997). This means the habitat of a bluefin tuna is not the same as that of a white grunt. Therefore, special attention must be given to the selection of the study species and the corresponding sites. The most important criterion that needs to be met by the chosen organism(s) is that it must depend on the habitat for a critical life process, for example feeding or reproduction. By ensuring this criterion is met, any changes in habitat quality will cause accompanying changes in the fitness of that organism(s). The selection of the study site is also critical. The most important criterion is that the site must be able to fulfill some basic requirement of the organisms that is directly related to its growth, survival, reproduction, or population persistence.

2. The more environmental factors considered the more robust the conclusions.

Although ten spatial, abiotic, and biotic factors that potentially have the greatest impact on the habitat quality of the system investigated were selected, it was still not possible to definitively attribute some of the results obtained to the factors considered. For example, the factor contributing most to Haemulidae condition at GI was suspected to be food quantity as determined by the amount of feeding habitat present (Chapter 3).

However, this conclusion was not definitive because the amount of food consumed by each individual was not explicitly measured.

3. <u>A large number of biological characteristics of the focal species should be used to measure habitat quality.</u>

Haemulidae community structure, distribution pattern, condition, and growth were used to demonstrate quality differences among IHMs and habitat types. The results of Chapter 2 showed that WILL was the IHM of highest quality based on the Haemulidae community structure and distributions pattern investigated. However, Chapter 3 indicated that GI was the IHM of highest quality based on weight-at-length relationships and condition indices. These results highlight the need for the incorporation of a large number of biological characteristics of the focal species to ensure robust conclusions.

Major Theoretical Questions not Addressed but Deserving Further Investigation

There are some major theoretical questions that were not addressed in this research but deserve further investigation. These are:

1. <u>How does the quantity and nutritional quality of the food available in each IHM influence Haemulidae community structure, distribution pattern, condition and growth?</u>

Two of the environmental characteristics that may have had a big influence on Haemulidae growth and condition that were not explicitly measured were the amount and nutritional quality of food resources present in each IHM. Increases in the amount and nutritional quality of food resources can potentially cause an expansion in the amount of suitable habitat where fish can experience positive growth, and in habitats already suitable for fish, can cause enhanced growth rates of individuals (Rosenfeld and Boss 2001, Railsback et al. 2003). Gut content analysis and studies on the protein to lipid to carbohydrate ratio of the gut contents of fish may elucidate food quantity and nutritional quality differences among IHMs.

2. How does the simultaneous action of the environmental parameters present in each habitat, influence Haemulidae growth and condition?

Laboratory studies investigating the influence of different combinations of the abiotic parameters present in each IHM and discrete habitat type (at the levels present in the natural environment), may help elucidate the direct influence of the action of different combinations of these parameters on Haemulidae condition and growth.

3. How important are habitat linkages to fish distribution, growth and survival?

One approach to validate the importance of the movement of coral reef fish among marine habitats would be to measure macronutrient and trace element ratios on fish otoliths. This would provide a unique trace of the temporary residence of given life stages of fish species in different habitats (Gillanders 2003, Werner 2002). In addition, diet analysis using isotope ratios may help elucidate movement among habitats to feed, and a determination of how much of the food consumed is obtained from surrounding habitats (Nagelkerken and van der Velde 2004a, 2004b).

APPENDIX I

A HABITAT CLASSIFICATION SCHEME FOR ANTIGUA

The exact terminology used to describe habitat types within marine coastal systems depends on the geographic location and the classification scheme being considered. Due to the benefits and challenges of the numerous habitat classification schemes available for use by ecologists there is no one that is universally accepted (Lund and Wilbur 2007). However, the majority of marine habitat classification schemes are defined down to the scale of an individual habitat type such as mangroves, soft bottoms (seagrass and bare sand) and hard bottoms (nearshore and offshore coral reefs, reefal hard bars etc.) (Allee et al. 2000, Brown 2002, Madley 2002, Madden et al. 2005, Kutcher et al. 2005), each of which have specific spatial relationships to adjacent habitats. One major benefit of habitat classification schemes is that they facilitate the organization of information about habitats used by marine organisms into a standard format so that comparisons can be made between different areas. Some of the most important applications of marine classification schemes as it relates to the marine environment include the delineation of areas that need protection due to their ecological significance or because they are critical hotspots for conservation, the identification of essential fish habitats, and the investigation and monitoring of ecosystem-based processes and mechanisms of coastal systems (Madden et al. 2005). The Coastal Marine Ecological Classification Scheme (CMECS) scheme was developed by NatureServe, NOAA and other US national partners to fulfill these application needs. It is an "ecosystem-oriented, science-based framework for the identification, inventory, and description of coastal and marine habitats and biodiversity" (Madden et al. 2005). This classification scheme was suitable for Antigua because it is applicable at different spatial scales (1 m^2 to thousands of m^2) and encompasses the marine area that extends from the high tide mark in the coastal zone to the deep ocean. The CMECS is a hierarchal classification scheme that organizes the marine waters and substrates surrounding islands and continents into six discrete levels (Figure A1.1):

Regime, Level 1 – is differentiated by a combination of salinity, geomorphology and depth and is organized into five categories: estuarine, fresh water-influenced marine, nearshore marine, neritic and oceanic (spatial scale - $10km^2$ to > $1000km^2$).

Formation, Level 2 – is relatively large physical structures formed by water (currents) or substrate (islands) (spatial scale - $10,000m^2$ to $100km^2$).

Zone, Level 3 – distinguishes between water column, littoral or sea bottom ($100m^2$ to $10,000km^2$).

Macrohabitat, Level 4 – is large physically complex structures that typically contain several habitats, such as a red mangrove stand (spatial scale - $100m^2$ to $1,000m^2$).

Habitat, Level 5 – is a specific combination of physical (i.e. grain size) and energy characteristics that create a suitable place for colonization or use by biota (spatial scale - 1 m^2 to $100m^2$).

Biotope, Level 6 – is identified by characteristic biology associated with a specific habitat (spatial scale - $1m^2$ to $100m^2$).

This Appendix deals with the classification of the marine benthic substrates seen at the four different IHMs around Antigua at the levels of macro-habitat (Level 4) and habitat (Level 5). The classification was limited to these two levels of the CMECS because they were most applicable to the geographic scale at which the studies completed were conducted. The CMECS defines macro-habitats as spatially large, complex vegetative structures of the coastal and marine environment that contain many habitats and support multiple distinct biological associations (Madden et al. 2005). In each IHM, the macro-habitats that were critical to the growth and survival of the focal fish family (Haemulidae) and thus, had a great impact on their fitness were mangrove stands, seagrass beds, coral reefs/hardbottom areas and bare sand. The CMECS defines a habitat as a physical unit of the environment that is directly used by the biota for food, shelter, spawning and/or refuge and includes specific substrate, energy, composition and biological classifiers (Madden et al. 2005). The different habitat types that occurred within each of the four IHMs studied in Antigua are: mangroves - red mangroves; seagrass - patchy seagrass, sparse seagrass, dense seagrass; coral reefs/hardbottom - fringing reefs, patch reefs, and nearshore hard bottom; and bare sand (Tables A1.1 and A1.2).

IHM Macro-habitat Description

CAD was located on the southwest coast of Antigua (Table A1.3). It stretched from Johnson Point to Morris Old Mill and out to sea. The depth of this IHM ranged from the shore to waters up to approximately 10 meters deep. The three macro-habitat types; mangroves, coral reefs/hardbottom and seagrass meadows were present at CAD (Figure A1.2). CAD had two red mangrove (*Rhizophora mangle*) stands that fringed the coastline. The larger stand was located between Johnson's Point and the Fisheries Complex at Urlings and was separated from the seaward seagrass beds and coral communities by a ridge of coral rubble, which was only inundated when the tide was high. Thus, at low tide, the mangroves and their accompanying biological communities were separated from the other habitats by this coral rubble ridge. The other smaller *H. mangle* stand fringed Cades Bay. The major benthic habitat component at CAD was an extensive area of low relief hardbottom. This hard substratum was scattered with numerous small, low-relief coral heads and a high abundance of gorgonians. These hardbottom areas stretched from the shore to over 300m out to sea in some areas followed by a steep drop off into seagrass and sand communities. The most common species of corals belonged to the genera *Diploria*, *Porites* and *Montastrea*. There was a high abundance of gorgonians and much of the hardbottom areas were covered by turf and calcareous algae. The majority of the seagrass communities at this site were very dense (30-60% of seagrass species) and the dominant seagrass species was *Thalassia testudinum*. CAD was a multi-use area (tourism, fishing etc.) that was designated an MPA in 1999 (pers com Antigua Fisheries Division). However, during the course of this research the management plan had not yet been implemented. A number of fishers practiced gill netting, handlining, seining, spearing and trapping (fish traps) at this IHM.

GI was the area surrounding Guiana Island; a small island located on the northeast coast of Antigua (Table A1.3). Much of the area of this IHM was very shallow with approximate maximum depth of 8.5 meters. GI had an abundance of mangroves, coral reefs and dense seagrass meadows (Figure A1.2). Much of the coastline to the west and south of Guiana Island was fringed with red mangroves (*Rhizophora mangle*). Dense seagrass meadows spread out all around the area and numerous coral reefs (patch reefs) were distributed around this IHM. The most abundant coral genera observed during surveys were *Acropora*, *Montastrea* and *Porites*. The dominant seagrass species observed was *Thalassia testudinum*. This site had a greater coverage of calcareous and fleshy macroalgae and crustose coralline algae than any of the other IHMs, with the dominant macroalgae species being *Halimeda* spp. and *Dictyota* spp. respectively. At GI, fish traps, spears and gill nets were the dominant gear types used by fishermen.

JB, which was located on the north of Antigua, was seaward of the coastline that stretches from Boons Point to Shoal Point (Table A1.3). This IHM was composed of seagrass meadows and coral reefs, and had no mangrove stands (Figure A1.2). Buttress and canyon formations of reef development were located approximately 90m off shore in certain areas and at closer or further distances in others. The buttress formations rose out of the water in many locations, were exposed regardless of the tides in a number of areas, and were mainly covered by species of corals from the genera *Acropora*, *Montastera*, *Portites* and *Diploria*. Much of the corals at this IHM were killed and piled up by hurricane Hugo (CCA 1991); however, there were numerous live coral heads. The buttress formations were separated by sand canyons or in some cases by low relief coral rubble and coral heads that gave the appearance of a continuous reef structure. At this IHM, there were a number of different calcareous and fleshy macroalgae species. The seagrass beds were very dense and occurred between the shoreline and coral formations and were composed mainly of *Thalassia testudinum*. Based on fisher interviews and data from the Antigua Fisheries Division, JB was the least fished of the four IHMs. In fact, for the duration of the study it was not possible to identify any subsistence fishermen that engaged in fishing activities at this IHM. The coastal areas of JB were the most developed of all the IHMs with a number of hotels and restaurants along the entire stretch of the coastline.

WILL was located on the southeast coast of Antigua at Willoughby Bay (Table A1.3). The macro-habitats present in this IHM were mangroves, seagrass meadows and coral reefs (Figure A1.2). There was only one large mangrove stand located at the curve of the bay. The area of the bay closest to the mangroves was very turbid. This turbidity was possibly the result of run-off from a number of agricultural farms located behind the mangrove stand that caused enhanced sedimentation in the area of the mangroves. Dense mixed seagrass beds (mainly *Thalassia testudinum* and *Syringodium filiforme*) and sand corridors separated this mangrove stand from the coral formations that lined the entrance to the bay. There were isolated coral heads, small rock formations, patches of algal plain and patch reefs distributed throughout the seagrass and sandy areas. However, the extensive reef development occurred close to the mouth of the bay. This area was colonized by mountains of *Montastraea*, *Diploria* and *Porites* species, and there were extensive areas where coral rubble was piled up by hurricane Hugo. There was a high abundance of gorgonians along the west coast of the bay. At its mouth, the bay received flushing from the incoming sea currents so the waters were clear with good visibility. Fishing activities were restricted to the mouth of the bay with fishers employing fish traps, spear guns and gill nets as the main gear types.

Table A1.1: The different habitat types within each macro-habitat of the four IHMs around Antigua. A short description of each habitat types is provided.

Macro-habitat	**Habitat**	**Habitat Description**
Mangroves	Red Mangroves	The benthic substrate in this macro-habitat is mud (particles with a grain size of less than 0.07 mm). Red mangroves (*Rhizophra mangle*) have colonized these muddy environments wherever they occur along the coastline of Antigua. These red mangroves are salt tolerant plants so they are able to survive in these hyperhaline, low energy areas of the coastline, containing anoxic muddy sediments, and covered by moderately turbid waters.
Seagrasses	Patchy Seagrass	Sandy bottom substrate with between 10% and 30% of either or all of the three seagrass species (*Thalassia testudinum*), manatee grass (*Syringodium filiforme*), and shoal grass (*Halodule wrightii*).
	Sparse Seagrass	Sandy bottom substrate with between 30-60% of either or all of the three seagrass species (*Thalassia testudinum*), manatee grass (*Syringodium filiforme*), and shoal grass (*Halodule wrightii*).
	Dense Seagrass	Sandy bottom substrate with greater than 30-60% or either or all of the three seagrass species (*Thalassia testudinum*), manatee grass (*Syringodium filiforme*), and shoal grass (*Halodule wrightii*).
Coral Reefs/ Hardbottom	Patch Reefs	In nearshore areas, patch reefs tend to be adjacent to sea grass beds. They are typically small, quite variable in size, and have a roughly circular in shape. They are structured by massive frame-building corals, and can exhibit substantial variability in the relative abundance patterns of algae, corals, sponges, and gorgonians.
	Fringing Reefs	Fringing reefs are the dominant platform margin reef type in Antigua. They are represented by three structural types: 1) those occurring immediately offshore on the island platform, 2) those that form ridges parallel to shore, and 3) those that occur in both shallow (< 5 m) and deep (> 10 m) water with spur and groove topography.
	Nearshore hardbottom	Several natural processes of cementation, lithification and levels of crystallization result in a hard underwater surface. Nearshore hardbottom communities in Antigua are typically expressed as an extension of the island platform.
Bare Bottom	Bare Bottom	Large expanses of subtidal clean white 'sand' composed of skeletal and oolite sediments with less than 10% coverage by sea grasses and algae are identified as the sand bare bottom habitat. They are often described as underwater deserts, with little or no overtly apparent flora or fauna.

Table A1.2: Benthic habitat classification of the four IHMs based on the CMECS scheme. The areas that are being described were all coastal and marine.

Macro-habitat	Habitat	CAD	GI	JB	WILL
Mangroves	Mud with red mangroves	X	X		X
Seagrass	Patchy seagrass	X	X	X	X
	Sparse seagrass	X	X	X	X
	Dense seagrass	X	X	X	X
Coral Reefs/ Hardbottom	Patch reef (nearshore)		X	X	X
	Fringing reef	X		X	X
	Nearshore hardbottom	X	X	X	X
Bare Sand	Bare sand	X	X	X	X

Figure A1.1: Diagrammatic representation of the classification scheme (CMECS) used to describe habitat types within IHMs in Antigua

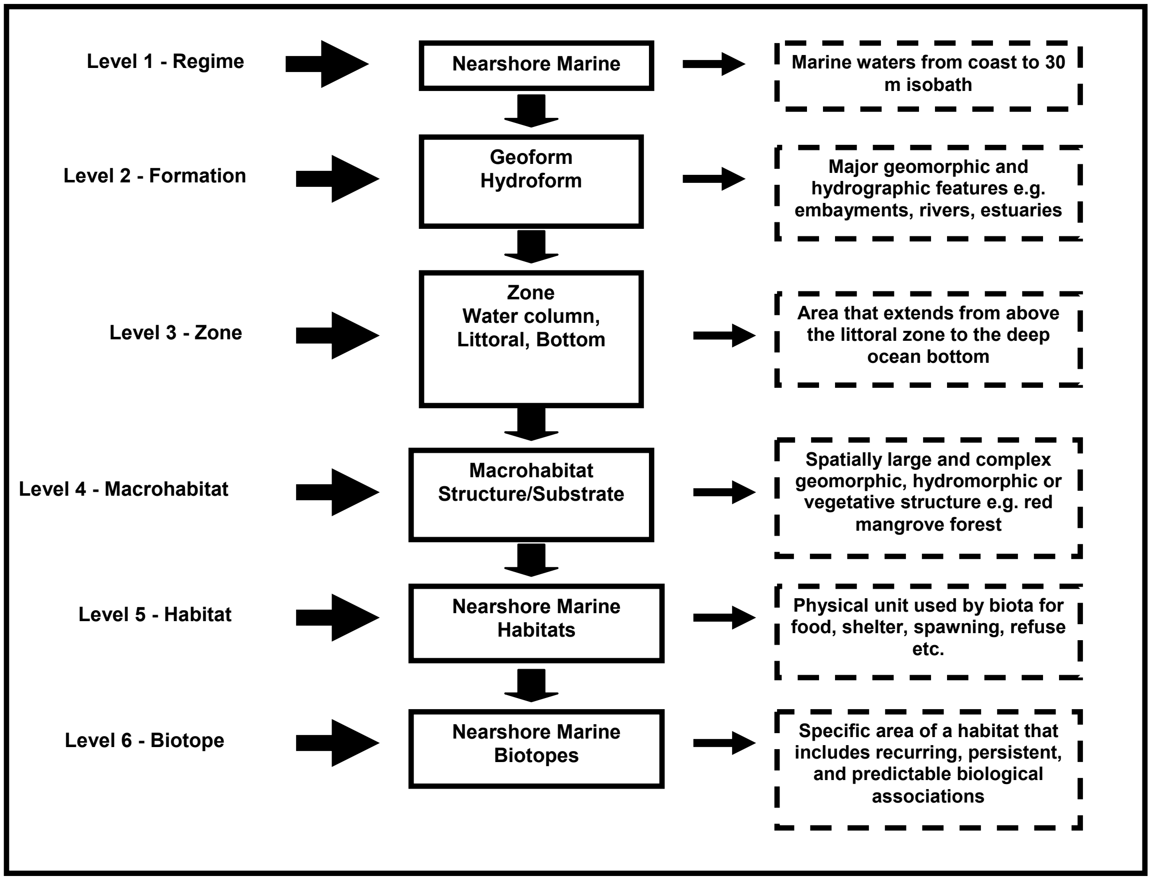


Figure A1.2: Diagrammatic representation of the benthic habitat types in each of the four interconnected habitat mosaics studied in Antigua. M - mangroves, S - seagrass, CR - coral reefs/hardbottom

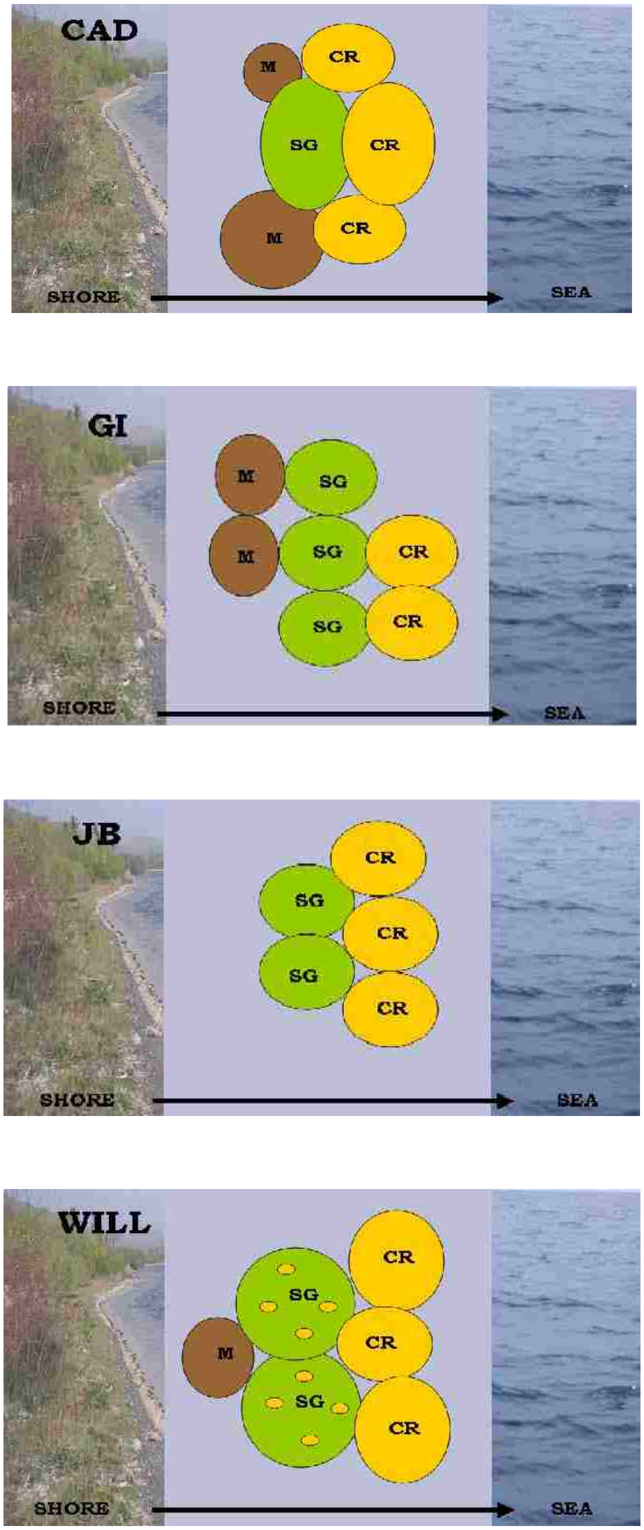


Figure A1.3: Photographs of some of the different habitat types present in the IHMs studied in Antigua.

Red mangroves at GI

Dense seagrass bed at JB

Fringing reef at WILL

Panoramic view of WILL – fringing reefs, bare sand and dense seagrass areas

Nearshore hard bottom at CAD

APPENDIX II

ENTIRE FISH COMMUNITY COMPOSITION AT THE FOUR INTERCONNECTED HABITAT MOSAICS

A2.1: Feeding diets and mean relative density 60m-^{2} ± SD (based on the logarithmic scale 1 = single; 2-10 = few; 11-100 = many; and > 100 = abundant) of the fish families observed during underwater visual survey at the IHMs in Antigua. The species are placed into their trophic groups based on Claro and García-Arteaga (2001) P – piscivorous; PI – piscivorous and invertebrate predator; B – benthophagous; Pk – planktivorous; O – omnivorous; H – herbivorous. * represents fish species that feed either on Haemulidae, their eggs or their larvae.

Family/ Scientific Species Name	Common Name	Trophic Group	CAD	GI	JB	WILL
Acanthuridae						
Acanthurus bahianus	Ocean Surgeonfish	H	2.5 ± 0.15	2.82 ± 0.15	2.9 ± 0.15	3.18 ± 0.12
Acanthurus chirurgus	Doctorfish	H	1.1 ± 0.18	1.4 ± 0.22	1.5 ± 0.24	0.18 ± 0.10
Acanthurus coeruleus	Blue Tang	H	2.62 ± 0.15	1.82 ± 0.23	2.7 ± 0.19	2.67 ± 0.18
Apogonidae						
Apogon maculates	Flamefish	Pk	0.18 ± 0.12	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Astrapogon stellatus	Conchfish	B	0.00 ± 0.00	0.12 ± 0.07	0.00 ± 0.00	0.00 ± 0.00
Apogon townsendi	Belted Cardinalfish	B	0.18 ± 0.10	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.09
Atherinidae, Clupeidae, Engraulidae						
Atherinidae, Clupeidae, Engraulidae	Silversides	PK	0.00 ± 0.00	0.64 ± 0.21	0.00 ± 0.00	0.00 ± 0.00
Aulostomidae						
Aulostomus maculates	Trumpetfish	P*	0.04 ± 0.04	0.16 ± 0.06	0.28 ± 0.09	0.25 ± 0.07
Balistidae						
Balistes vetula	Queen Triggerfish	B	0.04 ± 0.04	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Melichthys niger	Black Durgon	H	0.04 ± 0.03	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Belonidae						
Tylosusus crocodiles crocodilus	Houndfish	P*	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.06 ± 0.06
Blenniidae						
Ophioblennius macclurei	Redlip Blenny	Pk	1.04 ± 0.17	0.00 ± 0.00	0.04 ± 0.04	0.45 ± 0.13
Bothidae						
Bothus lunatus	Peacock Flounder	P*	0.00 ± 0.00	0.02 ± 0.02	0.02 ± 0.02	0.00 ± 0.00
Carangidae						
Caranx latus	Horse-eye Jack	P*	0.00 ± 0.00	0.00 ± 0.00	0.14 ± 0.08	0.00 ± 0.00
Caranx rubber	Bar Jack	P*	0.54 ±	0.14 ±	0.54 ±	0.76 ±

			0.15	0.07	0.13	0.18
Chaenopsidae						
Acanthemblemaria spinosa	Spinyhead Blenny	Pk	1.04 ± 0.17	0.12 ± 0.07	0.2 ± 0.06	0.92 ± 0.15
Chaetodontidae						
Chaetodon capistratus	Foureye Butterflyfish	B	0.5 ± 0.13	0.92 ± 0.16	0.66 ± 0.12	0.92 ± 0.17
Chaetodon ocellatus	Spotfin Butterflyfish	B	0.00 ± 0.00	0.02 ± 0.02	0.00 ± 0.00	0.00 ± 0.00
Chaetodon striatus	Banded Butterflyfish	B	0.24 ± 0.08	0.34 ± 0.10	1.12 ± 0.15	0.57 ± 0.13
Dasyatidae						
Aetobatus narinaris	Spotted Eagleray	B*	0.00 ± 0.00	0.00 ± 0.00	0.02 ± 0.02	0.00 ± 0.00
Dasyatis americana	Southern Stingray	B*	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.02 ± 0.02
Diodontidae						
Diodon holocanthus	Balloonfish	B	0.00 ± 0.00	0.06 ± 0.03	0.02 ± 0.02	0.00 ± 0.00
Diodon hystrix	Porcupinefish	B	0.04 ± 0.03	0.00 ± 0.00	0.04 ± 0.03	0.06 ± 0.04
Echeneidae						
Echeneis naucrates	Sharksucker	Pk*	0.1 ± 0.04	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Gerreidae						
Eucinostomus lefroyi	Mottled Mojarra	B	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.04 ± 0.04
Gerres cinereus	Yellowfin Mojarra	B	0.18 ± 0.07	0.08 ± 0.06	0.5 ± 0.13	0.29 ± 0.11
Gobiidae						
Coryphopterus glaucofraenum	Bridled Goby	B	0.62 ± 0.13	0.22 ± 0.87	0.48 ± 0.14	0.20 ± 0.12
Elacatinus genie	Cleaning Goby	B	0.08 ± 0.06	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Gnatholepis thompsoni	Goldspot Goby	B	0.08 ± 0.08	0.56 ± 0.19	0.12 ± 0.08	0.20 ± 0.12
Grammatidae						
Gramma loreto	Fairy Basslet	Pk	0.04 ± 0.04	0.00 ± 0.00	0.00 ± 0.00	0.04 ± 0.04
Haemulidae						
Anisotremus virginicus	Porkfish	B	0.00 ± 0.00	0.00 ± 0.00	0.08 ± 0.05	0.00 ± 0.00
Haemulon aurlineatum	Tomtate	B	0.08 ± 0.06	0.08 ± 0.08	0.22 ± 0.13	0.00 ± 0.00
Haemulon chrysargyreum	Smallmouth Grunt	B	0.14 ± 0.09	0.16 ± 0.1	1.06 ± 0.23	0.67 ± 0.18
Haemulon flavolineatum	French Grunt	B	1.00 ± 0.21	2.30 ± 0.25	1.94 ± 0.23	1.45 ± 0.22
Haemulon parra	Sailors Choice	B	0	0.12 ± 0.07	0.30 ± 0.10	0.16 ± 0.08
Haemulon plumieri	White Grunt	B	0.52 ± 0.18	1.66 ± 0.23	1.34 ± 0.23	1.62 ± 0.26
Haemulon sciurus	Bluestriped Grunt	B	0.22 ± 0.09	0.76 ± 0.16	1.36 ± 0.19	0.92 ± 0.19
	Unidentified juveniles	B	0.68 ± 0.21	2.2 ± 0.28	0.64 ± 0.2	0.74 ± 0.22

Holocentridae						
Holocentrus adscensionis	Squirrelfish	B	1.2 ± 0.18	1.7 ± 0.20	1.56 ± 0.19	1.61 ± 0.21
Holocentrus rufus	Longspine Squirrelfish	B	0.62 ± 0.16	0.3 ± 0.12	0.42 ± 0.14	0.39 ± 0.13
Myripristis jacobus	Blackbar Soldierfish	Pk	0.12 ± 0.07	0.04 ± 0.04	0.04 ± 0.04	0.49 ± 0.14
Sargocentron coruscum	Reef Squirrelfish	B	0.06 ± 0.03	0.18 ± 0.09	0.00 ± 0.00	0.00 ± 0.00
Sargocentron vexillarium	Dusky Squirrelfish	B	0.02 ± 0.02	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Kyphosidae						
Kyphosus sectatrix/incisor	Bermuda/Yellow Chub	H	0.12 ± 0.08	0.00 ± 0.00	0.14 ± 0.08	0.27 ± 0.13
Labridae						
Bodianus rufus	Spanish Hogfish	B	1.04 ± 0.17	0.00 ± 0.00	0.00 ± 0.00	0.10 ± 0.05
Clepticus parrae	Creole Wrasse	Pk	0.00 ± 0.00	0.00 ± 0.00	0.14 ± 0.1	0.00 ± 0.00
Halichoeres bivittatus	Slippery Dick	B	2.68 ± 0.22	3.54 ± 0.07	2.98 ± 0.16	3.10 ± 0.21
Halichoeres garnoti	Yellowhead Wrasse	B	1.14 ± 0.17	0.24 ± 0.09	0.02 ± 0.02	0.67 ± 0.16
Halichoeres maculipinna	Clown Wrasse	B	2.32 ± 0.2	1.54 ± 0.23	2.98 ± 0.14	2.84 ± 0.22
Halichoeres poeyi	Blackear Wrasse	B*	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.16 ± 0.11
Halichoeres radiatus	Puddingwife	B	1.70 ± 0.14	0.1 ± 0.05	1.46 ± 0.16	1.33 ± 0.18
Thalassoma bifasciatum	Bluehead Wrasse	B	3.64 ± 0.16	3.5 ± 0.14	1.64 ± 0.2	3.59 ± 0.16
Xyrichthys splendens	Green Razorfish	Pk*	0.00 ± 0.00	0.08 ± 0.06	0.26 ± 0.10	0.55 ± 0.17
Labrisomidae						
Malacoctenus macropus	Rosy Blenny	B	0.00 ± 0.00	0.12 ± 0.07	0.00 ± 0.00	0.00 ± 0.00
Malacoctenus triangulatus	Saddled Blenny	B	0.24 ± 0.10	0.50 ± 0.14	0.24 ± 0.11	0.37 ± 0.15
Lutjanidae						
Lutjanus apodus	Schoolmaster	PB*	0.80 ± 0.19	0.40 ± 0.14	1.02 ± 0.19	0.84 ± 0.17
Lutjanus griseus	Gray Snapper	P*	0.10 ± 0.07	0.24 ± 0.12	0.10 ± 0.07	0.22 ± 0.10
Lutjanus mahogoni	Mahogany Snapper	P*	0.24 ± 0.11	0.22 ± 0.09	0.46 ± 0.13	0
Lutjanus synagris	Lane Snapper	PB*	0.3 ± 0.11	0.32 ± 0.13	0.62 ± 0.18	0.76 ± 0.17
Ocyurus chrysurus	Yellowtail Snapper	PBI*	0.96 ± 0.18	1.86 ± 0.20	1.88 ± 0.18	2.02 ± 0.21
Monacanthidae						
Aluterus scriptus	Scrawled Filefish	O	0.20 ± 0.06	0.22 ± 0.06	0.00 ± 0.00	0.00 ± 0.00
Cantherhines macrocerus	Whitespotted Filefish	B	0.34 ± 0.08	0.10 ± 0.04	0.00 ± 0.00	0.22 ± 0.07
Cantherhines pullus	Orangespotted Filefish	O	0.22 ± 0.07	0.04 ± 0.03	0.00 ± 0.00	0.12 ± 0.06

Mullidae						
Mulloidichthys martinicus	Yellow Goatfish	B	0.32 ± 0.14	0.54 ± 0.15	0.86 ± 0.20	1.34 ± 0.25
Pseudupeneus maculates	Spotted Goatfish	B*	0.56 ± 0.16	0.88 ± 0.18	1.4 ± 0.18	2.37 ± 0.24
Muraenidae						
Gymnothorax funebris	Green Eel	P*	0.02 ± 0.02	0.02 ± 0.02	0.00 ± 0.00	0.00 ± 0.00
Gymnothorax moringa	Spotted Morray	P*	0.00 ± 0.00	0.02 ± 0.02	0.00 ± 0.00	0.00 ± 0.00
Opistognathidae						
Opistognathus aurifrons	Yellowhead Jawfish	Pk*	0.14 ± 0.05	0.08 ± 0.04	0.00 ± 0.00	0.00 ± 0.00
Ostraciidae						
Acanthostracion polygonius	Honeycomb Cowfish	B	0.04 ± 0.03	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Lactophrys bicaudalis	Spotted Trunkfish	B	0.02 ± 0.02	0.24 ± 0.06	0.00 ± 0.00	0.06 ± 0.04
Lactophrys triqueter	Smooth Trunkfish	B	0.02 ± 0.02	0.00 ± 0.00	0.00 ± 0.00	0.06 ± 0.04
Pempheridae						
Pempheris schomburgki	Glassy Sweeper	Pk	0.00 ± 0.00	0.00 ± 0.00	0.16 ± 0.11	0.14 ± 0.10
Pomacanthidae						
Holacanthus ciliaris	Queen Angelfish	B	0.00 ± 0.00	0.04 ± 0.04	0.12 ± 0.07	0.00 ± 0.00
Holacanthus tricolor	Rock Beauty	B	0.06 ± 0.04	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Pomacanthus paru	French Angelfish	B	0.00 ± 0.00	0.04 ± 0.03	0.04 ± 0.03	0.08 ± 0.08
Pomacentridae						
Abudefduf saxatilis	Sergeant Major	B*	1.82 ± 0.22	0.90 ± 0.19	2.26 ± 0.22	1.10 ± 0.22
Chromis cyanea	Blue Chromis	Pk	0.18 ± 0.11	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Chromis multilineata	Brown Chromis	Pk	1.62 ± 0.25	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Chromis scotti	Purple Reeffish	Pk	1.28 ± 0.18	0.58 ± 0.15	0.70 ± 0.14	1.22 ± 0.21
Microspathodon chrysurus	Yellowtail Damselfish	H	1.88 ± 0.20	0.26 ± 0.11	0.60 ± 0.15	1.22 ± 0.21
Stegastes adustus	Dusky Damselfish	O*	0.78 ± 0.16	0.04 ± 0.04	0.00 ± 0.00	0.06 ± 0.06
Stegastes leucostictus	Beaugregory	O*	2.98 ± 0.02	3.32 ± 0.12	2.84 ± 0.06	3.00 ± 0.00
Stegastes partitus	Bicolor Damselfish	O	1.00 ± 0.21	0.24 ± 0.11	0.00 ± 0.00	0.08 ± 0.06
Stegastes planifrons	Threespot Damselfish	O	1.12 ± 0.19	1.82 ± 0.21	0.12 ± 0.07	0.61 ± 0.19
Stegastes variabilis	Cocoa Damselfish	O	0.38 ± 0.12	0.00 ± 0.00	0.00 ± 0.00	0.08 ± 0.06
Priacanthidae						
Heteropriacanthus cruentatus	Glassyeye Snapper	Pk*	0.12 ± 0.06	0.00 ± 0.00	0.04 ± 0.03	0.08 ± 0.04
Scaridae						
Scarus iserti	Striped Parrotfish	H	2.54 ±	3.86 ±	3.22 ±	3.33 ±

			0.23	0.05	0.21	0.20
Scarus taeniopterus	Princess Parrotfish	H	0.36 ± 0.13	2.72 ± 0.23	0.10 ± 0.07	0.86 ± 0.21
Scarus vetula	Queen Parrotfish	H	0.00 ± 0.00	0.20 ± 0.10	0.00 ± 0.00	0.10 ± 0.07
Sparisoma aurofrenatum	Redband Parrotfish	H	1.96 ± 0.18	0.72 ± 0.18	0.22 ± 0.1	0.80 ± 0.2
Sparisoma radians	Bucktooth Parrotfish	H	0.26 ± 0.10	2.56 ± 0.19	1.24 ± 0.21	2.76 ± 0.17
Sparisoma rubripinne	Yellowtail Parrotfish	H	1.74 ± 0.17	0.88 ± 0.19	2.78 ± 0.12	2.20 ± 0.20
Sparisoma viride	Stoplight Parrotfish	H	2.12 ± 0.18	1.82 ± 0.20	2.36 ± 0.19	3.00 ± 0.13
Scombridae						
Scomberomorus maculatus	Spanish Mackerel	P*	0.02 ± 0.02	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Scorpaenidae						
Scorpaena plumieri	Spotted Scorpionfish	B*	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.02 ± 0.02
Serranidae						
Cephalopholis cruentata	Grasby	PB*	0.22 ± 0.07	0.00 ± 0.00	0.00 ± 0.00	0.08 ± 0.05
Cephalopholis fulva	Coney	PB*	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.12 ± 0.07
Epinephelus adscensionis	Rock Hind	B*	0.16 ± 0.06	0.00 ± 0.00	0.08 ± 0.04	0.00 ± 0.00
Epinephelus guttatus	Red Hind	PB*	0.42 ± 0.1	0.00 ± 0.00	0.02 ± 0.02	0.00 ± 0.00
Epinephelus striatus	Nassau Grouper	PBI*	0.02 ± 0.02	0.14 ± 0.06	0.06 ± 0.03	0.45 ± 0.13
Hypoplectrus puella	Barred Hamlet	B*	0.04 ± 0.03	0.00 ± 0.00	0.00 ± 0.00	0.14 ± 0.08
Hypoplectrus sp.	Tan hamlet	B*	0.02 ± 0.02	0.04 ± 0.04	0.00 ± 0.00	0.00 ± 0.00
Hypoplectrus unicolor	Butter Hamlet	B*	0.02 ± 0.02	0.04 ± 0.04	0.00 ± 0.00	0.00 ± 0.00
Serranus tigrinus	Harlequin Bass	B*	0.06 ± 0.04	0.00 ± 0.00	0.00 ± 0.00	0.04 ± 0.03
Sparidae						
Archosargus rhomboidalis	Sea Bream	H	0.00 ± 0.00	0.00 ± 0.00	0.16 ± 0.08	0.00 ± 0.00
Calamus calamus	Saucereye Porgy	B	0.00 ± 0.00	0.02 ± 0.02	0.08 ± 0.06	0.02 ± 0.02
Sphyraenidae						
Sphyraena barracuda	Great Barracuda	P*	0.04 ± 0.03	0.02 ± 0.02	0.00 ± 0.00	0.04 ± 0.03
Sphyraena picudilla	Southern Sennet	P*	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.08 ± 0.08
Synodontidae						
Synodus intermedius	Sand Diver	P*	0.00 ± 0.00	0.06 ± 0.03	0.02 ± 0.02	0.00 ± 0.00
Synodus saurus	Bluestriped Lizardfish	P*	0.00 ± 0.00	0.10 ± 0.04	0.04 ± 0.03	0.00 ± 0.00
Tetraodontidae						
Canthigaster rostrata	Sharpnose Puffer	O	0.24 ±	0.10 ±	0.00 ±	0.08 ±

	0.08	0.06	0.00	0.04

A2.2: Summary of the entire fish community distribution pattern observed at each IHM. B – benthophagous; H – herbivorous; P – piscivorous; PI – piscivorous and invertebrate predator; Pk – Planktivorous; O – Omnivorous

Characteristic	**CAD**	**GI**	**JB**	**WILL**	**ALL**
# of Species	83	73	66	75	111
# of Families	32	29	27	31	40
Number of Species in the 7 Dominant Families					
Haemulidae	5	6	7	5	8
Holocentridae	5	4	3	3	5
Labridae	6	6	7	8	9
Lutjanidae	5	5	5	4	5
Pomacentridae	10	7	5	7	11
Scaridae	6	7	6	7	7
Serranidae	8	3	3	5	9
Number of Species in Each Trophic Group					
B	39	35	31	36	53
H	12	11	12	12	14
P	7	10	8	6	14
PB	4	2	3	4	5
PBI	2	2	2	2	2
Pk	11	6	8	8	15
O	8	7	2	7	8
# of fish that consume fish, fish eggs or fish larvae	25	22	20	23	38

APPENDIX III

ASSIGNING AGES TO WHITE GRUNT (*HAEMULON PLUMIERI*) CAUGHT IN ANIGUAN WATERS

For age analysis, three transverse (dorsoventral) sections were taken from each otolith using a low speed saw. One section was made on either side of the core, and the other encompassed the core. Sections were mounted on glass slides with thermal cement. Without knowledge of fish size, site or capture date and using a compound microscope equipped with transmitted light, annuli were counted on each otolith section at 40x magnification. Annuli in sections viewed under transmitted light appear as opaque black rings (opaque zone) against an otherwise translucent background (translucent zone). Ages were assigned based on the number of opaque zones. The zones on each otolith section were counted independently by two readers. The results of the two readings were compared and if there was a discrepancy in the counts between readers, the section was re-examined and independently aged by each reader a second time. An age was assigned only after three out of the four ages agreed. If per chance ages did not agree, the otolith was discarded and not included in analyses. All *H. plumieri* were assigned an age based on the international birth date of January 1st (Chilton and Beamish, 1982). This was necessary so that *H. plumieri* collected throughout the year could be correctly assigned to the appropriate age class based on the year of their birth. The periodicity in the opaque zone formation in sagittal otoliths (marginal increments) was assumed to be annual (Potts and Manooch 2001, Murie and Parkyn 2005, Araújo and Martins 2007).

There were a number of interesting facts that were realized when the otoliths were aged. Some of these are listed below.

1. Age Assignments (Figure A3.1)

When viewed with transmitted light, white grunt otoliths had opaque (dark) annuli that alternate with translucent (light) zones. Opaque zones were enumerated along either the dorsal or ventral area of the sulcus. Of the 635 sectioned otoliths from *H. plumieri* landed in Antigua, 629 (99 %) of the otoliths were assigned ages between 0 – 15 years based on the agreement between the readings of the primary and secondary reader (all ageing disagreements were ± 1 year difference).

2. Differences in length-at-age for *H. plumieri* (Figure A3.2)

For all ages, the length-at-age values for *H. plumieri* had a wide range (see Age-length key Table 3.5). The otoliths in Figure A3.2 were all from 4 year old *H. plumieri,* however, the total lengths ranged from 23.4 cm to 26.4 cm. In addition, there was also a large amount of overlap among length-at-age values; for example a 4 year old fish was 26.4 cm (Figure A3.2) while a 5 year old fish was 26.5 cm (Figure A3.1).

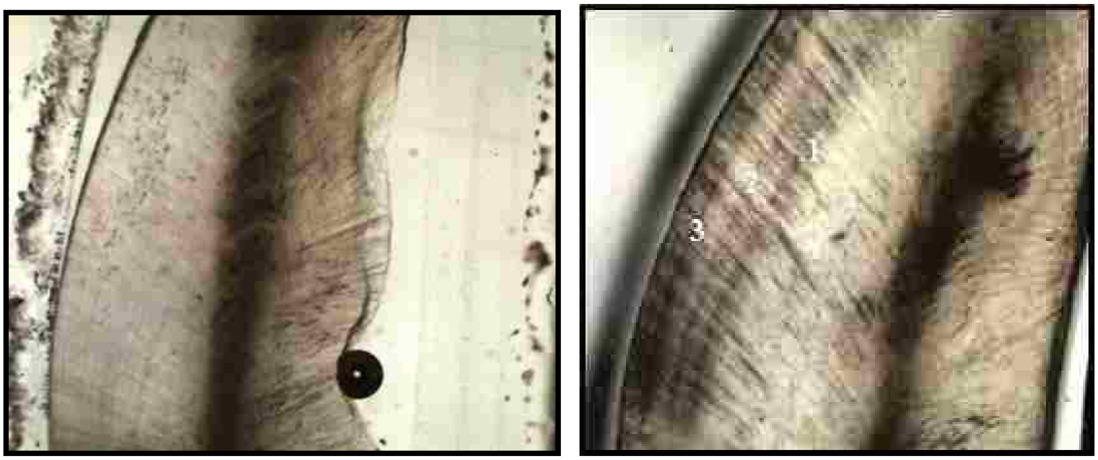
3. Clarity of Age Marks on Otoliths (Figure A3.3)

In some individuals the annuli were indistinct and irregular in appearance, which made age estimation difficult. Of the 635 sectioned otoliths from *H. plumieri* landed in Antigua, 629 (99 %) of the otoliths were assigned ages based on the agreement between the readings of the primary and secondary reader (all ageing disagreements were ± 1 year difference).

Figure A3.1: The range of ages assigned to *H. plumieri* caught in each of the three IHMs, based on the counting of opaque rings on sagittal otoliths.

Fork Length: 16 cm
Total Length: 18.1 cm
Age (years): 0

Fork Length: 19.2
Total Length: 21.6 cm
Age (years): 3



Fork Length: 23.2cm
Total Length: 26.5 cm
Age (years): 5

Fork Length: 26.6
Total Length: 30.2 cm
Age (years): 14

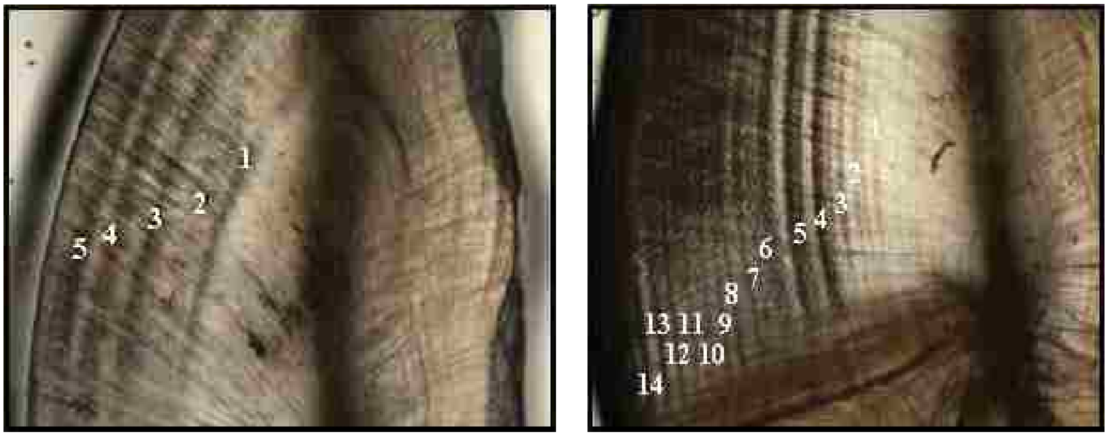
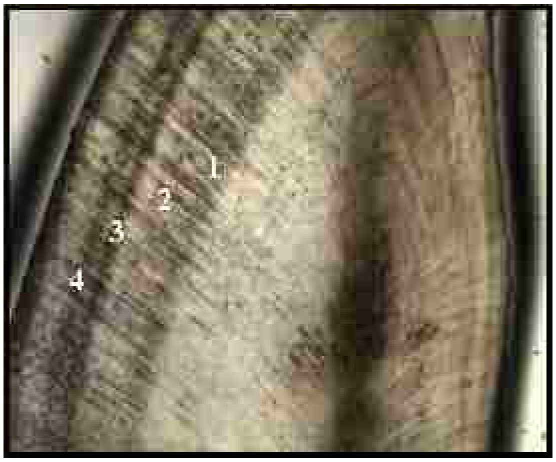
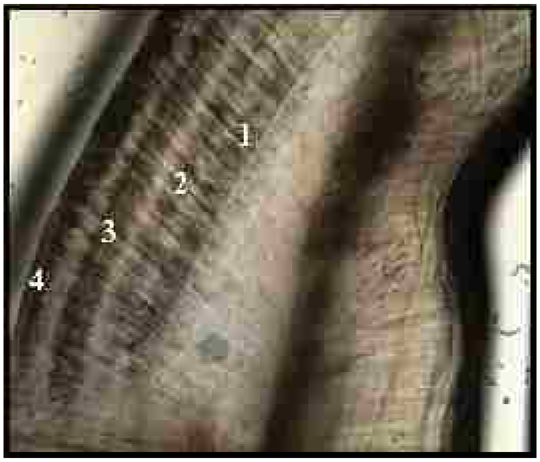


Figure A3.2: Differences in the length-at-age values of *H. plumieri* caught in the three different IHMs. In the four slides below the total length of four different 4 year old fish ranges from 23.4 to 26.4 cm.

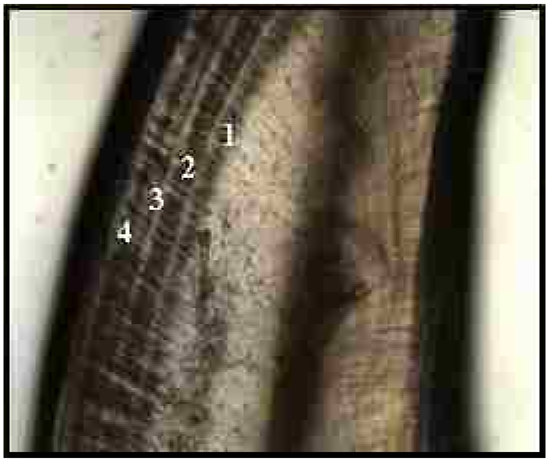
Fork Length: 23.2cm
Total Length: 26.4 cm
Age (years): 4



Fork Length: 22.5
Total Length: 25.2 cm
Age (years): 4



Fork Length: 20.5cm
Total Length: 23.4 cm
Age (years): 4



Fork Length: 23.0
Total Length: 25.8 cm
Age (years): 4

Figure A3.3: Slides of two otoliths where the annuli were indistinct and irregular in appearance, and therefore, made age estimation difficult. In the first round of annuli counting 1 independent reader assigned and age of 2 years and the other an age of 3 years to the 3 year old fish below (Slide a). The slide was re-read and an age of 3 was agreed upon. For Slide b, in the first round of annuli counting 1 independent reader assigned and age of 3 years and the other an age of 4 years to the 4 year old fish below. The slide was re-read and an age of 4 was agreed upon.

Fork Length: 23.0 cm
Total Length: 26.2 cm
Age (years): 3
Slide (a)

Fork Length: 23.7
Total Length: 26.7 cm
Age (years): 4
Slide (b)

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