

**USING LANDSCAPE ECOLOGY TO DESCRIBE HABITAT
CONNECTIVITY FOR CORAL REEF FISHES**

by

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A dissertation submitted in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY
in
MARINE SCIENCES
(Biological Oceanography)

UNIVERSITY OF PUERTO RICO
MAYAGÜEZ CAMPUS
2009

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ABSTRACT

Some coral reef fishes depend on specific habitats to complete ontogenetic migrations. The distribution of these nursery species may be influenced by the connectivity between nursery habitats, used during early life stages, and coral reefs. The lack of nursery habitats can potentially limit the development or presence of fish populations depending on the nature of the fish-habitat relationships. Mangroves and seagrasses have been shown to support the ecological nursery function; therefore the lack of mangroves at a remote oceanic island (Mona, Puerto Rico) presents an opportunity to explore habitat connectivity at the island scale. Landscape composition and habitat configuration were tested to explain the presence and abundance of ontogenetic stages of reef fishes. Mona Island's insular shelf was sampled by quantifying habitat metrics and fishes in 613, randomly stratified belt-transects (60 m²). Nursery habitats (nearshore seagrass, hardbottom (bedrock), coral reef) were species-specific and cross-shelf ontogenetic migrations were identified for the coral reef fish assemblage. When compared to La Parguera (with abundant mangroves and seagrass), the presence and abundance of some species at Mona were limited. A notable exception was *Lutjanus apodus*, which occupied nearshore hardbottom at Mona during juvenile stages. Habitat metrics correlated with fish density at distinct spatial scales and varied between species, suggesting ontogenetic requirements are species-specific and scale dependent. Depth, substratum vertical relief as well as percent cover of some epibenthic groups were important correlates to fish abundance for the different ontogenetic stages. At landscape scales, areas with small patches (~100 m²) of coral habitat located in proximity to each other supported higher fish densities, although their arrangement on

the shelf influenced this relationship. The distribution and replication of key habitats within Mona Island's marine reserve suggest that this protection is sufficient to encompass inter-habitat connectivity for reef fishes. However, the limited distribution of nursery habitat in nearshore areas implies that land-based threats may present greater potential impacts to juvenile fishes. Landscape ecology served to detect patterns of habitat use and ontogenetic connectivity of reef fishes applicable to evaluating the ecological value of a particular arrangement of habitats within spatial-based protection.

RESUMEN

Algunos peces asociados a los arrecifes de coral dependen de hábitats diferentes para completar su ciclo de vida a través de migraciones ontogénicas. Dichas especies requieren de combinaciones de hábitats durante etapas juveniles, que de estar ausentes, bien podrían limitar el desarrollo o la presencia de sus poblaciones. Por lo general los manglares y las praderas de hierbas marinas proveen la función de hábitat de crianza para peces juveniles. La Isla de la Mona, distante, oceánica y desprovista de manglares, ofrece una oportunidad para estudiar el grado de interdependencia de peces y hábitats críticos durante su ontogenia. La composición del paisaje submarino y la configuración de los hábitats fueron cuantificados para evaluar la conectividad entre hábitats usados por los peces en sus diversas etapas ontogenéticas. Para describir la relación entre peces y hábitats, en esta investigación se muestrearon los peces visualmente y se colectaron características de hábitat en 613 transectos de banda (60 m²) escogidos al azar y estratificados por profundidad en toda la plataforma insular de la Isla de la Mona. Los hábitats de crianza fueron identificados mediante comparaciones de los tamaños de los peces y las densidades observadas durante sus etapas ontogenéticas por hábitat. Las zonas de crianza son específicas para cada especie y están compuestas por fondos rocosos, hierbas marinas y arrecifes de coral en aguas someras. En este estudio se describieron migraciones ontogenéticas a través de la plataforma insular para varias especies. La ausencia de manglares en la Isla de la Mona parece limitar la abundancia algunas poblaciones, en comparación con La Parguera, un área con abundantes manglares. No obstante, en la Isla de Mona, el pargo amarillo (*Lutjanus apodus*) utiliza el fondo rocoso como un hábitat de crianza, en

sustitución de los mangles. Las características de los hábitats, a distintas escalas espaciales, se correlacionaron con las densidades de peces, aunque variaron por etapas ontogenéticas y por especies. En escalas de 30 metros el relieve del sustrato, la profundidad y la proporción de cobertura de algunos grupos epibentónicos están relacionados a la presencia y abundancia de peces. A escalas mayores los parches de hábitat de menor tamaño (~100 m²) albergaron mayores densidades de peces. La localización y abundancia de hábitats, a nivel del paisaje, también influyen sobre la distribución de peces, asunto que depende también de su etapa ontogenética. La inclusión de varios hábitats importantes dentro de la reserva marina de la Isla de la Mona sugiere que su configuración es suficiente para acaparar la mayoría de la conectividad entre hábitats críticos. Sin embargo, la localización de hábitats de crianza cercanos a la costa apunta a su vulnerabilidad a impactos potenciales provenientes de actividades terrestres. Dado a que consideraciones de la ecología del paisaje sirvieron para describir los patrones de usos de hábitats por peces, es recomendable su aplicación para diseñar y evaluar la efectividad del manejo basado en el ecosistema.

To my family . . .

For always being supportive, no matter what

ACKNOWLEDGEMENTS

Throughout my graduate studies at the University of Puerto Rico several persons and institutions collaborated in the development of my academic career. With their support I was able to grow professionally and personally. This section is a small representation of the great appreciation that I have for those individuals.

I am grateful to my chairman, Dr. Richard Appeldoorn for his patience, guidance and supervision. In addition I acknowledge my graduate committee for their input throughout this study. Dr. Paul Yoshioka provided ideas and suggestions during all phases of this study. Dr. Ernesto Weil initiated my interest for underwater research on a cruise to Mona Island in 1998. Dr. Ron Hill has provided ample opportunities to collaborate on research field trips at Mona Island since 2001. Dr. Edwin Hernández-Delgado has also provided me with opportunities in the field of marine studies and conservation.

During my professional development Dr. M. Valdés-Pizzini and R. Chaparro were supportive and always provided uplifting comments that boosted my self-confidence and motivated me to reach my goals. The complete staff of the Sea Grant College Program always provided a positive and encouraging work attitude to help me reach my potential. I am indebted to the Department of Marine Sciences for providing the administrative support essential for this dissertation, especially the Magueyes Island staff, A. Santiago, Z. Martinez, L. Valle, M. Pagán and M. Casiano.

Fellow students and alumni of the Department of Marine Sciences provided insight throughout the years and helped me move forwards, especially A. Aguilar-Perera, I. Bejarano M. Prada, I. Ruiz-Valentín, H. Ruiz, and F. Pagán. The following scientific

divers were an essential component of field data collection: A. Zuluaga-Montero A. Álvarez, I. Bejarano, C. Diez, C. Ellsworth, K. Ferrán, K. Flynn, J. García, F. García-Huertas, C. Hincapié, E. Irizarry, E. McLean, M. Nemeth, N. Pérez, C. Prada-Montoya, S. Rivero, H. Ruiz, I. Ruiz-Valentín, D. Ruiz, D. Stansbury, B. Todd, and C. Toledo. Mona Aquatics provided dive and travel logistics and I am especially grateful to the crew of *Orca Too*, Captains F. García-Huertas and C. Velez for their professional, efficient and safe operations at sea. During fieldwork O. Lugo, D. Flores, J. Montalvo, B. Montalvo and H. Collazo provided logistical support on land. Video transects were processed and partially analyzed by K. Sepúlveda and I. Ruiz-Valentín provided significant assistance in data entry. Ken Buja and T. Battista provided much needed help with GIS software. Last, but not least, M. Nemeth was instrumental in conceptualizing, planning, diving safely, collecting data and supporting me (literally) through all stages of this degree.

The Department of Natural and Environmental Resources provided research permits (# 04-IC-004) and logistical support at Mona Island in order to complete this study. This research was partially funded by the National Oceanic and Atmospheric Administration, Center for Sponsored Coastal Ocean Research, under awards NA04NOS4260206 to the University of Puerto Rico for the Caribbean Coral Reef Institute. In addition the Sea Grant College Program of the University of Puerto Rico Mayagüez provided a seed money award for this project. Throughout most of my graduate work a research fellowship was granted by the Central New York - Alliances for Graduate Education and the Professoriate (AGEP) at the University of Puerto Rico and I thank Dr. L. Antonio Estévez for the opportunity.

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1 INTRODUCTION

Nursery habitats

Marine ecosystems are under increasing threats that undermine ecological functions. Coastal benthic habitats provide nursery functions that impact other ecosystem components. Nurseries support the early life stages of marine organisms including coral reef invertebrates and fishes. Nearshore habitats such as mangroves, seagrass, rubble, coral reef patches and hardbottom are classified as nursery habitats when they contain early juvenile stages of species whose adults are located elsewhere (Thayer et al. 1987, Baelde 1990, Ley et al. 1999, Nagelkerken et al 2000). These habitats provide shelter, refuge and food for juvenile fishes and are a source to adult populations of nearby coral reefs. This is an ecological process, which is important to understand as it provides additional value to specific areas that deserve prioritization in the protection of ecosystems (Mumby et al. 2004, Sanchirico and Mumby 2009).

An important aspect of nursery habitats is undoubtedly their location, which may be subject to larval recruitment and settlement patterns although these are often variable and difficult to predict. Areas that accumulate or somehow entrap water masses and associated larvae during pelagic, floating or surface stages prior to metamorphosis and settlement may have a greater impact on the nursery function. This is commonly seen in estuaries, bays, lagoons and back-reef areas where habitats may or may not provide the ecological requirements (food, structure, refuge) for settlers to survive their early benthic life stages. When conditions favorable for post-settlement survival are met the habitats that harbor greater numbers of juveniles and provide a source to adult populations are considered nursery habitats (Parrish 1989).

Mumby et al. (2004) suggested that the lack of mangroves specifically affects the presence of some coral reef fishes (i.e. *Haemulon sciurus* and *Scarus guacamaia*) on nearby reefs. The proposed mechanism is outlined in Figure 1-1, where the ecosystem without mangroves (below) has reduced survival of these species during early life stages, when mangroves are more commonly used. However other species are able to recruit in seagrass, and survive to move on to coral reefs as juveniles.

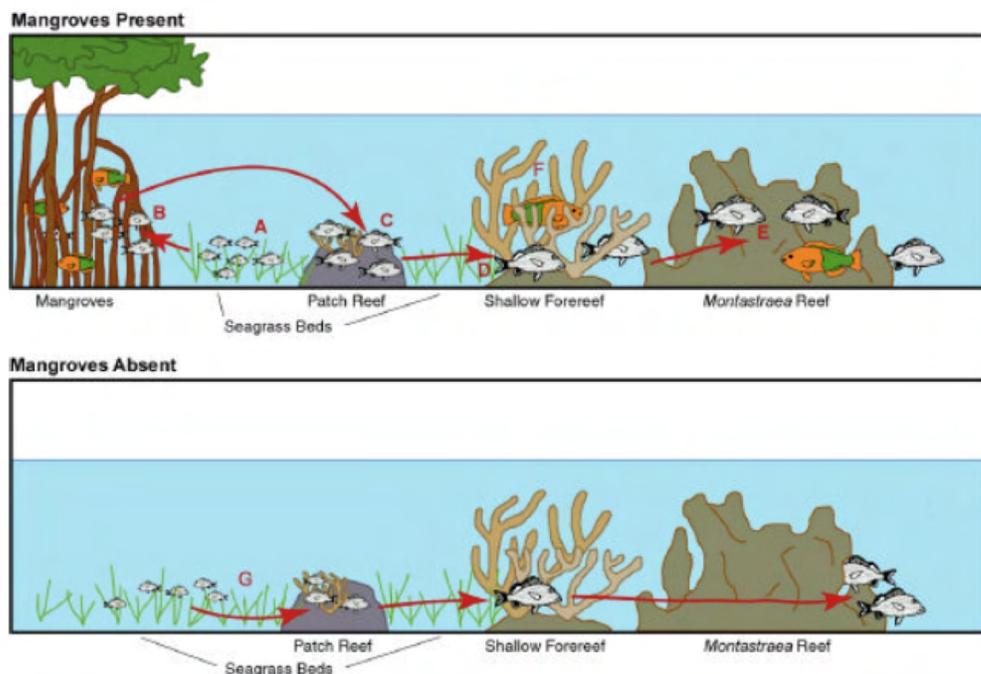


Figure 1-1 Conceptual figure of habitat connectivity between alternate habitats used by coral reef fishes (from Mumby et al. 2004 supplemental information).

It has also been suggested that the relationship of some fishes with a specific nursery habitat is facultative or opportunistic; it is beneficial to the fishes but not essential for their survival (CSA International, 2009). Obligate dependence upon one habitat is not common in motile species such as coral reef fishes; therefore, the relationship to specific habitats may be the result of a specific need that is being met

usually the basic requirement of food or structure in the case of small sized fishes. It seems that mangroves are not obligate habitats for juvenile coral reef fishes, although frequently used by early life stages (Nagelkerken 2007). Nursery habitats are believed to have higher prey abundance (Nagelkerken et al. 2000) and / or lower predation risk (Shulman 1985) for juveniles compared to adult habitats. Changes in diet (Cocheret de la Morinière 2003) as fishes grow and the ability to occupy habitats that maximize growth and minimize predation risk (Werner and Gilliam 1984) can lead to ontogenetic migrations, also known as post settlement migrations (Cocheret de la Morinière 2002). Yet not all habitats used by juveniles are nursery habitats, according to the definition proposed by Beck et al. (2001); only those that have a juvenile contribution function or higher than average number of juveniles per-unit area basis should be identified as nursery habitats. The higher than average contribution to the adult population may be a result of a combination of fish density, growth, survival and movement patterns (Beck et al. 2001).

Quantifying the juvenile contribution of a habitat requires specific research, often using methods that may be difficult to replicate. Because habitats are commonly used as surrogates for species abundances in marine ecosystems it is important to know what drives their ecological function. Although simplifying assumptions have been generated for well-studied, abundant species, there is a chance of underestimating nursery habitat requirements for other species or ecosystems where the nursery habitat of a species is lacking. Variability in nursery habitat use must also be considered, i.e., when other habitat types may substitute nurseries as long as ecological needs are met.

In order to better understand the nature of nursery habitat relationships of coral reef fishes, studies that quantify habitat use by ontogenetic stages are required.

Connectivity of habitats

For the purposes of this study the term “connectivity” will be used to refer to inter-habitat or ontogenetic connectivity. In this sense connectivity includes those habitats linked by the migration of fauna during ontogenetic stages (Cocheret de la Morinière 2003, Nakamura and Sano 2004) and by daily migrations or movements (Sogard et al. 1989, Unsworth et al. 2007). Most coral reef fishes are believed to be relatively site attached and studies of fish movements have revealed high site-fidelity (Eristhee and Oxenford 2001), although the duration of these studies is generally short termed. Habitat connectivity is considered a function of distance, abundance, size and arrangement of suitable habitat patches (Vega-Fernández et al. 2008) and is usually inversely related to isolation (Robertson 1988, Ault and Johnson 1998, Dorenbosch et al. 2007). Distance and isolation of habitat patches could serve as a measure of connectivity, yet limited knowledge of fish movement patterns, survival rates by habitat and other ecological interactions suggest connectivity is substantially more complex.

Understanding linkages between nursery and adult habitats, or connectivity, is important for studies of ecosystem function and fish ecology. Methods that have been employed to determine ontogenetic migrations include changes in size- or age-structure of organisms in different habitats, tagging studies and indirect sources such as differences in distribution and abundance (Gillanders et al. 2003) and otolith microchemistry (Chittaro et al. 2004, 2004, 2006; Mateo 2009). In order to infer

connectivity between nursery and adult habitats both juvenile and adult fishes must be quantified in all available habitats. While sampling in the field, it could be assumed juveniles move to different habitats as adults, when their disappearance may be due to predation or mortality. In addition, sampling all habitats should help detect areas that although not harboring high abundances of juveniles may serve as corridors between other important habitats. Studies of habitat use during ontogenetic migrations will help determine habitats critical for ecosystem based fisheries management and the conservation of endangered species.

Habitat use during ontogenetic migrations has been studied by inferring cross-shelf migrations using a variety of different habitats (Appeldoorn et al. 1997, Lindeman et al. 2000, Cocheret de la Morinière et al. 2002, Aguilar-Perera 2004, Cerveny 2005). In addition artificial tagging with the use of hydro acoustic technology has provided some evidence of movements across habitats, although at short temporal scales (Tulevech and Recksiek 1994, Friedlander and Monaco 2007). Otolith microchemistry measures are also being used to discriminate nursery habitat use of juvenile fishes (Chittaro et al. 2004, 2004, 2006; Mateo 2009). For this study the spatial distribution of all ontogenetic stages will be used to elucidate connectivity patterns of selected species.

Landscape ecology

Landscape ecology is derived largely from a combination of island biogeography theory (MacArthur and Wilson 1967), meta-population theory (Hanski 1999), and patch dynamics (Pickett and White 1985). Recently, this research framework has been applied to understanding the distribution of organisms in spatial terms emphasizing

relatively broad scales and the ecological effects of spatial patterns (Turner 1989; Turner et al. 2001). Landscape ecology is concerned with the abundance and arrangement of important ecological components (Turner et al. 2001). Quantifying spatial patterns at broader scales is possible thanks to recent developments in remote sensing technologies, in which larger areas can be mapped, quantified and statistically tested at distinct spatial scales.

Landscape ecology has been applied to try to understand causes of spatial patterns, organism's distributions, effects of fragmentation and to construct spatially explicit models. The purpose of these applications can be explicative or predictive in nature. Regardless, landscape ecology provides a suite of new hypotheses regarding interactions between organisms and space occurring at different scales.

Landscape ecology studies in marine systems are limited, and only recently have studies focused on coral reefs and the seascape (Ault and Johnson 1998, Nagelkerken et al. 2002, Appeldoorn et al. 2003, Kendall et al. 2003, Kendall 2005, Dorenbosch et al. 2007, Grober-Dunsmore et al. 2007 and 2008, Pittman et al. 2007a, 2007b, 2008). In marine ecosystems hard substratum patches may function as islands in the basic sense that they are surrounded by a matrix, which is a background type of habitat, characterized by extensive cover and high connectivity although not all landscapes have a definable matrix (Turner et al. 2001). This matrix is assumed to be less favorable to the organism or community studied, however the distances between patches of suitable habitat and the nature of their boundary will determine how ecological processes are affected by the landscape structure. In the Caribbean, coral reefs located near seagrasses or mangroves generally support greater species diversity and

abundances, while those that are isolated are relatively poor (Dorenbosch et al. 2007). Habitat patches can also act as sources or sinks relevant to meta-population theory for species with reduced vagility or ability to move around. Nonetheless much remains to be discovered in landscape aspects of marine systems and the connectivity between habitat elements.

In order to apply landscape ecology theory towards understanding reef fish distributions, the first step is to choose the appropriate spatial scale at which this process occurs and determine what habitats are suitable for a species. In coral reef ecosystems this becomes increasingly complicated due to migrations that occur at different temporal and spatial scales, variability in habitat requirements with size, intra and inter specific influences of the organisms, habitat preferences or use patterns as well as variability in habitat quality due to environmental or other ecological factors (succession, disturbance, etc.). For example, suitable feeding habitat for an adult fish may be seagrass, but due to the lack of refuge for its body size it spends the day in a nearby coral reef, which may be less suitable for feeding. Therefore the highest densities of adults are observed on coral reefs. This is where landscape scale studies can be employed to improve our understanding of species-habitat relationships at varying spatial scales, and the aims of this investigation.

The purpose of this study is to identify nursery habitats, map ontogenetic migrations and determine the influence of habitat metrics on coral reef fishes. The idea is to describe these spatial patterns occurring at the ecosystem level by sampling all habitats of an offshore, remote insular platform with known habitat distributions from which landscape metrics can be extracted. The influence of in-situ habitat

characteristics, patch metrics and the distribution of habitats is sought to explain fish distributions at distinct ontogenetic stages at the landscape level.

Summary of following chapters

In Chapter 2 I determine which reef fishes conduct ontogenetic habitat shifts at Mona Island and identify their nursery habitats. The distribution, size and abundance of coral reef fishes were used to determine habitat use during three main life stages (early juvenile, juvenile and adult). By sampling the complete insular platform the main ontogenetic shifts in habitats are inferred and habitat use by life stage is quantified. I also wanted to answer the question: How essential are mangroves for juvenile coral reef fish? For this I compared fish community structure and density of adults between Mona Island (which lacks mangroves) and La Parguera (with abundant mangroves). It is hypothesized that species that were absent or in low abundances at Mona Island require mangroves or greater amounts of seagrass habitats during ontogeny.

Chapter 3 relates habitat characteristics and landscape ecology metrics with five reef fishes shown to conduct ontogenetic migrations. The presence and abundance of three grunts and two snappers were correlated with habitat and landscape attributes in order to determine which features influenced distribution and abundance of the distinct ontogenetic life stages for each species. Habitat characteristics were quantified at small scales (60 m^2) in-situ while landscape scale (5 hectares or 0.05 km^2) metrics were extracted with geographic information system (GIS) software. The information on habitat requirements at distinct spatial scales provides the opportunity to identify important ecological patterns that may scale up in nature.

In Chapter 4 I summarize the findings of this study and suggest applications towards the design of marine reserves using inter-habitat connectivity criteria. Given the recent emphasis on ecosystem based management approaches and the increasing use of habitat as a surrogate for species distributions, this information can be applied to the protection of fishes in coral reef ecosystems. Critical habitats and their context or configuration within the landscape have important considerations for protected area planning and marine reserve design.

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2 NURSERY HABITAT HYPOTHESIS: HOW ESSENTIAL ARE MANGROVES FOR JUVENILE CORAL REEF FISHES?

Ecological links between marine organisms and benthic habitats are an integral part of ecosystem function. In tropical marine systems some coral reef fish depend (in varying degrees) on marine nurseries, typically identified as coastal mangrove and seagrass habitats. It has been suggested that the relationship of some fishes with a specific nursery habitat is facultative or opportunistic; it is beneficial to the fishes but not essential for their survival (CSA International, 2009). Obligate dependence upon one habitat is not common in motile species such as coral reef fishes; therefore, the relationship to specific habitats may be the result of a specific need that is being met usually the basic requirement of food or structure in the case of small sized fishes. In order to investigate the influence of habitat type upon what has been referred to as a 'nursery species' I assessed the abundance and distribution of coral reef fishes throughout Mona Island where the absence of mangroves and limited amounts of seagrass allow us to determine the nature of the nursery habitat association. Fish abundances and lengths were estimated throughout the non-sand habitats of the insular platform of the island to determine relations with depth, habitat use throughout ontogeny (based on size classes) and community structure. Results indicate that some species are absent or rare, others only occur in seagrass during early juvenile stages and the rest seem to have a facultative or opportunistic relation with habitat as they utilized alternate habitat types during early life stages. Finally the density of adult coral reef fishes at Mona Island was compared with the mangrove rich ecosystem of La Parguera highlighting those species influenced by the lack of mangroves. Results showed

differences in the nature of species-habitat linkages throughout ontogeny, which affects community structure at certain locations. The effects of habitat upon different ontogenetic stages of fishes should be taken into consideration when studying coral reef ecosystems function.

Introduction

Some coral reef fish exhibit life histories in which the distribution of juveniles is different from that of adults (Beck et al., 2001). These differences in distribution can be related to specific habitats or depths. Juvenile fishes may rely on marine nurseries, which provide ecological functions essential for early life stages that are distinct, spatially and ecologically from adults. Therefore, species that shift habitats with ontogeny create a functional link between distinct habitats in ecological terms, and understanding the strength of these linkages will provide a better understanding of how inter-habitat connectivity affects fish distributions.

Beck et al. (2001) contend that a nursery habitat contains one or more of the following traits compared to non-nursery habitat: (1) greater densities of young fishes; (2) lower predation rates; (3) higher growth rates; and (4) more successful migration to subsequent habitats. Following this definition, nursery habitats are only those that contribute the greatest number of individuals to the adult population on a per-unit-area basis, regardless of the overall contribution that a juvenile habitat makes to the adult population (Dahlgren et al. 2006). Yet, other habitats with lower contributions of individuals to the adult population, but that due to their extent provide significant numbers of individuals must be considered of equal, or even greater, importance for supporting viable populations (Dahlgren et al. 2006). Nonetheless the importance of nursery habitats must be determined by their linkages to adult habitats in order to be ecologically functional.

Habitats that provide nursery functions are generally referred to as 'nursery habitats' and species that depend on these are sometimes labeled 'nursery species'

(Nagelkerken et al. 2000a). The latter rely on one or a combination of habitats during early life stages and generally migrate to other habitats (mainly coral reefs) to complete their life history (Cocheret de la Morinière et al. 2002, Nagelkerken and van der Velde, 2003). Some of these changes occur in response to changes in feeding habits, and ensuing tradeoffs between growth and predation (Werner and Gilliam 1984) affect the distribution of individuals. Ontogenetic habitat shifts are generally associated with cross-shelf movement, where fish at greater depth or distance from shore have larger sizes (Appeldoorn et al. 1997). Cocheret de la Morinière et al. (2002) describe post-settlement migrations related to ontogenetic shifts, including stepwise migrations where fish move progressively closer to the reef as they grow, using a succession of different habitats. In the Caribbean 31 species have been identified as nursery species of which most undergo ontogenetic habitat shifts (Table 2-1).

Table 2-1 Species considered ontogenetic habitat shifters and nursery habitat reported. Nursery species identified by Nagelkerken et al. 2000 are in bold. Nursery habitats: CR=coral reef, HB=hardbottom, SG=seagrass, MG=mangrove, AL=algae.

Species	Common Name	CR	HB	SG	MG	AL	References*
<i>Abudefduf saxatilis</i>	Sergeant Major	X	X				6,22
<i>Acanthurus bahianus</i>	Surgeonfish	X	X	X			6,7,12,14
<i>Acanthurus chirurgus</i>	Doctorfish	X	X	X	X		1,6,7,8,11,12,14,17
<i>Anisotremus surinamensis</i>	Black margate	X	X				6,7
<i>Anisotremus virginicus</i>	Porkfish		X				5,6
<i>Chaetodon capistratus</i>	Four-eye butterflyfish	X		X	X		1,7,11,14,17,24
<i>Epinephelus striatus</i>	Nassau grouper			X		X	3,21
<i>Gerres cinereus</i>	Yellowfin mojarra	X		X	X		10,11,14,17,24
<i>Haemulon carbonarium</i>	Caesar grunt		X				5,6
<i>Haemulon chrysargyreum</i>	Smallmouth grunt	X	X				5,7
<i>Haemulon flavolineatum</i>	French grunt	X	X	X	X		1,5,7,8,9,10,11,12,14,15,17,23,24
<i>Haemulon macrostomum</i>	Spanish grunt		X				5,6
<i>Haemulon parra</i>	Sailor's choice		X	X	X		5,6,11,17,24
<i>Haemulon plumieri</i>	White grunt	x	X	X			4,5,8,11,14,15,24
<i>Haemulon sciurus</i>	Bluestriped grunt		X	X	X		5,7,8,9,11,13,14,17,24
<i>Lutjanus analis</i>	Mutton snapper			X	X		5,11,14,17
<i>Lutjanus apodus</i>	Schoolmaster	X	X	X	X		1,2,5,7,8,11,12,13,14,15,17,18,24
<i>Lutjanus cyanopterus</i>	Cubera snapper		X				20
<i>Lutjanus griseus</i>	Gray snapper			X	X		1,5,7,11,12,13,15,17,24
<i>Lutjanus jocu</i>	Dog snapper				X		5,15
<i>Lutjanus mahogoni</i>	Mahogany snapper	X	X	X	X		5,7,10,11,13,14,17,24
<i>Lutjanus synagris</i>	Lane snapper		X				5,6
<i>Ocyurus chrysurus</i>	Yellowtail snapper	X	X	X	X		5,6,8,11,12,13,14,15,16,17,24
<i>Scarus coeruleus</i>	Blue parrotfish			X			11,17
<i>Scarus guacamaia</i>	Rainbow parrotfish				X		11,13,14,22
<i>Scarus iserti</i>	Striped parrotfish			X	X		11,12,13,14,17
<i>Scarus taeniopterus</i>	Princess parrotfish			X	X		12
<i>Sparisoma chrysopterygum</i>	Redtail parrotfish	X	X	X	X		6,7,8,11,13,17,24
<i>Sparisoma rubripinne</i>	Yellowtail parrotfish		X		X		6,8,11,13,14
<i>Sparisoma viride</i>	Stoplight parrotfish	X		X	X		7,14
<i>Sphyraena barracuda</i>	Great barracuda			X	X		1,7,8,11,13,14,17,24

Table 2-1 Continued

*References:

1 Dennis 1992	2 Rooker 1995	3 Eggleston 1995
4 Appeldoorn et al. 1997	5 Lindeman 1997	6 Lindeman and Snyder 1999
7 Nagelkerken et al 2000b	8 Murphy 2001	9 Recksiek et al. 2001
10 Nagelkerken et al. 2001	11 Nagelkerken et al. 2002	12 Cocheret de la Morinière et al. 2002
13 Nagelkerken and van der Velde 2002	14 Nagelkerken and van der Velde 2003	15 Appeldoorn et al. 2003
16 Christensen et al. 2003	17 Dorenbosch et al. 2004	18 Halpern 2004
19 Mumby et al. 2004	20 Lindeman and De Maria 2005	21 Aguilar-Perera et al. 2006
22 Dorenbosch et al. 2006	23 Verweij et al. 2006	24 Aguilar-Perera and Appeldoorn 2007

The degree to which nursery habitats represent a limiting factor affecting the composition of reef fish assemblages, specifically among nursery species (Nagelkerken et al. 2000a), has been investigated in various Caribbean locations (Nagelkerken et al. 2000b, 2001, Nagelkerken and van der Velde 2002, Appeldoorn et al. 2003, Aguilar-Perera and Appeldoorn 2007). The facultative dependence of nursery species upon a specific habitat (or combination of habitats) during early stages is still debatable, particularly in the case where a combination of seagrass and mangrove habitats exists. In the Caribbean mangroves alone are not viewed as obligate nursery habitats for juveniles except perhaps for *Scarus guacamaia* (Nagelkerken and van der Velde 2002, Mumby et al. 2004, Dorenbosch et al. 2006).

Nagelkerken et al. (2002) concluded that nursery species are less abundant in seascapes or islands without mangrove or seagrass habitats associated with embayments or lagoons. Furthermore, Nagelkerken et al. (2001) suggest there is an interaction between seagrass and mangrove habitats, which enhances nursery species

richness in seagrass beds near mangroves. In La Parguera, Puerto Rico, Pittman et al. (2007) found more nursery species in mangroves near seagrasses. The biomass of several coral reef fish was enhanced in mangrove rich systems of Belize (Mumby et al. 2004) suggesting the combination of seagrass and mangroves provides an advantage to some populations.

To assess the relationship of ontogenetic habitat shifters or nursery species with mangrove habitat I investigated species-habitat linkages at Mona Island. This remote oceanic island has no submerged mangroves and a very limited amount of seagrass, which only occurs in shallow (< 5 m depth) near shore areas. Therefore, we would not expect significant populations of species dependent upon mangroves to occur at Mona Island. In addition, where species dependence on seagrass is high, populations at Mona Island should be significantly reduced in comparison to other species. By sampling throughout the insular platform of Mona Island, so that possible immigration and emigration of post-settlement fishes can be assumed to be zero, the presence of distinct life stages will identify potential nursery habitats. This information will help determine which species are dependant upon and will be most affected by the loss of either mangroves or seagrasses. In addition it will allow us to elucidate which coral reef fishes are influenced by the abundance and distribution of nursery habitats.

In order to identify species that are dependent upon nursery habitats I compared the abundances and sizes of fish found throughout the available habitats of the insular platform (< 25 m depth) of Mona Island. The first objective was to determine which species occur in shallow areas at smaller sizes and in deeper areas at larger sizes, thus following a cross-shelf migration pattern (Appeldoorn et al. 1997). Secondly I quantified

the abundance of early juveniles (i.e. post-settlement) to determine in which habitats they occur in higher densities. With this information we can infer which habitats are necessary and how their relative abundances (in area) compare in providing effective juvenile habitat (Dahlgren et al. 2006). For species that have been reported as dependent upon mangrove or seagrass habitat for nursery functions and occur at Mona Island, alternate nursery habitats are described. Finally we compared the density of adult coral reef species on reefs and associated hard substrata habitats between Mona Island and La Parguera, a mangrove-rich system off Southwestern Puerto Rico. In this comparison we would expect higher densities of adults of nursery species in La Parguera, due to the greater abundance of seagrass and presence of mangrove nursery habitats. On the other hand, species that are more opportunistic or have facultative associations to mangroves should be in equal or greater abundances at Mona Island.

The data were used to identify the nursery habitats available at Mona Island, detect the species that rely on specific nursery habitats, and those that are more opportunistic during early life stages. The information will be used to determine the ontogenetic shifts of fishes and identify the ecological links between habitats. In addition I describe the facultative nature of the dependence upon mangroves and seagrass for nursery species. Finally the presence of significant abundances of adults of nursery species at Mona Island could help identify those that are more opportunistic and able to complete their life cycle despite the lack of mangroves and limited seagrass.

Identifying high quality nursery habitats is a basic objective of ecosystem-based management as it is an essential fish habitat (EFH) for critical life stages of many

species. The EFH is defined as “those waters and substrate necessary to fish for spawning, breeding, feeding or growth to maturity” (Sustainable Fisheries Act of 1996). Identifying EFH is an important step in recognizing the ecological importance and translating it into a fisheries management tool that must now consider the spatial distribution of these important habitats. These habitats were determined to support highly important ecological functions; a primary criterion for EFH and habitat areas of particular concern (HAPC) designation under the federal Sustainable Fisheries Act (1996).

The ecological function of nursery habitats for coral reef fisheries is an important part of ecosystem-based management and applicable to the design of fisheries management as well as coral reef conservation strategies. Populations of species requiring distinct habitats for the completion of their life cycle may be less able to cope with threats if critical habitats are absent, disconnected or non functional. Within an ecosystem-based management approach, critical habitats as well as linkages between nursery and coral reef habitats need to be better understood in order to design management strategies for the conservation of coral reef fish populations that depend on them.

Materials and methods

2.1.1 Study Site

Mona and Monito Islands are located in the Mona Passage between the Dominican Republic (66 km) and Puerto Rico (68 km). The islands lie due east of Saona Island, southern Dominican Republic and due west of Puerto Real, Cabo Rojo in Puerto Rico (Figure 2-1). The Insular platform of Mona is located at longitude 67.89 W and latitude 18.09 N and measures approximately 81.6 km². Both islands lie on separate (by depths of 250 m) carbonate platforms formed approximately 15 million years ago (Late Miocene to early Pliocene) and uplifted from the seafloor due to tectonic movements (Frank et al. 1998). Mona Island occupies most of its insular platform (55 km²), and only the southern half of the island is bordered by relatively shallow waters with coral reef and associated habitats. Vertical cliff walls rising to 40 m above and below sea level surround the northern coast of Mona Island and all of Monito Island. Trade winds and North Equatorial Currents predominantly arise from the east or northeast generating oceanic currents in the Mona Passage (Capella, pers. com.). Because Mona Island is located upon a platform isolated from other large islands, we expect very limited immigration of post-settlement fish and therefore our sampling of all the habitats available around the island should provide a good estimate of the habitat use patterns of coral reef fishes of the insular platform.

Historically the island was occupied by Taíno aboriginal cultures previous to Spanish colonization that relied mainly on marine fishery resources as evidenced in middens from archeological excavations at Mona Island (Dávila 2003). Subsistence fishing during pre-Columbian times evolved into a subsistence fishery during guano

mining at the island (Cardona-Bonet 1985) and later into a commercial fishery targeting groupers and snappers that significantly declined during the 1970's. This decline was due to the reduced catches of reef fishes over time according to interviews with experienced fishers of the region (unpublished data). Most commercial fishing around Mona Island targets deeper (100 to 300 m) habitats for snappers (Valdés-Pizzini 1985), while recreational fishing occurs throughout near shore and pelagic areas around both islands (pers. obs).

Mona and Monito Islands as well as the waters up to 9 nautical miles from shore compose the Mona and Monito Natural Reserve, which is the largest marine protected area (MPA) in Puerto Rico. The Department of Natural and Environmental Resources (DNER) designated the Natural Reserve in 1986 (Aguilar-Perera et al. 2006). Both islands are uninhabited except for DNER staff (rangers and biologists) on Mona Island. Due to the distance from the main island of Puerto Rico visitors to Mona Island are limited to hunting season (December to April) or fishing and camping trips, which occur year-round. All campers require an advanced permit from the DNER to camp on land, however boaters that remain on-board do not. Within the Natural Reserve a no-take zone was designated in 2004 extending 0.5 nautical miles from shore around all of Monito and most of Mona Island. This zone was modified in 2007 to include most of both island's platform up to the 100 fathom (182 m) depth contour except for a swath on the western coast (Figure 2-1) where recreational fishing is allowed (DNER, 2007). However, enforcement at this site is limited due to logistical reasons (i.e. lack of patrol boat).

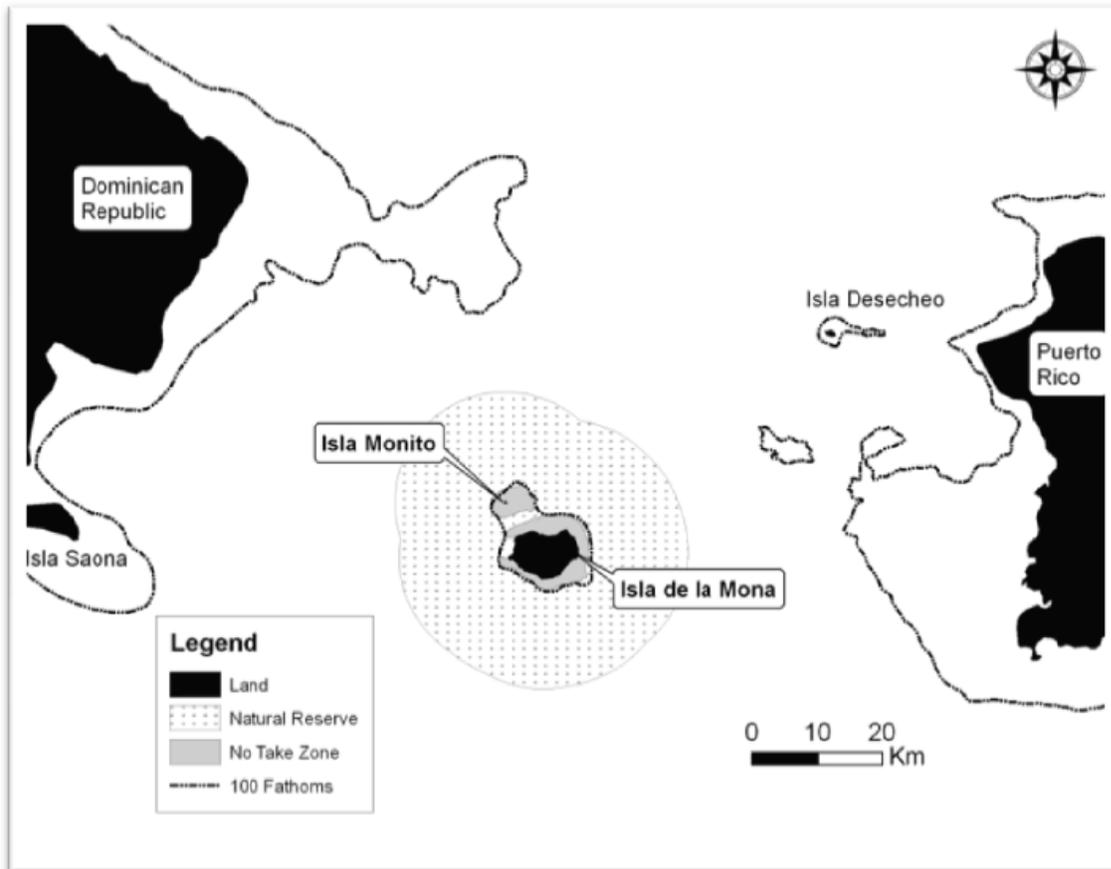


Figure 2-1 Mona Passage and associated islands west of Puerto Rico.

2.1.2 Data Collection

Data on coral reef fish distributions were collected randomly throughout the non-sand habitats of Mona Island by underwater visual census (UVC) techniques. Monito Island was not surveyed due to water depths greater than 25 m, the limit for SCUBA diving surveys. Data on fish size and abundance were collected snorkeling or with SCUBA between 7:00 and 17:00 h at sampling sites chosen randomly from a 50 m grid superimposed upon a GIS layer of the insular platform. The coordinates for each sampling site were uploaded to a handheld GPS and located in the field where a weighted buoy line was dropped from the surface to mark the starting point for each

UVC transect. At this point the depth of the beginning of a transect was measured with an underwater dive gauge and noted before recording fish observations. A 30 m tape was extended parallel to the coast or at a constant depth, while counting each fish observed within a 2 m wide band of the tape for an area of 60 m². All fish encountered in the 30 X 2 m belt were enumerated, identified to species when possible and fork length (FL) was estimated visually to the nearest centimeter.

Each sampling site was then given a habitat classification based on a benthic habitat map in GIS. The habitat map used for this study was re-digitized from the same aerial photography used by NOAA (2002) at a reduced minimum mapping unit of 100 m². The four main categories of habitat considered for this study were; submerged vegetation (SV), rubble and other unconsolidated sediments (RB/SD), hard bottom (HB) and coral reef (CR). The only SV habitats available at Mona are seagrass areas in shallow (< 5 m), backreef lagoons near the shorelines of the southern and eastern coast and amount to approximately 78 Ha. Seagrass beds are composed of mixed stands dominated by *Thalassia testudinum* and *Syringodium filiforme* and *Halodule wrightii* to a lesser extent. Most of the RB/SD habitat was also located in lagoon areas covering approximately 18 Ha. The greatest amount of habitat available at Mona Island (922 Ha) is made up of HB, including pavement and bedrock low relief areas that may be covered by a thin layer of sand such as mixed habitats of pavement with sand channels. Finally CR habitats, which amount to 656 Ha, are made up of patch, linear or spur and groove reefs usually of greater vertical relief and live coral cover than HB habitats. Within the shallow areas (< 5m depth) the dominant habitats are CR and HB (Table 2-2).

Table 2-2 Total area of shallow water (< 5 m depth) habitats at Mona Island.

Habitat	Area (km²)	Percentage
coral reef (CR)	4.93	49%
hardbottom (HB)	3.73	37%
submerged vegetation (SV)	0.78	8%
rubble/sediment (RB/SD)	0.56	6%

2.1.3 Ontogenetic migration determination

Fish size data were correlated with depth to identify species with ontogenetic cross-shelf migrations. Non-parametric Spearman's correlations of fork length (FL) and depth were considered significant at $\alpha < 0.05$. For species showing a positive correlation between size and depth, fork length was compared between habitats to determine in which habitats the smallest (post-settlement) individuals occurred. Non-parametric Kruskal-Wallis test of medians was utilized and is considered significant at $\alpha < 0.05$. Data on the frequency of occurrence, total number of individuals and density for each species observed during sampling were calculated from the 60 m² transects (sampling sites). Species observed in less than 5 transects or in low numbers (total < 5 individuals) were not analyzed.

For each species life stages were based on fork length (FL) classes (Early = FL less than half the reported size at maturity; Juvenile = FL less than size at maturity and; Adult = FL greater than size at maturity), (Table 2-3). Size at maturity data was taken from Fishbase Life History Tool (Froese and Pauly, 2003). In order to identify nursery habitats the density (individuals/60 m²) used by early juveniles, those individuals with FL less than half their reported size at maturity, was compared among all available habitat

types. Furthermore to describe ontogenetic shifts in habitat use throughout Mona Island the density for each of three life stages was compared. Differences in density by habitat type were tested with non-parametric Kruskal Wallis, considered significant at $\alpha < 0.05$.

Table 2-3 Size classification (fork length in cm) used for life stage classification for species occurring at Mona Island, size at maturity data from (Froese and Pauly, 2003).

Species	Early	Juvenile	Adult
<i>Acanthurus bahianus</i>	< 9	9 - 16	> 16
<i>Acanthurus chirurgus</i>	< 8	8 - 14	> 14
<i>Acanthurus coeruleus</i>	< 9	9 - 16	> 16
<i>Anisotremus surinamensis</i>	< 15	15 - 30	> 30
<i>Cantherines pullus</i>	< 5	5 - 10	> 10
<i>Caranx crysos</i>	< 15	15 - 29	> 29
<i>Chaetodon capistratus</i>	< 3	3 - 5	> 5
<i>Chaetodon striatus</i>	< 3	3 - 6	> 6
<i>Haemulon carbonarium</i>	< 8	8 - 15	> 15
<i>Haemulon chrysargyreum</i>	< 7	7 - 14	> 14
<i>Haemulon flavolineatum</i>	< 6	6 - 13	> 13
<i>Haemulon parra</i>	< 9	9 - 17	> 17
<i>Haemulon plumierii</i>	< 8	8 - 15	> 15
<i>Kyphosus sectator</i>	< 15	15 - 29	> 29
<i>Lactophrys triqueter</i>	< 10	10 - 20	> 20
<i>Lutjanus apodus</i>	< 14	14 - 27	> 27
<i>Lutjanus mahogoni</i>	< 10	10 - 20	> 20
<i>Melichthys niger</i>	< 11	11 - 22	> 22
<i>Ocyurus chrysurus</i>	< 16	16 - 30	> 30
<i>Scarus iserti</i>	< 8	8 - 15	> 15
<i>Sparisoma chrysopterum</i>	< 9	9 - 17	> 17
<i>Sparisoma rubripinne</i>	< 10	10 - 20	> 20
<i>Sparisoma viride</i>	< 13	13 - 26	> 26

2.1.4 Comparison with a mangrove-rich site

For species that co-occurred in Mona Island and the nursery rich ecosystem of La Parguera, the density of adults observed in CR and HB habitats was compared. Fish abundances from La Parguera were taken (Dec. 2008) from an on-line database (NOAA, 2008). These data were collected at randomly selected sampling sites from stratified habitats mapped by the National Ocean Service (NOAA), as part of a larger Caribbean Coral Reef Ecosystem Monitoring Project. Underwater visual surveys along 25m X 4m (100 m²) belt transects were conducted to quantify fishes in all benthic habitats. Density data were converted to individuals / 60 m². Comparisons were made between sites with the non-parametric Kruskal Wallis test, pooling the selected habitat types within site. In La Parguera all hard substrate habitats are pooled into one class - Coral reef and colonized hardbottom, therefore at Mona Island the CR and HB sites were pooled for this comparison.

Results

2.1.5 Nearshore habitats

The larger island of Mona is surrounded by a variety of hardbottom habitats ranging from shore to the shelf break, which is generally between 20 and 100 m in depth. Based on a benthic habitat map re-digitized from aerial photography these habitats have been quantified and their distribution is known. The dominant nearshore habitats that provide putative nursery habitats for coral reef fishes of Mona Island are presented in Figure 2-2 and described below.

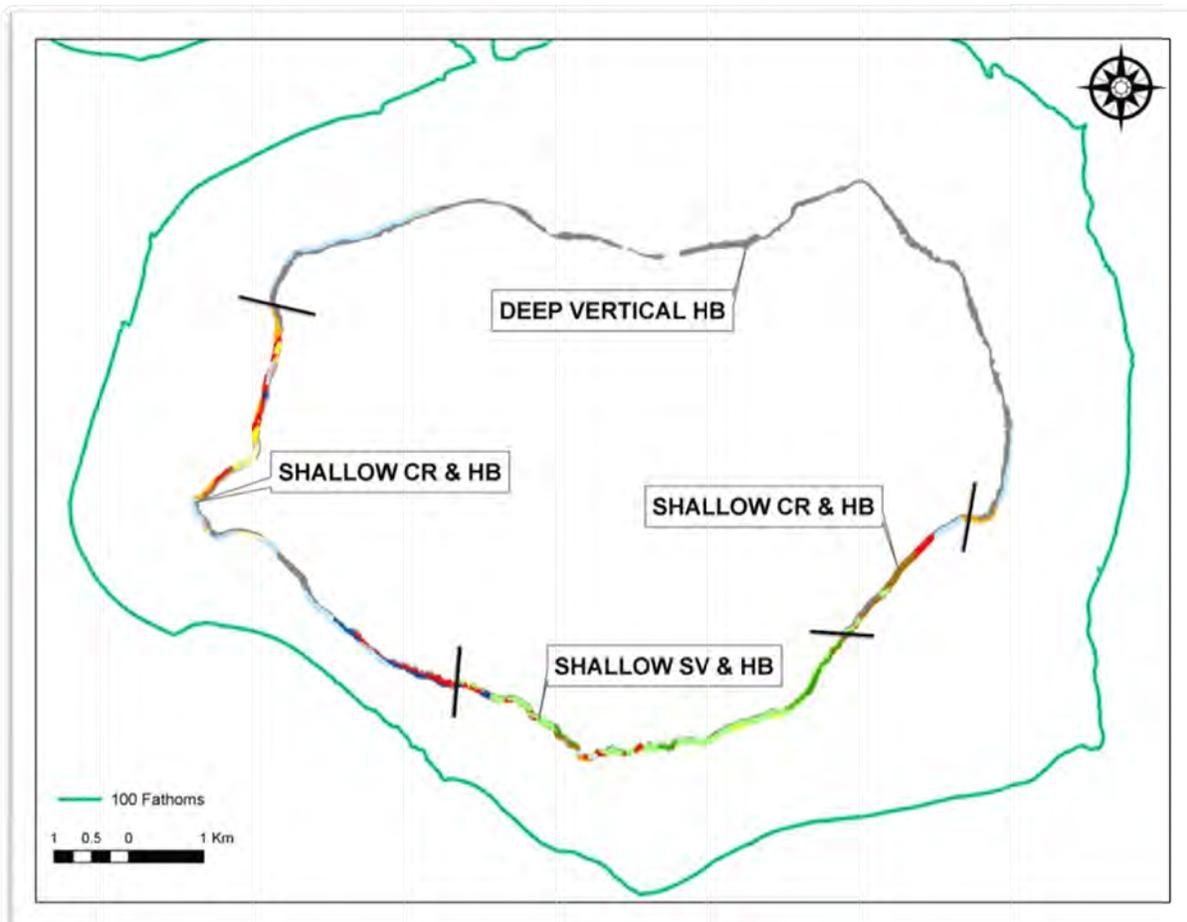


Figure 2-2 Nearshore habitats of Mona Island (HB = hardbottom, CR = coral reef and SV = submerged vegetation).

Nearshore hardbottom habitats of Mona Island are composed of limestone mainly of fossilized Pleistocene coral reefs and hence of biogenic origin. On the southern shores raised reef flats composed mainly of *Acropora palmata* facies make up the geological foundation of this habitat. Pavements of beach rock (eolianite) are frequently buried and exposed by fine carbonate sands. In general most nearshore bedrock habitats are located in shallow waters at the land and sea interface. Due to the geologic origins of Mona Island the nearshore hardbottom habitat of the northern shores is deep (~ 30m) and provides a different functional habitat to marine organisms. Generally this habitat on the northern shores of Mona Island and completely surrounding Monito Island is a sheer, vertical limestone wall that may have cracks and fissures through which freshwater percolates. Encrusting organisms such as sponges, algae and octocorals generally colonize these walls.

Sandy beaches can be found intermittently with nearshore hardbottom habitats where the underlying beach rock is sloping and not vertical. Most of the beaches of Mona Island are composed of white carbonate sand grains with red foraminifera giving the beaches a pink coloration. These beaches are highly dynamic and dependent upon the longshore transport generated by swells, currents and tidal influences upon shore. Seagrass beds are one of the most restricted nearshore habitats of Mona Island amounting to less than 1 km². Seagrass beds are composed mainly of *Syringodium filiforme* and *Thalassia testudinum* located in backreef lagoons that do not exceed 5m in depth. The greatest area of continuous seagrass is found on the southeastern shore of Mona Island covering most of the backreef lagoon. This seagrass area extends approximately 4 km parallel to shore with a maximum width of 250 meters. The majority

(83%) of total seagrass is considered patchy seagrass interspersed by smaller areas of bedrock, rubble, rocky outcrops, coral colonies and sand blow-outs. The remaining (17%) seagrass patches are composed of continuous (100% coverage) of seagrass blades.

Rubble habitats of calcareous and *Peyssonellia* spp. algae are the less abundant nearshore habitat type usually surrounded by coarse sediment with coral or carbonate outcrops. Among these patches of rubble and sediment there may be developed patches of live coral in backreef lagoon areas. Colonies of *Porites porites*, *Montastrea annularis* and *Acropora palmata* can create continuous patches of live coral near the shore in shallow water.

At present no submerged mangroves forest are present at Mona Island yet a small patch of *Rhizophora mangle* exists approximately 100 m from shore on the southwest coast. This mangrove stand is located in a low lying area on the coastal plain where brackish water accumulates although separated from the shore at present sea level by extensive sand deposits and coastal vegetation. In addition other species of mangroves (*Laguncularia racemosa* and *Conocarpus erectus*) can be observed on the coastal plain among other coastal vegetation as well as further inland.

All sampling was conducted from early August 2005 to March 2006 during 11, multi-day expeditions to Mona Island. Throughout the insular platform, 613 belt transects (Appendix 2-1) were conducted, and 126 species were observed in the four major habitat types sampled (Appendix 2-2). Some species considered to be nursery dependent or ontogenetic shifters (Table 2-1) were not observed at Mona Island, including *Gerres cinereus*, *Lutjanus synagris*, *Scarus coeruleus* and *Scarus guacamaia*.

Several additional species were found in abundances too low to be analyzed (occurred in less than 5 transects), including *Anisotremus virginicus*, *Epinephelus striatus*, *Haemulon macrostomum*, *Lutjanus analis*, *L. cyanopterus*, *L. griseus* and *L. jocu*. Only one species, the buck-tooth parrotfish (*Sparisoma radians*) was unique to submerged vegetation (SV) at all sizes and occurred in no other habitat. Of the remaining species, those that occurred in SV or are considered nursery habitat dependent (Table 2-1) were analyzed.

2.1.6 Cross-shelf habitat use

Of the species observed in SV habitat or reported to have ontogenetic migrations (Table 2-1), 23 exhibited significant (Spearman Rank test; $\alpha = 0.05$) positive correlations between fork length (FL) and depth (Table 2-4). Two species (*Scarus taeniopterus* and *Sphyraena barracuda*) demonstrated significant negative correlations between FL and depth. Ten of these 23 species had significantly smaller mean FL in SV habitats (Kruskall-Wallis H test; $p < 0.05$), while six species were smaller in SV, but not significantly so. Four species tended towards smaller sizes in hardbottom (HB) although differences were not significant. All nursery species had smaller sized individuals in SV except *Sparisoma chrysopterus*, which was smaller in HB.

Table 2-4 Trends in mean size (fork length, FL in cm) by habitat type observed for species (nursery species in bold) with FL positively correlated with depth. CR=coral reef, HB=hardbottom, SV=submerged vegetation. Significant Kruskal-Wallis H test indicated by (*) p-values < 0.05 and (**) p-values < 0.005.

Family	Species	Trends by habitat
Acanthuridae	<i>Acanthurus bahianus</i>	Smaller in SV **
	<i>Acanthurus chirurgus</i>	Larger in HB and CR
	<i>Acanthurus coeruleus</i>	Smaller in SV
Carangidae	<i>Caranx crysos</i>	Larger in HB
Chaetodontidae	<i>Chaetodon capistratus</i>	Smaller in SV *
	<i>Chaetodon striatus</i>	Smaller in SV **
Haemulidae	<i>Anisotremus surinamensis</i>	Smaller in HB
	<i>Haemulon carbonarium</i>	Smaller in SV **
	<i>Haemulon chrysargyreum</i>	Smaller in SV *
	<i>Haemulon flavolineatum</i>	Smaller in SV **
	<i>Haemulon parra</i>	Smaller in SV **
	<i>Haemulon plumierii</i>	Smaller in SV
Kyphosidae	<i>Kyphosus sectator</i>	Smaller in SV
Lutjanidae	<i>Lutjanus apodus</i>	Smaller in SV **
	<i>Lutjanus mahogoni</i>	Smaller in SV **
	<i>Ocyurus chrysurus</i>	Smaller in SV *
Monacanthidae	<i>Cantherines pullus</i>	Smaller in SV
Ostraciidae	<i>Lactophrys triqueter</i>	Smaller in HB
Pomacanthidae	<i>Pomacanthus arcuatus</i>	Smaller in SV
Scaridae	<i>Scarus iserti</i>	Smaller in SV
	<i>Sparisoma chrysopterum</i>	Smaller in HB
	<i>Sparisoma rubripinne</i>	Smaller in HB
	<i>Sparisoma viride</i>	Smaller in HB

2.1.7 Ontogenetic habitat shifts

Evidence of ontogenetic migration, in terms of correlations in fork length (FL) and depth, as well as differential habitat use among life stages, is given in Table 2-5.

Species present at Mona Island, although not in significant numbers to fully analyze ontogenetic habitat shifts (less than 5 individuals per life stage), include: *Abudefduf saxatilis*, *Acanthurus chirurgis*, *Caranx crysos*, *Haemulon plumieri*, *H. sciurus*, *Ocyurus chrysurus* and *Sphyraena barracuda*. In the case of *A. chirurgis*, considered a nursery species, only 3 individuals were quantified in the early life stage. For *C. crysos* and *O. chrysurus* sufficient early and juvenile individuals but few adults were quantified. In the case of *O. chrysurus* many large adults were seen in deeper (> 25 m) areas. Statistical results are only presented for early and juvenile life stages of *C. crysos* and *O. chrysurus* and only totals for adults.

All 27 species tested showed a significant correlation between FL and depth. Twenty-five had a positive and two (*S. taeniopterus* and *S. barracuda*) a negative relationship. Of species with significant correlations between FL and depth as well as sufficient occurrences to quantify habitat use, 20 had lower median FL in one habitat type (Kruskall-Wallis H test). Of these, 10 had significantly higher density in SV and two (*A. surinamensis* and *M. niger*) in HB. For another five species the smallest individuals were also found in SV but the trend was not significant.

Table 2-5 Evidence for ontogenetic migrations: Fork length (FL) correlations with depth, habitat with the smallest FL individuals, and habitats of highest density of early, juvenile and adult life stages. Nursery species in bold. Significant trends and differences in density by habitat type are indicated with *. Total = total number of individuals quantified, CR = coral reef, HB = hardbottom, RB/SED = rubble and sediment, SV = submerged vegetation, VAR = variable.

Family	Species	Occurrence	Total	FL and depth	Smallest FL	Density Early	Density Juvenile	Density Adult
Acanthuridae	<i>Acanthurus bahianus</i>		5,722	positive *	SV *	RB/SD*	VAR	CR & HB
	<i>Acanthurus chirurgus</i>	< 5 per life stage	68	positive *	VAR	HB	RB/SED*	CR & HB
	<i>Acanthurus coeruleus</i>		3,857	positive *	SV	CR *	CR *	CR
Balistidae	<i>Melichthys niger</i>		2,091	positive *	HB *	CR & HB	CR & HB	CR *
Carangidae	<i>Caranx crysos</i>	< 5 per life stage	111	positive *	VAR	VAR	SV *	CR & HB
Chaetodontidae	<i>Chaetodon capistratus</i>		244	positive *	SV *	VAR	VAR	CR & HB
	<i>Chaetodon striatus</i>		145	positive *	SV *	SV *	SV *	CR & HB
Gerreidae	<i>Gerres cinereus</i>	absent	0	-	-	-	-	-
Haemulidae	<i>Anisotremus surinamensis</i>		45	positive *	HB *	HB *	CR & HB	CR & HB
	<i>Anisotremus virginicus</i>	< 5 transects	5	-	-	-	-	-
	<i>Haemulon carbonarium</i>		1,289	positive *	SV *	SV & RB/SD*	VAR	CR
	<i>Haemulon chrysargyreum</i>		607	positive *	SV *	VAR	VAR	CR
	<i>Haemulon flavolineatum</i>		597	positive *	SV *	SV	SV *	CR & HB
	<i>Haemulon macrostomum</i>	< 5 transects	3	-	-	-	-	-
	<i>Haemulon parra</i>		249	positive *	SV *	SV & HB*	VAR	CR & HB
	<i>Haemulon plumieri</i>	< 5 per life stage	7	positive *	SV	-	-	-
	<i>Haemulon sciurus</i>	< 5 per life stage	8	positive *	N/A	-	-	-
Kyphosidae	<i>Kyphosus sectator</i>		527	positive *	SV	VAR	CR *	CR & HB

Family	Species	Occurrence	Total	FL and depth	Smallest FL	Density Early	Density Juvenile	Density Adult
Lutjanidae	<i>Lutjanus analis</i>	< 5 transects	5	-	-	-	-	-
	<i>Lutjanus apodus</i>		224	positive *	SV *	SV & HB*	VAR	CR & HB
	<i>Lutjanus cyanopterus</i>	< 5 transects	1	-	-	-	-	-
	<i>Lutjanus griseus</i>	< 5 transects	12	-	-	-	-	-
	<i>Lutjanus jocu</i>	< 5 transects	1	-	-	-	-	-
	<i>Lutjanus mahogoni</i>		417	positive *	SV *	RB/SD*	CR *	CR & SV
	<i>Lutjanus synagris</i>	absent	0	-	-	-	-	-
	<i>Ocyurus chrysurus</i>	< 5 per life stage	24	positive *	SV *	SV *	HB	CR & HB
Monacanthidae	<i>Cantherines pullus</i>		36	positive *	SV	VAR	RB/SD*	CR & HB
Ostraciidae	<i>Lactophris triqueter</i>		62	positive *	HB	CR & HB	CR *	CR & HB
Pomacentridae	<i>Abudefduf saxatilis</i>	< 5 per life stage	25	positive *	CR	-	-	-
Scaridae	<i>Scarus coeruleus</i>	absent	0	-	-	-	-	-
	<i>Scarus guacamaia</i>	absent	0	-	-	-	-	-
	<i>Scarus iserti</i>		287	positive *	SV	CR	CR *	CR & HB
	<i>Scarus taeniopterus</i>		790	negative *	CR	-	-	-
	<i>Sparisoma chrysopterus</i>		272	positive *	HB	SV	SV *	VAR
	<i>Sparisoma rubripinne</i>		1,278	positive *	HB	SV & RB/SD*	SV & RB/SD*	CR & HB
	<i>Sparisoma viride</i>		406	positive *	HB	CR *	CR & HB	CR & HB
Serranidae	<i>Epinephelus striatus</i>	< 5 transects	4	-	-	-	-	-
Sphyraenidae	<i>Sphyraena barracuda</i>	< 5 per life stage	44	negative *	-	-	-	-

Family Acanthuridae

Acanthurus bahianus was observed in all habitat types and was the most abundant species at Mona Island. Significantly smaller individuals were observed in SV, while significantly higher median density of early life stages was observed in rubble and sediment (RB/SD) habitat. Juveniles were in all habitats with significantly lower median density in SV and highest density of adults was in CR (Figure 2-2). Although occurrences were quite low, *Acanthurus chirurgus* had a positive relationship between FL and depth and occurred in all habitats. Only three early stage individuals were seen, all in HB habitat. Juveniles had significantly greater density in RB/SD habitats, and although no significant differences were detected, the highest adult density was observed in HB (Figure 2-3). For the third most numerous species, *Acanthurus coeruleus*, FL was also positively correlated with depth, and the smallest individuals were in SV. Nonetheless, all life stages had significantly higher density in CR, although all habitats were occupied (Figure 2-3). For all figures in this section the point illustrated is the mean, boxes include standard error (SE) whiskers are the 95% confidence limits (CL) and N is the number of transects in which that ontogenetic stage was present out of the 613 transects.

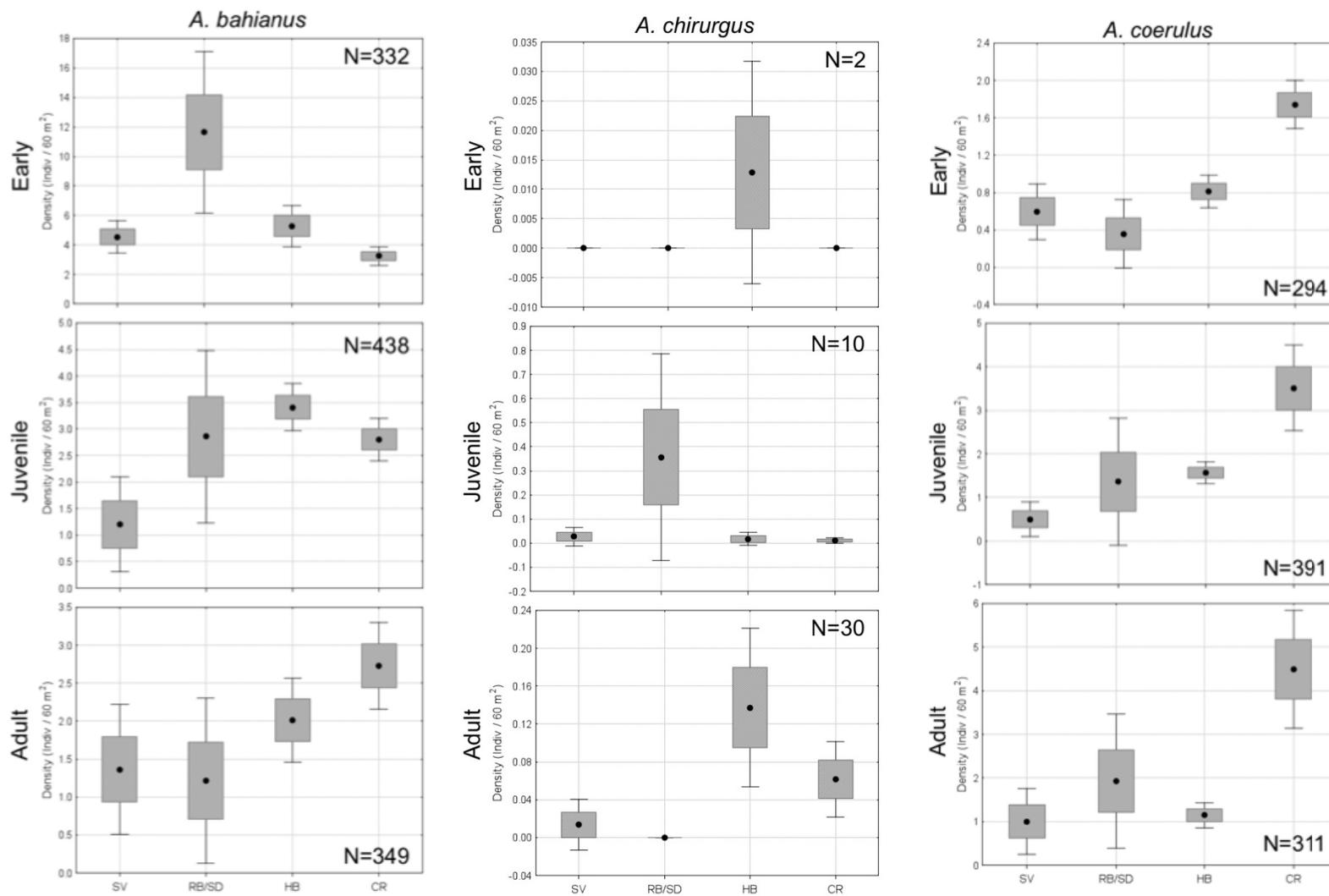


Figure 2-3 Density (individuals / 60 m²) of each life stage by habitat type for *A. bahianus*, *A. chirurgus* and *A. coeruleus* N= transects in which present (Mean, SE and 95% CL).

Family Balistidae

Melichthys niger had a significantly positive relationship between FL and depth. Smaller individuals occurred mostly in HB where early life stages had higher densities (although not significantly different from CR). Juveniles had significantly higher median density in HB and CR habitats although present in very low density in SV and RB/SD. Adults were only in HB and CR, with significantly higher density in CR habitat (Figure 2-4). *Balistes vetula*, *Canthidermis sufflamen* and *Xanthichtys ringens* were in CR and HB.

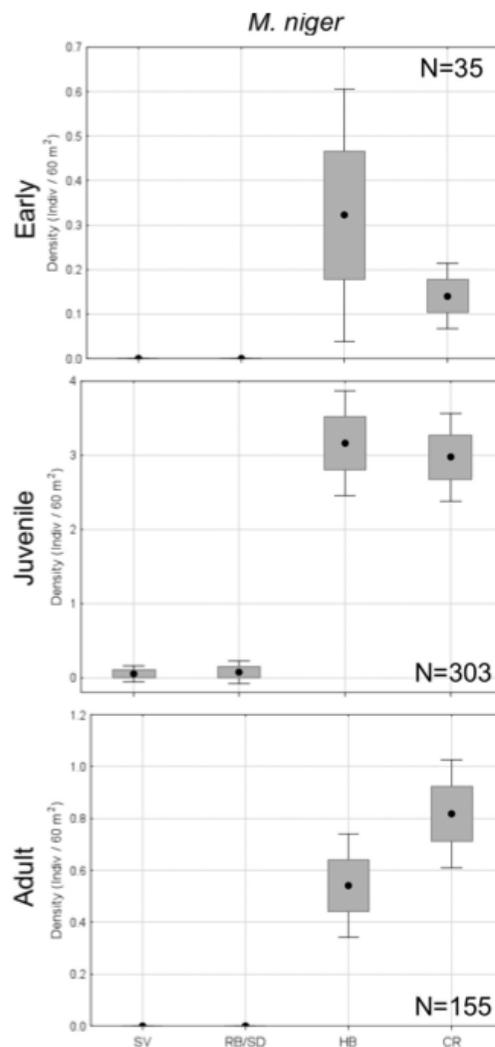


Figure 2-4 Density (individuals / 60 m²) of each life stage by habitat for *M. niger* N= transects in which present (Mean, SE and 95% CL).

Family Carangidae

Caranx crysos had a positive relationship between FL and depth and smaller sizes occurred in most habitats with the exception of RB/SED. No differences in the density of early stages were detected due to low occurrences, however juveniles were significantly higher in SV. Only 3 adults were observed, in HB and CR habitat (Figure 2-5). Other jacks were seen as adults, including *Caranx latus*, *C. lugubris*, *Carangoides bartholomaei*, *C. rubber*, *Elagatis bipinnulata*, *Trachinotus falcatus* and *T. goodei*.

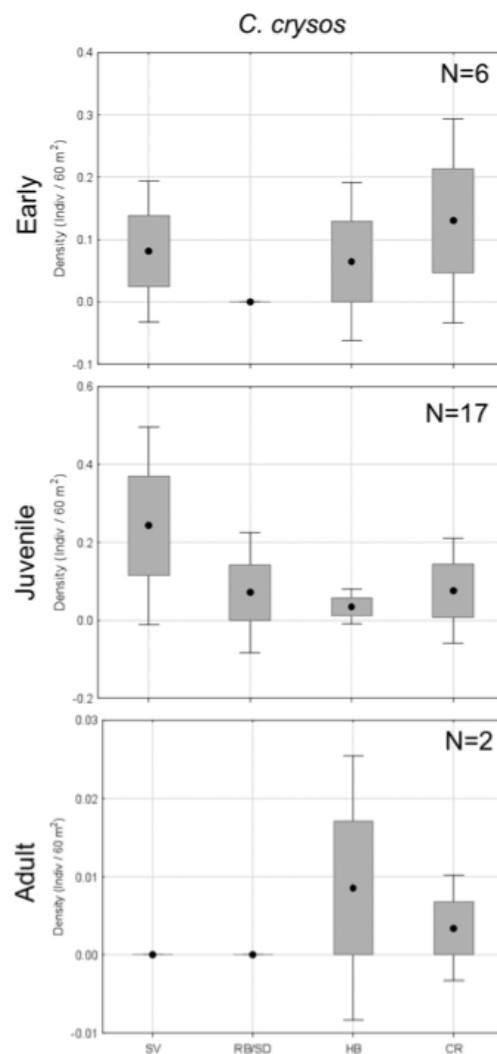


Figure 2-5 Density (individuals / 60 m²) of each life stage by habitat type for *C. crysos* N= transects in which present (Mean, SE and 95% CL).

Family Chaetodontidae

Chaetodon capistratus had significantly smaller sized individuals in SV, although early life stages were distributed in all habitats except RB/SD. No significant differences in density were detected by habitat in early or juvenile stages perhaps due to low occurrences, yet adults showed significantly lower density in SV (Figure 2-6).

Chaetodon striatus had a positive relationship between FL and depth as well as significantly smaller sized individuals in SV. Early and juvenile individuals were found in significantly higher density in SV. Although no significant differences by habitats were observed for adults, the highest density was observed in HB followed by CR habitat (Figure 2-6). Other butterflyfishes observed included *Chaetodon ocellatus* and *C. sedentarius* although these were in very low frequency.

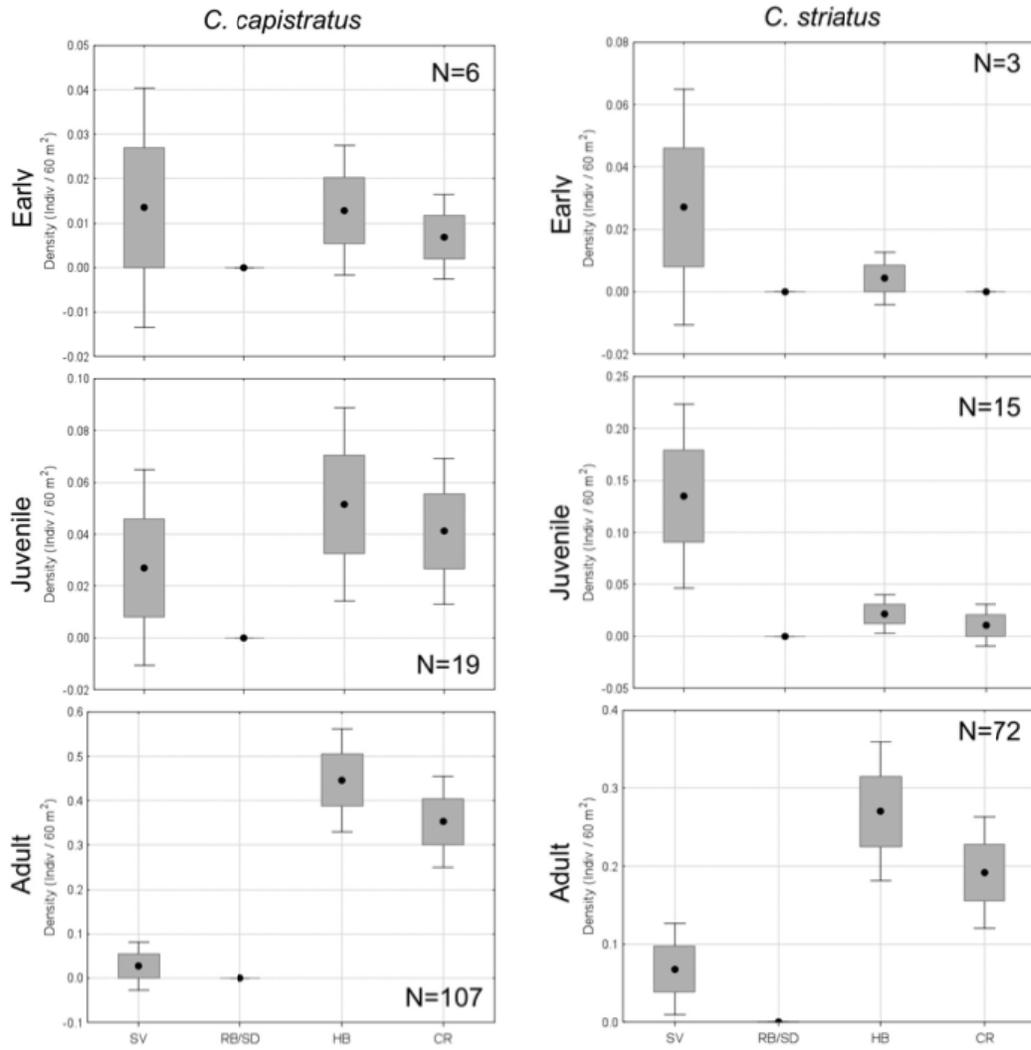


Figure 2-6 Density (individuals / 60 m²) of each life stage by habitat type for *C. capistratus* and *C. striatus* N= transects in which present (Mean, SE and 95% CL).

Family Haemulidae

Anisotremus surinamensis only occurred in 5% of transects, yet a positive relationship between size and depth was detected at all stages; individuals were only found in HB and CR habitats. The FL was significantly smaller and early individuals had significantly higher density in HB. For juvenile and adult stages the trend was reversed but not significantly so, although frequency of occurrences were lower for adults (Figure 2-7). *Haemulon carbonarium* was the most abundant grunt species and exhibited a significant positive relationship between FL and depth. Individuals in SV were significantly smaller, and early stages had significantly higher median density in SV and RB/SD. Juveniles had high density in RB/SD and SV although not significantly different, while adults were observed in significantly higher density in CR (Figure 2-7). *Haemulon chrysargyreum* were significantly smaller in SV although early stages occupied all habitat types. No significant differences in density were observed for early or juvenile stages, while adults had significantly higher median density in CR habitat (Figure 2-7).

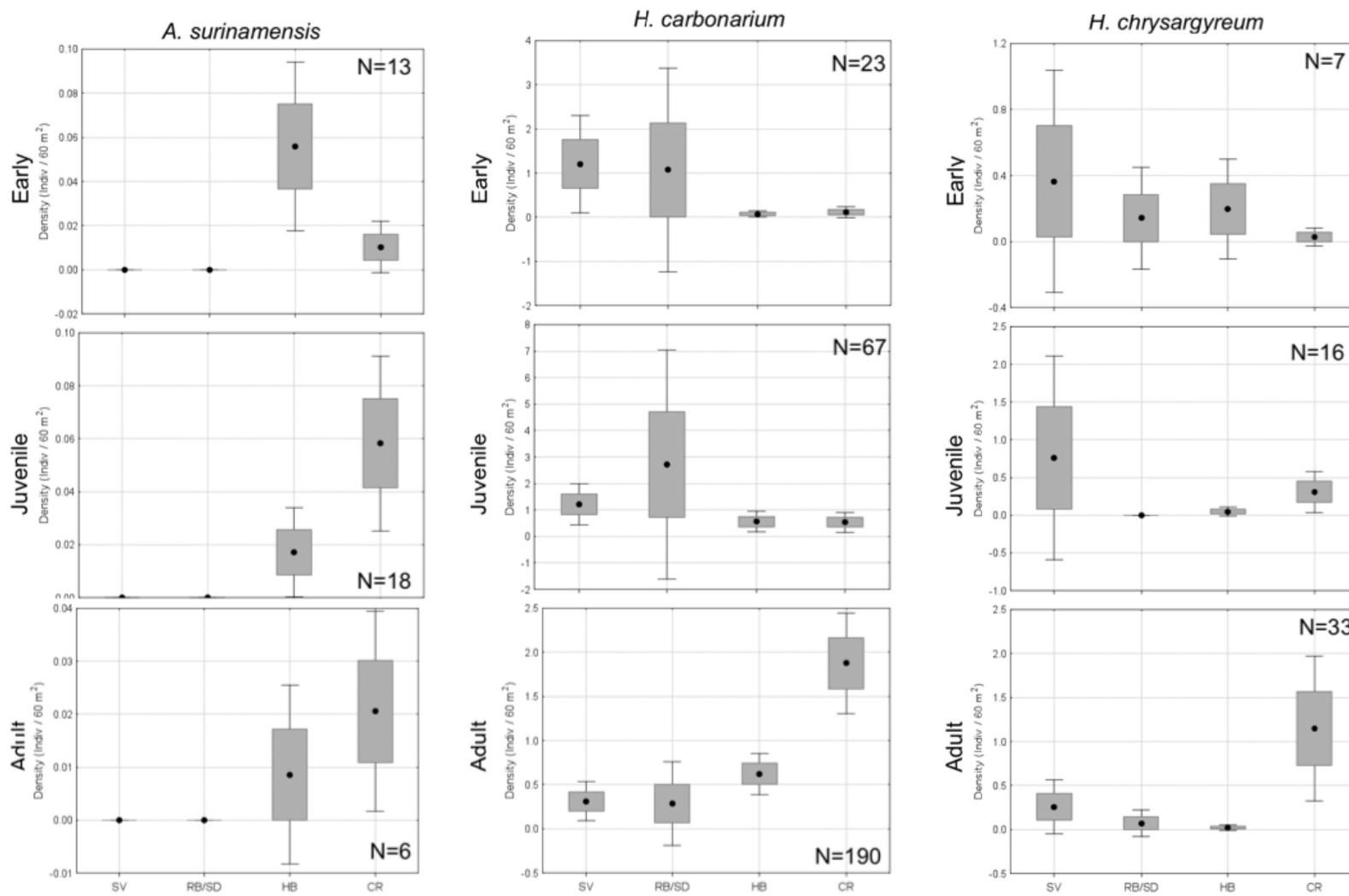


Figure 2-7 Density (individuals / 60 m²) of each life stage by habitat type for *A. surinamensis*, *H. carbonarium* and *H. chrysargyreum* N= transects in which present (Mean, SE and 95% CL).

Haemulon flavolineatum was significantly smaller, and early stages were found in higher density in SV but not significantly so. Juveniles had significantly higher median density in SV. Adults were distributed mainly in CR and HB habitat where median density was significantly greater than SV (Figure 2-8). *Haemulon parra* were significantly smaller in SV and significantly higher median density occurred in SV and HB habitat for early life stages. Juveniles were distributed in all habitats except RB/SD, but no significant differences were observed, but adults were only seen in CR and HB habitats (Figure 2-8). Other haemulids observed in lower densities include *Anisotremus virginicus*, *H. macrostomum*, *H. plumierii* and *H. sciurus*.

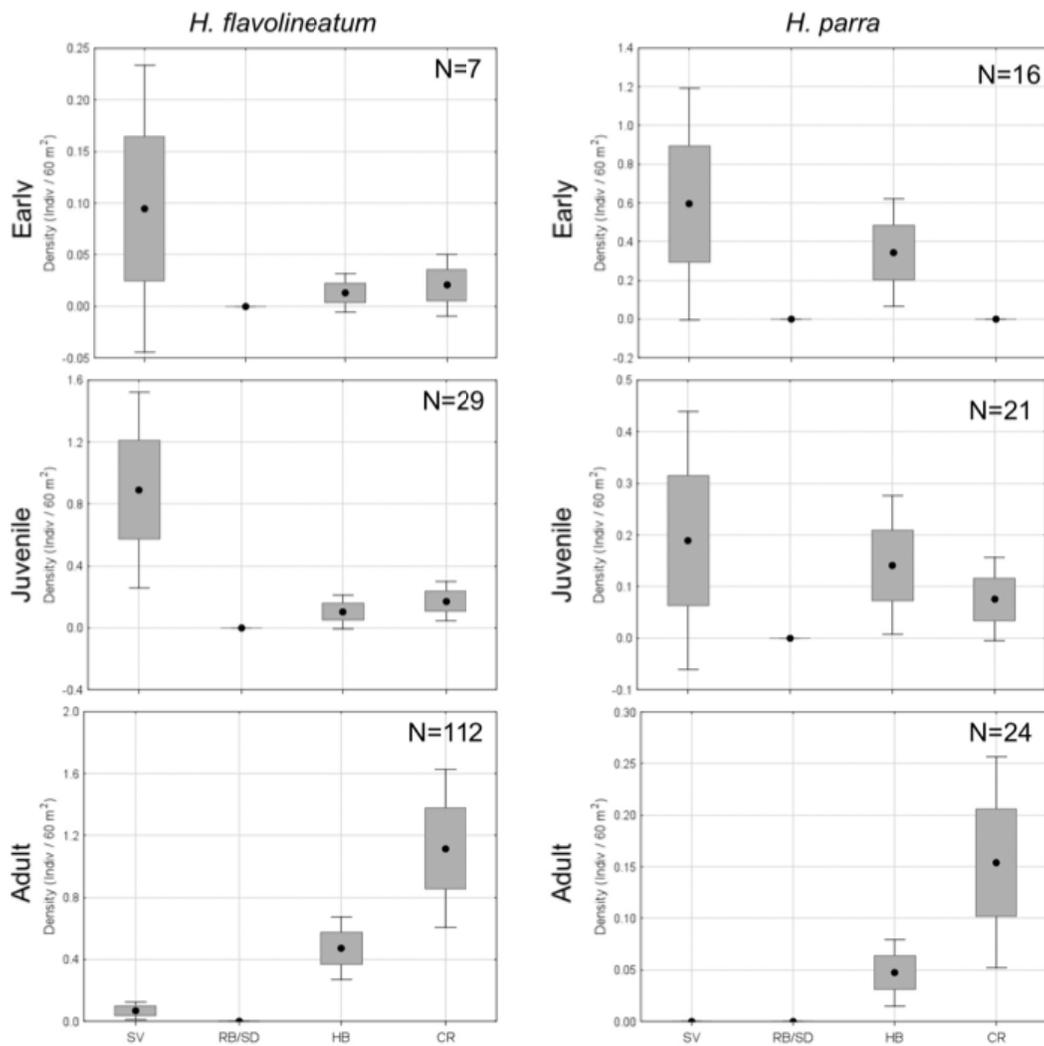


Figure 2-8 Density (individuals / 60 m²) of each life stage by habitat for *H. flavolineatum* and *H. parra* N= transects in which present (Mean, SE and 95% CL).

Family Kyphosidae

Kyphosus sectator had smaller individuals in SV, and although early stages showed no significant difference in density by habitat higher densities of all stages occurred in HB and CR. Juveniles and adults had significantly higher median density in CR followed by HB, whereas adults were exclusively in CR and HB (Figure 2-9).

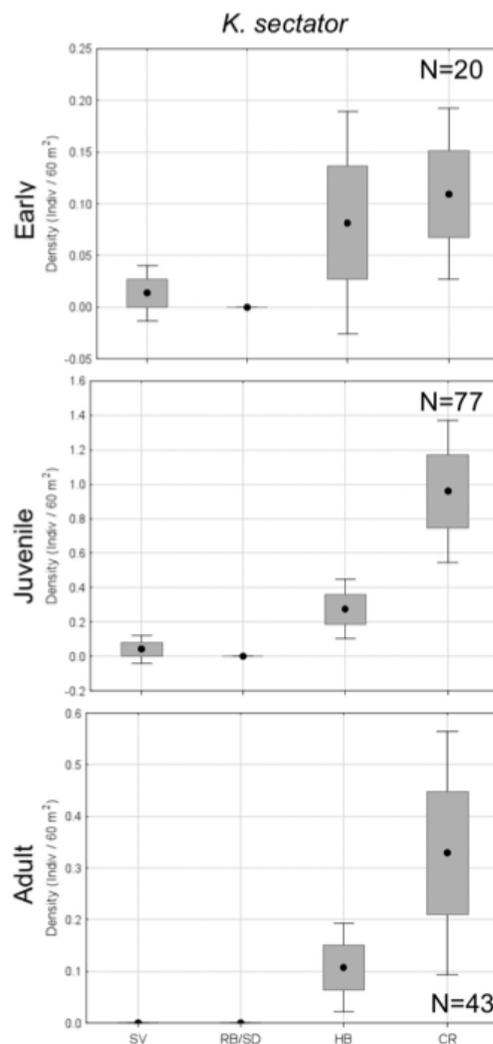


Figure 2-9 Density (individuals / 60 m²) of each life stage by habitat for *K. sectator* N= transects in which present (Mean, SE and 95% CL).

Family Lutjanidae

Lutjanus apodus had a significant positive relationship between FL and depth, and significantly smaller sizes occurred in SV. Early life stages were only seen in SV and HB, whereas juvenile stages were seen in all habitat types with significantly lower median density in SV. Adults were only observed in CR and HB habitats (Figure 2-10). *Lutjanus mahogoni* was the most frequent snapper species recorded at Mona Island, and had a significant positive relationship between FL and depth. Submerged vegetation harbored significantly smaller FL; although early stages were distributed in all habitat types with significantly higher median density in RB/SD. Juveniles had significantly higher median density in CR and adults in both CR and SV (Figure 2-10). *Ocyurus chrysurus* also had a significantly positive relationship between FL and depth, and SV had significantly smaller sized individuals. Early life stages had significantly higher density in SV, while juveniles and adults were observed in HB and CR (Figure 2-10). Large bodied lutjanids such as *L. analis*, *L. cyanopterus* and *L. jocu* were observed in very low densities mainly in CR. A school of 12 adult *L. griseus* were seen in one transect in CR near the shelf break.

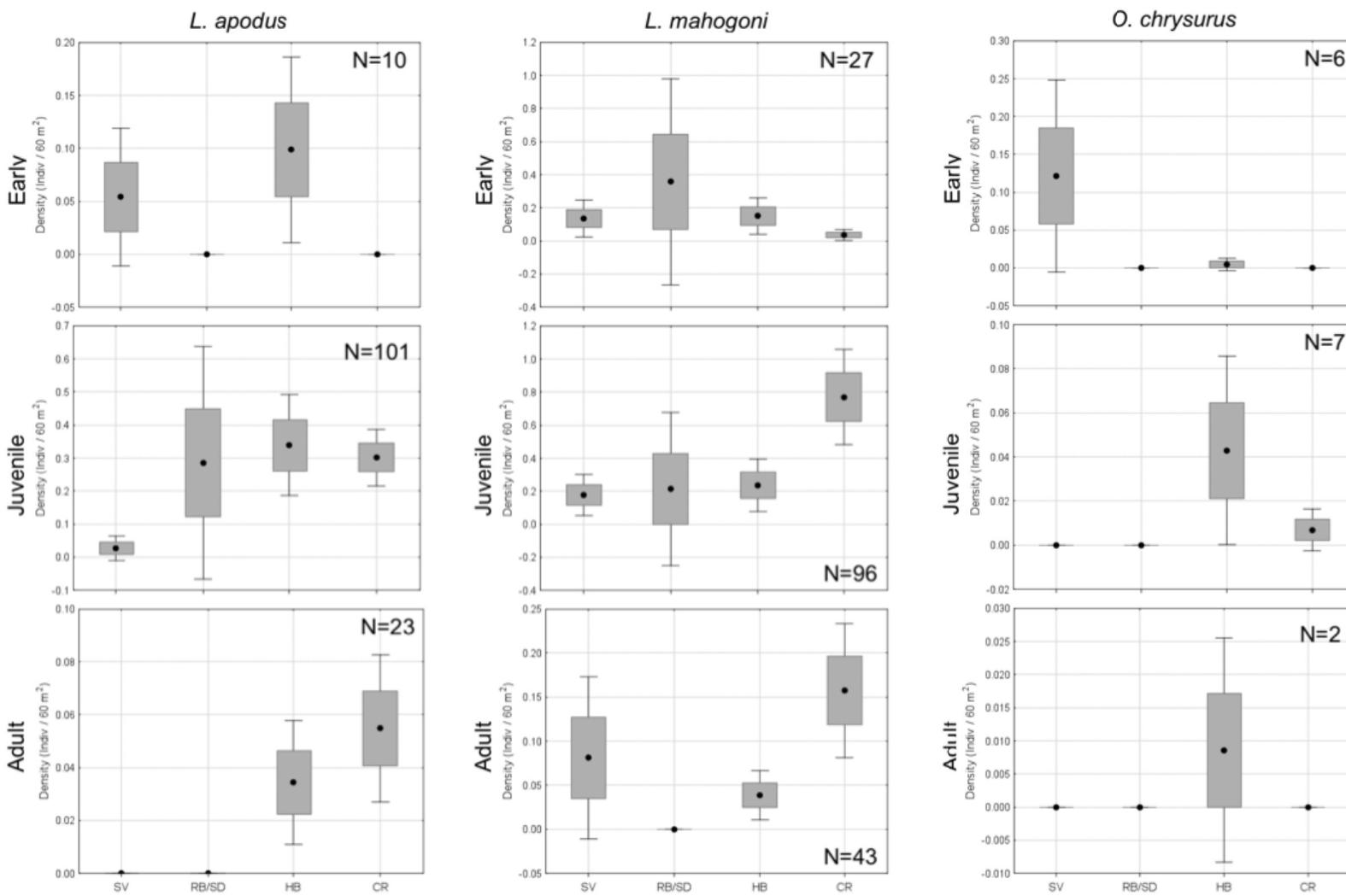


Figure 2-10 Density (individuals / 60 m²) of each life stage by habitat for *L. apodus*, *L. mahogoni* and *O. chrysurus* N= transects in which present (Mean, SE and 95% CL).

Family Monacanthidae

Cantherines pullus had the smallest individuals in SV although not significantly so. Fish were distributed in all habitat types except early stages that were not found in RB/SD. Juveniles had significantly higher median density in RB/SD. Adults were only observed in HB and CR habitat with no significant differences in density (Figure 2-11). *Aluterus scriptus* and *Cantherines macrocerus* were observed in very low densities

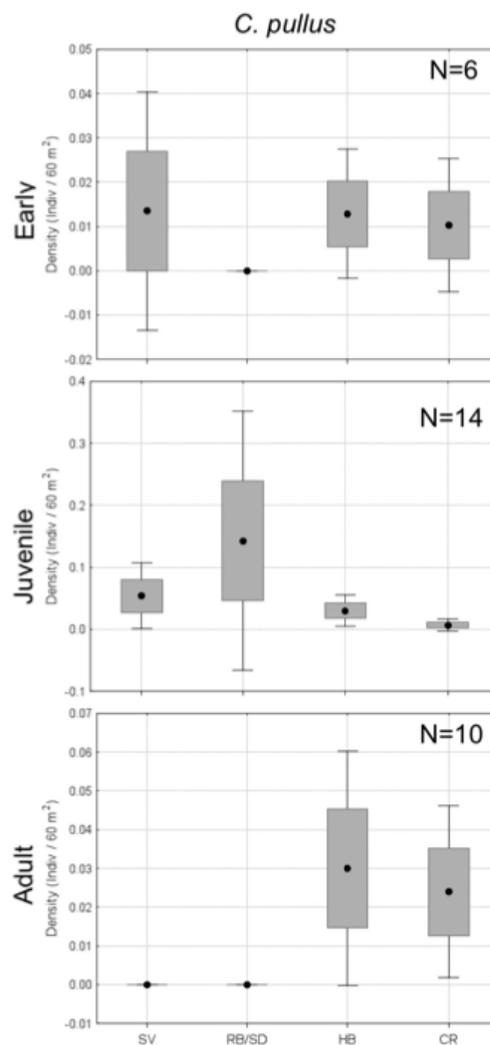


Figure 2-11 Density (individuals / 60 m²) of each life stage by habitat type for *Cantherines pullus* N= transects in which present (Mean, SE and 95% CL).

Family Ostraciidae

Early stages of *Lactophris triqueter* were only seen in HB and CR with similar densities, although smaller individuals tended to occur in HB. Juveniles had significantly higher median density in CR and HB, although they occurred in SV. Adults were only in CR and HB, yet the frequency of occurrence was very low (Figure 2-12).

Acanthostracion polygonius, *A. quadricornis*, *Lactophrys bicaudalis* and *L. trigonus* were also observed although quantified in much lower densities.

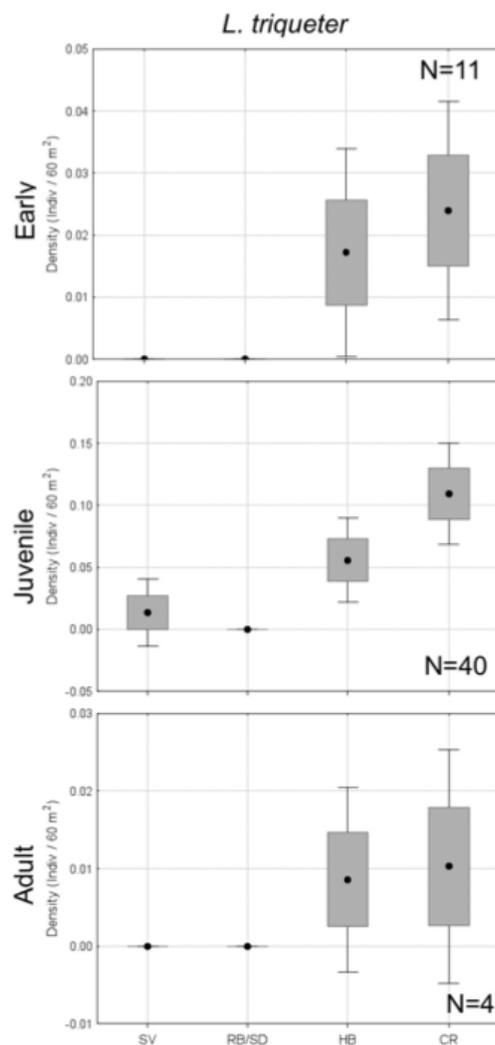


Figure 2-12 Density (individuals / 60 m²) of each life stage by habitat for *L. triqueter* N= transects in which present (Mean, SE and 95% CL).

Family Scaridae

Scarus iserti had a significantly positive relation between FL and depth as smaller individuals occurred in SV. Early stages had higher density in CR although not significantly different from other habitats. Juveniles had significantly higher median density in CR over HB although for adults the difference was not significant (Figure 2-13). *Scarus taeniopterus* did not present evidence of ontogenetic habitat shifts although it was very common in deeper areas. *Scarus vetula* did not demonstrate a shift in habitat use as all life stages occurred in CR and HB. Although early juvenile *S. vetula* was limited to shallow CR many adults were also distributed in this habitat type obscuring any relations of size and depth. *Scarus guacamaia* and *S. coelestinus* were not observed within transects.

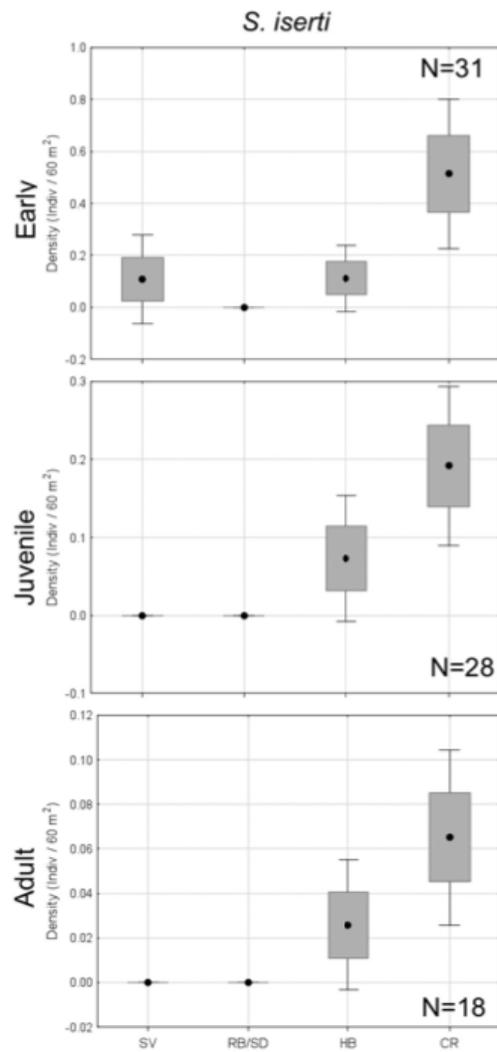


Figure 2-13 Density (individuals / 60 m²) of each life stage by habitat for *Scarus iserti* N= transects in which present (Mean, SE and 95% CL).

Sparisoma chrysopterum had a significantly positive relationship between FL and depth, and HB tended to harbor smaller sized individuals. Early stages had higher density in SV although this was not significant. Juveniles had significantly higher median density in SV and adults occurred in similar densities in SV, HB and CR habitat (Figure 2-14). *Sparisoma rubripinne* was the most abundant parrotfish at Mona Island and also had a significantly positive relationship between FL and depth. Smallest sized individuals tended to occur in HB habitat although early and juvenile life stages occurred in significantly higher median density in SV and RB/SD habitats. Adults on the other hand had significantly higher median density in HB and CR (Figure 2-14). *Sparisoma viride* had a significantly positive relationship between FL and depth and HB tended to harbor the smallest sized individuals. Early juveniles and juveniles had significantly higher median density in CR habitat. Adults had higher density in CR although this was not significantly different from HB (Figure 2-14). Other parrotfishes included *S. atomarium*, which was limited to deep CR and *S. aurofrenatum* that occurred commonly in CR and HB.

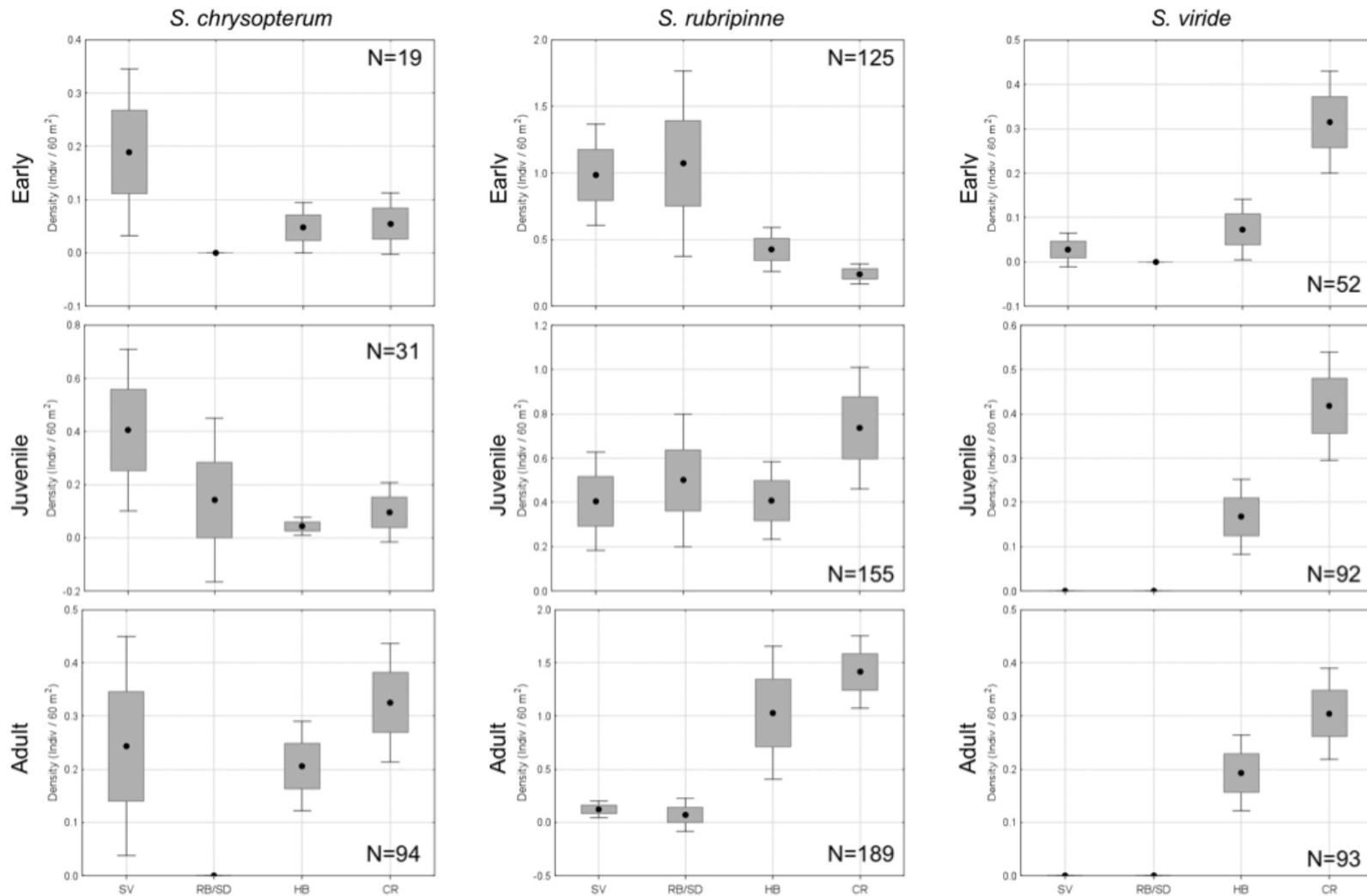


Figure 2-14 Density (individuals / 60 m²) of each life stage by habitat for *S. chrysopterum*, *S. rubripinne* and *S. viride* N= transects in which present (Mean, SE and 95% CL).

2.1.8 Comparison with a mangrove-rich site

The comparison of density of juveniles and adults in hard substratum (CR and HB habitats) between La Parguera (NOAA, 2008) and Mona Island was not possible for all species. Differences in methodology required minimum size cutoff in order to compare similar size classes in similar substrata (lumping CR and HB). Minimum fork length (FL) cutoff values for species that co-occurred are summarized in Table 2-6. A few species were not comparable between these two sites including *A. surinamensis*, which was absent from the La Parguera dataset and *C. crysos*, *C. pullus*, *H. parra*, *K. sectator*, *L. triqueter* and *L. mahogoni* that were reported in low abundances (< 10 individuals). Four of the seven co-occurring nursery species (Table 2-6) were significantly more abundant in La Parguera (*A. chirurgus*, *C. capistratus*, *O. chrysurus* and *S. iserti*). All other species (except *H. chrysargyreum*) were significantly more abundant at Mona Island, including the reported nursery species *H. flavolineatum*, *L. apodus* and *S. chrysopterum*.

Table 2-6 Comparison of fish density (individuals / 60 m²) for species (nursery species in bold) between Mona Island and La Parguera. Minimum fork length (cm) used as cutoff to include individuals considered juveniles/adults. Significant differences of Kruskal Wallis test indicated with (*) for $p < 0.05$.

Species	Min FL (cm)	La Parguera	Mona Island
<i>Acanthurus bahianus</i>	15	0.79	* 4.35
<i>Acanthurus chirurgus</i>	15	* 0.33	0.10
<i>Acanthurus coeruleus</i>	15	0.34	* 5.02
<i>Chaetodon capistratus</i>	5	* 1.32	0.41
<i>Chaetodon striatus</i>	5	0.11	* 0.24
<i>Haemulon carbonarium</i>	10	0.04	* 1.84
<i>Haemulon chrysargyreum</i>	10	0.03	0.85
<i>Haemulon flavolineatum</i>	10	0.69	* 0.94
<i>Lutjanus apodus</i>	20	0.03	* 0.30
<i>Melichthys niger</i>	15	0.19	* 3.17
<i>Ocyurus chrysurus</i>	20	* 0.20	0.03
<i>Scarus iserti</i>	10	* 1.96	0.19
<i>Sparisoma chrysopterum</i>	15	0.08	* 0.31
<i>Sparisoma rubripinne</i>	15	0.06	* 1.70
<i>Sparisoma viride</i>	15	0.54	* 0.55

Discussion

2.1.9 Ontogenetic migrations

Species described as nursery or ontogenetic habitat shifters (sensu Nagelkerken et al 2002 and Adams et al. 2006) include species of grouper (Serranidae), snapper (Lutjanidae), grunt (Haemulidae), parrotfish (Scaridae) and the barracuda (Sphyraenidae). The results of this investigation suggest that at Mona Island 22 species of coral reef fishes undergo cross shelf migrations towards deeper areas using a combination of habitats (Table 2-5). Fifteen of the 17 nursery species (sensu Nagelkerken et al. 2002) were present, of which a few occurred in extremely low abundances and frequencies as might be expected due to the limited nursery habitats available.

Family Acanthuridae

Acanthurus bahianus depended mostly on SV habitat in combination with RB/SED in shallow areas, whereas HB habitats contained the few early stage *A. chirurgus* observed, and *A. coeruleus* was dependent upon SV and CR. In La Parguera *A. bahianus* was predominantly in non-seagrass and mangrove habitats as early juveniles while *A. coeruleus* were not in seagrass or mangroves at all (Aguilar-Perera and Appeldoorn 2007). The lower abundance of *A. chirurgus* adults on Mona Island reefs suggests the lack of mangroves, or some other habitat function, limits this population. Nagelkerken et al. (2000b) determined that seagrass was the most important nursery habitat for *A. chirurgus*, yet subsequent studies (Nagelkerken et al. 2002, Dorenbosch et al. 2004) concluded that this species did not depend on mangroves or seagrass beds

as nurseries. This contrasts to the situation at Mona Island where some combination of critical habitats seems lacking.

Family Balistidae

Hardbottom and CR habitats around Mona Island provide an important nursery function for *Melichthys niger*. Dennis et al. (2005) described *M. niger* as shelf-edge associated, although at Mona it is not limited to the shelf edge as in La Parguera. This species has also been reported to form large aggregations or swarms at remote oceanic islands and is able to remain more time in pelagic larval phases compared to most reef fishes (Kavanagh and Olney 2006). Being one of the most abundant reef fish at Mona Island (56% frequency of occurrence and overall mean density = 3.4 individuals / 60 m²) in HB and CR it is evident that habitats to support ontogenetic migration and development of this species were sufficiently abundant at Mona Island. This species does not require mangrove or seagrass as indicated by the patterns observed at Mona Island and the lower density of adults in La Parguera.

Family Carangidae

Caranx crysos undergoes cross shelf movements with size and shifts habitats through ontogeny. At early life stages it was most common in shallow areas in all habitat types, suggesting they are opportunistic during early stages. Interestingly juveniles showed an association to SV. This species is a coastal pelagic, which would explain why adults were only observed in deep CR and HB.

Family Chaetodontidae

Seagrass was the most important nursery habitat for smaller sized individuals and, along with HB and CR, supported high densities of early life stages of *Chaetodon*

capistratus and *C. striatus*. Nagelkerken and van der Velde (2002) observed a strong mangrove to reef ontogenetic migration for *C. capistratus*, although Nagelkerken et al. (2002) concluded that this species showed little dependence upon seagrass and or mangroves. *Chaetodon capistratus* showed preference for shallow coral reef habitats over seagrass and mangrove sites in La Parguera (Aguilar-Perera 2004). This suggests that there is significant variability in the possible nursery roles of shallow water habitats (Nagelkerken 2007). Yet the low density of *C. capistratus* adults at Mona Island compared to La Parguera (Table 2-6) suggests the habitats available at the former site do not provide sufficient nursery function and that perhaps seagrasss and/or mangroves are, indeed, essential to this species. This trend was not observed for *C. striatus*, where adults were significantly more abundant at Mona Island.

Family Haemulidae

Seagrass was the most important nursery habitat for smaller sized individuals and supported higher densities of early life stages of *H. carbonarium*, *H. flavolineatum* and *H. parra* at Mona Island. The smallest individuals of *H. flavolineatum* were found in SV, *H. carbonarium* occurred mostly on SV habitat in combination with RB/SED in shallow areas and *H. parra* relied on HB habitat in addition to SV for early life stages. Most of the grunts were aggregated in multi-species schools closely associated with structure within the patches of hard bottom, rock or coral interspersed within the seagrass. This association of small grunts to structure (corals, rock, urchin spines, etc.) has been reported in back reef habitats of La Parguera as well (Hill 2001).

Hardbottom habitats mainly composed of bedrock provide an important nursery function for *A. surinamensis*. Similar habitats consisting of invertebrates and HB in

exposed areas less than 10 m in depth were identified as the primary settlement areas of early juveniles in Biscayne Bay, Florida (Lindeman et al. 1998). The early juveniles observed at Mona Island were significantly more abundant in HB habitats near shore and seem to migrate to CR habitats utilizing a combination of HB and CR in their cross-shelf movements.

Haemulon chrysargyreum had significantly smaller individuals in SV and larger sizes in CR. Early life stages were distributed in all near shore habitats (seagrass, coral, bedrock and pavement sites) suggesting a facultative relationship during early and juvenile stages while adults were restricted to CR. Nagelkerken and van der Velde (2004) found this species utilizing mangroves as a feeding habitat while occupying seagrass areas, although (Nagelkerken 2007) concluded that the role of mangroves in the life cycle of this species is probably minimal. Although differences were not significant, the higher density of adults at Mona Island compared to La Parguera, suggests this species is more opportunistic during early juvenile life stages.

The density of adult *H. carbonarium* on CR and HB habitats at Mona Island suggests it completes ontogenetic migrations with the habitats available. Although cross-shelf migration has been documented for this species (Cervený 2006) few studies reported on the habitats that provide the nursery function for this species. Although *H. carbonarium* was found in various habitats, seagrass with patches of rock, coral or rubble are important for early and juvenile stages. For adults the main habitats were relatively shallow CR. Mona Island supports a thriving population, with greater adult density than in La Parguera (Table 2-6) suggesting mangroves are not necessary for the early stages of this species.

In Curaçao *H. flavolineatum* and *H. parra* were originally described as obligate mangrove residents (Nagelkeken and van der Velde 2002), yet *H. parra* and *H. sciurus* showed a high dependence on seagrass beds, but not mangroves (Nagelkerken et al. 2001), suggesting they are more flexible in their nursery habitat dependence. Lagoons were considered nursery areas for various coral reef species in Tortoloa (BVI) where *H. flavolineatum* preferred rocky areas (Gratwicke et al. 2006). Mangroves with adjacent seagrass in the seascape had higher densities of *H. flavolineatum* in La Parguera (Pittman et al. 2007), supporting the hypothesis that they can use alternate nursery habitats. However at Mona Island *H. flavolineatum* was associated with SV, HB and CR during early and juvenile life stages moving from lagoons towards deeper offshore CR habitats as sizes increased. Due to its daily migratory behavior and scale of movements of approximately 100 m (Boumeester, 2005) *H. flavolineatum* may be favored by the distribution of habitats at Mona Island. In St Croix the probability of juvenile *H. flavolineatum* presence on hard bottom sites was inversely correlated with distance to soft bottom in lagoon areas suggesting juveniles remain relatively near feeding areas (Kendall et al 2003). At Mona Island this species was found in greater abundance in SV during early and significantly so for juvenile stages migrating towards deeper CR as adults. The distribution of habitats at Mona Island seems favorable for the ontogenetic migration and development of *H. flavolineatum* as it was found in greater adult density than in La Parguera.

Haemulon parra seems to be less opportunistic as it was abundant in SV and HB habitats of Mona Island during early and juvenile stages. As adults they occurred in CR and HB habitats (although their distribution was patchy). Abundances of *H. parra* are

extremely low in La Parguera, despite large areas of seagrass, therefore the association with HB could be more restrictive during early life stages. Nagelkerken and van der Velde (2002) suggested a strong mangrove to reef ontogenetic migration, and Nagelkerken et al. (2001) found few or no juveniles of this species in bays lacking mangroves. Yet the lack of mangroves apparently does not restrict this species at Mona Island.

At Mona Island very few *H. sciurus* were observed (juvenile in SV and adults in CR). This was expected as it has been described as a mangrove dependent species (Nagelkerken et al 2002, Mumby et al. 2004); in the absence of mangroves abundances are greatly reduced and juveniles move from seagrass to patch reefs at smaller sizes (Mumby et al. 2004). In Old-Providence, Colombia juveniles were only abundant near limited mangrove habitats (Appeldoorn et al. 2003). In addition to mangroves, SV is required for daily foraging migrations of larger fish as the movement of *H. sciurus* from reefs to seagrass beds was recorded in St. John (Beets et al. 2003).

Family Kyphosidae

Kyphosus sectator is an important demersal herbivore that is commonly observed in large schools over reefs. This schooling behavior resulted in wide variation in density among transects. The smallest individuals were found in SV, and this habitat also harbored some early and juvenile stages. However, the main habitat types occupied were CR and HB in all life stages. There was a significant correlation between the FL and depth suggesting cross-shelf movement towards deeper areas albeit in similar types of habitats.

Family Lutjanidae

Lutjanus analis had very low abundance at Mona Island, which may be caused by the reduced amount of seagrass and mangroves, which are described as important nursery habitat for this species (Nagelkerken et al. 2002, Appeldoorn et al. 2003, Dorenbosch et al. 2004). Similarly *L. analis* was found in low abundances in Aruba although Dorenbosch et al. (2007) suggests the low abundances are due to other factors besides the lack of mangroves and seagrass.

Seagrass was the most important nursery habitat for smaller sized individuals and supported higher densities of early life stages of *L. apodus*. At Mona Island early stages of *L. apodus* occurred in a combination of SV and HB habitats. The latter habitat was composed of rocky vertical structure, which may provide an effect similar to that created by mangrove prop roots. In Curaçao *L. apodus* occurred predominantly in seagrass beds, but not in mangroves (Nagelkerken et al. 2001), yet it is reported as a mangrove dependent species (Rooker and Dennis 1991, Rooker 1995, Cocheret de la Morinière et al. 2002, Nagelkerken and van der Velde 2002, Halpern 2004, Mumby et al. 2004). In Tortola, BVI lagoons were considered nursery areas for *L. apodus*, where it was associated with mangroves (Gratwicke et al. 2006). The early juvenile life stages of *L. apodus* show higher abundances in mangroves or mangrove rich coral reef systems in various continental and island sites (Nagelkerken et al. 2000a, 2000b, Appeldoorn et al. 2003, Aguilar-Perera and Appeldoorn 2007). Although Dennis et al. (2005) considered them rare at Mona Island this species was relatively common (19% of sampling sites) and additionally large numbers of adults were seen aggregated at depths greater than 30 m at nearby Monito Island (which lacks shallow habitats). This

suggests their association to mangroves is not obligate and they are using near shore HB at Mona Island as alternate nursery habitat. Verweij et al. (2006) demonstrated this species responds to shade of artificial structure more than to food items, which suggests that this nocturnal feeder seeks shaded areas during the daytime. Near shore vertical rocky habitats at Mona Island seem to provide that shade and should be considered an important alternate nursery habitat for this important fishery species. Other factors that may influence the association of *L. apodus* with mangroves are food availability, structural complexity, shade, and reduced predation (Beck et al. 2001, Adams et al. 2006, Dahlgren et al. 2006), which seem to be met by HB at Mona Island.

Small (< 5 cm SL) early juvenile *L. apodus* were seen among algae and seagrass detritus accumulations on the seafloor or in depressions in the sand or rubble among seagrass habitats in backreef lagoons at Mona Island. Small sized early juveniles were also seen in tidal pools where less than a meter of seawater accumulated at high tide. The presence of *L. apodus* may be more related to settlement processes. Larvae were observed associated with floating vegetation, which would drift into shallow areas where both naturally deposit to the benthos. At this stage the loose vegetation and accumulations of detritus continue to offer small fish protection and foraging habitat.

The lack of mangroves at Mona Island limits the population of *L. griseus*. Mangroves are considered important habitat for all life stages of *L. griseus* (Rooker and Dennis 1991), a species with an affinity for coastal bays (Faunce and Serafy 2007). Although *L. griseus* showed a high dependence on seagrass beds, but not on mangroves (Nagelkerken et al. 2001) in Curaçao, which would suggest they are more

flexible in their nursery habitat dependence. Nonetheless only 12 adult individuals were observed, all in one transect at Mona Island.

Lutjanus mahogoni were observed in various habitats at Mona Island. Early and juvenile stages depended mostly on HB, SV and RB/SED in shallow areas. Adults were absent from RB/SED and most abundant in CR and SV. At both Bonaire and Curaçao juvenile *L. mahogoni* were most abundant in seagrass (Nagelkerken and van der Velde 2003), and associated with mangroves as juveniles (Rooker and Dennis 1991, Nagelkerken and van der Velde 2002). Nonetheless their occurrence on reefs far away from seagrass or mangroves was attributed to this species ability to recruit onto shallow CR habitat (Dorenbosch et al. 2004). Shallow coral reefs had been proposed as the nursery habitat for *L. mahogoni* (Nagelkerken et al. 2000b) yet at Mona Island very few early life stage individuals were observed in CR, although it was the most important habitat for juvenile stages. Nonetheless the distribution of nursery habitats for this species at Mona Island supports a higher density of adults than in La Parguera where abundances were too low for any comparisons to be made. Equivalent HB habitats along the coastline used as nursery habitat by *L. mahogoni* are missing at La Parguera due to the almost complete coverage of coastal mangroves, and this could partially explain the lower density of this species at the latter site.

In this study SV was the main nursery habitat for smaller sized individuals and supported significant densities of early life stages of *O. chrysurus*. Settlement of this species into seagrass was followed by high site-fidelity up to sizes of 7.5 cm (TL) in the BVI (Watson et al 2002). Mateos and Tobias (2001) reported seagrass as the main nursery habitat and Nagelkerken et al. (2002) determined it is highly dependent upon

seagrass and mangrove habitat due to their absence on islands without these. Cocheret de la Morinière et al. (2004) determined that juvenile *O. chrysurus* were attracted to the shade in mangroves and not the structural complexity. In Curacao there were decreasing counts of this species as distance of reef to mangrove and seagrass bays increased (Dorenbosch et al. 2004). The abundance of *O. chrysurus* at Mona Island is reduced (an order of magnitude) in comparison with La Parguera (Table 2-6) in line with the nursery habitat hypothesis that the presence of mangroves and or seagrass at the island scale influences the density of reef fishes (Nagelkerken et al. 2002, Halpern 2004). Nonetheless larger *O. chrysurus* were observed in deeper areas off the shelf edge, although not quantified due to limits in the sampling depth, suggesting the limited amount of seagrass provides nursery habitat for a reduced population of adults at Mona Island when compared to La Parguera. This would suggest that they are not obligate dependents of mangroves although perhaps limited by the reduced seagrass at Mona Island.

Family Monacanthidae

Cantherines pullus had smaller sizes in SV although density was equal in all habitat types at early life stages. Adults were only observed in CR and HB habitats suggesting a shift in habitats with ontogeny. Randall (1964) described the genus and indicated pre-juveniles were taken at sea far from land. Information on nursery habitat is lacking and abundances in La Parguera were too low for comparison. Nonetheless this species seems to have a cross-shelf movement pattern towards deeper CR and HB habitats from a diversity of nursery habitat types making it an opportunistic species.

Family Ostraciidae

Coral reef and HB habitats provide an important nursery function for *L. triqueter* and individuals seem to migrate to deeper areas as they attain larger sizes. Although a few juveniles were seen in SV, the CR and HB habitat supported greater density of individuals. This species has been reported as forming spawning aggregations on the shelf edge at depths of 25-30 m in Gladden Spit, Belize (Heyman and Kjerfve 2008) and at Mona Island they have been observed with courtship coloration at a multi species aggregation site near the shelf break (pers. obs.). Therefore during adult stages they undergo reproductive migrations to deeper CR and HB habitat. No significant numbers of adult *L. triqueter* were quantified in La Parguera for comparison, perhaps because the local fishery targets this species heavily.

Family Scaridae

Scarus coeruleus and *S. guacamaia* were not observed at Mona Island, although the latter has been sighted in deep (> 30 m) waters at Monito Island (pers. obs.). Mangroves have been identified as a nursery habitat for *S. guacamaia* (Nagelkerken and van der Velde 2002, Mumby et al. 2004) therefore we would not expect to see any significant numbers of this species, although anecdotal evidence of their occurrence in large numbers near shore exists (unpublished data and Yoshioka, pers. comm.). In Puerto Rico these larger species are the target of recreational spear fishing as they commonly hold large parrotfish tournaments. Mumby et al. (2004) suggested *S. guacamaia* has a functional dependency on mangroves during juvenile stages, while Dorenbosch et al. (2006) demonstrated the distance to mangroves affected the

presence of adults on reefs. In addition the distribution of *S. coeruleus* is significantly related to the presence of seagrass and mangroves (Dorenbosch et al. 2004).

Scarus iserti had smaller sizes in SV with high density of early, juvenile and adult stages occurring mainly in CR. This species is limited in depth range and did not occur in areas deeper than 20 m. The density of adults was significantly lower compared to La Parguera suggesting the lack of mangroves or differences in seagrass habitat limit this population. Nagelkerken and van der Velde (2002) proposed juveniles prefer seagrass beds and mangroves, although Dorenbosch et al. (2004) conclude that *S. iserti* are not highly dependent upon seagrass beds and mangroves. For the congener *S. taeniopterus* the distribution of all life stages was limited to the deeper areas of the platform including some sites along the deep eastern cliff wall habitat; therefore no differences by depth or habitat were detected. This suggests that *S. taeniopterus* does not undergo habitat shifts or cross-shelf ontogenetic migrations.

Hardbottom habitats provide an important nursery function for larger sized parrotfishes (*S. chrysopterus*, *S. rubripinne* and *S. viride*) at Mona Island. Nagelkerken and van der Velde (2002) suggested mangroves as a juvenile habitat for *S. chrysopterus*, although in Curaçao *S. chrysopterus* showed a high dependence on seagrass beds, but not on mangroves (Nagelkerken et al. 2001) suggesting they are more flexible in their nursery habitat dependence. Finally Nagelkerken et al. (2002) and Dorenbosch et al. (2004) concluded that this species did not depend on mangroves or seagrass beds as nurseries. In La Parguera *S. chrysopterus* was not observed in mangrove or seagrass (Aguilar-Perera and Appeldoorn 2007) although Cerveny (2006) suggested early juveniles occurred in vegetated habitats. At Mona Island density of *S.*

chrysopteron adults was much higher than in La Parguera, which suggests that during early juvenile stages there is no obligate dependence upon mangroves for *S.*

chrysopteron and the limited seagrass is providing habitat for all stages as the highest density was consistently in SV. As adults they spawn on the shelf break at depths greater than 20 m at a multi species aggregation site (pers. obs.).

The total abundance of *S. rubripinne* was 4 times greater than *S. chrysopteron* and both demonstrated ontogenetic habitat shifts from shallow SV and RB/SED towards deeper CR and HB habitats at Mona Island. The higher abundance of *S. rubripinne* at Mona Island contrasts with sampling conducted in seagrass bays with mangroves in Guadeloupe (Baelde 1990) where *S. chrysopteron* was much more abundant than *S. rubripinne*. Similarly in the Bahamas, a mangrove rich site, *S. chrysopteron* was reported as 'common' and *S. rubripinne* was 'rare' (Layman and Silliman 2002). Nagelkerken and van der Velde (2002) determined *S. rubripinne* favored shallow (<2 m) forereef habitat throughout ontogeny and compared to *S. chrysopteron* it is less affected by the lack of mangroves and limited seagrass. *Sparisoma rubripinne* was restricted to areas less than 20 m in depth and only single individuals were observed deeper than 15 m except during spawning aggregations, which generally occurred deeper (pers. obs.) similar to that described by Randall and Randall (1963).

Sparisoma viride occurred mainly in CR and HB habitats and were smaller in HB, suggesting they are limited to these two habitats during early stages. There seems to be a cross-shelf migration as FL was positively correlated with depth although no switch in habitat type was observed. Nagelkerken et al. (2000) as well as Nagelkerken and van der Velde (2003) identified seagrass beds as the most important habitat for juvenile *S.*

viride along with reef habitats, nonetheless in shallow back-reef areas of St. Croix, USVI (Mateo and Tobias 2004) they were not observed and at Mona Island early life stages were only observed in SV in very low density. If shallow CR or HB is available it seems that *S. viride* can use these as nursery habitats and move to deeper similar habitats during adult stages. Because adults were observed in significantly higher density at Mona Island compared to La Parguera we can infer that SV is not necessary and CR habitat of varying depths is sufficient for the ontogenetic migration of this species.

Family Sphyraenidae

Sphyraena barracuda is commonly referred to as a mangrove dependent species due to the occurrence of very small sized fish within submerged prop roots. In Curaçao *S. barracuda* showed a high dependence on seagrass beds, but not on mangroves (Nagelkerken et al. 2001) suggesting they are more flexible in their nursery habitat dependence. At Mona Island relatively few (44) *S. barracuda* were quantified and the FL was not correlated with depth although data suggest that HB is preferred at all life stages.

2.1.10 Influence of nursery habitats at Mona Island

According to Dennis et al. (2005) the coral reef fish assemblage at Mona Island is relatively impoverished due to lack of nursery habitats (specifically mangroves). Some species observed in the present study yet not reported by Dennis et al. (2005) included *A. virginicus*, *H. macrostomum*, *L. cyanopterus* and *L. jocu*. This may be due primarily to their low abundances or patchy distribution, differences in sampling effort (time spent underwater) and partly due to differences in sampling techniques.

Nonetheless, other nursery species and ontogenetically migrating species (Table 2-1) were observed, suggesting that Mona Island provides alternate habitats, which despite the lack of mangroves and limited areas of seagrass provide the nursery function some species require.

The lack of mangrove habitats at Mona Island presumably influences the presence and abundance of mangrove dependant species. Notable absences at Mona Island include *Gerres cinereus*, *L. synagris*, *S. coeruleus* and *S. guacamaia* although the latter two have been the target of recreational spear fishing by divers at Mona Island. According to experienced fishers interviewed over the past decade (unpublished data) *S. guacamaia* used to be common in near shore areas. Therefore it is not clear if the patterns observed for this species are the result of one factor or a combination of nursery habitat limitation and selective take of this large-bodied parrotfish. The low abundances of *H. macrostomum*, *H. plumieri*, *H. sciurus*, *L. analis* and *L. griseus* also seem to respond to the lack of mangroves. According to Mumby et al. (2004) mangroves are essential for significant biomass of both *H. sciurus* and *S. guacamaia* and this pattern was consistent at Mona Island.

Tests of dependence require consistent evidence that at least one life stage is restricted only to the habitat in question (CSA International 2009). Therefore if a species can be found in more than one habitat it can be considered opportunistic and the impact of nursery habitats upon their abundances may be under- or overestimated unless the alternate habitats are characterized and the underlying ecological process is understood. In the case of Mona Island seagrass was the most important nursery habitat for *Chaetodon capistratus*, *C. striatus*, *H. flavolineatum*, *H. parra*, *L. apodus* and *O.*

chrysurus. *Haemulon parra* and *L. apodus* also relied on HB while *A. bahianus*, *H. carbonarium* and *L. mahogoni* depended mostly on SV and RB/SED in shallow areas. *Cantherines pullus* and *K. sectator* had smaller sizes in SV although variable density of early life stages suggesting they are more opportunistic. Hardbottom habitats supported an abundance of early juveniles of *Acanthurus chirurgus*, *A. surinamensis*, *L. triqueter*, *M. niger* as well as for the three most common parrotfishes (*S. chrysopterus*, *S. rubripinne* and *S. viride*).

The species present, although less abundant as adults at Mona Island compared to La Parguera suggests there is a facultative dependence upon mangroves or seagrasses and could not find sufficient nursery habitat at Mona. These species (*A. chirurgus*, *C. capistratus*, *O. chrysurus* and *S. iserti*) have been reported as mangrove or seagrass dependent at other locations (Nagelkerken 2007). Although they occupy alternate habitats during early life stages at Mona Island, their lower growth, survival, subsequent habitat migrations or recruitment to the adult populations may be affecting the adult populations observed at Mona Island. No Haemulids and reduced densities of *O. chrysurus* were observed at another remote oceanic site, Navassa Island, where mangroves and seagrass are absent (Miller and Gerstner 2002).

The results of this study highlight the facultative relationship of some species to the combination of mangroves and seagrass as nursery habitats (Nagelkerken et al. 2000b, Aguilar-Perera and Appeldoorn, 2007). *Haemulon flavolineatum*, *H. carbonarium* and *L. mahogoni* were common at Mona Island, and in addition the density of adults was higher than La Parguera, although differences could be attributed to other factors, for example fishing effects, mainly traps and spearfishing in La Parguera

(Valdés-Pizzini et al. 1997, Schärer et al. 2004). These species in addition to three parrotfishes (*S. chrysopterus*, *S. rubripinne* and *S. viride*) seem opportunistic (or facultative) nursery species, using alternate HB habitats at Mona Island. Nearshore hardbottom habitats maintain high numbers of early juveniles along the eastern Florida coast providing the main nursery habitat for a diverse group of species (CSA International 2009).

Finally it must be stressed that the association of many of these early juvenile fishes with nursery habitats may be related to the spatial scale at which habitats are mapped. Many of the 60 m² transects in SV where high abundances of early stages were detected covered heterogeneous micro-scale (<10 m) habitats where hard structure (reef, rock, rubble, bedrock, etc.) was interspersed with seagrass. Fish (mainly haemulids and lutjanids) were associated with the small-scale vertical structure yet the dominant benthic cover in these transects was seagrass. All transects in which early stages of haemulids and lutjanids were quantified at Mona Island had seagrass mixed with rubble, patches of bedrock or rocky reef smaller than the transect's total area (pers. obs.). Only early stages of *O. chrysurus* used seagrass of continuous cover within the transect. Therefore, not all seagrass beds are equal in the nursery habitat function; areas of heterogeneous seagrass cover or mixed seagrass categories with structure supported significantly more nursery species than continuous cover of seagrass. Settlement of grunts in back-reef areas was associated with structure provided by the supportive elements of organisms (algae, coral, urchins) or other abiotic features such as rocks or sand mounds (Hill, 2001).

The results of the present study indicate that some nursery species use alternate near shore habitats during early life stages and exhibit greater adult densities at Mona Island when compared to La Parguera despite the lack of mangroves. Another possible explanation for the difference in density between these two locations is the landscape configuration of habitats available, which may favor distinct fish assemblages due to other ecological factors such as habitat distribution, connectivity, productivity, competition or predation. In addition, differences in fishing pressure undoubtedly affects these comparisons since fish traps and nets are commonly used in La Parguera but are rarely used at Mona Island. Fishing effects in La Parguera were deemed responsible for lower size and catch-per-unit effort of grunts indicating growth overfishing (Dennis 1992). In this case it is possible that overall patterns in fish abundance due to the availability of nursery habitats are affected by differences in fishing mortality as the density of species of similar size and habits would have consistently demonstrated higher densities at Mona Island, and this was not the case.

I propose that coral reef fishes that undergo ontogenetic migrations are positioned along a gradient of nursery dependence that is species specific (Figure 2-15). Most restricted species dependent upon mangroves and to a lesser extent seagrass including: *A. chirurgis*, *C. capistratus*, *A. virginicus* and *L. griseus*. Another group requires both mangroves and seagrass as a nursery habitat but may also require vegetated or sediment dominated habitats for subsequent life stages, such as: *H. plumieri*, *H. sciurus*, *L. analis*. Some species require seagrass as nursery habitat *O. chrysurus*, *S. chrysopterum*, *S. rubripinne* and *S. iserti*. Further along this dependence gradient is a group of opportunistic species using multiple habitats during early life

stages: *A. bahianus*, *A. coeruleus*, *H. carbonarium*, *H. parra*, *H. flavolineatum* and *L. apodus*. Finally the group considered HB habitat dependent for early life stages includes: *A. surinamensis*, *L. triqueter* and *M. niger*.

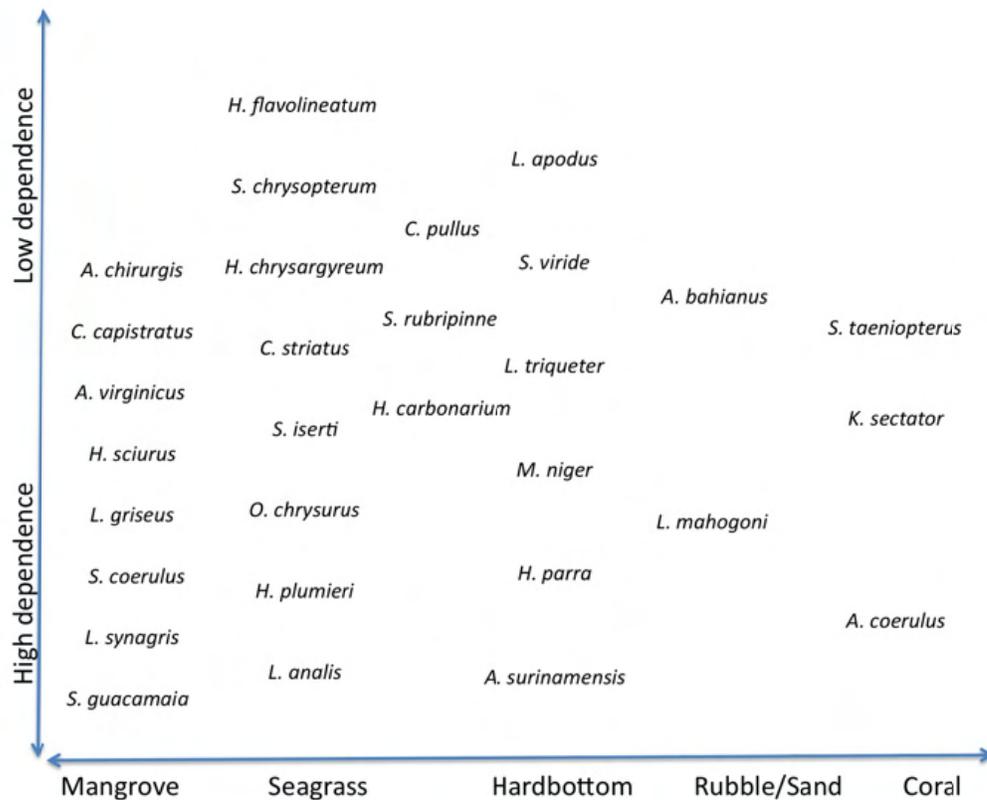


Figure 2-15 Species position along a nursery habitat and relative dependence gradient.

At Mona Island there is a high dependence of most early juvenile coral reef fishes on seagrass or hardbottom habitats located in backreef lagoons. The near shore hardbottom habitats with vertical relief may provide an ecological substitute for mangroves. This suggests that nursery function should not be attributed to a specific species (i.e. *Rhizophora mangle*), but must consider the characteristics or attributes (i.e. shading) that create conditions promoting the ecological processes required by early life stages. In addition, the location of a habitat patch in the landscape context is an

important consideration that must be done on a case-by-case scenario. These results highlight the need for a species-specific and landscape approach to the nursery habitat question. This information should be integrated in the decision making process where specific habitats are prioritized over others in spatial management measures, without a comprehensive evaluation of their potential nursery function, especially within the ecosystem based management approach.

Conclusion

Coral reef fishes that undergo migrations from juvenile habitats distinct from adult habitats showed a cross shelf migration towards deeper habitats, but the degree to which early juveniles stages depended on one specific habitat types varied between species. The full range of habitats used throughout ontogeny is variable and previously un-reported habitats are used by some species. For example the presence of mangrove habitats during early life stages is not essential for *L. apodus* as they were significantly abundant at Mona Island despite the lack of mangroves. The composition of habitats in tropical ecosystems influences the biodiversity and abundance of reef associated fishes. However the magnitude of this relationship is variable among species, life stage and depends on the ability of alternate habitats to provide the ecological functions required as well as the species capability to migrate. Linkages between habitats used by coral reef fish should not be generalized as their function is not uniform and constrains biodiversity at different taxonomic levels. The influence of nursery habitat upon assemblages of coral reef fish species needs to take into consideration the availability of alternate habitats when mangroves are lacking in order to make accurate conclusions about the impact of this habitat. In addition the impacts of historical fishing on certain species may skew the interpretation of these results.

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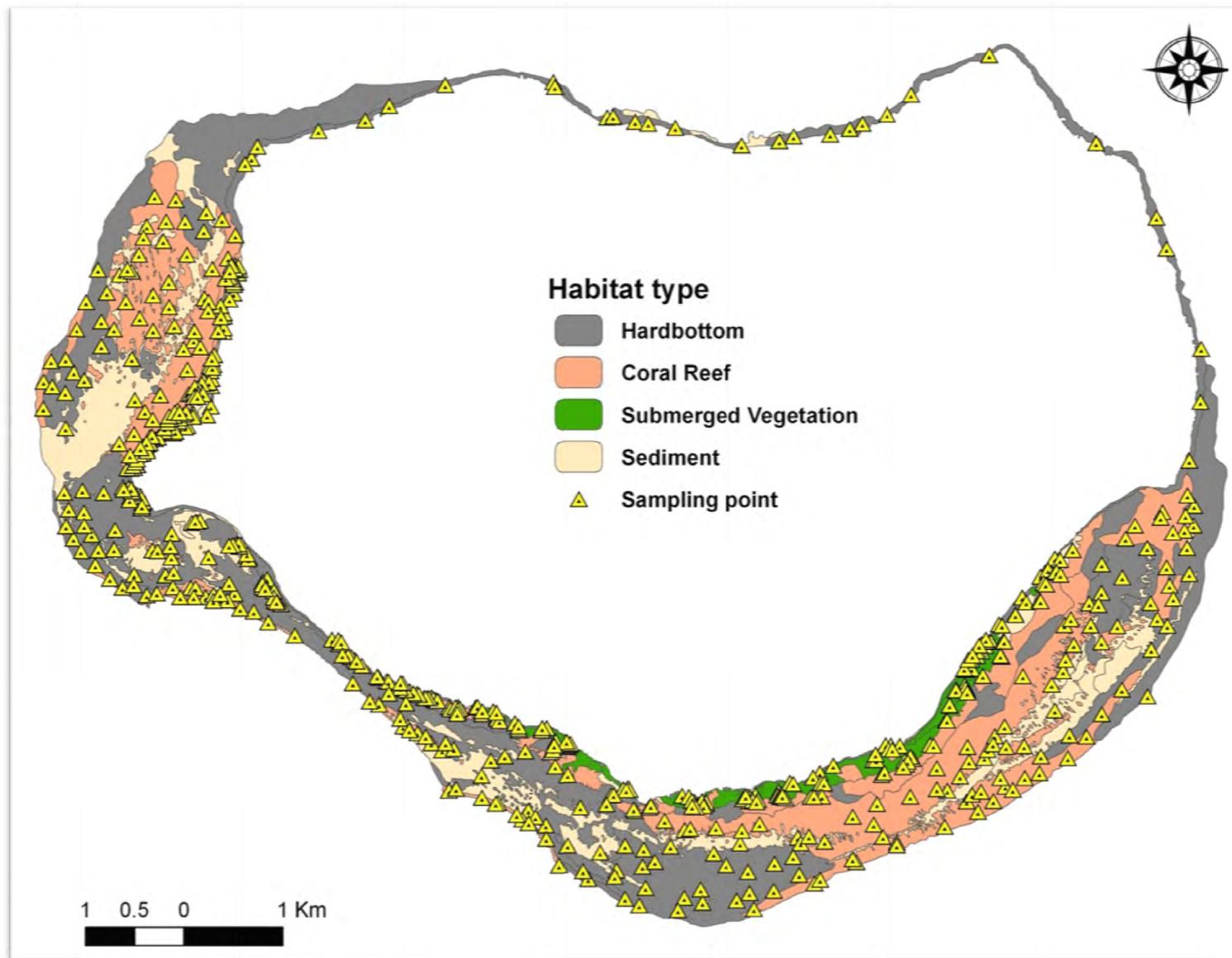
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Appendices

Appendix 2-1 Sampling sites around Mona Island by habitat type.

Appendix 2-2 Frequency of occurrence and density of all species observed by habitat type.

Appendix 2-1 Sampling sites around Mona Island by habitat type.



Appendix 2-2 Frequency of occurrence and density of all species observed by habitat type.

Table 1 All species observed within belt transects. Freq. = frequency of occurrence or percentage of transects where that species was present, N = total number of individuals, Overall = mean density (individuals / 60 m²) pooled by all habitats, and by habitat type SV = submerged vegetation, RB = rubble and unconsolidated sediment, HB = hardbottom habitats and CR = coral reef habitats.

Genus	Species	Common Name	Freq.	N	Overall (N=613)	SV (N=74)	RB (N=14)	HB (N=233)	CR (N=292)
<i>Abudefduf</i>	<i>saxatilis</i>	Sergeant Major	2.3%	25	0.041	-	-	0.026	0.065
<i>Abudefduf</i>	<i>taurus</i>	Night Sergeant	0.2%	1	0.002	-	-	0.004	-
<i>Acanthostracion</i>	<i>polygonius</i>	Honeycomb Cowfish	2.3%	14	0.023	-	-	0.030	0.024
<i>Acanthostracion</i>	<i>quadricornis</i>	Scrawled Cowfish	0.8%	5	0.008	-	-	0.013	0.007
<i>Acanthurus</i>	<i>bahianus</i>	Ocean Surgeon	91.5%	5722	9.334	7.108	15.714	10.361	8.774
<i>Acanthurus</i>	<i>chirurgus</i>	Doctorfish	6.5%	68	0.111	0.041	0.357	0.167	0.072
<i>Acanthurus</i>	<i>coeruleus</i>	Blue Tang	86.0%	3857	6.292	1.851	3.643	3.524	9.753
<i>Alphestes</i>	<i>afer</i>	Mutton Hamlet	0.3%	2	0.003	0.014	-	0.004	-
<i>Aluterus</i>	<i>scriptus</i>	Scrawled Filefish	0.2%	1	0.002	-	-	-	0.003
<i>Amblycirrhitus</i>	<i>pinos</i>	Hawkfish	6.4%	52	0.085	-	-	0.112	0.089
<i>Anisotremus</i>	<i>surinamensis</i>	Black Margate	5.1%	45	0.073	-	-	0.082	0.089
<i>Anisotremus</i>	<i>virginicus</i>	Porkfish	0.7%	5	0.008	-	-	0.013	0.007
<i>Apogon</i>	<i>pseudomaculatus</i>	Cardinalfish	0.2%	1	0.002	-	-	-	0.003
<i>Apogon</i>	<i>townsendi</i>	Belted Cardinalfish	0.2%	1	0.002	-	-	-	0.003
<i>Aulostomus</i>	<i>maculatus</i>	Trumpetfish	1.8%	11	0.018	-	-	0.017	0.024
<i>Balistes</i>	<i>vetula</i>	Queen Trigger	11.7%	91	0.148	-	-	0.288	0.082
<i>Bodianus</i>	<i>rufus</i>	Spanish Hogfish	29.4%	360	0.587	-	-	0.768	0.620
<i>Cantherines</i>	<i>macrocerus</i>	Whitespotted File	0.8%	7	0.011	-	-	0.017	0.010
<i>Cantherines</i>	<i>pullus</i>	Orangespotted File	4.4%	36	0.059	0.068	0.143	0.073	0.041
<i>Canthidermis</i>	<i>sufflamen</i>	Ocean Triggerfish	1.8%	42	0.069	0.014	-	0.009	0.134
<i>Canthigaster</i>	<i>rostrata</i>	Sharpnose Puffer	3.4%	24	0.039	-	-	0.039	0.051
<i>Carangoides</i>	<i>bartholomaei</i>	Yellow Jack	0.3%	2	0.003	-	-	0.009	-
<i>Carangoides</i>	<i>ruber</i>	Bar Jack	36.7%	487	0.794	0.959	0.714	0.742	0.798
<i>Caranx</i>	<i>crysos</i>	Blue Runner	4.1%	111	0.181	0.324	0.071	0.107	0.209
<i>Caranx</i>	<i>latus</i>	Horse Eye Jack	1.5%	74	0.121	-	-	0.013	0.243
<i>Caranx</i>	<i>lugubris</i>	Black Jack	2.6%	22	0.036	-	-	0.026	0.055
<i>Carcharhinus</i>	<i>perezi</i>	Reef Shark	0.2%	1	0.002	-	-	-	0.003
<i>Cephalopholis</i>	<i>cruentata</i>	Graysby	17.0%	149	0.243	-	-	0.210	0.342

Genus	Species	Common Name	Freq.	N	Overall (N=613)	SV (N=74)	RB (N=14)	HB (N=233)	CR (N=292)
<i>Cephalopholis</i>	<i>fulva</i>	Coney	44.0%	939	1.532	0.014	0.143	2.464	1.240
<i>Chaetodon</i>	<i>capistratus</i>	Foureye Butterflyfish	19.7%	244	0.398	0.068	-	0.519	0.404
<i>Chaetodon</i>	<i>ocellatus</i>	Spotfin Butterflyfish	0.3%	2	0.003	0.014	-	-	0.003
<i>Chaetodon</i>	<i>sedentarius</i>	Reef Butterflyfish	0.2%	2	0.003	-	-	0.009	-
<i>Chaetodon</i>	<i>striatus</i>	Banded	14.0%	145	0.237	0.230	-	0.296	0.202
<i>Chromis</i>	<i>cyanea</i>	Blue Chromis	33.3%	2995	4.886	-	-	3.373	7.565
<i>Chromis</i>	<i>multilineata</i>	Brown Chromis	25.8%	2418	3.945	-	-	3.867	5.195
<i>Clepticus</i>	<i>parrae</i>	Creole Wrasse	11.3%	1368	2.232	-	-	1.343	3.613
<i>Coryphopterus</i>	<i>personatus</i>	Masked goby	0.2%	10	0.016	-	-	-	0.034
<i>Dasyatis</i>	<i>americana</i>	Southern Stingray	0.3%	2	0.003	0.014	-	0.004	-
<i>Elagatis</i>	<i>bipinnulata</i>	Blue Runner	0.3%	6	0.010	-	-	-	0.021
<i>Epinephelus</i>	<i>adscensionis</i>	Rock Hind	0.7%	5	0.008	-	-	0.009	0.010
<i>Epinephelus</i>	<i>guttatus</i>	Red Hind	3.9%	25	0.041	0.014	-	0.073	0.024
<i>Epinephelus</i>	<i>striatus</i>	Nassau Grouper	0.3%	4	0.007	0.054	-	-	-
<i>Equetus</i>	<i>punctatus</i>	Spotted Drum	0.7%	4	0.007	-	-	0.009	0.007
<i>Eucinostomus</i>	<i>lefroyi</i>	Mottled Mojarra	0.5%	14	0.023	0.162	-	-	0.007
<i>Eucinostomus</i>	<i>melanopterus</i>	Flagfin Mojarra	0.3%	9	0.015	0.108	-	0.004	-
<i>Gobiosoma</i>	<i>genie</i>	Cleaning Goby	0.5%	6	0.010	-	-	0.004	0.017
<i>Gramma</i>	<i>loreto</i>	Fairy Basslet	18.8%	1529	2.494	-	-	3.421	2.507
<i>Gynglymostoma</i>	<i>cirratum</i>	Nurse Shark	0.8%	5	0.008	-	-	0.004	0.014
<i>Haemulon</i>	<i>carbonarium</i>	Cesar's Grunt	36.4%	1270	2.072	2.716	4.071	1.279	2.445
<i>Haemulon</i>	<i>chrysargyreum</i>	Smallmouth Grunt	6.7%	607	0.990	1.378	0.214	0.266	1.507
<i>Haemulon</i>	<i>flavolineatum</i>	French Grunt	21.0%	597	0.974	1.054	-	0.588	1.308
<i>Haemulon</i>	<i>macrostomum</i>	Spanish Grunt	0.5%	3	0.005	0.014	-	-	0.007
<i>Haemulon</i>	<i>parra</i>	Sailor's Choice	8.3%	249	0.406	0.784	-	0.532	0.229
<i>Haemulon</i>	<i>plumierii</i>	White Grunt	1.1%	7	0.011	0.027	-	0.004	0.014
<i>Haemulon</i>	<i>sciurus</i>	Bluestriped Grunt	1.1%	8	0.013	-	-	-	0.027
<i>Haemulon</i>	<i>species</i>	Unknown Grunt	0.5%	11	0.018	0.081	-	0.021	-
<i>Haemulon</i>	<i>species</i>	Unknown Grunt	0.5%	3	0.005	-	-	-	0.010
<i>Halichoeres</i>	<i>bivittatus</i>	Slippery Dick	4.1%	63	0.103	-	-	0.176	0.075
<i>Halichoeres</i>	<i>garnoti</i>	Yellowhead Wrasse	14.4%	425	0.693	-	-	0.948	0.699
<i>Halichoeres</i>	<i>maculipinna</i>	Clown Wrasse	9.1%	191	0.312	-	-	0.270	0.438
<i>Halichoeres</i>	<i>pictus</i>	Rainbow Wrasse	0.2%	1	0.002	-	-	-	0.003
<i>Halichoeres</i>	<i>poeyi</i>	Blackear Wrasse	0.7%	9	0.015	-	-	0.034	0.003
<i>Halichoeres</i>	<i>radiatus</i>	Puddingwife	6.5%	57	0.093	-	-	0.086	0.127
<i>Holacanthus</i>	<i>ciliaris</i>	Queen	1.8%	17	0.028	-	-	0.052	0.017

Genus	Species	Common Name	Freq.	N	Overall (N=613)	SV (N=74)	RB (N=14)	HB (N=233)	CR (N=292)
<i>Holacanthus</i>	<i>tricolor</i>	Rock Beauty	12.1%	109	0.178	-	-	0.253	0.171
<i>Holocentrus</i>	<i>adscensionis</i>	Squirrelfish	9.6%	117	0.191	-	-	0.343	0.127
<i>Holocentrus</i>	<i>rufus</i>	Longspine Squirrelfish	24.5%	288	0.470	-	-	0.785	0.360
<i>Hypoplectrus</i>	<i>chlorurus</i>	Yellowtail Hamlet	0.3%	2	0.003	-	-	-	0.007
<i>Hypoplectrus</i>	<i>puella</i>	Barred Hamlet	0.3%	2	0.003	-	-	-	0.007
<i>Hypoplectrus</i>	<i>unicolor</i>	Butter Hamlet	1.3%	9	0.015	-	-	0.004	0.027
<i>Kyphosus</i>	<i>sectator</i>	Bermuda Chub	17.0%	527	0.860	0.054	-	0.494	1.397
<i>Lactophrys</i>	<i>bicaudalis</i>	Spotted Trunkfish	1.5%	9	0.015	-	-	0.009	0.024
<i>Lactophrys</i>	<i>trigonus</i>	Trunkfish	0.3%	2	0.003	0.014	-	-	0.003
<i>Lactophrys</i>	<i>triqueter</i>	Smooth Trunkfish	8.6%	62	0.101	0.014	-	0.082	0.144
<i>Lutjanus</i>	<i>analis</i>	Mutton Snapper	0.8%	5	0.008	0.054	-	-	0.003
<i>Lutjanus</i>	<i>apodus</i>	Schoolmaster	19.4%	223	0.364	0.081	0.286	0.468	0.356
<i>Lutjanus</i>	<i>cyanopterus</i>	Cubera Snapper	0.2%	1	0.002	-	-	-	0.003
<i>Lutjanus</i>	<i>griseus</i>	Grey Snapper	0.3%	12	0.020	-	-	-	0.041
<i>Lutjanus</i>	<i>jocu</i>	Dog	0.2%	1	0.002	-	-	-	0.003
<i>Lutjanus</i>	<i>mahogoni</i>	Mahogany	21.5%	417	0.680	0.392	0.571	0.425	0.962
<i>Malacanthus</i>	<i>plumieri</i>	Sand Tilefish	1.0%	7	0.011	-	-	0.009	0.017
<i>Malacoctenus</i>	<i>triangulatus</i>	Saddled Blenny	1.1%	13	0.021	-	-	0.026	0.024
<i>Megalops</i>	<i>atlanticus</i>	Tarpon	0.2%	23	0.038	-	-	0.099	-
<i>Melichthys</i>	<i>niger</i>	Black Durgon	56.3%	2091	3.411	0.054	0.071	4.026	3.932
<i>Microspathodon</i>	<i>chrysurus</i>	Yellowtail Damselfish	27.2%	395	0.644	-	-	0.515	0.942
<i>Mugil</i>	<i>curema</i>	White Mullet	0.2%	5	0.008	-	-	0.021	-
<i>Mulloidichthys</i>	<i>martinicus</i>	Yellow Goatfish	2.9%	52	0.085	-	-	0.052	0.137
<i>Mycteroperca</i>	<i>interstitialis</i>	Yellowmouth Grouper	0.5%	3	0.005	-	-	0.004	0.007
<i>Mycteroperca</i>	<i>tigris</i>	Tiger Grouper	0.3%	2	0.003	-	-	0.004	0.003
<i>Mycteroperca</i>	<i>venenosa</i>	Yellowfin Grouper	0.3%	2	0.003	-	-	-	0.007
<i>Myripristis</i>	<i>jacobus</i>	Blackbar Soldierfish	13.7%	181	0.295	-	-	0.395	0.305
<i>Neoniphon</i>	<i>marianus</i>	Longjaw Squirrelfish	7.2%	69	0.113	-	-	0.112	0.147
<i>Ocyurus</i>	<i>chrysurus</i>	Yellowtail Snapper	2.1%	24	0.039	0.122	-	0.056	0.007
<i>Ophioblennius</i>	<i>macclurei</i>	Redlip Blenny	3.8%	41	0.067	-	-	0.056	0.096
<i>Opistognathus</i>	<i>aurifrons</i>	Yellowhead Jawfish	0.2%	4	0.007	-	-	0.017	-
<i>Paranthias</i>	<i>furcifer</i>	Creole Fish	0.2%	2	0.003	-	-	-	0.007
<i>Pomacanthus</i>	<i>arcuatus</i>	Grey Angelfish	1.8%	16	0.026	0.014	-	0.052	0.010
<i>Pomacanthus</i>	<i>paru</i>	French Angelfish	2.0%	16	0.026	0.014	-	0.034	0.024
<i>Priacanthus</i>	<i>cruentatus</i>	Glasseye Snapper	0.3%	2	0.003	-	-	0.009	-
<i>Prognathodes</i>	<i>aculeatus</i>	Longsnout	3.4%	24	0.039	-	-	0.021	0.065

Genus	Species	Common Name	Freq.	N	Overall (N=613)	SV (N=74)	RB (N=14)	HB (N=233)	CR (N=292)
<i>Pseudupeneus</i>	<i>maculatus</i>	Spotted Goatfish	6.5%	52	0.085	-	-	0.150	0.058
<i>Rypticus</i>	<i>saponaceus</i>	Greater Soapfish	1.6%	10	0.016	-	-	0.013	0.024
<i>Sargocentron</i>	<i>vexillarium</i>	Dusky Squirrelfish	0.7%	5	0.008	-	-	0.004	0.014
<i>Scarus</i>	<i>iseri</i>	Striped Parrotfish	10.3%	287	0.468	0.108	-	0.210	0.788
<i>Scarus</i>	<i>taeniopterus</i>	Princess Parrotfish	30.2%	790	1.289	-	-	1.519	1.493
<i>Scarus</i>	<i>vetula</i>	Queen Parrotfish	9.8%	117	0.191	-	-	0.064	0.349
<i>Scomberomorus</i>	<i>regalis</i>	Cero	0.3%	2	0.003	-	-	-	0.007
<i>Serranus</i>	<i>tigrinus</i>	Harlequin Bass	4.2%	31	0.051	-	-	0.082	0.041
<i>Sparisoma</i>	<i>atomarium</i>	Greenblotch Parrotfish	0.3%	5	0.008	-	-	-	0.017
<i>Sparisoma</i>	<i>aurofrenatum</i>	Redband Parrotfish	36.2%	783	1.277	-	-	1.185	1.736
<i>Sparisoma</i>	<i>chrysopteron</i>	Redtail Parrotfish	20.1%	272	0.444	0.838	0.143	0.296	0.476
<i>Sparisoma</i>	<i>radians</i>	Bucktooth Parrotfish	4.2%	121	0.197	1.635	-	-	-
<i>Sparisoma</i>	<i>rubripinne</i>	Redfin Parrotfish	46.8%	1278	2.085	1.514	1.643	1.863	2.428
<i>Sparisoma</i>	<i>viride</i>	Stoplight Parrotfish	31.0%	406	0.662	0.027	-	0.433	1.038
<i>Sphyraena</i>	<i>barracuda</i>	Great Barracuda	5.9%	44	0.072	-	-	0.103	0.068
<i>Stegastes</i>	<i>adustus</i>	Dusky Damselfish	7.3%	233	0.380	-	-	0.052	0.757
<i>Stegastes</i>	<i>diencaeus</i>	Longfin Damselfish	0.2%	1	0.002	-	-	0.004	-
<i>Stegastes</i>	<i>leucostictus</i>	Beaugregory	3.1%	39	0.064	-	-	0.017	0.120
<i>Stegastes</i>	<i>partitus</i>	Bicolor Damselfish	43.7%	4609	7.519	-	-	9.412	8.274
<i>Stegastes</i>	<i>planifrons</i>	Threespot Damselfish	5.9%	113	0.184	-	-	0.017	0.373
<i>Stegastes</i>	<i>variabilis</i>	Cocoa Damselfish	0.5%	4	0.007	-	-	0.009	0.007
<i>Thalassoma</i>	<i>bifasciatum</i>	Bluehead Wrasse	2.9%	496	0.809	-	-	1.614	0.411
<i>Trachinotus</i>	<i>falcatus</i>	Permit	0.5%	3	0.005	-	0.071	-	0.007
<i>Trachinotus</i>	<i>goodei</i>	Palometa	0.8%	30	0.049	-	-	0.004	0.099
<i>Urobatis</i>	<i>jamaicensis</i>	Yellow Stingray	2.0%	13	0.021	0.014	-	0.021	0.024
<i>Xanthichthys</i>	<i>ringens</i>	Sargassum Triggerfish	1.5%	13	0.021	-	-	0.043	0.010

3 HABITAT AND ONTOGENETIC MIGRATIONS OF REEF FISHES IN THE LANDSCAPE

The relationship between habitat and reef fish distributions throughout ontogeny was investigated at distinct spatial scales within a remote oceanic island. Data included habitat metrics ranging from in-situ measures of benthic cover to patch and landscape scale metrics. Correlations between habitat metrics and the abundance of early, juvenile and adult stages of 5 reef fishes were based on video transects and a high-resolution benthic habitat map. Fish density correlated significantly with distinct metrics at transect, patch and landscape scales, although some trends were consistent (depth and vertical relief) others were more variable (coral, crustose coralline algae and sand) across ontogenetic stages. Habitat patch variables such as size, perimeter to area ratio as well as distance from land and nursery habitats were positively correlated for *H. flavolineatum* and *L. apodus* but not for the other species, and position on the shelf, nearby habitat area and number of habitat patches in the landscape differed by ontogenetic stage and species. Although many metrics (depth, distance to land, patch size etc.) were co-varying due to the arrangement of habitats in the landscape some species-specific differences were observed in the distribution of ontogenetic stages. Comparing habitat metrics between sites with and without fish in coral reef habitat demonstrated preferences for coral, crustose coralline algae, higher vertical relief as well as smaller patch size and lower perimeter to area. Results suggest that habitat variables of distinct spatial scales vary by ontogenetic stage and the influence of habitat connectivity affects species differentially.

Introduction

Coral reefs are an important part of marine tropical ecosystems, which support high biodiversity. How fishes use the ecosystem and what determines their spatial distribution is dependent upon a variety of physical and ecological factors operating at distinct scales. Differences due to scale are not always addressed (Syms 1995) in ecological studies of reef fishes. Relationships between fish and habitat variables at smaller scales have shown rugosity and depth to influence the distribution and abundance of fishes (Luckhurst and Luckhurst 1978, Roberts and Ormond 1987, Friedlander and Parrish 1998, Gratwicke and Speight 2005). At larger scales habitat richness (Ault and Johnson 1998), abundance (Tolimieri 1998) and complexity (Jones and Syms 1998) seem to explain the abundance and species richness. In addition to species-habitat associations the concept of habitat connectivity, which is a combination of distance and abundance or size of habitat patches in the landscape, probably influences large-scale fish distributions.

Fish-habitat relationships at distinct spatial scales determining ontogenetic habitat connectivity may result from distinct ecological processes that determine their spatial distribution (Lecchini and Galzin 2005), which in many cases is scale dependent (Fahrig 2003, Mellin et al. 2007). The combination of large scale remote sensing and small scale in situ observations were used to create models of reef fish diversity (Pittman 2007a) and to determine important metrics to predict the distribution of corals and reef fishes (Pittman et al. 2009). However, factors influencing the distribution of ontogenetic stages and hence habitat connectivity need to be considered over a range

of spatial scales to provide better estimates of the interactions that support this ecosystem function.

Landscape ecology seeks to describe ecological processes and spatial patterns (Turner et al. 2001). A landscape generally refers to a heterogeneous area composed of locally interacting units (habitat patches) and their composition or spatial arrangement is known as landscape structure (Forman and Godron 1986). The landscape is made up of a habitat patches embedded in a matrix, which is the background most abundant habitat type that provides less suitable habitat for a species (Turner et al. 2001). In the case of coral reef ecosystems there may be no clearly definable matrix, because the most abundant habitat type (usually sand or hardbottom), is utilized by fishes to some degree. Although by definition patches are homogeneous, at smaller spatial scales the within patch heterogeneity is revealed. Within the landscape or mosaic of all patches and matrix combined the habitat connectivity can be structural, based on the spatial arrangement of habitats or functional, incorporating the behavioral response of organisms to the physical structure of the landscape.

The use of landscape ecology theory, derived largely from island biogeography theory (MacArthur and Wilson 1967), meta-population theory (Hanski 1999), and patch dynamics (Pickett and White 1985) has been used to understand the distribution of organisms in terrestrial communities (Turner 1989; Turner et al. 2001). However, the application to marine systems is limited, and only recently have more studies focused on coral reefs (Ault and Johnson 1998, Nagelkerken et al. 2002, Appeldoorn et al. 2003, Kendall et al. 2003, Kendall 2005, Dorenbosch et al. 2007, Grober-Dunsmore et al. 2007 and 2008, Pittman et al. 2007a, 2007b, 2008, 2009). Organisms in three-

dimensional submerged habitats may respond differently to inter-habitat boundaries compared to terrestrial systems. Therefore we would expect inter-habitat connectivity of reef fishes to be influenced by spatial scales reflecting different ecological processes (within patch heterogeneity, patch quality, quantity of habitat, distances between patches, boundary effects and the quality of the surrounding matrix).

Ontogenetic migrations from settlement areas to adult habitats are thought to occur in response to changes in habitat requirements related to fish size and the ensuing tradeoffs in predator avoidance and feeding strategies (Werner and Gilliam 1984, Dahlgren and Eggleston 2000). A basic assumption is that fishes respond to habitat cues at small spatial scales (within patches) at shorter temporal scales (i.e. daily), and as they grow characteristics at greater spatial scales within the habitat mosaic become more relevant. For example species that undergo nightly foraging migrations may respond to within patch or patch characteristics (type, size, perimeter to area ratio, neighboring habitats, etc.) that match the range of their movements at daily scales, but the influence of the landscape acts upon the ontogenetic migrations at long-term scales. In order to understand the requirements of ontogenetic migrations greater areas of the habitat mosaic become relevant, hence the opportunity to apply landscape ecology to describe the spatial distribution of reef fishes.

This study seeks to determine habitat preferences during reef fish ontogeny in order to determine the inter-habitat connectivity within the landscape. The goal is to detect the effects of habitat variables, at different spatial scales, on fish distributions in order to elucidate connectivity requirements. Although the relative importance of habitat variables is not compared between spatial scales, the influence upon ontogenetic

stages is used to infer which processes are important at distinct scales and can be used to understand habitat connectivity in a coral reef ecosystem. Conducting this analysis at a remote, uninhabited, oceanic island (Mona Island) and by sampling all available habitats, the spatial distribution of fish is assumed to be the result of relatively undisturbed habitat connectivity, with lower fishing impacts in comparison with inhabited islands (Stallings 2009).

The main habitat types used by ontogenetic stages (early, juvenile and adults) of fishes were previously determined for Mona Island (Chapter 2). The spatial distributions of three grunts (family Haemulidae) and two snappers (family Lutjanidae) were further analyzed throughout all available habitats in order to determine the influence of habitat metrics at distinct spatial scales upon connectivity. The following questions were posed:

1. Which habitat metrics, of distinct spatial scales affect the abundance of ontogenetic stages?
2. Which landscape scale metrics influence the distribution of ontogenetic stages?
3. Within coral reef habitat, which habitat metrics were abundant where fish were present?

If patterns of fish-habitat relationships remained constant throughout ontogeny the connectivity requirements of that species would be relatively simple to conceptualize, and for some site-attached species this is probably the case. However, changing habitat preferences during ontogeny increase the complexity at greater spatial scales within a species. Understanding differences in habitat requirements may help identify essential or critical habitat connectivity for species with ontogenetic requirements. It is expected

that habitat metrics influencing the spatial distribution of fishes will be variable due to changes in ontogenetic requirement as well as differences in landscape structure.

Materials and Methods

3.1.1 Study Site

Mona and Monito Islands are located in the Mona Passage between the Dominican Republic (66 km) and Puerto Rico (68 km), (Figure 3-1). These two islands lie on separate (by depths of 250 m) carbonate platforms formed approximately 15 million years ago (Late Miocene to early Pliocene) and uplifted from the seafloor due to tectonic movements (Frank et al. 1998). Mona Island (18.09 N, 67.89 W) covers 55 km² and is surrounded by narrow submerged insular shelf of 2,657 km², with only the southern half of the island bordered by relatively shallow (< 30 m) waters with coral reefs and associated habitats. Mona Island's location upon a relatively isolated platform located ~ 70 km from any large island suggests limited immigration of post-settlement sized fish, and therefore sampling throughout the platform should provide a comprehensive estimate of habitat use patterns by fish.

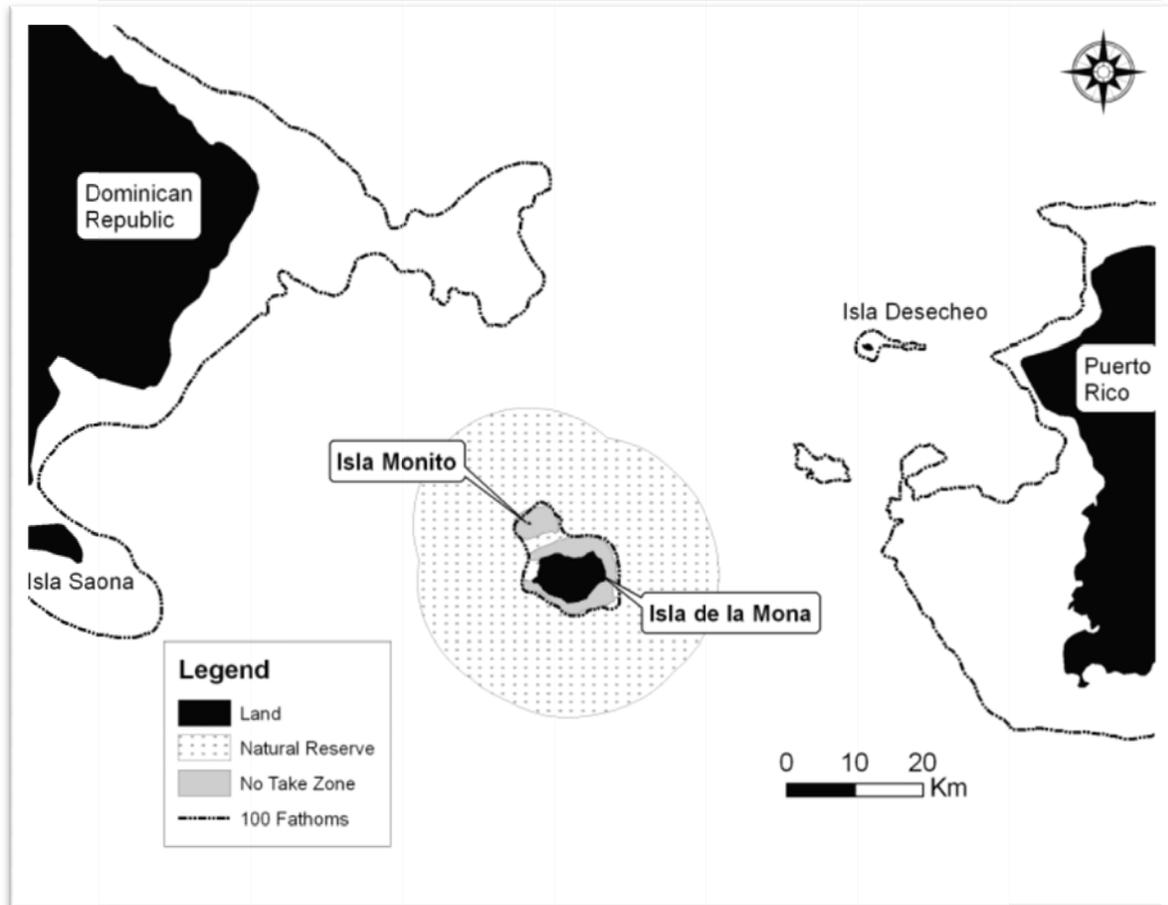


Figure 3-1 Mona Passage and associated islands west of Puerto Rico.

The waters surrounding both islands up to 9 nautical miles from shore compose the Mona and Monito Natural Reserve, which is the largest marine protected area (MPA) in Puerto Rico (Figure 3-1). The Department of Natural and Environmental Resources (DNER) established the Natural Reserve in 1986 (Aguilar-Perera et al. 2006). The islands are uninhabited except for the DNER staff on Mona Island. Due to its remote location, few persons venture to Mona Island except during hunting season and camping trips. Commercial fishing occurs mainly in areas deeper than 100 m for deep-water snappers, while recreational diving and fishing occurs throughout near shore and pelagic areas around both islands. Within the Natural Reserve a no-take zone was

designated in 2004 extending 0.5 nautical miles from shore around all of Monito and most of Mona Island. The limits of this zone were modified in 2007 to include most of both island's platform up to the 100 fathom (182 m) depth contour (Figure 3-2).

Excluded is a swath on the western coast where recreational hook and line as well as spearfishing are permitted (DNER, 2007).

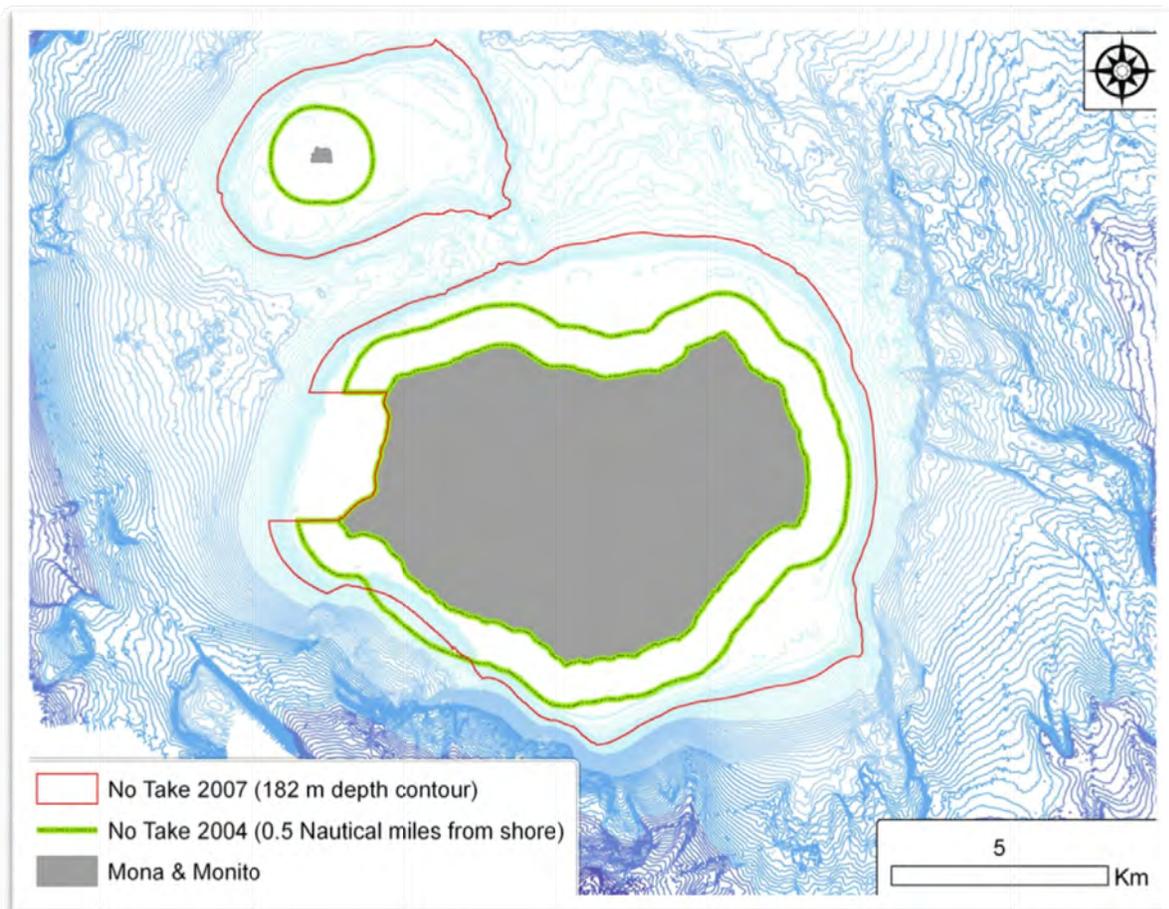


Figure 3-2 No take zone limits for 2004 and 2007 around Mona and Monito Islands.

3.1.2 Benthic habitat characteristics

Random sites throughout the insular platform to depths of 25 m were sampled with SCUBA (> 5m depth) for in situ habitat and fish characterizations. Sampling sites were selected using Hawth's Tools extension in Arc Map 9.3 from a 50 m grid

superimposed on the insular platform of Mona Island. Coordinates for each sampling point were uploaded to a handheld GPS and located in the field.

At each site (sampling point) a weighted buoy was dropped from the surface to mark the starting point of a 30 m linear transect parallel to the coast or depth contour. For each transect depth was estimated with a depth gauge at the start and vertical relief was estimated by measuring depth at 5 equidistant points along a 30 m tape. Vertical relief was the difference between minimum and maximum values in meters.

Video was recorded along 15 m (three 5-m sections) of each transect with a Sony digital (mini-DV) video camera in Ikelite housing. Video images were recorded in planar view although distance between the camera and the seafloor was not always constant due to organisms growing vertically such as octocorals. Nonetheless an effort was made to maintain the camera 50 cm from the seafloor to minimize variations in area covered by the frame. Still images were extracted to quantify the relative proportion of area covered by major benthic components.

Each video transect was downloaded from mini-DV tape into separate digital, high quality video (.avi) files. From each video transect file 10 equally spaced still images were captured, exported (.jpg) and analyzed with Coral Point Count with Excel extensions program (CPCe, Kohler and Gill 2006). Forty-nine uniformly distributed points were overlaid upon each image to quantify major benthic organisms. A hierarchical benthic habitat classification scheme was created for this study. This scheme included coral (to species level), coralline crustose algae (CCA), sponge, algae (some recognizable genera or functional groups), octocoral (some recognizable species), bare pavement, rubble and sand. The mean percentage cover for each

transect was calculated by pooling data from all 10 images. Percent cover data was arcsine transformed for statistical analyses.

A comparison of the major benthic categories estimated by video images for coral reef (CR) and hardbottom (HB) habitats was performed with the mann-Whitney U test ($\alpha = .05$). Throughout the insular platform of Mona, 213 benthic video transects were conducted to characterize the two dominant benthic habitats of depths greater than 5 meters. The relative abundances of epi-benthic categories in habitats used by adult fishes was estimated with 123 video transects in coral reef (CR) and 90 in hardbottom (HB) habitats.

3.1.3 Habitat use by fish through ontogeny

Data on fish densities were collected via underwater visual census (UVC) along each 30-m transect. Data on fish size and abundance were collected snorkeling or with SCUBA between 7:00 and 17:00, counting each fish observed to cross or within a 2-m wide band of the centerline (30-m tape). All fish were identified to species when possible and their fork length (FL) was visually estimated to the nearest centimeter. Observers had previously tested size estimation on labeled wooden fish models underwater (Rooker and Recksieck).

Based on known ontogenetic habitat shifts and significant abundances at Mona Island (Chapter 2), five species were chosen for study, three grunts (Family Haemulidae) and two snappers (Family Lutjanidae). As adults all five inhabit coral reefs or hard substratum areas to at least 30 m depth. The species reported mean total length (TL)

and maximum TL as well as the cutoff values in fork lengths (FL) used to discriminate ontogenetic life stages (described below) are summarized in Table 3-1.

For each species three ontogenetic or life stages were defined based on size classes (Early = FL less than half the reported size at maturity; Juvenile = FL less than size at maturity and; Adult = FL equal to or greater than size at maturity). Size at maturity data (Table 3-1) were taken from Fishbase Life History Tool (Froese and Pauly, 2003) and published scientific literature Anderson 2002 and Lindeman 2002). Sampling sites where each stage (E, J, A) was present were plotted in GIS in order to calculate landscape scale variables.

Table 3-1 Mean and maximum fork length (FL) in cm reported for grunts and snappers (Anderson 2002, Lindeman 2002). Ontogenetic stage classification of FL (cm) based on size at maturity data (Froese and Pauly 2003).

Species	Mean FL	Max FL	Early FL	Juvenile FL	Adult FL
<i>Haemulon carbonarium</i>	23	37	<8	8 to 15	>15
<i>Haemulon flavolineatum</i>	17	26	<6	6 to 13	>13
<i>Haemulon parra</i>	28	38	<9	9 to 17	>17
<i>Lutjanus apodus</i>	36	59	<14	14 to 27	>27
<i>Lutjanus mahogoni</i>	33	46	<10	10 to 20	>20

Density (individuals / 60 m²) for each ontogenetic stage was calculated by species. The median density of each ontogenetic stage was compared across habitat types. Each transect was classified by habitat based on a high-resolution benthic habitat map digitized from aerial photos (1:28,000) (Kendall et al. 2004). The digitalization was made using a 100 m² minimum mapping unit (MMU) with the aid of the NOAA habitat digitizer extension (Buja pers. com.) in Arc Map 9.3 editor. Habitats were classified as

submerged vegetation (SV), unconsolidated sediments (SED), hard bottom (HB), coral reef (CR) or deep (> 30 m depth) habitat (DH), i.e., areas too deep to visually interpret.

The only SV habitat available was dominated by seagrass in shallow (< 5 m), back reef lagoons near the south and east coasts of Mona Island. Most SED habitat near shore is sandy or dead coral rubble while in deeper areas sediment may be interspersed with coral or rock smaller than the MMU. HB habitats include level pavement and bedrock areas sometimes covered by a thin veneer of sand or with sand channels. Finally, CR habitats are composed of patch, linear or spur and groove formations. For the landscape analysis the northern and eastern coasts were excluded, as these areas are mainly vertical limestone walls that extend deeper than 30 m.

3.1.4 Fish and habitat characteristics

In order to detect differences in habitat preferences during ontogenetic stages correlations were made between fish density and habitat metrics. In-situ habitat metrics include depth, vertical relief and proportions of benthic cover estimated from video transects. Distances from each sampling point to land or the nearest nursery habitat (polygons created of the preferred nursery habitat, Chapter 2) and habitat polygon metrics such as patch area and perimeter were calculated using geographic information systems (GIS) software (Arc Map 9.3). Perimeter to area ratio (PAR) of each habitat patch (polygon) was calculated by dividing the perimeter by the corrected area (square root transformation of area). Patch and distance measurements were extracted with the Arc Map toolbox and those variables were joined to each transect with data collected in-situ. Non-parametric Kendall Tau ($\alpha = .05$) correlations were performed between density

of each life stage and habitat metrics. Non-parametric methods were used for statistical comparisons, as transformations did not normalize data or achieve homogeneity of variances.

3.1.5 Habitat distribution in the landscape

Landscape scale habitat metrics independent of the specific patch in which fishes were observed and within a consistent spatial range were compared to quantify the influence of habitat connectivity. The southern continuous area of the insular platform was gridded with contiguous hexagons measuring 5 Ha (250 m maximum diameter within the hexagon, Figure 3-3) using the Patch Analyst scripts (Elkie et al. 1999) in Arc Map. The distribution of contiguous habitats was chosen in order to minimize the chances of using the same habitat areas in correlations since some transects were located nearby each other due to the narrow shelf area surrounding the island.

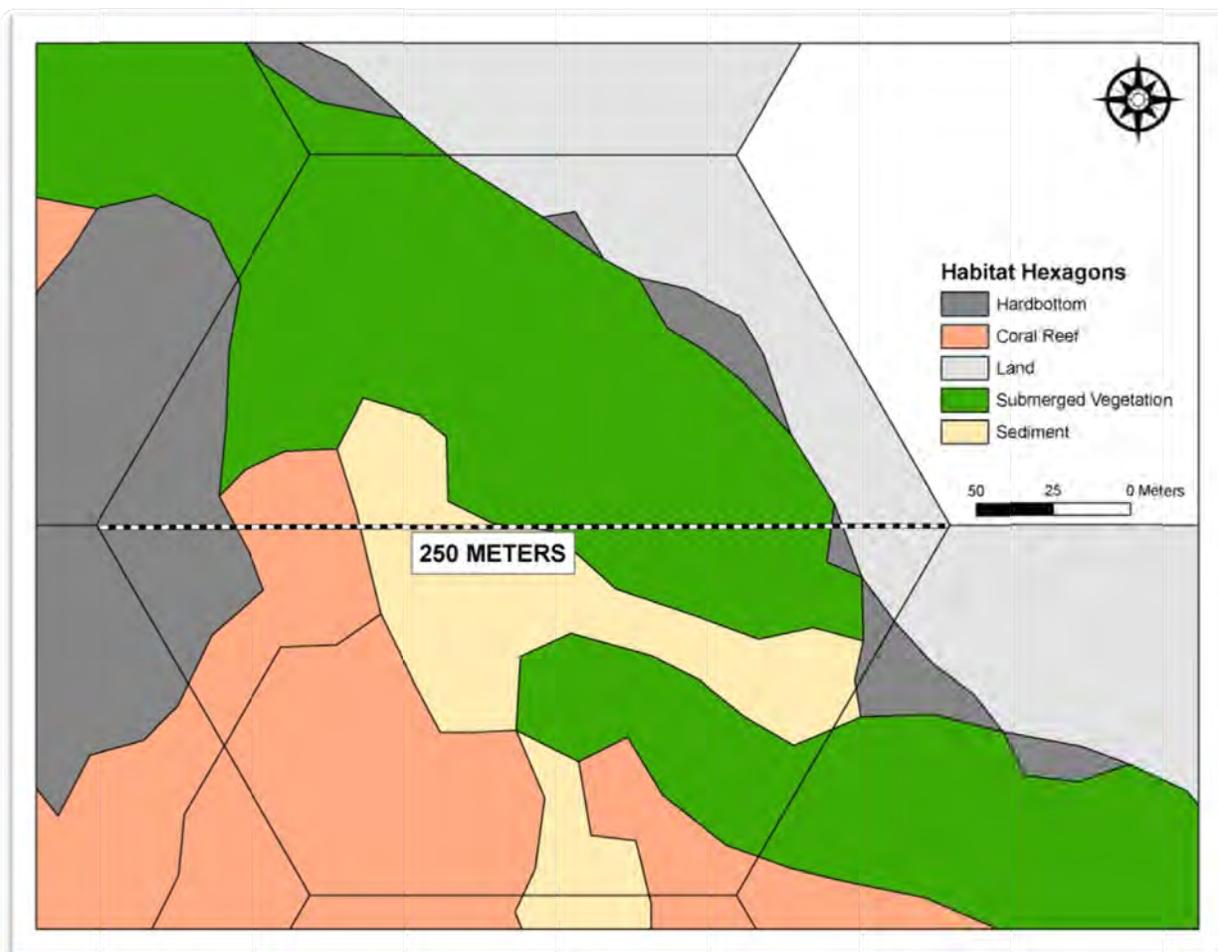


Figure 3-3 Close up of one 5 Ha hexagon intersecting habitat patches digitized at 100 m² MMU.

The spatial scale (i.e. hexagon size) selected for quantifying habitats in surrounding areas as landscape metrics is assumed to incorporate the distances covered by grunts and snappers in daily migrations. Kendall et al. (2003) suggested the range of daily foraging for *H. flavolineatum* is limited to approximately 300 m and fish movements assessed by tagging studies revealed transit distances of 100–400 m for adult haemulids (*H. plumieri*, Tulevech and Recksiek 1994; *H. sciurus*, Beets et al. 2003). In Barbados the maximum distance between tagging and recapture sites of *H. carbonarium* and *H. flavolineatum* was approximately 60 m. For lutjanids, specifically *L.*

apodus this distance was 616 m (Chapman and Kramer 2000). Meyer et al. (2007) measured distances of 10 to 100 m for a snapper (*Aprion virescens*) in Hawaii.

A new GIS layer was created of hexagons with benthic habitat patch attributes (patch size and PAR) intersected. Subsequent layers were created of hexagons with sampling sites where ontogenetic stages (E, J and A) were present as well as a layer composed of a random sample (R) of hexagons (N = 100). The total area of each habitat type, the number of habitat patches and habitat richness within a hexagon was compared between layers of ontogenetic stages and a random sample with the Kruskal-Wallis H-test ($\alpha = .05$). Table 3-2 summarizes the metrics correlated with density of ontogenetic stages.

Table 3-2 Landscape metrics derived from GIS calculated for each sampling unit (t=transect, p=patch, h=hexagon).

Metric	Definition
Patch size (p)	Total area of individual habitat patch polygon (meters ²)
Perimeter to area ratio (p)	Ratio of perimeter to the square root of area for each habitat patch polygon (PAR = perimeter / $\sqrt{\text{area}}$)
Number of patches (h)	Sum of patches digitized for each habitat within a hexagon
Habitat area (h)	Sum of area of all patches of the same habitat within a hexagon (meters ²)
Habitat richness (h)	Number of habitat classes represented within a hexagon
Distance to land (t)	Straight line distance between a transect and the nearest boundary of the land patch (meters)
Distance to nursery (t)	Straight line distance between a transect and the nearest boundary of a patch of the nursery habitat layer * (meters)

* Presence of early juveniles was used to select polygons and merge them into a nursery habitat layer for each species.

3.1.6 Discriminant function analysis

A discriminant function analysis (multivariate statistic) was applied to determine the variables that discriminated between the presence and absence of adults at a given site pooling all habitat types. The purpose was to determine which metrics were important in discriminating the presence of adults. A forward stepwise analysis was used to build a model of discrimination in which all variables are evaluated and the ones that contribute most to the discrimination between groups are included in the model, leaving out those that do not discriminate. The F value to enter the model was set to 1 and the variable is only entered into the model if the F value is greater. Tolerance

values are based on a multiple correlation (R-square) for each variable with all other variables included in the model. Therefore, the tolerance value is a measure of the redundancy of a variable and was set at 0.01. The results for the discriminant function analysis are presented as Wilks' Lambda that is the standard statistic that is used to denote the statistical significance of the discriminatory power of the model. If Wilks' Lambda is equal to 0.0 it has perfect discriminatory power and ranges to 1 in which the model has no discriminatory power. Values presented are the Wilks' Lambda statistic after the respective variable is entered into the model. Variables entered into the analysis included transect based metrics (depth, rugosity, video transect benthic cover), distance metrics (distance to land and to nursery habitat), patch metrics (patch size and PAR) and landscape metrics within hexagons (area of surrounding habitat, number of patches of each habitat and habitat richness).

3.1.7 Preferences within coral reefs

Coral reef was the main habitat for latter ontogenetic stages of grunts and snappers (Chapter 2); therefore the sites with presence of juveniles and adults provides an estimation of preferences within CR. Habitat metrics of different spatial scales were compared between sites occupied by fishes and those where they were absent in CR habitat. In-situ measures (benthic cover, depth, vertical relief) as well as patch and distance metrics were compared with the Mann-Whitney U test ($\alpha = .05$) as data violated the assumptions of normality and homogeneity of variances.

Results

3.1.8 Benthic habitat characteristics

The percent cover of major benthic groups is summarized in Table 3-3 for CR and HB habitats as well as pooling both habitat types. Algae and abiotic components (sand, rubble and pavement) were the dominant benthic classes. The non-algal live epibenthic categories (coral, sponges and octocorals) combined made up less than 30% of the total cover. Percent cover estimates of macro-algae, coralline crustose algae (CCA) and coral were significantly higher in CR, while sponge and pavement categories were higher in HB.

Table 3-3 Mean percent cover of major benthic categories from video transects of habitat categories from GIS map. CR - coral reef, HB - hardbottom, ALL – CR and HB combined. Significant differences (Mann-Whitney U test $p < 0.05$) between CR and HB habitats indicated with (*).

Benthic Component	CR	HB	All
Live coral	* 12.5	7.4	10.3
Octocorals	5.1	5.4	5.3
Sponges	3.9	* 7.2	5.4
Algae	* 39.6	31.8	36.2
Dead coral with algae	1.5	0.6	1.1
Coralline crustose algae (CCA)	* 5.8	2.5	4.2
Sand, pavement & rubble	31.4	* 41.4	35.6

Macroalgae were the dominant live benthic category by percent cover and were sub classified into 8 functional groups of which *Dictyota* spp. and turf or filamentous algae dominated in both CR and HB (Figure 3-4). One of the species identified within the filamentous algae functional group consisted of 'golden noodle algae' *Chrysoecystis*

fragilis, which has recently been reported for the Atlantic Ocean (Ballantine et al. 2009) and was observed covering large expanses in shallow (<15 m depth) flat areas of the shelf over hard or sediment substrata overgrowing benthic organisms.

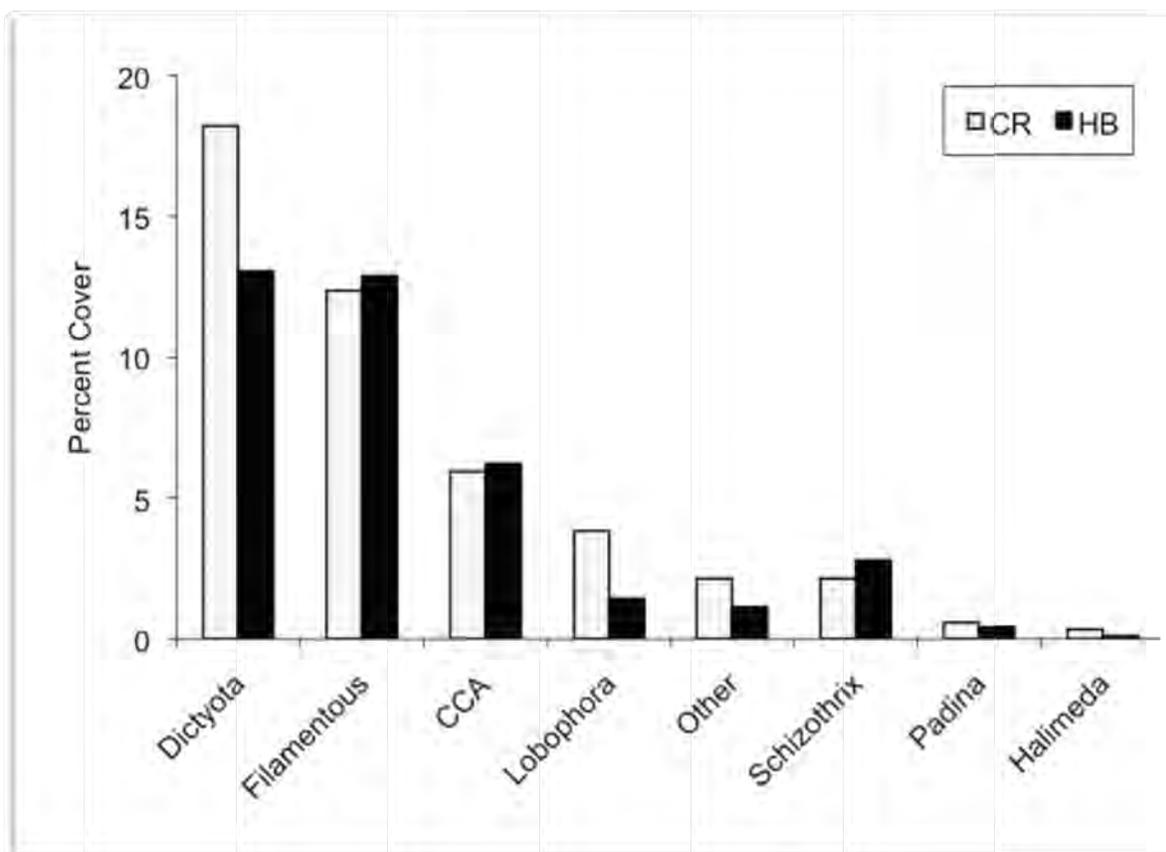


Figure 3-4 Mean percent cover of benthic algae functional groups and species from video transect analysis for coral reef (CR) and hardbottom (HB) habitats.

Cover of live coral ranged from 0.2 % to 55 % in CR and was significantly higher than in HB, which ranged from 0 to 38 %. Coral cover was slightly higher in areas deeper than 15 m but it was also more variable. In CR habitats the principal scleractinian coral species were: *Montastraea franksi*, *M. annularis*, *M. faveolata*, *M. cavernosa*, *Diploria strigosa*, *D. clivosa*, *Porites porites*, *P. astreoides*, *Colpophyllia natans*, *Meandrina memorialis*, *Agaricia spp.*, *Siderastrea spp.*, *Dendrogyra cylindrus*, *Eusmyllia fastigata* and *Acropora spp.* Sampling coincided with the 2005-2006 massive

bleaching event of corals (Schärer and Sepúlveda 2007) and octocorals (Prada et al. 2009).

Vertical relief, depth and hence position on the insular shelf of the two main habitats (CR and HB) were also significantly different. Vertical relief within transects was significantly higher in CR habitats ($p < 0.001$). Depth and distance to shore were significantly greater in HB habitats ($p < 0.05$), although these metrics co-vary due to the arrangement of habitats at Mona Island. Large expanses of HB were generally deeper while CR habitats were variable yet found in greater abundance in shallow nearshore areas.

3.1.9 Habitat use by fish through ontogeny

Underwater visual transects to quantify fish abundances were conducted at 613 sites throughout the insular platform between August 2005 and March 2006. Density (individuals / 60 m²) values of the each life stage by habitat are summarized in Table 3-4. *Haemulon carbonarium* was most abundant (total N= 1,289) followed by *H. flavolineatum* (N=597) and *H. parra* (N=249). Snappers were mostly represented by *L. mahogoni* (N=417) and *L. apodus* (N=224). Adults were consistently in highest density in CR and HB, while early and juvenile stages used a variety of habitats including HB, submerged vegetation (SV), or a combination of rubble and sediment (RB /SED).

Table 3-4 Sum, mean density (DEN) and standard deviation (SD) of ontogenetic stages by habitat type (N= transects). SV – submerged vegetation, RB/SED – rubble & sediment, HB – hardbottom, CR – coral reef, ALL – pooling all habitats.

Species (life stage)	SV (N=47)			RB/SED (N=14)			HB (N=233)			CR (N=292)			ALL (N=613)		
	SUM	DEN	(SD)	SUM	DEN	(SD)	SUM	DEN	(SD)	SUM	DEN	(SD)	SUM	DEN	(SD)
<i>H. carbonarium</i> (early)	89	1.20	4.75	15	1.07	4.01	17	0.07	0.56	33	0.11	1.10	154	0.25	1.97
(juvenile)	89	1.20	3.35	38	2.71	7.48	131	0.56	2.96	157	0.54	3.24	415	0.67	3.32
(adult)	23	0.31	0.95	4	0.29	0.83	145	0.62	1.80	548	1.88	4.97	720	1.17	3.68
<i>H. flavolineatum</i> (early)	7	0.09	0.60	0	-	-	3	0.01	0.15	6	0.02	0.26	16	0.02	0.29
(juvenile)	66	0.89	2.73	0	-	-	24	0.10	0.83	50	0.17	1.11	140	0.23	1.34
(adult)	5	0.07	0.25	0	-	-	110	0.47	1.56	326	1.12	4.44	441	0.72	3.24
<i>H. parra</i> (early)	44	0.59	2.59	0	-	-	80	0.34	2.15	0	-	-	124	0.20	1.61
(juvenile)	14	0.19	1.08	0	-	-	33	0.14	1.04	22	0.08	0.70	69	0.11	0.89
(adult)	0	-	-	0	-	-	11	0.05	0.25	45	0.15	0.89	56	0.09	0.64
<i>L. apodus</i> (early)	4	0.05	0.28	0	-	-	23	0.10	0.68	0	-	-	27	0.04	0.43
(juvenile)	2	0.03	0.16	4	0.29	0.61	79	0.34	1.19	88	0.30	0.74	173	0.28	0.90
(adult)	0	-	-	0	-	-	8	0.03	0.18	16	0.06	0.24	24	0.04	0.20
<i>L. mahogoni</i> (early)	10	0.14	0.48	5	0.36	1.08	35	0.15	0.85	10	0.03	0.29	60	0.10	0.61
(juvenile)	13	0.18	0.53	3	0.21	0.80	55	0.24	1.24	225	0.77	2.49	296	0.48	1.91
(adult)	6	0.08	0.40	0	-	-	9	0.04	0.21	46	0.16	0.66	61	0.10	0.50

The results of non-parametric correlations (Kendall Tau) between density of ontogenetic stage and benthic habitat characteristics (of all habitat types sampled) at the transect scale are summarized in Table 3-5. The percent cover of sand was significantly positively correlated with the density of juvenile *H. carbonarium*, while the percent cover of rubble was positively correlated with juvenile *L. mahogoni*. Significant negative correlations with percent cover of pavement were detected for adult *H. carbonarium*, *H. flavolineatum* as well as for juvenile and adult *L. apodus*. All correlations between coralline crustose algae (CCA) and density were positive although significant only for adult *H. carbonarium*, adult *H. flavolineatum* and juvenile *L. mahogoni*. Percent cover of macroalgae was significantly positively correlated with density of adult *L. apodus*. Percent cover of sponges was significantly negatively correlated with early and juvenile *H. flavolineatum*, adult *L. apodus* and juvenile *L. mahogoni*. Octocorals showed a significant negative correlation with juvenile *H. carbonarium*, while live coral cover was significantly (positively) correlated with the density of juvenile *H. flavolineatum* as well as juvenile and adult *L. apodus*. Early stages were rarely sampled in habitats deeper than 5 m therefore in-situ habitat variables for sites with early life stages in deeper habitat are only available for a few cases where *H. flavolineatum* and *L. mahogoni* were observed.

Table 3-5 Correlations between fish density and percent cover of benthic categories estimated with video transects. (*) Indicates significance at $p < 0.05$ using the Kendall Tau test. CCA – coralline calcareous algae, POS – positive, NEG – negative.

Species (life stage)	Coral	CCA	Algae	Octo-corals	Sponge	Pave-ment	Rubble	Sand
<i>H. carbonarium</i> (early)	-	-	-	-	-	-	-	-
(juvenile)	NEG	POS	NEG	NEG *	POS	NEG	POS	POS *
(adult)	POS	POS *	POS	NEG	NEG	NEG *	POS	POS
<i>H. flavolineatum</i> (early)	POS	POS	NEG	POS	NEG *	POS	NEG	NEG
(juvenile)	POS	POS	POS	POS	NEG *	NEG	NEG	NEG
(adult)	POS *	POS *	POS	POS	NEG	NEG *	POS	POS
<i>H. parra</i> (early)	-	-	-	-	-	-	-	-
(juvenile)	NEG	POS	POS	NEG	POS	POS	NEG	POS
(adult)	POS	POS	NEG	NEG	NEG	POS	POS	POS
<i>L. apodus</i> (early)	-	-	-	-	-	-	-	-
(juvenile)	POS *	POS	POS	POS	POS	NEG *	POS	POS
(adult)	POS *	POS	POS *	POS	NEG *	NEG *	NEG	NEG
<i>L. mahogoni</i> (early)	NEG	POS	POS	NEG	POS	POS	NEG	POS
(juvenile)	POS	POS *	NEG	NEG	NEG *	NEG	POS *	POS
(adult)	NEG	POS	POS	NEG	NEG	NEG	POS	NEG

Correlations of fish density with depth, vertical relief and patch metrics are summarized in Table 3-6. Many of the metrics calculated at the landscape level were co-varying due to the spatial arrangement of habitats within this insular platform. For example depth, patch size, PAR and distance from land were positively correlated. Nonetheless, trends were not consistent between species. Correlations with depth were generally negative except adult *H. flavolineatum* and *L. apodus* whose densities were significantly positively correlated with depth. Variations in fish density by depth are summarized in Appendix 3-1. Vertical relief within transects was, in general, positively correlated with fish density, although non-significant for early *H. flavolineatum*, juvenile *H. parra* and early *L. mahogoni*. Negative correlations with vertical relief were detected for juvenile *H. carbonarium* and *H. flavolineatum* although these were not significant.

Significant inverse correlations were observed between patch size (area) and density of most species, although not significant for juvenile *L. apodus*. Patch size was positively correlated with density of adult *H. flavolineatum* and *L. apodus*, although only the latter was significant. Perimeter to area ratio (PAR) was negatively correlated with fish density, significantly so for juvenile stages of *H. flavolineatum*, *H. parra* and early *L. mahogoni*. In the case of adult *H. flavolineatum* and juvenile *L. apodus* the correlation with PAR was positive and significantly so for adult *L. apodus*.

Table 3-6 Correlations between fish density and patch metrics quantified *in-situ* (depth and vertical relief) and with GIS. (*) Indicates significance at $p < 0.05$ with Kendall Tau test. PAR – perimeter to area ratio, POS – positive, NEG – negative.

Species (life stage)	Depth (m)	Vertical Relief (m)	Patch Size (m ²)	PAR	Distance to Land	Distance to Nursery
<i>H. carbonarium</i> (early)	NEG *	-	NEG *	NEG	NEG *	NEG *
(juvenile)	NEG *	NEG	NEG *	NEG	NEG *	NEG *
(adult)	NEG	POS *	NEG *	NEG	NEG *	NEG *
<i>H. flavolineatum</i> (early)	NEG *	POS	NEG *	NEG	NEG	NEG *
(juvenile)	NEG *	NEG	NEG *	NEG *	NEG *	NEG *
(adult)	POS *	POS *	POS	POS	POS *	POS *
<i>H. parra</i> (early)	NEG *	-	NEG *	NEG	NEG *	NEG *
(juvenile)	NEG *	POS	NEG *	NEG *	NEG *	NEG *
(adult)	NEG	POS *	NEG *	NEG	NEG *	POS
<i>L. apodus</i> (early)	NEG *	-	NEG *	NEG	NEG *	NEG *
(juvenile)	NEG	POS *	NEG	POS	POS	NEG
(adult)	POS *	POS *	POS *	POS *	POS	POS *
<i>L. mahogoni</i> (early)	NEG *	POS	NEG *	NEG *	NEG *	NEG *
(juvenile)	NEG *	POS *	NEG *	NEG	NEG *	NEG *
(adult)	NEG *	POS *	NEG *	NEG	NEG *	NEG *

3.1.10 Fish distribution in the landscape

Landscape metrics were calculated within an area of 21.4 km² (2,144 Ha) of contiguous insular shelf on the western and southern coasts of Mona Island (Figure 3-5). The two most abundant habitats mapped in this portion of the insular platform are HB (780 Ha, 36%) and CR (660 Ha, 31 %) followed by SED (379 Ha, 18%), deep habitat DH (247 Ha, 11%) and SV (79 Ha 4%).

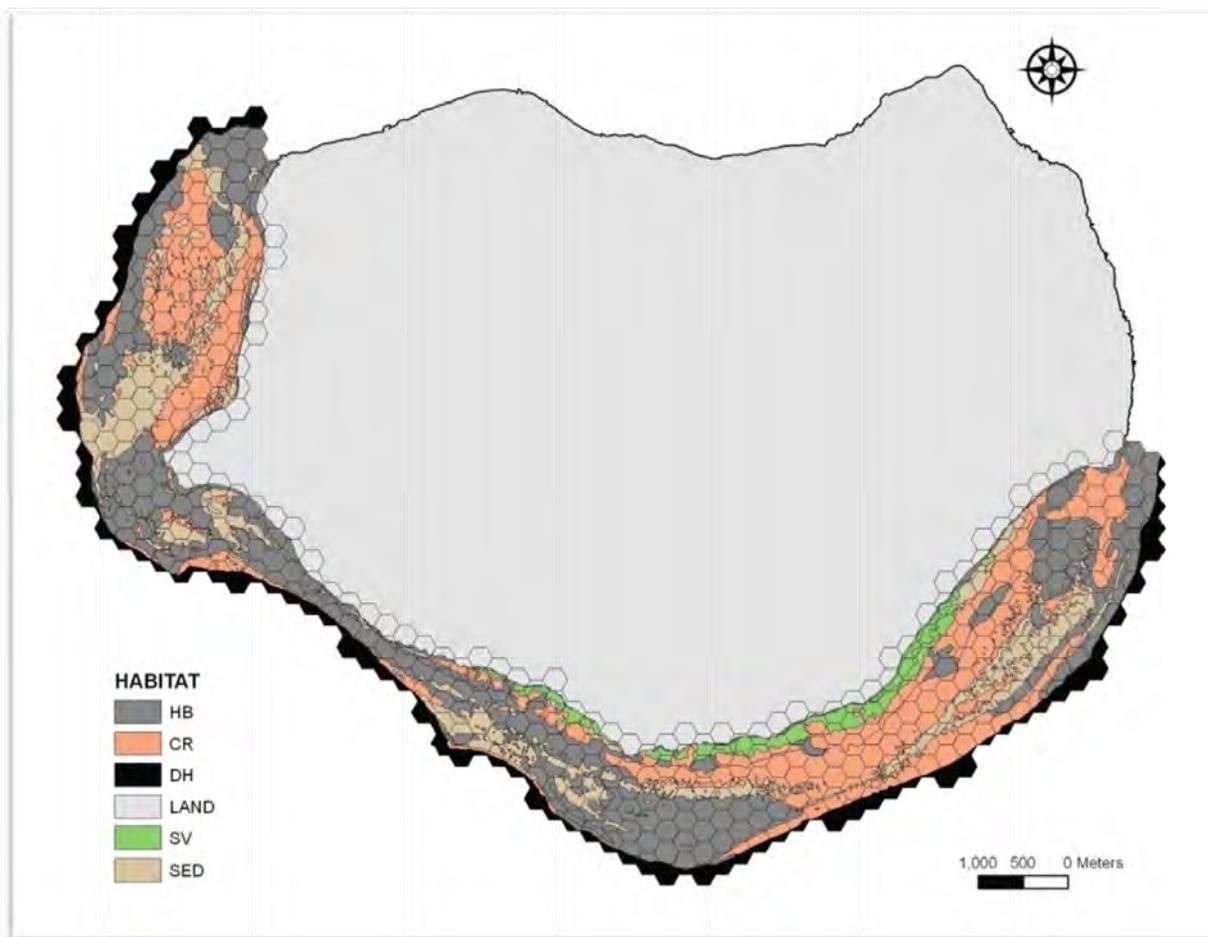


Figure 3-5 Map of Mona Island with landscape sampling units (hexagons) intersected with habitat polygons. HB – hardbottom, CR – coral reef, DH – deep habitat, SV – submerged vegetation, SED - sediment.

The total area of shelf (represented by the number of hexagons) occupied by the ontogenetic stages is illustrated in Figure 3-6. During early and juvenile life stages of *L. mahogoni* had the widest distribution. Adult *H. carbonarium* and *H. flavolineatum* covered greater area than all other species as adults. In relation to other species *H. parra* did not show much variation across life stages, although early stage were more widespread than *H. flavolineatum* and *L. apodus*. The two dominant grunt species occupied more area during adult stages, while snappers were more widespread as juveniles. In the case of the snappers *L. apodus* occupied less area in all stages compared to *L. mahogoni*.

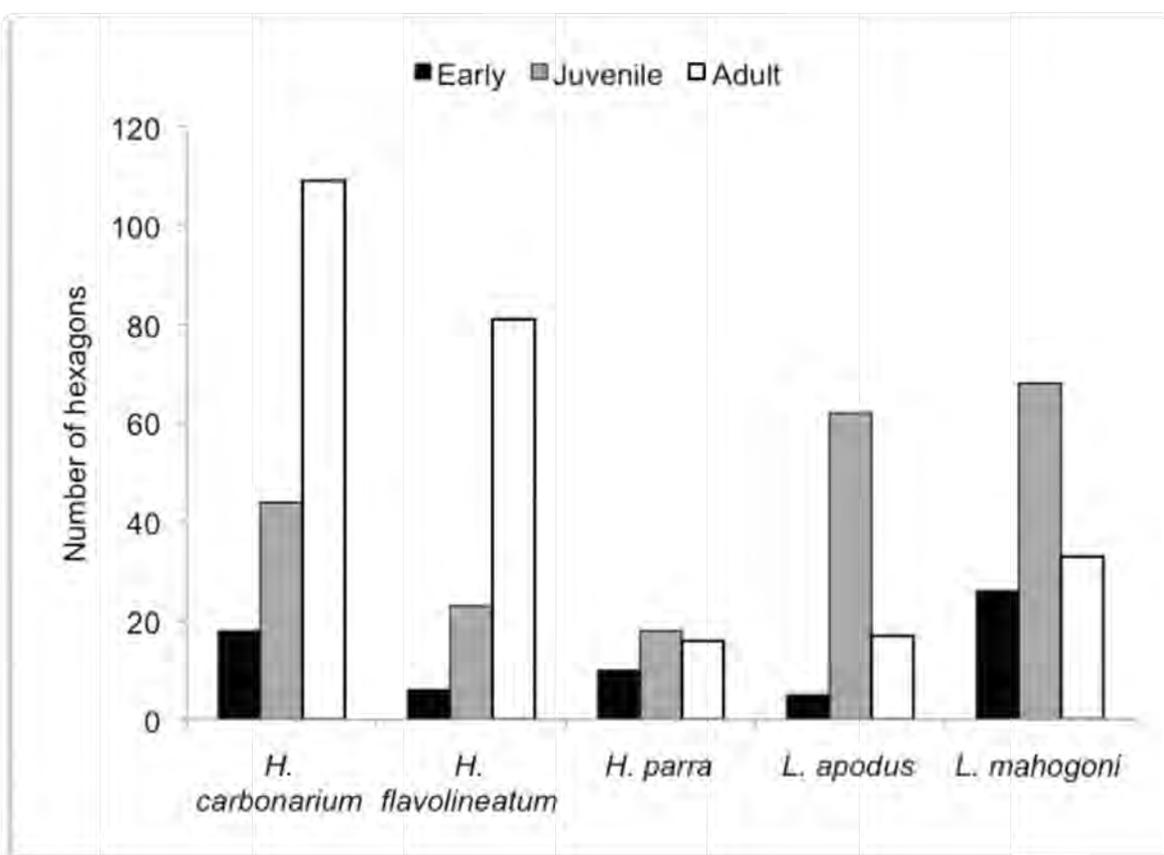


Figure 3-6 Total area represented by the number of hexagons (5 Ha) occupied by ontogenetic stages of the three grunt and two snapper species.

Comparisons of patch and landscape metrics between hexagons of each life stage (E, J, A) between ontogenetic stages and versus randomly chosen areas (R) revealed significant differences in total area (m²) of habitat type, number of habitat patches and habitat richness (Table 3-7). A description of the results observed for each species is given below by ontogenetic stage. Metrics that were not statistically significant at this scale are not reported. In this analysis the same caveat regarding the distribution of habitats may affect the interpretation of results in the sense that patch size and depth are correlated.

Early *H. carbonarium* occupied areas with more patches of SV than adults and more than a random sample of hexagons. They also occupied areas with less patches of SED than adults or a random sample. Juvenile stages followed the same pattern as early stages with respect to SV and SED, but in addition they occupied areas with less patches of DH as well as more patches of HB than random. Adults occupied areas with less patches of SV and more patches of SED than early or juvenile stages. In addition they were located in areas with less area of DH and more patches of CR than random as well as less patches of HB than juveniles.

For *H. flavolineatum* early life stages occupied areas with less HB than adults or a random sample of hexagons. Juveniles followed that early stage pattern and in addition were located in areas with less DH and greater number of SV patches than adults or a random sample. Adults were located in areas with more DH although fewer SV patches than juveniles as well as more CR patches than a random sample.

Early and juvenile stages of *H. parra* had more SV patches than adults or a random sample, while juveniles occupied areas with less HB area than random. Adults were present in areas with fewer SV patches than early and juvenile stages but not distinct from random.

The number of patches of SV for early *L. apodus* was higher than all other life stages or a random sample. Total CR area was significantly higher than a random selection of hexagons for juveniles and adults). In addition adults occupied areas with more patches of DH than all other life stages or a random sample as well as more CR patches, increased HB area and greater habitat richness than random.

In the case of early *L. mahogoni* there were less patches of DH, more SV patches and greater CR area as well as greater habitat richness than random. Juveniles remained in areas with less area and fewer patches of DH, near more CR patches. Adults were present in areas with fewer patches of DH, and more CR patches.

Table 3-7 Comparisons of landscape metrics between ontogenetic stages and with a random sample. Only significant results of the Kruskal-Wallis H-test are reported. DH – deep habitat, CR – coral reef, HB – hardbottom, SED – sediment, SV – submerged vegetation, E – early, J – juvenile, A – adult, R – random.

Species (life stage)	DH Area	DH Patches	CR Area	CR Patches	HB Area	HB Patches	SED Patches	SV Patches	Habitat Richness
<i>H. carbonarium</i> (early)							< A, R	> A, R	
(juvenile)		< R				> A, R	< A, R	> A, R	
(adult)	< R			> R		< J	> E, J	< E, J	
<i>H. flavolineatum</i> (early)					< A, R				
(juvenile)		< A, R			< A, R			> A, R	
(adult)		> J		> R				< J	
<i>H. parra</i> (early)								> A, R	
(juvenile)					< R			> A, R	
(adult)								< E, J	
<i>L. apodus</i> (early)								> J, A, R	
(juvenile)			> R					< E	
(adult)		> E, J, R	> R	> E	> E			< E	> R
<i>L. mahogoni</i> (early)		< R	< R					> R	> R
(juvenile)	< R	< R		> R					
(adult)		< R		> R					

3.1.11 Discriminant function analysis

Benthic, patch, distance and surrounding habitat landscape variables (of hexagons) from 202 sites pooling all habitat types revealed differences in the discriminant function analysis. This analysis was performed for adults on the contiguous insular platform and the results for each species are presented in Appendix 3-2. Variables that entered the discriminant function model varied from 4 for *H. parra* to 12 for *H. carbonarium* (Table 3-8). Vertical relief at the transect scale was the variable that entered the models of most species. Other variables included in the model for more than 2 species were patch size, patches of deep habitat (DH), area of sediment habitat (SED), patches of CR and patches of land within the hexagon. Trends of these variables and adult abundances are presented in Tables 3-5, 3-6 and 3-7, although the datasets are dissimilar.

Table 3-8 Wilks' Lambda for variables included in the model of each species by the discriminant function analysis.

Metric	<i>H. carbonarium</i>	<i>H. flavolineatum</i>	<i>H. parra</i>	<i>L. apodus</i>	<i>L. mahogoni</i>
Coral %				0.86	
CCA %	0.82				
Algae %				0.84	
Octocoral %			0.94	0.84	
Pavement %		0.85			
Rubble %	0.81		0.95		
Depth		0.82			
Relief	0.84	0.83		0.84	0.93
Patch size		0.82	0.96		0.92
PAR		0.82			
Dist. Land	0.83			0.88	
Dist. Nursery					0.91
Area DH	0.81				
Patch DH	0.82	.85		0.85	
Patch HB	0.81			0.85	
Area SED	0.81		0.98	0.84	
Patch SED	0.81				0.91
Patch CR	0.82	0.83			0.94
Patch SV	0.82			0.84	
Patch Land	0.82	0.83			0.9
Habitat Richness				0.85	

3.1.12 Preferences within coral reefs

Comparisons of habitat variables between sites with and without juvenile and adult fishes within CR habitat revealed some significant differences (Table 3-9). Cover of live coral at the transect scale was higher for sites where most species were present except *H. parra* and were significantly higher for *H. flavolineatum* and *L. apodus*. Coralline crustose algae (CCA) cover was significantly higher for *H. carbonarium* and *H. flavolineatum* and *L. mahogoni* but not significant in the latter case. Percent cover of pavement within transects was generally lower, significantly for *H. flavolineatum* and *L. apodus*, although it was higher in the case of *H. parra*. Rubble was also generally more abundant, significantly for *L. mahogoni*, although less abundant for *H. parra*. Trends in the percent cover of algae, octocoral, sponge and sand were variable and only the cover of sponge for *L. mahogoni* was significantly lower.

Sites with *H. carbonarium* and *L. mahogoni* were significantly shallower while for the remaining species sites were deeper, significantly for *H. flavolineatum*. Vertical relief within transects was higher for all cases and this trend was significant for *H. carbonarium*, *H. flavolineatum* and *L. mahogoni*. Patches of CR were smaller in size and had lower PAR for *H. carbonarium*, *H. parra* and *L. mahogoni*, although the latter was not significant. *Haemulon carbonarium*, *H. parra* and *L. mahogoni* had less distance to land and to their nursery areas. *Haemulon flavolineatum*, on the other hand, occupied sites more distant from the coast and its nursery habitat. For *L. apodus* there was a greater distance from land combined with lower distance to nursery habitat although these trends were not significant.

Table 3-9 Trends in habitat metrics in CR sites of juveniles and adults pooled. Significant differences of Kruskal-Wallis H test (p values) are shaded. CCA – crustose coralline algae, PAR – perimeter to area ratio, nd – no difference.

Metric	<i>H. carbonarium</i>	<i>H. flavolineatum</i>	<i>H. parra</i>	<i>L. apodus</i>	<i>L. mahogoni</i>
Coral % Cover	lower (p=0.7)	higher (p=0.02)	lower (p=0.9)	higher (p=0.03)	nd
Octocoral % Cover	lower (p=0.9)	higher (p=0.1)	lower (p=0.9)	higher (p=0.3)	lower (p=0.9)
Algae % Cover	higher (p=0.6)	nd	lower (p=0.4)	higher (p=0.2)	nd
CCA % Cover	higher (p=0.02)	higher (p=0.04)	lower (p=0.7)	lower (p=0.4)	nd
Sponge % Cover	lower (p=0.2)	lower (p=0.4)	nd	lower (p=0.2)	lower (p=0.04)
Pavement % Cover	lower (p=0.5)	lower (p=0.03)	higher (p=0.4)	lower (p=0.01)	nd
Rubble % Cover	higher (p=0.5)	higher (p=0.4)	higher (p=0.2)	lower (p=0.8)	higher (p=0.00)
Sand % Cover	lower (p=0.7)	lower (p=0.8)	nd	nd	nd
Depth	shallower (p=0.03)	deeper (p=0.00)	deeper (p=0.7)	deeper (p=0.1)	shallower (p=0.02)
Vertical Relief	higher (p=0.04)	higher (p=0.00)	higher (p=0.3)	higher (p=0.2)	higher (p=0.00)
Patch Size	lower (p=0.00)	higher (p=0.6)	lower (p=0.00)	higher (p=0.3)	lower (p=0.2)
PAR	lower (p=0.02)	higher (p=0.5)	lower (p=0.04)	higher (p=0.3)	lower (p=0.4)
Distance to Land	lower (p=0.00)	higher (p=0.00)	lower (p=0.1)	higher (p=0.3)	lower (p=0.00)
Distance to Nursery	lower (p=0.00)	higher (p=0.00)	lower (p=0.00)	lower (p=0.1)	lower (p=0.00)

Discussion

3.1.13 Summary of species-specific patterns

Overall the correlations of fish density with habitat and landscape metrics reflect ontogenetic migrations towards deeper CR habitat type. A brief description of each species is discussed below and data from other studies are included. Table 3-10 summarizes the trends observed within and across ontogenetic stages and spatial scales.

Haemulon carbonarium

Early life stages were limited to shallow areas with highest density in relatively small patches of SV and RB/SD located in areas with relatively abundant SV and fewer SED patches than adults. Within lagoons in St. Croix small (< 10 cm FL) individuals were only observed in seagrass (Mateo and Tobias 2001). Juveniles were found in a variety of shallow habitats of small patches and correlated with high sand cover and low octocoral cover. Patches were located away from the shelf edge and were surrounded by fewer patches of SED, but more of SV and HB than adults. In La Parguera similar cross-shelf distributions with size were observed, although the highest density of juveniles was observed in intermediate shelf zones in coral reef habitats followed by seagrass (Cervený 2006).

Adults occupied small sized patches located away from the shelf edge in CR with high vertical relief and percent cover of CCA and low cover of pavement near more CR and SED patches and fewer HB and SV patches. This species was distributed to the farthest areas of deep HB habitat on the northern and eastern coasts, although in lower density. At Mona Island the location of unconsolidated sediments at the landscape scale

was significantly correlated with the density of *H. carbonarium* and the presence of juveniles was significantly correlated with the percent cover of sediment at the transect scale, which may be related to foraging habits. Higher vertical relief and percent cover of CCA were important for discriminating the presence of adults at small scales, while distance to land and the amount of deep habitat were important at the landscape level. In La Parguera adults were located exclusively in outer shelf shallow zones (Cervený 2006), while juveniles and adults occur in nearshore hardbottom habitats of eastern Florida (CSA International 2009).

Haemulon flavolineatum

The early life stages of *H. flavolineatum* occurred in small CR, HB and SV patches, near land and distant from HB, similar to that described by Lindeman et al. (2000). Highest densities of early stages at Mona Island correlated negatively with the abundance of sponges at the transect scale. In La Parguera early stages were common in seagrass and reef sites with varying levels of vertical relief (Cervený 2006). Appeldoorn et al. (2003) observed a similar pattern where the smallest size classes were located near the island and larger fishes further away towards the outer bank of Old Providence-Santa Catalina in Colombia. Juveniles at Mona Island used patches of small PAR in areas similar to early stages located away from the shelf edge. While at La Parguera mangroves were described as an important biotope during this stage (Burke et al. 2009), although Cervený (2006) described a shift away from vegetated sites towards hardbottom areas in the cross shelf habitat matrix. Mangroves are absent at Mona Island and nearshore reefs are used by this stage suggesting an association with reefs of vertical relief at this stage.

Adults occupied patches of CR and HB, which were larger with greater PAR located near the shelf edge similar to La Parguera, where no adults occupied the intermediate shelf (Cervený 2006). Density increased in sites with high vertical relief, percent cover of CCA and live coral and low cover of pavement at Mona Island. Adults were surrounded by more CR and DH and were detected in deep HB located farthest from nursery areas on the northern and eastern coasts as reported for other locations (Lindeman et al. 2000, Burke et al. 2009).

Haemulon parra

Density estimates of *H. parra* were very low throughout Mona Island; nonetheless early stages occurred in shallow, small HB patches in nearshore areas close to SV. Early stages and juveniles were located in a variety of habitats of small patches near SV, yet distant from large areas of HB. In La Parguera early and juvenile stages occurred in mangrove habitat as well as shallow dead coral areas (Cervený 2006).

Adults occupied small patches of CR and HB with high vertical relief distant from SV but nowhere near the shelf edge. Within CR percent cover of pavement and rubble at the transect scale were important. Adult *H. parra* were observed in distant HB habitat of the eastern and northern coasts of Mona Island suggesting long-distance (16 km) movements along the coast, distant from nursery habitats, suggesting that coastal habitats are an important corridor for ontogenetic migrations despite being composed of deep (> 25 m) habitats. Dorenbosch et al. (2004, 2007) observed a similar pattern where juvenile *L. apodus* and *L. mahogoni* were found distant from seagrass-mangrove habitats and they hypothesized fish migrated along the coastline rather than recruiting

directly to these reefs. It may be that this species prefers HB throughout all life stages; similar to the East coast of Florida (CSA International 2009) and at Mona Island this habitat extends continuously around the island although varying in depth.

Lutjanus apodus

Early juveniles occurred in shallow, small patches of SV and HB habitats remaining nearer to SV than subsequent life stages. Juveniles used various habitats near CR with high vertical relief, high percent cover of live coral, and low pavement. La Parguera had high density of early juveniles in vegetated habitats (mangroves and seagrass) as well as high relief coral reefs moving offshore to more coral dominated habitats (Cervený 2006). On the East coast of Florida the juveniles and adults occur in nearshore hardbottom habitats (CSA International 2009).

Adults occurred in deep CR and HB habitats with high vertical relief, high percent cover of algae and live coral as well as low pavement and sponges. Patches occupied by adults were larger than for other life stages near CR and the shelf edge, adjacent to HB and areas of higher habitat richness. *Lutjanus apodus* was distributed widely extending to HB habitat along the northern and eastern coasts. The increased abundance of adults in areas distant from land contrasts with the findings at Old Providence-Santa Catalina where abundance decreased with increasing distance from the island (Appeldoorn et al. 2003). However at La Parguera adults were seen mostly in outer shelf habitats (Cervený 2006). At Mona and Monito Island large schools of adult *L. apodus* were observed in habitats > 40 m (pers. obs.), up to 60 m in La Parguera, PR (Nemeth, pers. comm.) and are commonly associated with shelf breaks in Cuba (Claro and Lindeman 2004) suggesting suitable habitats extend beyond the areas sampled in

this study. The greater densities of *L. apodus* at Mona Island when compared to La Parguera suggest this species is opportunistic during all life stages and cross shelf movements are not restricted by the arrangement of specific habitat types. This is also supported by the positive association of adults with greater depth, patch size, PAR, habitat richness, and greater distances from land or nursery habitats, which differed from the other species evaluated here, except *H. flavolineatum*.

Lutjanus mahogoni

This species was distributed throughout shallow areas of the insular platform, yet it did not reach the farthest areas of the northern and eastern coasts. Early stages occurred in small sized patches with highest densities in RB/SED near SV far from CR or DH in areas of high habitat richness. Juveniles occurred in small patches of CR in shallow areas with high vertical relief, rubble and CCA with few sponges. In St. Croix early stages (< 5 cm FL) were quite indiscriminate occupying all available habitats within coral reef embayments with highest densities in rubble (Mateo and Tobias 2001), and in eastern Florida juvenile stages were observed in nearshore hardbottom habitats (CSA Int. 2009).

Adults remained near shore and relatively near nursery habitats, which were widely distributed along the southern coast of Mona Island. Adults occupied small SV and higher numbers of nearby CR patches with high vertical relief near land similar to the pattern observed in Old Providence-Santa Catalina of greater abundances at nearshore patch reefs (Appeldoorn et al. 2003). This species is less commonly observed in low energy environments dominated by fine sediments and associated vegetation types such as those abundant in La Parguera. Although differences in adult

density between Mona Island and La Parguera were partly attributed to the lack of suitable nursery habitats (Chapter 2) the landscape preferences detected in this study suggest their occurrence may also be affected by differences in habitat availability or distribution. For example all life stages of *L. mahogoni* occur in coastal reefs of Rincón, western Puerto Rico (pers. obs.) where high energy, rocky environments on a narrow shelf are similar to the habitat context at Mona Island. Additionally Dorenbosch et al. (2004) suggested migrations from seagrass to reefs occurred along the coastline, which supports the nearshore distribution observed at Mona Island.

Density of *L. mahogoni* was significantly higher in small patches of CR and SV during adult stages, distinct from other species whose adults were rarely abundant in SV. Adults were associated with higher vertical relief at smaller scales, while at the landscape scale it was associated with a high number of CR and land patches nearby. The distribution of adult *L. mahogoni* may be responding to the limited distribution of small CR patches near diverse habitat types. In St. John, Grober-Dunsmore et al. (2007) reported fish species richness and abundance increased with area of adjacent seagrass beds, particularly for juvenile Haemulids (although a different assemblage of species), *L. apodus* and *L. mahogoni*. This would suggest that *L. mahogoni* is influenced by habitat configuration and context.

Table 3-10 Summary of fish life stages and habitat metrics at distinct spatial scales. (-) negative relationship with light shading if significant, (+) positive relationship with dark shading if significant. Abbreviations as in Tables 3-5 and 3-7.

Scale	Metric	<i>H. carbonarium</i>			<i>H. flavolineatum</i>			<i>H. parra</i>			<i>L. apodus</i>			<i>L. mahogoni</i>					
		E	J	A	E	J	A	E	J	A	E	J	A	E	J	A			
Transect	Coral		-	+		+	+	+		-	+		+	+		-	+	-	
	CCA		+	+		+	+	+		+	+		+	+			+	+	
	Algae		-	+		-	+	+		+	-		+	+		+	-	+	
	Octocoral		-	-		+		+		-	-		+	+		-	-	-	
	Sponge		+	-		-	-	-		+	-		+	-		+	-	-	
	Pavement		-	-		+	-	-		+	+		-	-		+	-	-	
	Rubble		+	+		-	-	+		-	+		+	-		-	+	+	
	Sand		+	+		-	-	+		+	+		+	-		+	+	-	
	Depth	-	-	-		-	-	+		-	-	-	-	-	+		-	-	-
	Vertical relief		-	+		+	-	+		+	+		+	+		+	+	+	
Patch	Patch size	-	-	-		-	-	+		-	-	-	-	-	+		-	-	
	PAR	-	-	-		-	-	+		-	-	-	-	+	+		-	-	
Landscape	Dist. to land	-	-	-		-	-	+		-	-	-	-	-	+		-	-	
	Dist. to nursery	-	-	-		-	-	+		-	-	+	-	+	+		-	-	
	DH patches		-				-							+		-	-	-	
	DH area			-													-		
	CR patches			+				+						+			+	+	
	CR area												+	+		-			
	HB patches		+	-															
	HB area					-	-			-				+					
	SED patches	-	-	+															
	SV patches	+	+	-			+	-		+	+	-	+	-	-		+		
	Habitat richness														+		+		

3.1.14 Habitat use by fish through ontogeny

Vertical relief estimated at the transect scale consistently correlated with adult abundances. This variable could be assumed to correlate positively with structural complexity (Luckhurst and Luckhurst 1978) or topographic relief (Friedlander and Parrish 1998) known to structure reef fish assemblages (Friedlander et al. 2007).

Habitats with increased vertical relief provide greater structural complexity, topographic relief and surface rugosity with more microhabitats that support higher species diversity and abundances (Friedlander and Parrish 1998, Gratwicke and Speight 2005, Lirman 1999, Pittman et al. 2007b). The association with high vertical relief may reflect a common behavior of grunts and snappers, which form daytime resting aggregations, and move away nightly to feeding in a range of neighboring habitats returning to the same sites in the morning (Ogden and Ehrlich 1977).

Significant correlations of epi benthic cover with ontogenetic stages at transect and landscape scales reflected changes in the combination of characteristics towards those that more closely resemble a coral reef (i.e. high: coral, algae, CCA, vertical relief). Percent cover of live coral throughout all habitats was positively correlated with the density of adults and in CR sites this trend was significant for *H. flavolineatum* and *L. apodus*. This is consistent with a shift from non-reef habitats towards more reef-like characteristics. In some cases vertical relief was more important (with some variation) than live coral cover, even though the latter is often associated with areas of structural complexity or topographic relief. At Mona Island deeper sites with high vertical relief also had higher coral and macroalgae. Although coral cover was highly variable, combinations of low coral and high vertical relief provided suitable habitat for adult *L.*

mahogoni. Some studies suggested a positive relation between species richness and live coral cover (Bell and Galzin 1984, Lewis 1997) whereas others report none (Luckhurst and Luckhurst 1978, Roberts and Ormond 1987). In the case of Mona Island that relationship was only significant for certain life stages (Table 3-9). Additionally the amount of bare pavement in transects was negatively correlated with fish abundance except for *H. parra* and early stages of *L. mahogoni*. This variable was negatively related to fish abundance and species richness patterns at distinct spatial scales in St. Croix (Chittaro 2004) and may help explain the reduced abundances in HB habitats for coral reef species.

Ontogenetic stages demonstrated negative associations between fish density and patch size (with two exceptions) suggesting relatively smaller habitat patches supported greater abundances of fish per area as observed in a similar reef systems at smaller (10 m²) spatial (Prada 2002) scales. At Mona Island fish seem to prefer small patches with low PAR during juvenile and adult stages, although adult *H. flavolineatum* and *L. apodus* were significant exceptions. Within CR patch size was smaller for three species although the reverse trend was detected for *H. flavolineatum* and *L. apodus*. This suggests that despite being different sized as adults, the latter two may have relatively similar vagility and range of ontogenetic migrations, which led them to occupy similar patch and landscape areas. Another consideration is that within patch heterogeneity of larger patches was not detected by the benthic habitat map and is confounding this result (i.e. small CR patches occupied not mapped within a larger HB patch). It is always difficult to delineate boundaries on natural features at larger spatial scales with the human biases inherent in defining habitats. In addition during this study

the smaller patches were proportionally less sampled than larger ones due to differences in area. The larger patches had greater probability of getting selected randomly than smaller ones. Within CR 78% of the patches of small size (100 to 35,000 m²) were not sampled because the benthic habitat map was not available prior to sampling to stratify the habitat patches and be able to detect differences in patch size influence. However these preliminary data are available in order to gather high-resolution mapping data (multibeam or side-scan sonar) to address this question specifically.

Significant correlations between fish density (except *H. parra*) and the number of nearby CR patches suggest patches were small, relative to the area enclosed by the sampling unit (hexagons) and were located nearby, which are important factors in habitat connectivity. This was one of the advantages of conducting the landscape scale analysis, where without sampling every patch some inferences can still be drawn. Abundant small nearby patches at the landscape level are consistent with the results of within-habitat (CR) comparisons of patch size, which was lower for adult life stages, except for *H. flavolineatum* and *L. apodus*. Smaller patches may support greater numbers of fishes if these are responding to edge effects within a patch, the distribution of nearby patches or a combination of these two factors.

The edge of a habitat patch could provide distinct microhabitats i.e. higher vertical relief (which was correlated with abundance at transect scales, Table 3-6) compared to the rest of the patch. Fish may be attracted to edge habitat due to small-scale features associated with vertical relief of edges or to the edges proximity to nightly foraging migratory pathways. In addition the presence of conspecifics (or congeners),

which aggregate in daytime schools may attract fish. It remains to be determined how preferences for edge vs core areas affect fish distributions within a patch and if edges function as filters to fish movements between patches as other patch edge dynamics affect interactions between organisms (Fagan et al. 1999).

Small patches with more edge habitat contributed to greater species diversity of fish communities in Belize (Acosta and Robertson 2002) and may be driving the fish abundances in smaller patches at Mona Island. This finding highlights the importance of mapping small ($\sim 100 \text{ m}^2$) patches that are only depicted with high-resolution remote sensing techniques yet provide important features for reef fishes. However these results along with others in marine systems (Eggleston et al. 1998, 1999) contrast with terrestrial cases where large patches support a greater number of species (Turner et al. 2001) although this trend is also probably scale dependant.

In this study fish abundance and distribution trends were similar for patch size and PAR however these variables were significantly positively correlated. If edge effects are important both small patches and high PAR will be favorable for fishes, although difficult to tease apart in natural landscape studies. If patch size were held constant, a higher PAR would occur in patches with elongate or convoluted shapes, which also increase the amount of edge habitat. Another possibility is that elongated shaped (i.e. linear reef) patches have a greater probability of intersecting migratory pathways compared to circular ones. The PAR was not identified as a strong explanatory factor of fish abundances in St. John, USVI (Grober-Dunsmore et al. 2007), although this could also be scale dependent as the latter study was based on a coarse (1 acre MMU) benthic habitat map.

At Mona Island adult *H. carbonarium*, *H. parra* and *L. mahogoni* were limited to moderate depths, while *H. flavolineatum* and *L. apodus* ranged to the deeper sites of the shelf (Appendix 3-1). *Lutjanus mahogoni* seems to have an ontogenetic migration that is restricted to nearshore areas while *L. apodus* extended to areas beyond the shelf edge. Although other habitat variables (coral cover, patch size, distance from land, area of deep habitat, etc.) were positively correlated with depth and could be affecting the patterns observed, depth has been identified as an important factor structuring reef communities (Friedlander et al. 2007). Because relatively more area of the landscape occurs in deeper areas there may be a species-area relationship influencing these trends.

The distribution pattern of early juveniles may be driven by larval recruitment, settlement and post-settlement mortality at local scales. The environments where these occurred were similar in depth, location and patch characteristics (although these co-varied). Within this environment at Mona Island seagrass coincided with early *H. carbonarium*, *H. parra* and *L. apodus* on the southern and eastern coasts, while *H. flavolineatum*, were observed in lagoons with and without SV and *L. mahogoni* were not limited to back reef lagoons. Species-specific differences were also reflected at the landscape scale (Appendix 3-3), where the proportion of SV area nearby was highest for *H. parra* and *L. apodus* and lowest for *L. mahogoni* supporting habitat preferences at reduced spatial scales (Table 3-4). This suggests that some habitat preferences could be scaling up and may be applied to planning at landscape scales.

Although seagrass is considered critical habitat for grunts and snappers as a nursery, nearshore HB and rubble are also important for snappers (Lindeman et al.

1998, Table 3-4). The structure provided by SV reduces predation pressure of early stages (Dorenbosch et al. 2009). However at Mona Island HB (bedrock and reef rock) and small size rocky or coral patches in SED (unconsolidated sediments and rubble) near SV, seem to provide structure. Additionally these are located within range of movements the early stages could conduct. This could explain the landscape patterns observed for early stages, which were significantly correlated with SV. Landscape configuration of juvenile habitats influenced the composition of fish assemblage, species richness, fish density and fish size in Aruba, where distances from seagrass or mangrove affected the composition of fish assemblages (Dorenbosch et al. 2007).

The habitat matrix exerts strong influence on fish assemblages, perhaps as much as or more than within-patch characteristics (Grober-Dunsmore et al. 2008). This emphasizes the influence of post-settlement processes in the distribution of coral reef fishes (Ault and Johnson 1998), which are in part driven by distinct scales of habitat effects as many ecologically driven patterns are scale dependent (Levin 1992). Correlations of ontogenetic stages with habitat were scale dependent and patterns detected at Mona Island highlight the importance of habitat configuration upon the degree of connectivity. Landscape-scale metrics may serve as a proxy to quantifying functional connectivity of coral reef ecosystems, although caution regarding the species of choice is warranted due to within species differences (Drew and Eggleston 2008).

Unfortunately the unique habitat configuration at Mona Island prevents generalizations to be applied to other systems. Benthic habitat configuration varied by depth and nearshore areas were composed of greater diversity of habitat types due to relatively smaller patch size (range 500– 500,000 m²). In this case habitat preferences

at patch and landscape scales could be confounded by the distribution of habitats within this narrow shelf. Multiple variables of depth, patch size, distance to land and neighboring areas of deep habitat or hardbottom were correlated. In some cases connectivity among habitat patches and size are confounded by correlating environmental factors (Fahrig 2003). Therefore trends or hypotheses regarding the effects of landscape configuration in natural settings will often be confounded and additional large-scale studies in distinct habitat configurations may help identify important ecological patterns.

Although grunts and snapper are generally referred to as sedentary adults (Claro and Lindeman 2004), the patterns observed in this study indicate grunts and snappers conduct relatively distant (10's km) ontogenetic migrations through the habitat mosaic similar to that observed in Curaçao (Cocheret de la Morinière et al. 2002). Therefore the vagility of species is an important consideration in the measure of functional connectivity. The input of post-settlement fishes to Mona Island from other external sources is probably minimal, therefore the habitat use patterns observed seem to strongly reflect the result of ontogeny. The only other nearby source of adults is Monito Island from where fish would have to migrate through depths greater than 200 m and at least a distance of 6 km. Therefore inferences made from this study about habitat use are compelling evidence that connectivity should not be generalized by species, family or habitat types. Reef fish habitat connectivity requirements have been described as species-specific in other locations (Mellin et al. 2007), therefore diversity and abundance will respond to distinct factors depending on the habitat mosaic configuration.

Habitat connectivity has been shown to influence fish abundances in artificial reef scenarios in temperate reefs (Vega Fernández et al. 2008), and in the Caribbean ontogenetic movements necessitate a mix of habitat types (Nagelkerken et al. 2002, Christensen et al. 2003, Syms and Jones 2004). Therefore the connectivity between preferred habitats depends on specific patch and landscape characteristics. These principles could provide criteria to maintain the ecological function of connectivity. Marine reserves (MR) have a greater chance of protecting all life stages and ecological linkages by including representative portions of ecologically important habitat types (Ballantine 1997; Friedlander and Parrish 1998). This study serves to identify some of the linkages for coral reef fishes that could be incorporated into MR design for conservation or fisheries management. Trends observed at different spatial scales allowed us to infer connectivity requirements (Gillanders et al. 2003), that can be applied to the prioritizing and spatial planning methods of MR design and marine zoning for the conservation of coral reef fishes.

Conclusion

This study identified important habitat characteristics at distinct spatial scales for coral reef fishes during ontogeny. Distributions and abundances of ontogenetic stages were influenced by habitat metrics at distinct spatial scales including landscape level metrics. The effect of these variables upon fish changed in strength and direction depending on ontogenetic stage, reflecting shifts in habitat requirements at short and long temporal scales. Percent cover of coral, CCA and pavement were important variables at small scales as well as depth and vertical relief, depending on ontogenetic stage. Patch area and perimeter to area ratios were important and at landscape scales and the amount or configuration of deep habitat, coral reef, hardbottom, sediment, submerged vegetation and habitat richness correlated at larger spatial scales. Habitat heterogeneity at the landscape level with abundant small, relatively nearby CR patches provided better connectivity between habitats than large, continuous patches. Although habitat metrics co-varied, in some cases trends in different directions were observed, and the information provides a better understanding of the ecology and functional connectivity in coral reef ecosystems. Habitat requirements of ontogenetic migrations are species-specific and provide indication that spatially explicit models should be single species and the consistent trends detected in this study could be incorporated into marine planning exercises for conservation of coral reef ecosystems.

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Appendices

Appendix 3-1 Depth and density relationships for grunts and snappers.

Appendix 3-2 Results of discriminant function analysis for grunts and snappers.

Appendix 3-3 Habitat areas occupied by early stages of grunts and snappers.

Appendix 3-1 Depth and density relationships for grunts and snappers.

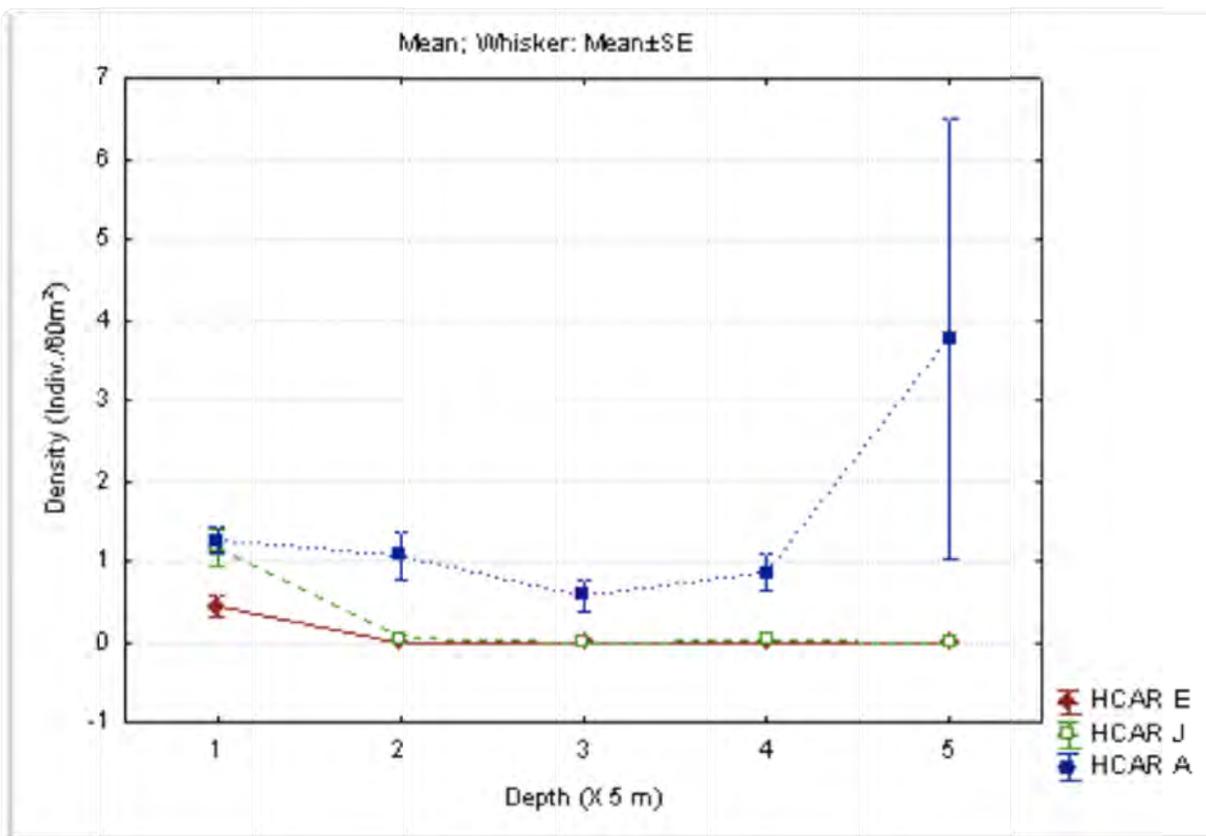


Figure 1 Density of *Haemulon carbonarium* (HCAR) ontogenetic stages (E – early, J – juvenile, A - adult) by 5 m depth intervals.

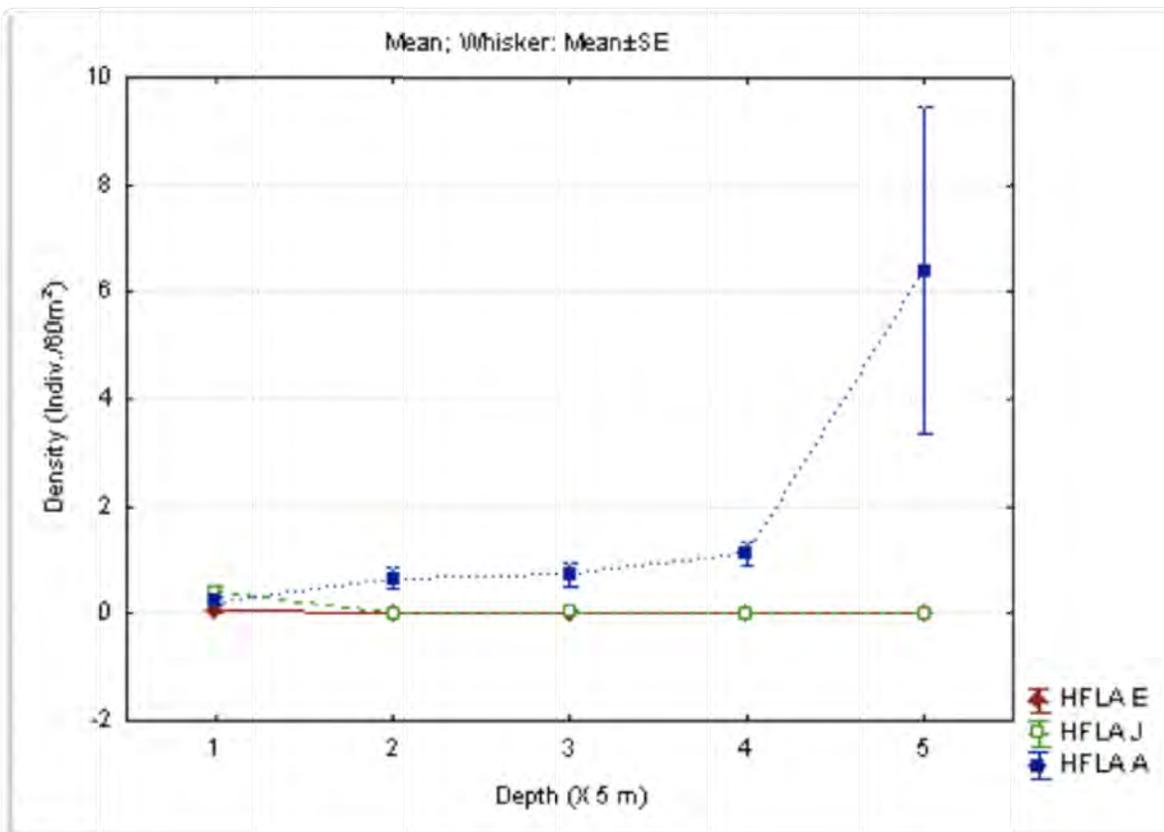


Figure 2 Density of *Haemulon flavolineatum* (HFLA) ontogenetic stages (E – early, J – juvenile, A - adult) by 5 m depth intervals.

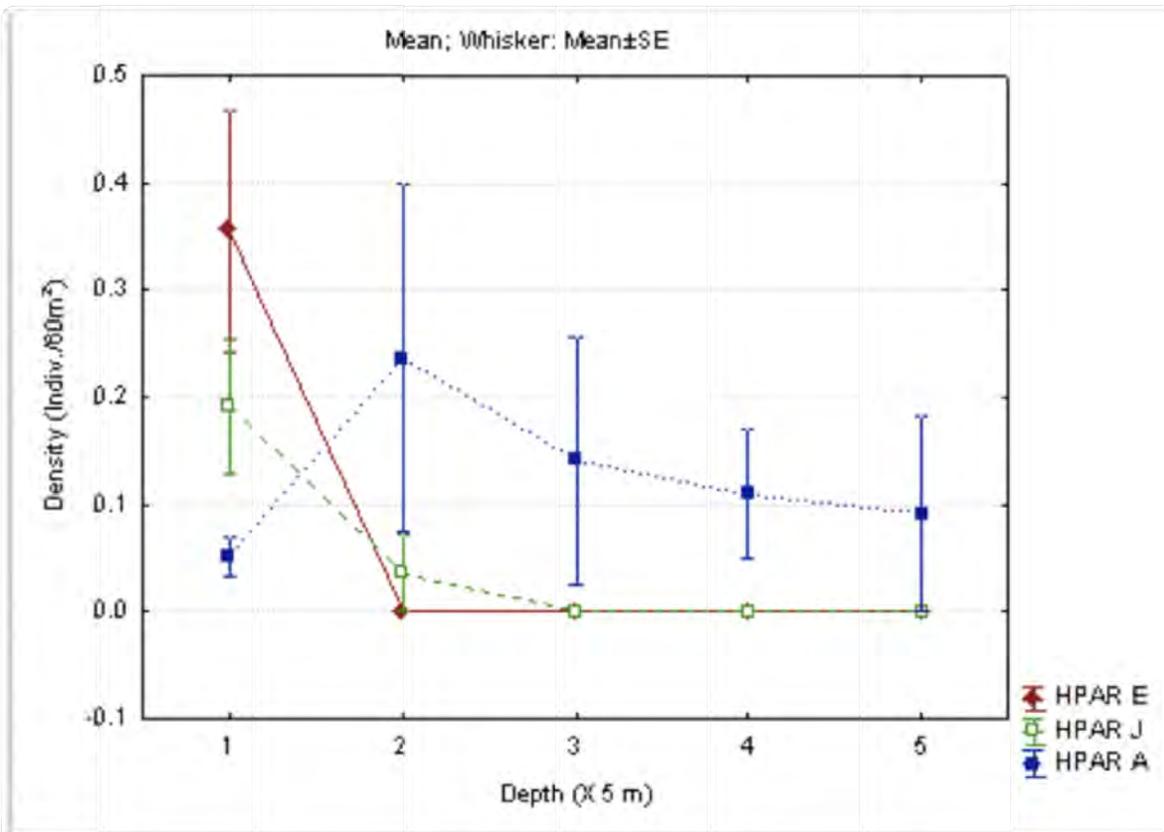


Figure 3 Density of *Haemulon parra* (HFLA) ontogenetic stages (E – early, J – juvenile, A - adult) by 5 m depth intervals.

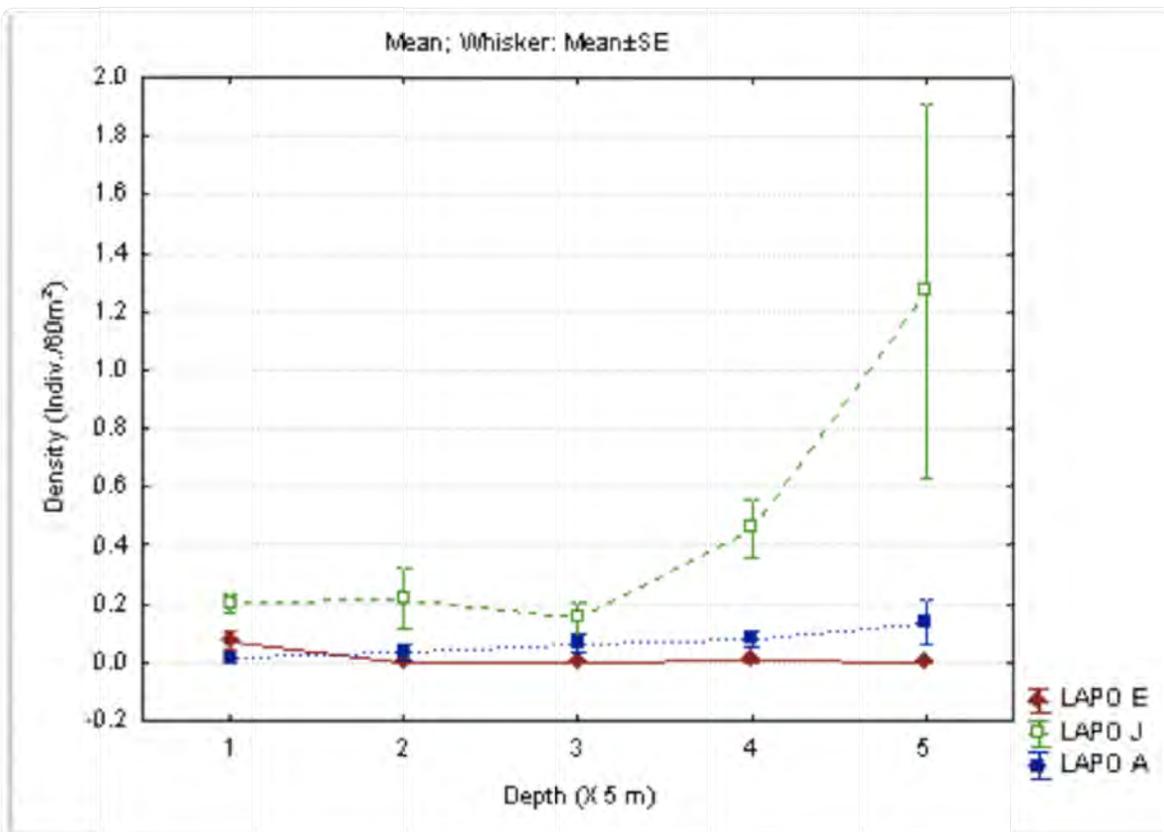


Figure 4 Density of *Lutjanus apodus* (LAPO) ontogenetic stages (E – early, J – juvenile, A - adult) by 5 m depth intervals.

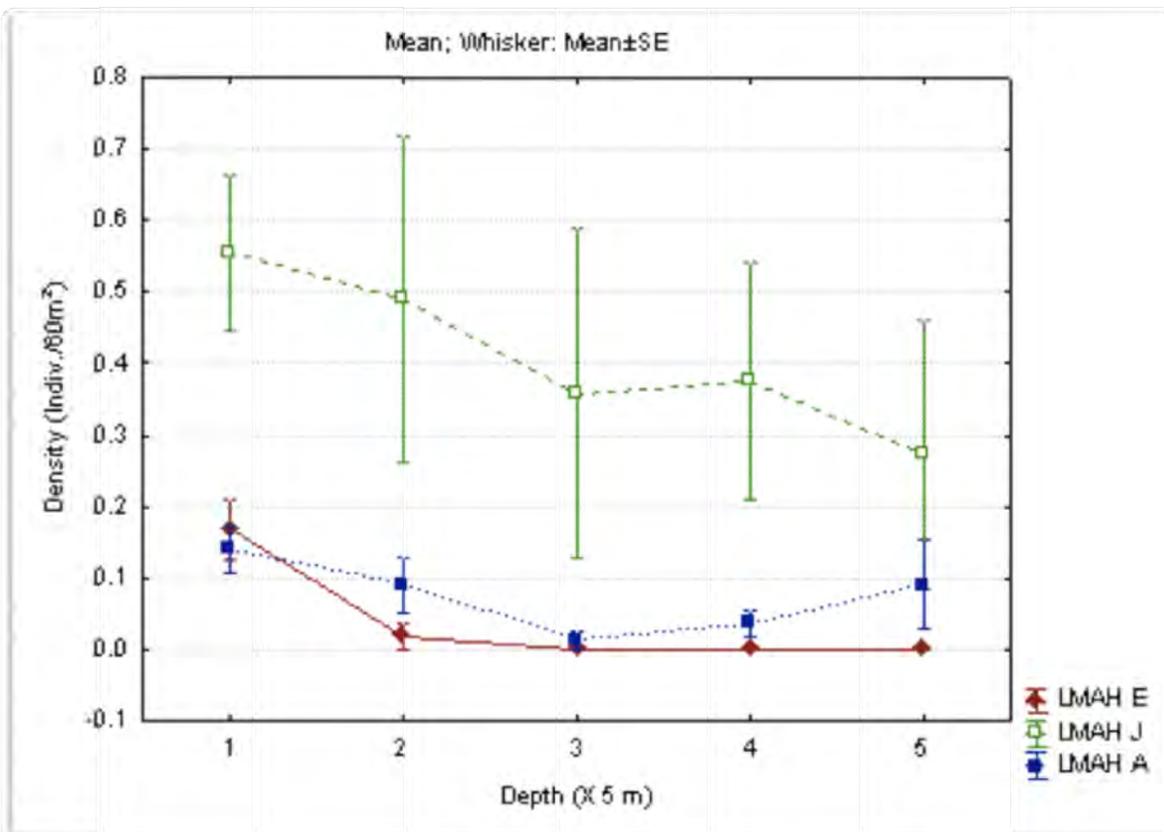


Figure 5 Density of *Lutjanus mahogoni* (LMAH) ontogenetic stages (E – early, J – juvenile, A - adult) by 5 m depth intervals.

Appendix 3-2 Results of discriminant function analysis for grunts and snappers.

Table 1 Values of discriminant function analysis for *Haemulon carbonarium* adults (N=202).

Discriminant Function Analysis Summary (HEX_dist_video) Step 12, N of vars in model: 12; Grouping: P_HCAR_A (2 grps)
Wilks' Lambda: .80456 approx. F (12,189)=3.8259 p< .0000

	Wilks'-Lambda	Partial-Lambda	F-remove- (1,189)	p-value	Toler.	1-Toler. - (R- Sqr.)
RELIEF	0.840563	0.957170	8.457182	0.004072	0.907254	0.092746
CR_Patches	0.815839	0.986177	2.649075	0.105276	0.708669	0.291331
LAND_Patches	0.818740	0.982682	3.330782	0.069573	0.941577	0.058424
CCA %	0.821673	0.979174	4.019744	0.046398	0.922014	0.077986
dist. land	0.832508	0.966431	6.564908	0.011180	0.795326	0.204674
SV_Patches	0.816570	0.985294	2.820961	0.094693	0.942418	0.057582
RUBB %	0.811302	0.991692	1.583447	0.209817	0.933135	0.066865
DH_Patches	0.821617	0.979242	4.006496	0.046756	0.365362	0.634637
DH_Area	0.810978	0.992089	1.507182	0.221097	0.371481	0.628519
SED_Patches	0.813793	0.988657	2.168453	0.142531	0.787357	0.212643
SED_Area	0.811398	0.991574	1.606023	0.206611	0.671128	0.328872
HB_Patches	0.809136	0.994347	1.074505	0.301255	0.859780	0.140220

Table 2 Values of discriminant function analysis for *Haemulon flavolineatum* adults (N=202).

Discriminant Function Analysis Summary (HEX_dist_video) Step 8, N of vars in model: 8; Grouping: P_HFLA_A (2 grps) Wilks' Lambda: .81548 approx. F (8,193)=5.4587 p< .0000						
	Wilks' - Lambda	Partial - Lambda	F-remove - (1,193)	p-value	Toler.	1-Toler. - (R-Sqr.)
PAVMT %	0.852772	0.956274	8.825061	0.003349	0.870632	0.129368
DH_Patches	0.849594	0.959850	8.072995	0.004975	0.819832	0.180168
CR_Patches	0.826627	0.986519	2.637406	0.106006	0.832170	0.167830
RELIEF	0.830980	0.981351	3.667585	0.056959	0.922321	0.077679
LAND_Patches	0.824648	0.988886	2.169114	0.142436	0.971295	0.028705
DEPTH	0.821113	0.993144	1.332404	0.249805	0.910931	0.089069
PATCH SIZE	0.823419	0.990362	1.878255	0.172125	0.147520	0.852480
PAR	0.820143	0.994318	1.102905	0.294943	0.149209	0.850791

Table 3 Values of discriminant function analysis for *Haemulon parra* adults (N=202).

Discriminant Function Analysis Summary (HEX_dist_video) Step 4, N of vars in model: 4; Grouping: P_HPAR_A (2 grps) Wilks' Lambda: .93758 approx. F (4,197)=3.2788 p< .0125						
	Wilks' - Lambda	Partial - Lambda	F-remove - (1,197)	p-value	Toler.	1-Toler. - (R-Sqr.)
PATCH SIZE	0.956612	0.980106	3.998566	0.046913	0.956778	0.043222
SED_Area	0.959082	0.977583	4.517520	0.034795	0.932146	0.067854
RUBB %	0.951982	0.984873	3.025826	0.083511	0.946893	0.053107
GORG %	0.943226	0.994016	1.185930	0.277482	0.948596	0.051404

Table 4 Values of discriminant function analysis for *Lutjanus apodus* adults (N=202).

Discriminant Function Analysis Summary (HEX_dist_video) Step 10, N of vars in model: 10; Grouping: P_LAPO_A (2 grps)
Wilks' Lambda: .83015 approx. F (10,191)=3.9080 p< .0001

	Wilks' - Lambda	Partial - Lambda	F-remove - (1,191)	p-value	Toler.	1-Toler. - (R-Sqr.)
DH_Patches	0.850936	0.975569	4.78315	0.029954	0.587402	0.412598
dist. land	0.886730	0.936189	13.01857	0.000394	0.726331	0.273669
CORAL %	0.852337	0.973966	5.10535	0.024982	0.746409	0.253591
HB_Patches	0.847601	0.979408	4.01576	0.046490	0.725821	0.274179
HAB RICHNESS	0.848040	0.978901	4.11686	0.043846	0.558901	0.441099
SED_Area	0.841822	0.986131	2.68619	0.102868	0.867894	0.132106
RELIEF	0.835530	0.993558	1.23847	0.267164	0.946886	0.053114
SV_Patches	0.835046	0.994134	1.12697	0.289762	0.926963	0.073037
ALGAE %	0.838569	0.989957	1.93769	0.165539	0.869194	0.130806
GORG %	0.838341	0.990226	1.88520	0.171354	0.777379	0.222621

Table 5 Values of discriminant function analysis for *Lutjanus mahogoni* adults (N=202).

Discriminant Function Analysis Summary (HEX_dist_video) Step 6, N of vars in model: 6; Grouping: P_LMAH_A (2 grps)
Wilks' Lambda: .90073 approx. F (6,195)=3.5818 p< .0022

	Wilks' - Lambda	Partial - Lambda	F-remove - (1,195)	p-value	Toler.	1-Toler. - (R-Sqr.)
CR_Patches	0.934563	0.963800	7.324244	0.007406	0.865864	0.134136
RELIEF	0.926803	0.971869	5.644432	0.018480	0.976232	0.023768
PATCH SIZE	0.918022	0.981165	3.743412	0.054463	0.916694	0.083306
SED_Patches	0.912662	0.986927	2.583051	0.109631	0.881763	0.118237
dist. Nursery	0.909530	0.990326	1.904832	0.169119	0.835487	0.164513
LAND_Patches	0.905362	0.994885	1.002638	0.317914	0.951693	0.048307

Appendix 3-3 Habitat areas occupied by early stages of grunts and snappers.

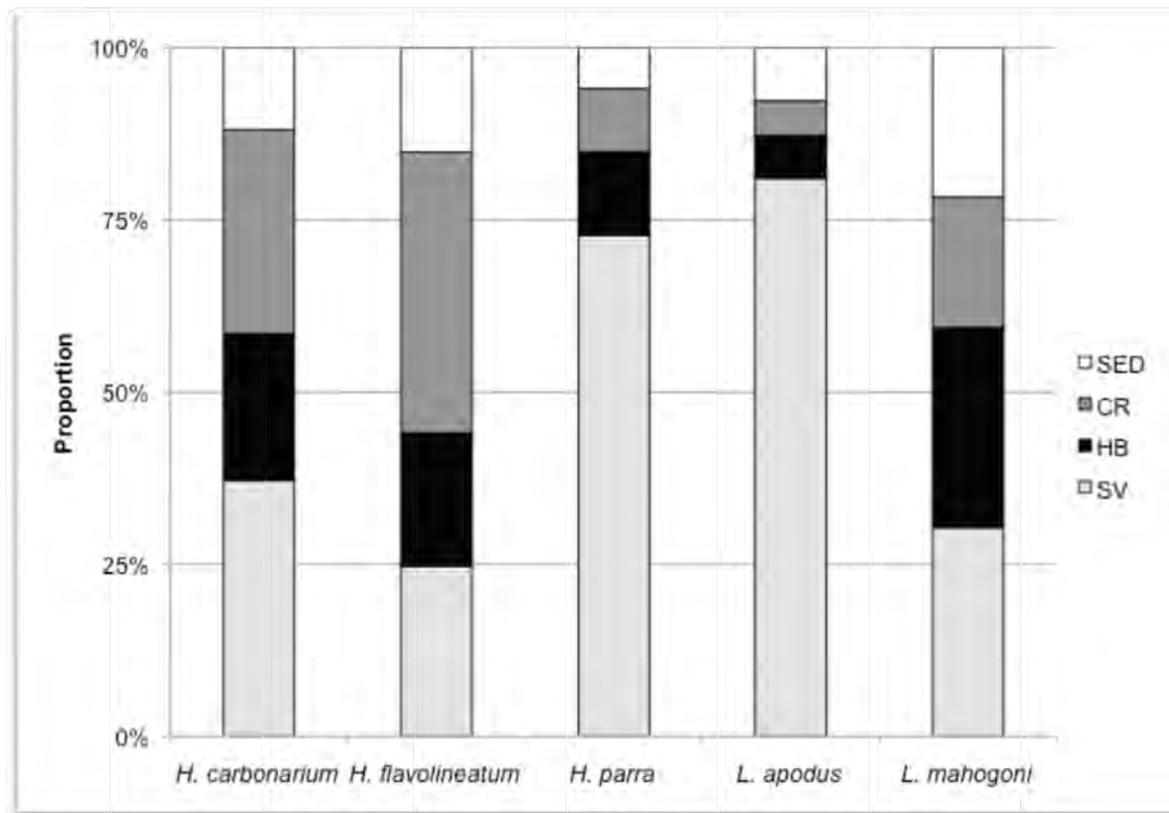


Figure 6 Proportion of habitat area within 5 Ha hexagons occupied by early stages. SED – unconsolidated sediment, CR – coral reef, HB – hardbottom, SV – submerged vegetation.

4 APPLICATIONS TO MANAGEMENT

Marine reserve design

Remote oceanic islands have unique attributes that make coral reef populations more vulnerable to changes in the environment. Some of these attributes include small area, bounded by wide seas, remote from potential sources of fauna and flora, high endemism and increased risk to introduced species (Wace 1982). Ecological processes occurring within the insular platform, such as recruitment, are less reliant upon external sources of larvae and more dependent on localized population dynamics. Therefore maintenance of local ecosystem function is critical for sustaining fish populations at remote sites, as they are less dependent upon external sources for replenishment of larvae (Perez-Ruzafa et al. 2006, Bell 2008). While this reduces the spatial scale at which management and conservation should operate, lower connections to other sites warrant higher levels of protection (Almany et al. 2007). Efforts to maintain healthy populations and ecosystem function at remote sites should include inter-habitat connectivity as well as other localized ecological processes within marine reserves (MR) in order to maximize overall system resilience.

Determining at what scales connectivity is most relevant to marine populations in tropical ecosystems remains debatable. Genetic connectivity between populations remains a significant uncertainty, which precludes our understanding of how larval connectivity affects populations. Much research has been directed towards the application of larval connectivity models towards MR design (Jones et al. 2009). However in the case of remote oceanic Mona Island, larval connectivity is probably very limited (Rojas-Ortega 2002, Taylor and Hellberg 2006, Baums et al. 2006) for many

species and self-recruitment processes, therefore, would be expected to be predominant. In addition it is unlikely that larval connectivity will be 'managed' or can somehow be manipulated to increase a population's self-sustainability. However habitat connectivity within a platform can be estimated to provide insight towards protecting critical habitats in a manner that they maximize ecosystem function and the production of spawning adults. This goal could be met by designing a MR that increase the probability of completing ontogenetic migrations for coral reef fishes that settle successfully at remote oceanic sites.

Marine protected areas (MPA) and MRs have been proposed as a tool for marine conservation and to help improve conservation and fisheries in general (Ballantine 1989, Roberts et al. 2001), through two potential mechanisms; 1) the spillover of adults to adjacent areas, and 2) the increased production of larvae to seed areas outside the reserve (Polunin and Roberts 1993, Gell and Roberts 2003). Studies have demonstrated increases in fish abundance, biomass and size within MR limits (Halpern 2003) as well as export to areas outside the MR (Gell and Roberts 2003, Russ et al. 2004). An important function of MRs for management is the maintenance of relatively undisturbed areas that may be used as controls to study important questions related to the ecology of marine systems and the impacts of fishing (Dayton et al. 2000). Other benefits of MRs include the protection of habitat from fishing gear impacts, conservation of spawning and nursery grounds and the potential for increases in biodiversity and biomass of the fish community (Polunin 2002).

In order to achieve sustainability of marine resources using MRs, these should be designed with scientific criteria based on biological, ecological as well as socio-

economic data (Agardy 2000). Some ecological aspects that have been proposed include the appropriate size, location, replication, shape and self-sustainability (Ballantine 1997, Botsford et al. 2003). Location, size and shape criteria are generally based on theories of connectivity in the larger genetic populations sense where larval recruitment patterns are believed to drive population connectivity (Levin 2006, Gaines et al. 2007). However, two aspects that should not be underestimated include location and management (Jameson et al. 2002), which suggests that no matter how good the management if the location is not adequate the reserve will not achieve its goals and vice versa. It is in the location, size, shape and hence, boundary designation that inter-habitat connectivity can provide critical ecological information. Unfortunately most existing MRs have not been designed on the basis of scientific criteria (Roberts 2000, Sladek-Nowlis and Friedlander 2004) as is the case of Puerto Rico (Aguilar-Perera et al. 2006). Additionally, after designation of an MR, basic ecological information will be necessary to measure the effectiveness of management. Therefore understanding the underlying ecological patterns will help incorporate scientific data into the design, designation and implementation of MRs.

For marine planning purposes it has been demonstrated that certain places in the ecosystem have greater importance than others for particular species (Crowder and Norse 2008), therefore the selection of areas to be included in MR boundaries can be optimized by applying basic ecological concepts, even though these may not be completely understood. One key concept applicable to the delineation of MR boundaries is the dependence upon critical habitats such as nursery, migrating and spawning areas, as well as recognizing differential habitat use by some species. Linkages between

habitats used in response to changes in the ecological requirements within a fish's lifetime are critical to prioritizing habitats to be included in a MR, although this becomes highly complex in situations where multiple species or biodiversity conservation are important goals.

In order to link habitats used by a species, and use them as a proxy for reef fishes, their ecological functions require a better understanding. For example, not all seagrass (or mangrove) patches (although they may cover the same area) support the same number or diversity of species nor do they all have the same nursery function for a species. This may be due to within habitat differences or the influence of the landscape (Dorenbosch et al. 2007) among other ecological factors. This information is essential for prioritizing habitats and incorporating the landscape approach to identify critical habitats (i.e. nursery function and ontogenetic connectivity).

Although mangroves are undoubtedly an important nursery habitat for some reef fishes (Nagelkerken et al. 2000, Mumby et al. 2004, Dorenbosch et al. 2006), this seems to be a facultative relationship for some species. Observing a species in high densities in a particular habitat is not always indicative of an obligate nursery function, as demonstrated for *L. apodus*. At Mona Island this species used bedrock and seagrass as nursery habitats, and adult densities on reefs were higher than in La Parguera, suggesting it was not affected by the lack of mangroves at this remote site. Instead we could argue that the lack of a particular nursery habitat can be overcome if alternate habitats provide an ecological substitute for this function. Because recruitment processes vary temporally and spatially, the spatial distribution of this species should be replicated at this location and at other sites lacking mangroves in order to support this

conclusion. It is also worth mentioning that fishing pressure at La Parguera could be seriously affecting this population and despite abundant mangroves for early juveniles adults are less abundant.

This finding highlights the importance of not generalizing nursery habitat function to a specific type of habitat or location. For example, in the prioritization of areas to be included in a MR, a site with mangroves may receive more importance than one without because of the high number of mangrove dependent reef fishes. However, a site without mangroves may still harbor high numbers of early juveniles of a different suite of species and should not be considered less valuable as a nursery (CSA International 2009). This should also be considered at the landscape level in which a nearby area of mangroves that may not be incorporated within the MR supports most of the nursery function and the non-mangrove areas nearby will provide less of a nursery function in comparison to that patch.

Mona Island Marine Reserve

The no take zone (NTZ) at Mona Island, which is essentially a MR is located within the larger Natural Reserve of Mona and Monito Islands. The Mona Island MR (although not named so) was designated in 2007 (DNER 2007) as an amendment of the MR designated in 2004 through the fisheries regulations (# 6768) based on the Puerto Rico Fisheries Law (Law # 278 of 1998). The original MR was limited to 0.5 nautical miles from shore except for the swath on the western coast. The complete MR is contained within a federally designated critical habitat for hawksbill sea turtles (*Eretmochelys imbricata*) that extends to 3 nautical miles from shore (part 226 of CFR 1998).

The limits of the current MR extend to the 182 m (100 fathoms) bathymetric contour (DNER 2007) except a swath on the western coast (Figure 4-1). This covers 114 km² of submerged area mainly composed of deep (> 30 m) habitats beyond the shelf edge. Within the insular platform of Mona Island the distribution of reef fishes was overlaid upon the benthic habitat map (100 m² MMU) to select habitat patches occupied by each species in relation to the limits of the MR to quantify essential fish habitat with and without protection from extractive activities (fishing and collecting).

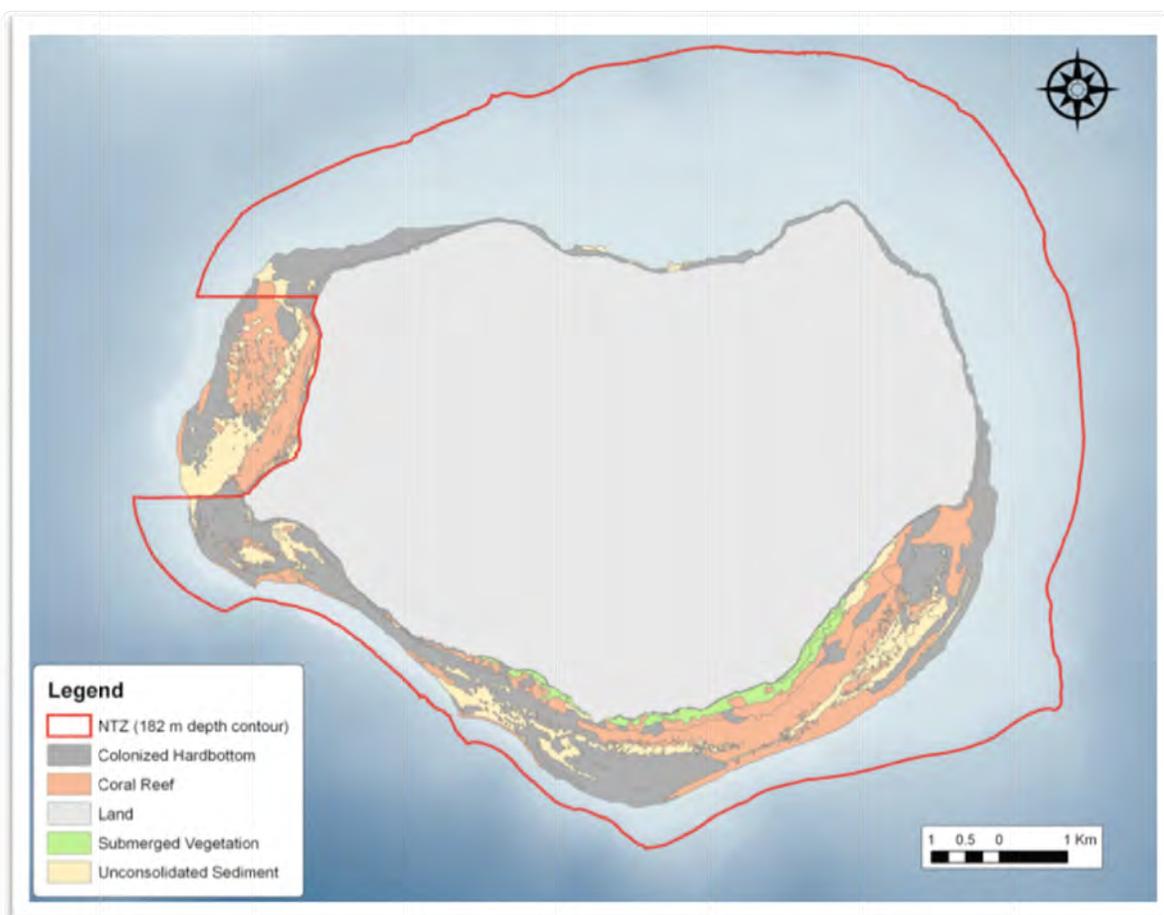


Figure 4-1 Benthic habitat map of Mona Island and the limits of the MR (NTZ) designated in 2007.

Approximately 20.5 km² of the insular was classified in the benthic habitat map and of these 16.1 km² (79%) are located within the MR limits. Submerged vegetation (SV) habitats are completely contained due to the discrete distribution of this habitat on the southern and southeastern coasts of the island. The remaining habitats are dominated by hardbottom (HB), coral reef (CR) and unconsolidated sediments (SED). The proportion of each habitat located outside the MR boundaries ranges from 13% (HB) to 32% (SED), while 29% of CR is outside (Figure 4-2).

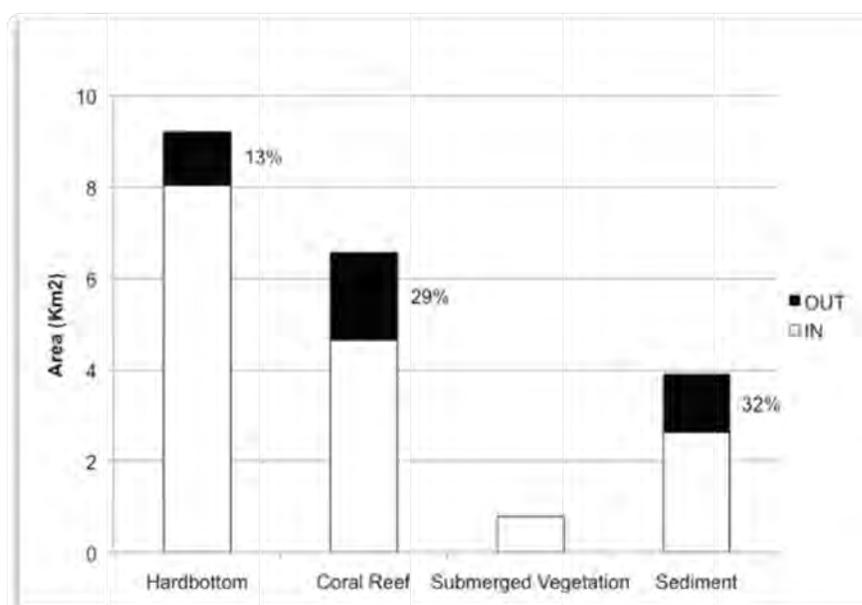


Figure 4-2 Total area of mapped habitat inside (white) and out (black) of the Mona Island MR.

In this analysis 3 Haemulid (*Haemulon carbonarium*, *H. flavolineatum* and *H. parra*) and 2 Lutjanid (*Lutjanus apodus* and *L. mahogoni*) species were selected due to their known ontogenetic migration patterns at Mona Island. Individual maps were created (Appendix 4-1) and the area of habitat excluded from the MR was calculated for each species.

Haemulon carbonarium

Over 12 km² of habitat were used by *H. carbonarium* at Mona Island, including sites on the northern coast composed of deep HB. The nursery habitat for this species, seagrass and sediment patches in shallow waters, is completely contained within the NTZ (Figure 4-3). The HB habitat was mostly contained within the MR although 18% of CR was not, including small patches of abundant staghorn coral (*Acropora cervicornis*) on the western shelf break that supported high adult densities.

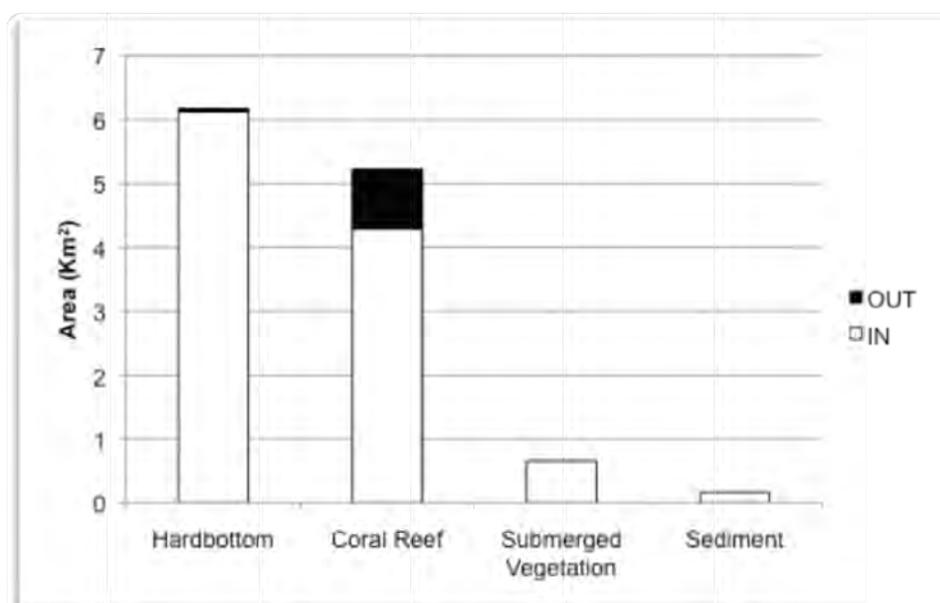


Figure 4-3 Area of habitats used by *H. carbonarium* located inside (IN) and outside (OUT) the MR.

Haemulon flavolineatum

The distribution of *H. flavolineatum* was widespread around Mona Island, including 6 km² of CR. All SV is located within the MR, although areas of shallow CR on the western coast nearshore also used as nursery habitat are excluded. Approximately one third of offshore CR used by adults is outside the MR limits (Figure 4-4) including small patches of abundant staghorn coral (*Acropora cervicornis*) on the western shelf break that supported high adult densities.

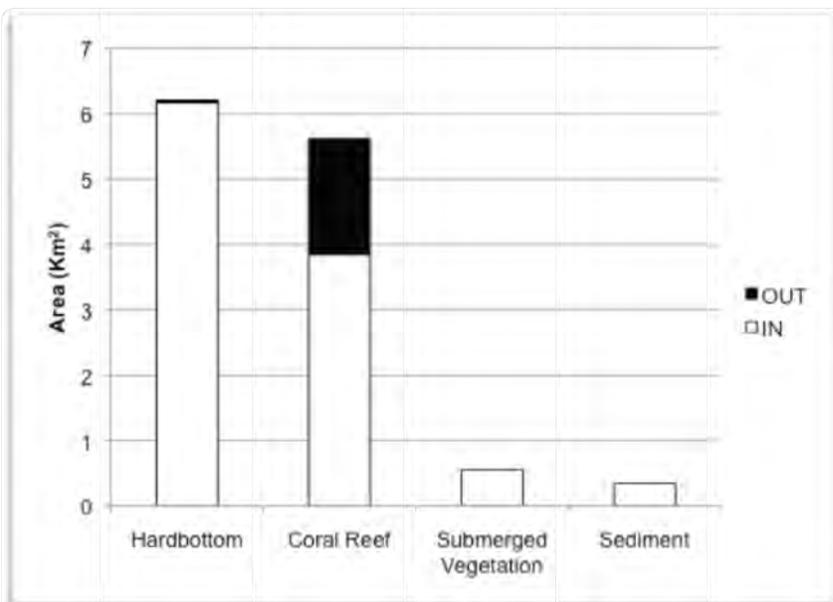


Figure 4-4 Area of habitats used by *H. flavolineatum* located inside (IN) and outside (OUT) the MR.

Haemulon parra

The areas used by *H. parra* were limited to nearshore habitats surrounding all coasts of the island. Only two small offshore CR patches on the western and southwestern shelf edge shelf were occupied by this species. The entire SV and HB nursery habitat is located within the MR however 46% of the CR occupied by adult *H. parra* is not (Figure 4-5).

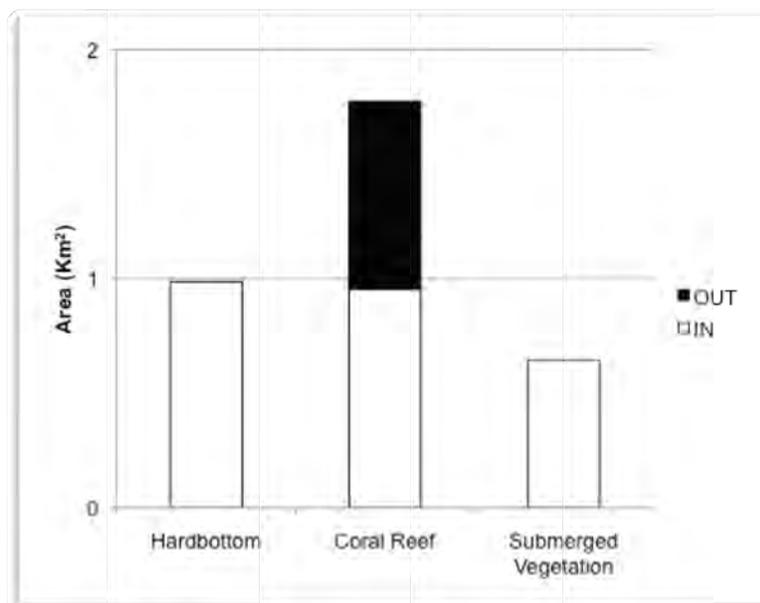


Figure 4-5 Area of habitat used by *H. parra* located inside (IN) and outside (OUT) the MR.

Lutjanus apodus

The distribution of *L. apodus* extends over 13 km² throughout the insular shelf. All of the SV and HB nursery habitats are contained within the MR limits although approximately 19% of the total adult habitat is not. Much of the juvenile and adult area is composed of CR at the shelf edge on the western shelf. The greatest proportion of area outside is of CR (29%) followed by HB (12%) summarized in Figure 4-6.

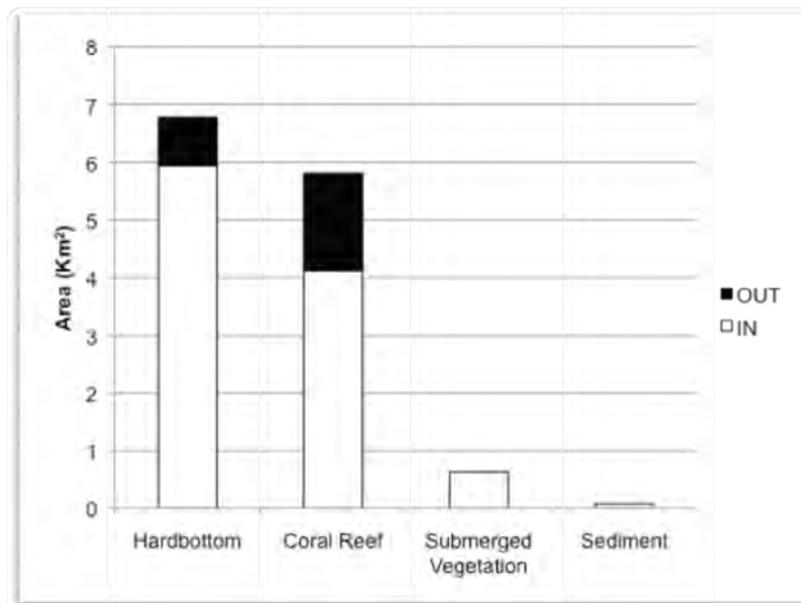


Figure 4-6 Area of habitat used by *L. apodus* located inside (IN) and outside (OUT) the MR.

Lutjanus mahogoni

Areas occupied by *L. mahogoni* extended around Mona Island including northern areas of deep HB. Although early juveniles were not limited to nearshore areas, some important nursery habitats were located outside the MR. Areas occupied by juveniles and adults outside the MR included 17% of CR (Figure 4-7).

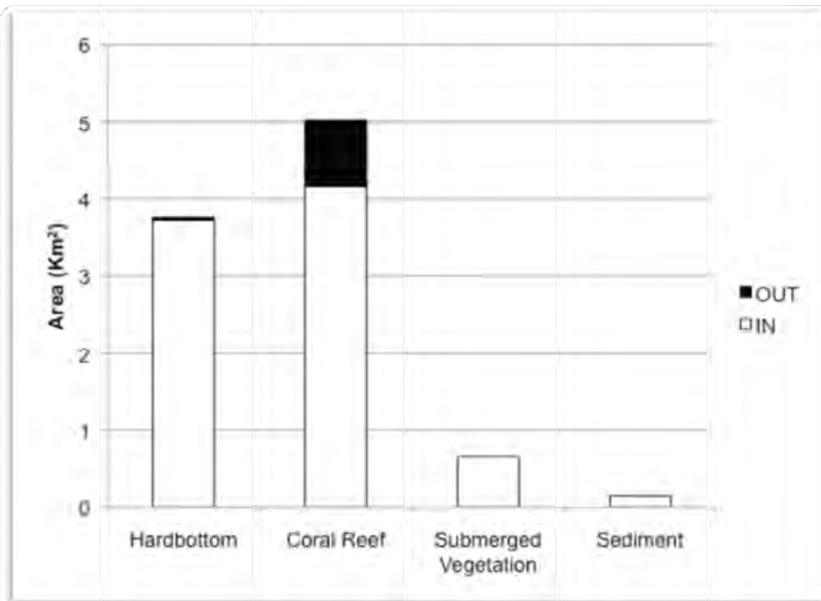


Figure 4-7 Area of habitat used by *L. mahogoni* located inside (IN) and outside (OUT) the MR.

The Mona Island MR excludes a minimal proportion of the nursery habitats of *H. carbonarium*, *H. flavolineatum* and *L. mahogoni* while for the other two species (*H. parra* and *L. apodus*) all nursery habitats were within its limits. Most of the nursery habitat for these haemulids and lutjanids is shallow nearshore SV and HB habitat and all of the SV is located within the MR limits. Although this analysis is limited to a few species, others that were shown to depend on SV as their main nursery habitat (Chapter 2) are equally protected from direct fishing impacts during early ontogenetic stages, although this may not be the main threat affecting the survival or growth of early stages of coral reef fishes.

The greatest area of adult habitat outside the MR was for *L. apodus*. This was mainly due to a large area of continuous HB habitat located near the shelf break on the northwestern insular platform. Of the CR habitat outside the MR a few isolated small patches were consistently occupied haemulids and lutjanids. These were small (mean < 0.04 km²) isolated patches surrounded by either SED or HB habitat near the shelf edge. Further investigation on the use of small sized CR patches is warranted in order to determine their influence upon the distribution of coral reef fishes and if these should be included in the MR.

For a reduced number of species the areas of adult habitat and the migration corridors connecting nursery to adult habitats are excluded from the MR. The degree to which juvenile or adult habitats were outside the limits seems to depend upon the abundance of the species, variability in the range of habitats used and the magnitude of their cross-shelf migrations. Most of the essential fish habitats composed of CR patches adjacent to nursery habitats were encompassed within the Mona Island MR.

A map overlaying nursery habitats and land facilities is presented in Figure 4-8. The main nursery habitats of the three grunt and two snapper species analyzed in detail are located in nearshore habitats that occur only on the southern coasts of Mona Island. All SV nursery habitats are within the MR yet are within close proximity of two sites where roads provide access to shore. These access points provide greater chances of impacts due to land-based sources of pollution and recreational activities. One of these sites is the Pajaros beach campground on the beach that has a pier where vessels load and unload passengers and equipment. Despite the MR regulations applicable to this site, visitors commonly use the pier for hook and line fishing. In addition the narrow lagoon at Pajaros has a series of mooring buoys that are commonly used by vessels, which may remain there for various days increasing the potential impact of vessel-generated pollution such as bilge, fuel or waste spills. This is extremely important at this site, which contains the largest expanse of SV on the island.

Although Mona Island is remote and uninhabited, based on field observations many activities (boating, fishing, camping, construction, etc.) occur precisely within nearshore habitats that provide the only nursery habitat for many species. Human activities occurring on the coast require special considerations in order to minimize impacts that may impair the nursery function. The small size of fishes found in nearshore nursery habitats at Mona Island suggests that they are probably not impacted by most common fishing practices. Potentially the beach seines or the use of chemicals would directly impact early juvenile stages in nursery habitats. However juvenile and adult fishes coincided in these areas and are caught by hook and line from shore and piers by campers. More importantly, applying the ecosystem based management

approach should consider the influence of land-based impacts to the nursery function specifically in nearshore habitats

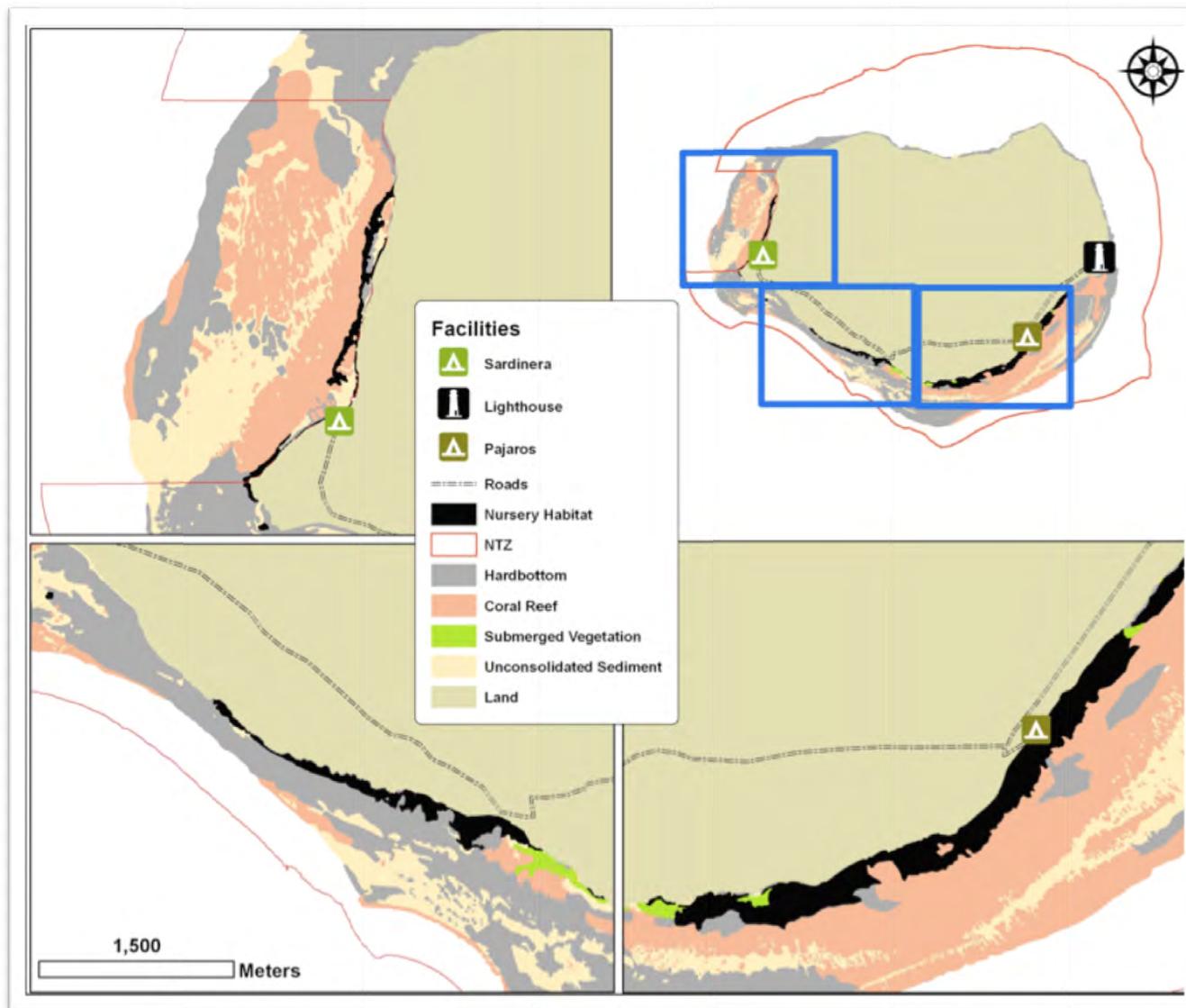


Figure 4-8 Nursery habitats and land-based facilities at Mona Island.

The other pier where vessels load and unload is located on the western shore, outside the MR near the main DNER facilities and campground called Sardinera. At this site there is a concrete pier where land vehicles come up to the pier's edge to unload fuel from transport vessels as well as passengers and equipment. Although this site does not contain SV patches, nearby CR and HB were used as nursery habitat for a few species. Because this is the main pier used on the island by staff and visitors it provides the greatest risk to the surrounding critical habitats. The Sardinera lagoon also has a group of mooring buoys used by recreational vessels. Other activities that have the potential of impacting the nursery habitats are the use of landing crafts that remain on the beaches within the lagoon. The high-traffic of vessels within the lagoon increases the risk of groundings, spills and other sources of pollution, which may impact the nursery function at this location.

The nursery function of a habitat may be based on specific requirements (food, refuge, or other) that are provided by particular characteristics, which would determine the nature of impacts that could potentially undermine their functionality. Any impact that reduces prey abundance or eliminates the structure that provides refuge will diminish the nursery function. For example, if seagrass blades provide physical structure that early juveniles use for refuge and blades are destroyed or removed (storm, grounding, dredge, burial by sedimentation, etc.) the area can't function as an effective nursery. In this case (and perhaps many other similar situations) impacts from land-based sources may be more significant than fishing. This is an important consideration in an MR that incorporates nursery habitats but do not protect these from land based impacts that may significantly reduce nursery function.

Nearshore HB and CR habitats provided essential fish habitats as nursery areas as well as migration corridors for species that were distributed to the most distant areas of the eastern and northern coasts of Mona Island. Although areas of deep HB habitat extended farthest from nursery areas they provide continuous habitat composed of vertical bedrock with ledges and overhangs as well as large boulders along the seafloor, which seems to provide a suitable corridor for fishes. Although total abundances of *H. parra* were low, adults were distributed throughout deep HB habitat, but rarely occurred in other deep areas of the insular platform. Vertical, deep HB is generally not considered significant reef fish habitat yet this study suggests they may provide important resting areas for migrating species.

The absence or limited distribution of some reef fishes at Mona Island highlights the importance of nursery habitats and connectivity patterns at the landscape scale. Cross-shelf migrations were detected for at least 20 fishes, and of these 15 were associated with seagrasses located nearshore. Nursery function was limited to one habitat type for some species; while for others it was flexible or adaptable using alternate habitats, as observed at other locations (Lecchini and Poignonec 2009). Those species with specific habitat requirements during early stages may have a reduced ability to overcome impacts to or degradation of nursery habitats. However, some nearshore nursery habitats may be intermittent or fluctuate such as nearshore hardbottom habitat that could be buried due to natural sediment accumulations over time, storms or beach renourishments. There are probably mechanisms for fishes to deal with changes in the distribution of nursery habitats that need to be better

understood in order to predict how the nursery function is affected by changes in the environment.

Although the design of the MR at Mona Island fortuitously includes most of the nursery habitats used by reef fishes and incorporated connectivity corridors of most of the insular platform, there are still potential threats to inter-habitat connectivity. Most nearshore habitats are threatened by human activities in coastal areas as well as the lack of compliance with no-fishing regulations. These two aspects remain critical in order to realize the goals of the MR and sustain this remote coral reef population's viability.

Conclusion

Including nursery habitats within MR boundaries is important for maintaining ontogenetic connectivity function, but the configuration of habitats (Dorenbosch et al. 2007) should also be considered. A population's productivity depends on the ability of fishes to complete their life cycle. Those species that conduct ontogenetic migrations will have a greater probability of capture if the MR is of area less than the range of ontogenetic migrations or it excludes habitats used in migrations. Therefore the location, size and shape criteria for a MR in a coral reef system must consider landscape inter-habitat connectivity between nursery and adult habitats to effectively protect populations that undergo ontogenetic migrations.

Although there is not sufficient data to determine which habitats each MR should include, there are some general principles to consider. First, nursery habitats for most species are located nearshore in shallow bays or lagoons. Therefore a MR should

incorporate these and nearby habitats progressively offshore to create a cross-shelf corridor for migration towards coral reef habitats offshore or at greater depths. In general, at Mona Island relatively small sized, nearby (< 250 m linear distance) coral patches in areas with high habitat richness (within 5 Ha) supported greater abundances of fishes. However, the relationship between fishes and patch shape or size remains confounded and requires further investigation. This must also consider important aspects of how we measure natural features (e.g. fractal theory) and the identification of 'homogeneous' patches in nature, which are scale dependent and will vary depending on the technology available to detect these features.

Cross-shelf habitat use suggests an MR should include areas perpendicular to shore instead of parallel to shore with increasing area of depths to cover habitats used by all ontogenetic stages. In order to maintain ontogenetic migrations within the MR, boundaries should be placed in less suitable habitats, where the possibilities of intersecting migration corridors are minimal. For example Bartholomew et al. (2007) found that reef fishes were more likely to move out of reserves when boundaries crossed reef habitats. Unfortunately this information will not be available for all species nor sites, but basic ecological patterns of fish distributions can also be elucidated from the landscape configuration of coral reef habitats

Ecological criteria for designing a MR can be improved by incorporating landscape patterns and habitat characteristics, which may be available or relatively worthwhile to attain. Although detailed habitat information (collected in-situ) is not always available, the use of GIS and remote sensing could be used to quantify habitat at 'larger' spatial scales, although a relevant minimum mapping unit proved to be

important for Mona Island. For example live coral cover did not have a strong relationship with the abundance of fishes in this study, as well as others (Roberts and Ormond 1987); therefore what defines a coral reef patch for fishes may be more related to vertical relief, complexity and rugosity at smaller scales. Although identifying these variables in the landscape context is often difficult, there are some useful correlations such as small patch size of coral reef habitats that can be mapped efficiently and have an ecological basis. The habitat mosaic should be connected ecologically in order for the coral reef ecosystem to be functional (Ogden 1988, Appeldoorn et al. 2003), and this connectivity can be quantified for some species with the information presented in this study.

Important species-habitat associations were detected for distinct ontogenetic stages of reef fishes that should be considered in reef fish studies. For example reef fish monitoring studies that seek to measure changes over time must consider in which habitat types sampling will be most effective for that species depending on the ontogenetic stage. Differences in fish-habitat associations observed at various scales suggest ontogenetic preferences for specific habitat types and elements of landscape configuration. Therefore sampling design can be directed towards specific habitat types or landscape context for more efficient use of limited resources in field studies. Further analysis of landscape level metrics should be conducted to identify patterns that support ontogenetic connectivity at sites with other combinations of habitats.

The identification of nursery habitats and ontogenetic connectivity patterns allows the integration of inter-habitat connectivity into MR design. This criterion can be considered more important in remote oceanic locations or areas that are otherwise

disconnected from their natural environment (i.e. habitat damage). However the best-designed MR cannot be expected to provide relevant ecosystem functions if land-based impacts and fishing pressure are not controlled.

The Mona Island MR incorporates the majority of the nursery habitats critical to at least 5 species of grunts and snappers during early life stages. However the lack of a management plan, effective law enforcement and the potential impacts of land based activities threatens the ecosystem functions of nearshore habitats. Most of the adult grunts and snappers analyzed in this section are widely distributed throughout the insular platform within the MR and would potentially benefit from the fisheries regulations. Nonetheless spatially replicated temporal patterns in fish abundance should be consistently measured in order to determine the long-term effectiveness of the Mona Island MR. This study provides a substantial baseline upon which the effects of fishing could be accurately quantified, given the remoteness from urban development and other impacts such as major sources of pollution and habitat degradation.

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Appendix

Appendix 4-1 Habitat connectivity maps for grunts and snappers and NTZ limits at Mona Island.

Appendix 4-1 Habitat connectivity maps for grunts and snappers and NTZ limits at Mona Island.

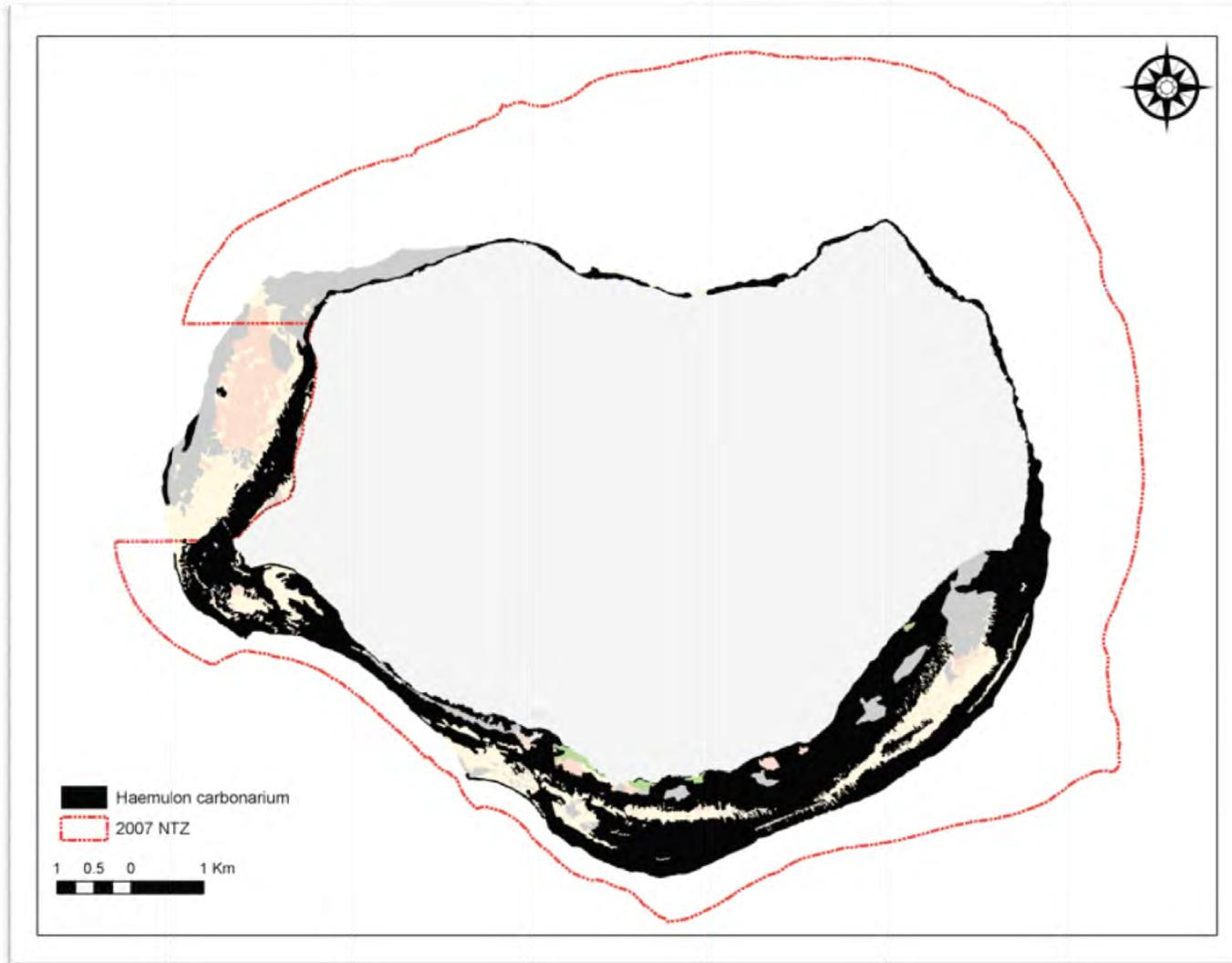


Figure 1 Habitat connectivity map for *H. carbonarium* (black patches).

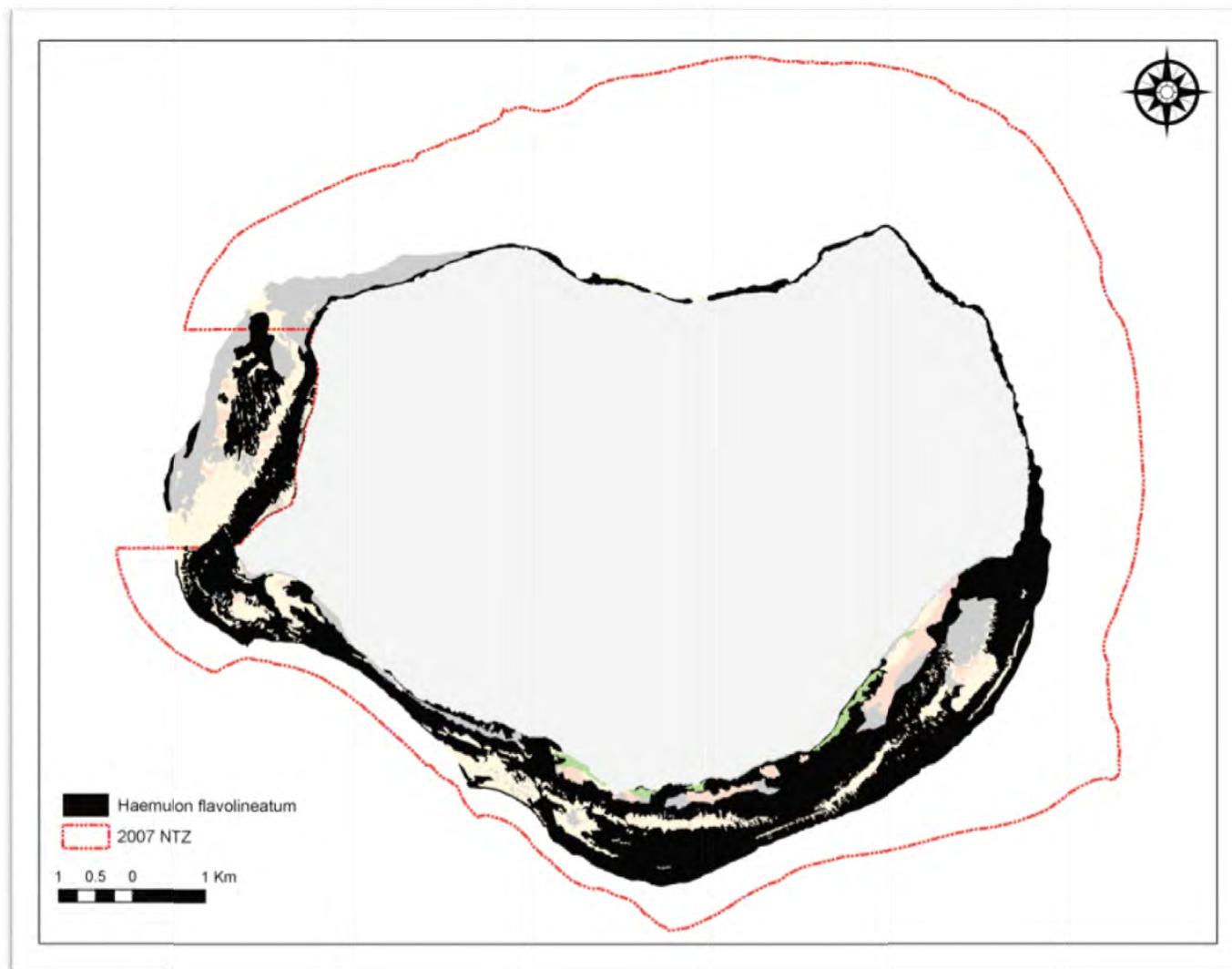


Figure 2 Habitat connectivity map for *H. flavolineatum* (black patches).

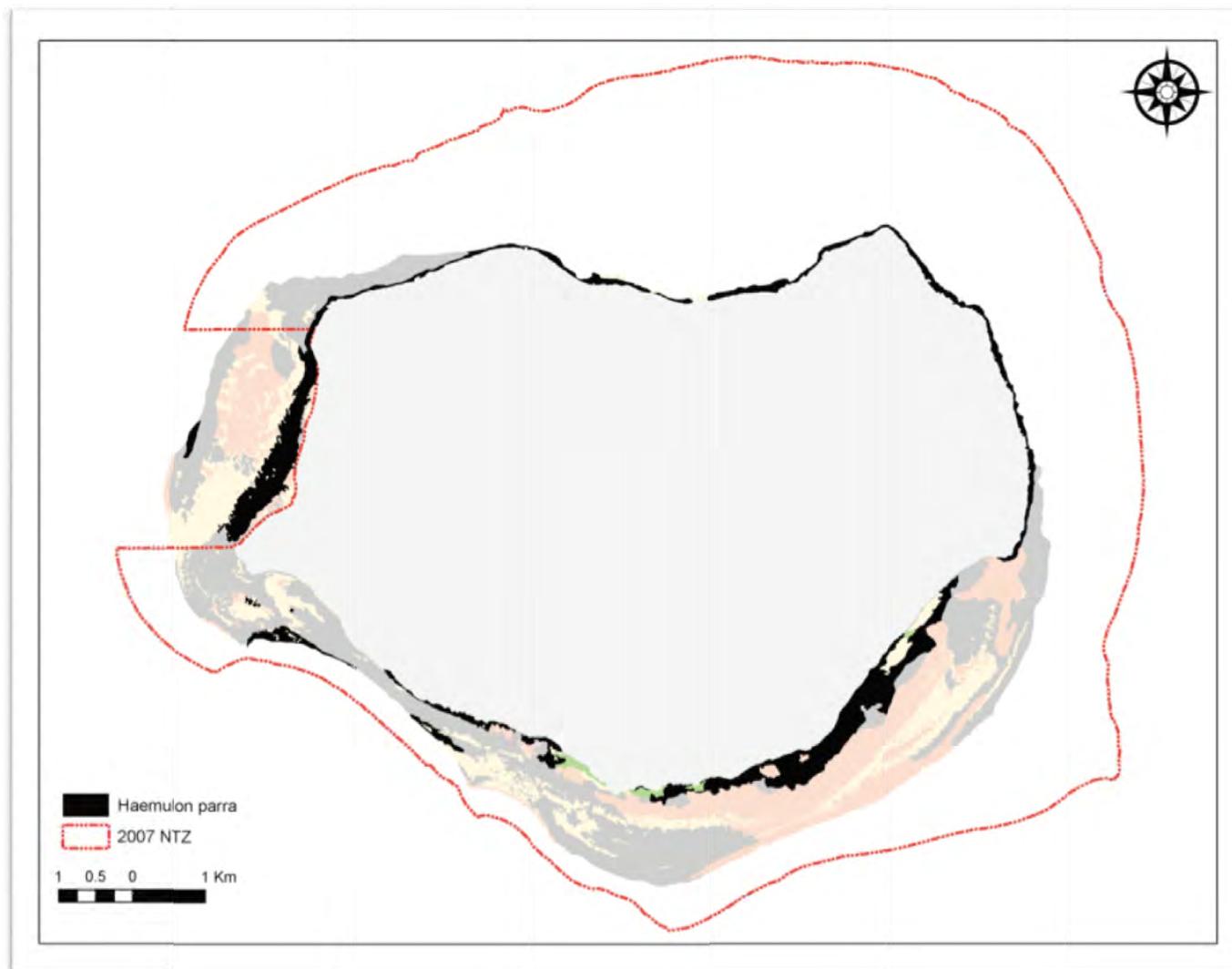


Figure 3 Habitat connectivity map for *H. parra* (black patches).

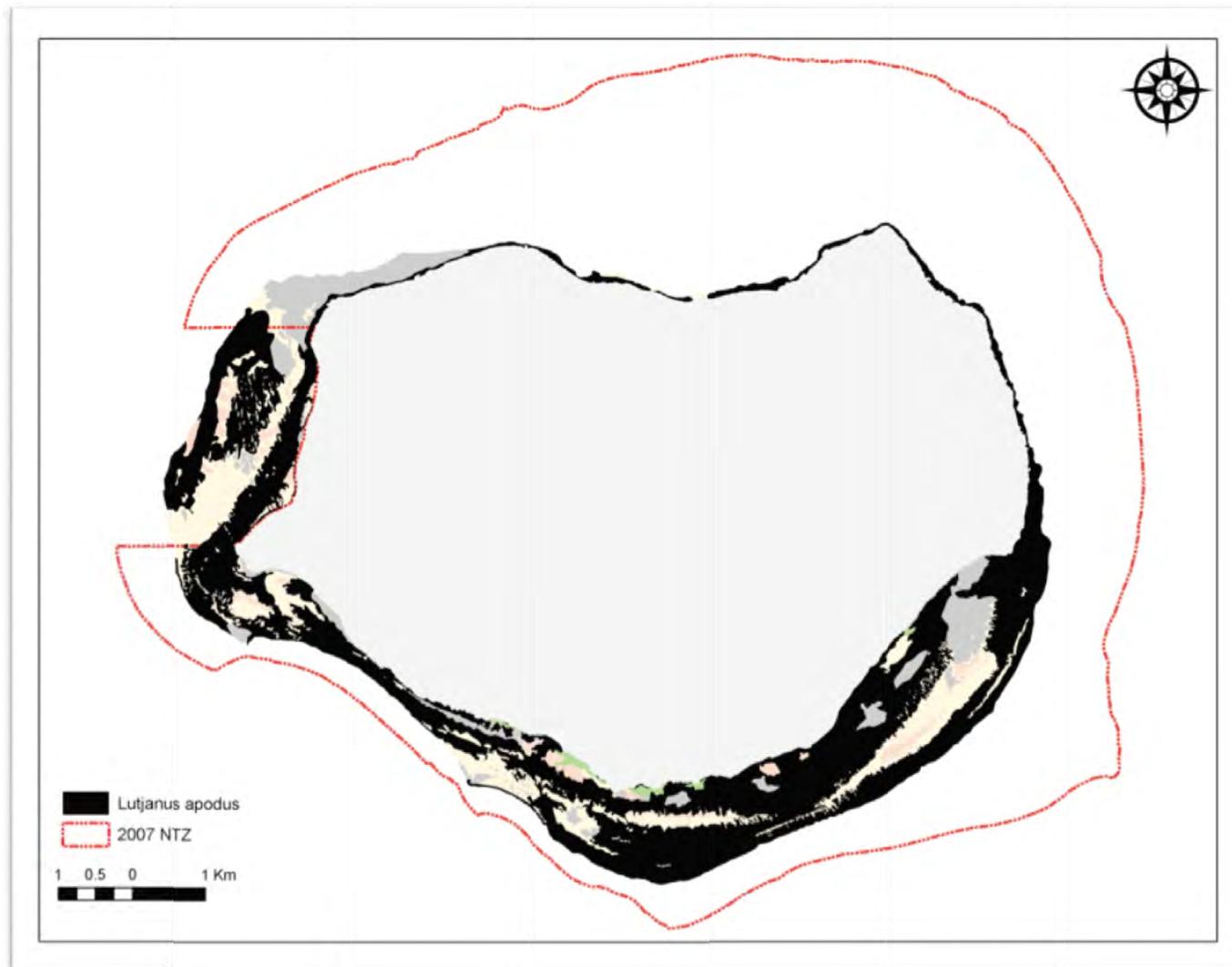


Figure 4 Habitat connectivity map for *L. apodus* (black patches).

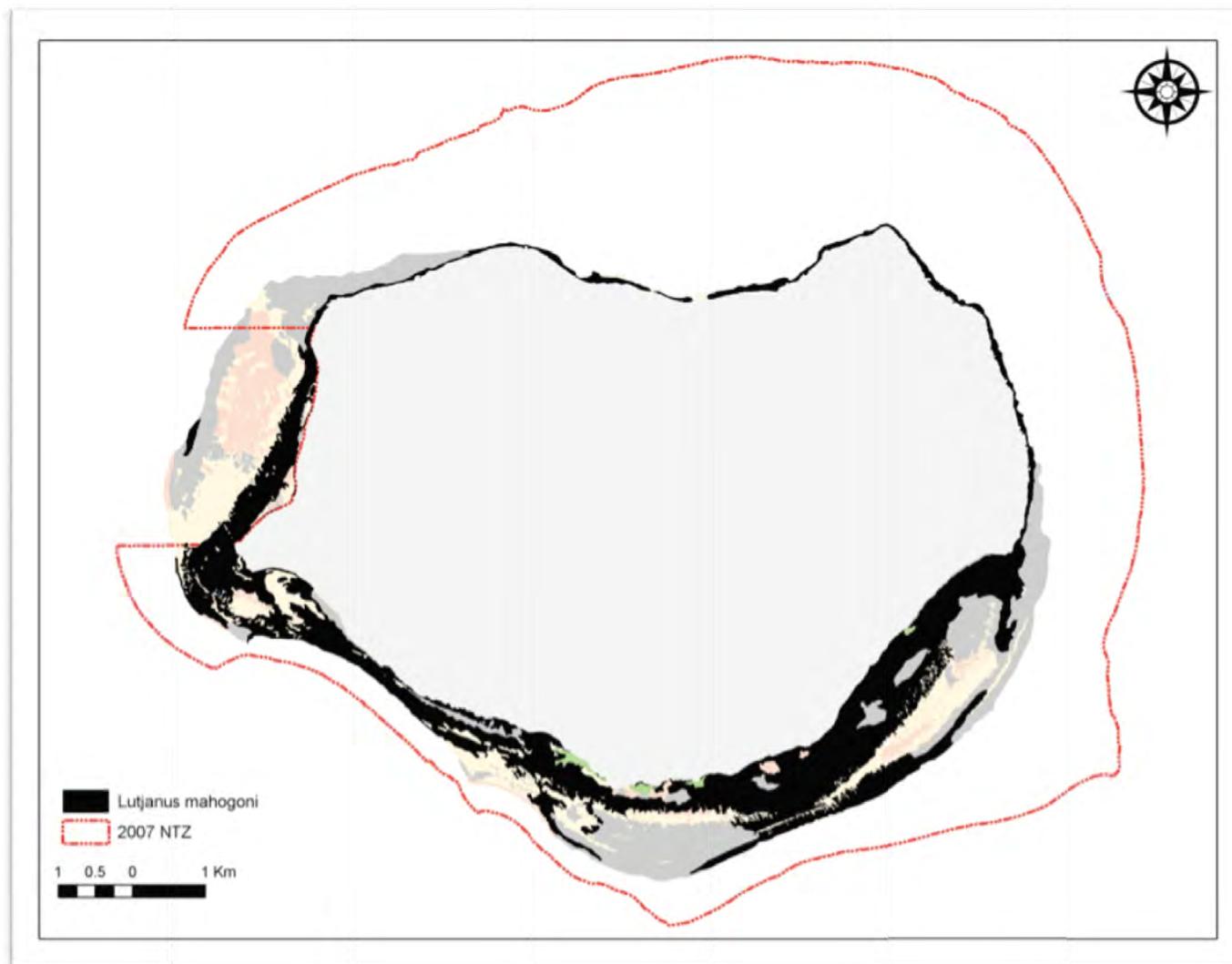


Figure 5 Habitat connectivity map for *L. mahogoni* (black patches).

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