

Ontogenetic Migration and Growth of French grunt (Teleostei: *Haemulon flavolineatum*) as Determined by Coded Wire Tags

by

Björn Lambert Karl Bouwmeester

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

MASTER OF MARINE SCIENCES
IN
BIOLOGICAL OCEANOGRAPHY

UNIVERSITY OF PUERTO RICO
MAYAGÜEZ CAMPUS
2005

Approved by

Richard S. Appeldoorn, Ph.D.
Chairman, Graduate Committee

Date

Dannie Hensley, Ph.D.
Member, Graduate Committee

Date

Paul Yoshioka, Ph.D.
Member, Graduate Committee

Date

Nilda Aponte, Ph.D.
Director of Department

Date

Edgardo Ojeda, Ph.D.
Representative of Graduate Studies

Date

Copyright

In presenting this dissertation in partial fulfillment of the requirements for a Master in Marine Sciences degree at the University of Puerto Rico, I agree that the library shall make its copies freely available for inspection. I therefore authorize the Library of the University of Puerto Rico at Mayagüez to copy my MS Thesis totally or partially. Each copy must include the title page. I further agree that extensive copying of this dissertation is allowable only for scholarly purposes. It is understood, however, that any copying or publication of this dissertation for commercial purposes, or for financial gain, shall not be allowed without my written permission.

Signed: John C. Bourne

Date: December 9, 2005

Abstract

The early life history of grunts was studied using mark-recapture techniques. Juvenile fish (*Haemulon flavolineatum*) were tagged with coded wires and the effects of tagging were investigated in controlled tank experiments. Results indicate monthly survivorship (0.96) and retention (≥ 0.87) are high and growth is unaffected by the tags. In the field, movements between juvenile schools were determined to be directional and individually determined. It is hypothesized that movement is initiated by antagonistic and territorial behavior. Large-scale movements were not observed, but subadult fish moved seaward to the adjacent reef front. Growth data covered a wider range of sizes than previously studied, yielding a robust estimation of growth. Estimates for L_{∞} and k of the von Bertalanffy growth equation were 28.323 cm (FL) and 0.166; respectively, t_0 was not determined. Observed and modeled growth suggest grunts remain in the back reef and school for a period of two years. Averaged daily growth was determined to be 0.0151 cm FL/day for small juveniles (7-12 cm) and 0.0063 cm FL/day for larger juveniles (≥ 10 cm).

Resume

La historia de vida temprana de los roncós fue estudiada usando técnicas de marcaje y recaptura. Los roncós (*Haemulon flavolineatum*) juveniles fueron marcados con alambre codificado con cifras decimales y los efectos de las marcas fueron estudiados en tanques controlados. Los resultados indican que la supervivencia mensual (0,96) y la retención ($\geq 0,87$) es alta y que las marcas no afectan el crecimiento. En el campo, los movimientos observados entre las escuelas juveniles fueron direccionales y determinados de manera individual. Se presume que el movimiento es iniciado por comportamiento antagónico y territorial. Movimientos a gran escala no fueron observados, pero los sub-adultos se movieron mar adentro, adyacentes al frontón arrecifal. Los datos de crecimiento cubrieron unos intervalos de tallas más amplios que los estudiados previamente, por lo que se obtuvieron unos estimados robustos en los parámetros de crecimiento. Las estimaciones de L_{∞} y k de la ecuación de crecimiento de von Bertalanffy fueron 28,323 (centímetro FL) y 0,166, respectivamente; t_0 no fue determinado. El crecimiento observado y modelado sugiere que los roncós se permanecen en la parte posterior del arrecife y se mantienen agrupados en cardúmenes por un período de dos años. El crecimiento diario promedio fue estimado en 0,0151 centímetros FL/día para los juveniles pequeños (7-12 cm) y 0,0063 centímetros FL/día para juveniles más grandes (≥ 10 cm).

Acknowledgments

I came to this school to create a stronger experimental background and develop confidence to organize projects. Through class and fieldwork, I have accomplished these goals.

At this moment I would like to acknowledge all those who have led me to this point in my life, for without them none of this would have been possible. I wish to begin with my committee members, whose patience and understanding I might have tested just a bit. Of those on my committee, I would especially like to thank my chairman, Dr. Richard Appeldoorn, for his infinite patience with the thousands of revisions until my writing skills returned from the grave, Dr. Paul Yoshioka, for his support and teaching early in my stay here in Mayagüez, and Dr. Hensley, for the exciting anecdotes on his travels through the world that reminded me of why I studied marine science in the first place.

My research was labor intensive, as were the revisions to this thesis, and I would like to thank the support of my lab mates and the workers of the school. I begin with acknowledging the teachings of Dr. Ron Hill and Dr. Conrad Recksiek, who introduced me to the world of grunts and the early mornings and late nights that accompany their capture. I wish to thank my lab mates Alfonso Aguilar, Francisco Pagan, Anthony Marshak, Cassandra Cerveny, Michael Nemeth, Idelfonso Ruiz, and Ivonne Bejarano whom I dragged off to depths and areas unknown on those early mornings and late nights. I thank them for their patience when I stranded them without gasoline or a broken motor and for their willing submission to the torture of editing my thesis. Of the *trabajadores* that figured prominently, I thank Marcos Rosado for helping me recover his lunches and dinners, to Neftali Figueroa and Angel L “Negrito” Camacho for fixing and switching boats for me when I needed a larger, safer boat to explore the outer areas, for dealing with my nuances, and for being all around amiable, and to Juan Traval for fixing my spear constantly after I broke it once again.

Finally, I would like to thank my fiancé for her patience, understanding, and love; for without her, I would have quit and taken another path through life.

Table of Contents

LIST OF TABLES	viii
LIST OF FIGURES	x
LIST OF APPENDICES	xi
CHAPTER 1: INTRODUCTION	1
CHAPTER 2: VIABILITY OF CODED WIRE TAGGING ON JUVENILE <i>HAEMULON FLAVOLINEATUM</i> (FRENCH GRUNT) AS DETERMINED BY GROWTH, SURVIVAL, AND TAG RETENTION UNDER EXPERIMENTAL CONDITIONS	7
1.0 Introduction	7
2.0 Materials and Methods	9
2.1 Collection of fish for tank studies	9
2.2 Experimental preparation	10
2.3 Tagging	10
2.4 Data analysis	11
3.0 Results	12
3.1 Survival	12
3.2 Growth	14
3.3 Retention	19
3.4 Length-weight relationships	19
4.0 Discussion	20
5.0 Implications	21
CHAPTER 3: DIRECTIONAL MOVEMENTS OF <i>HAEMULON FLAVOLINEATUM</i> (FRENCH GRUNT)	23
1.0 Introduction	23
2.0 Materials and Methods	25
2.1 The study site	25
2.2 Structural design of the study	29
2.3 Small-scale juvenile movement	29
2.4 Large juvenile/adult movement	31
2.5 Data analysis	32
3.0 Results	32
3.1 Small-scale juvenile movement	32
3.2 Large-scale juvenile/adult movement	35
4.0 Discussion	36
4.1 Small scale movements	36
4.2 Large scale movements	38
5.0 Implications	39

CHAPTER 4: GROWTH AND SURVIVORSHIP OF <i>HAEMULON FLAVOLINEATUM</i> AS DETERMINED BY MARK AND RECAPTURE STUDIES AT LA PARGUERA, PUERTO RICO WITH COMPARISONS TO LABORATORY RAISED SPECIMENS	41
1.0 Introduction	41
2.0 Materials and Methods	42
2.1 Study site.....	42
2.2 Tagging	44
2.3 Data analysis	45
3.0 Results	46
3.1 Recovery	46
3.2 Growth increments.....	46
3.3 Conversion equations.....	48
3.4 von Bertalanffy growth parameters	50
4.0 Discussion	50
CHAPTER 5: CONCLUSIONS AND RECOMMENDATIONS.....	53
LITERATURE CITED.....	54
APPENDIX A.....	65
APPENDIX B.....	67
APPENDIX C.....	68

List of Tables

<u>Tables</u>	<u>Page</u>
2.1 Number, survival, and cumulative survival of tagged and untagged juvenile <i>Haemulon flavolineatum</i> held in a 5-m diameter tank for 90 days. Ratio is the number of tagged to untagged fish at each sampling.....	13
2.2 Fork length (cm) and weight (g) for tagged and untagged <i>Haemulon flavolineatum</i> by sampling period during Experiment 1 (a) spanning March to June 2004, and Experiment 2 (b) spanning September to December 2004.....	15
2.3 Number of live and dead tagged and untagged juvenile <i>Haemulon flavolineatum</i> recorded at each sampling period over 90 days during Experiment 2.....	19
2.4 Selected conversion equations for FL (cm) to Wt (g) of <i>Haemulon flavolineatum</i> . The parameter (a) in the equation $Wt=a(FL)^b$ is condition index.....	20
3.1 Descriptive statistics for fork length (cm) by location of juvenile <i>Haemulon flavolineatum</i> and <i>H. plumieri</i> in resting schools found in the Majimo/Caracoles area of the initial mark-recapture study.....	28
3.2 Recovery data for ontogenetic movement of small-tagged juveniles of <i>Haemulon flavolineatum</i> (Flav) and <i>H. plumieri</i> (Plu) among school groups. The numbers before the dash in recovery column are the school group and the number after the dash is the visit.....	33
3.3 Recovery data for ontogenetic movement of large-tagged juveniles of <i>Haemulon flavolineatum</i> (Flav) to adult habitat. Days at liberty with stars (*) denote fish recovered at a location other than the tagging location.....	34
4.1 Recovery data for ontogenetic movement of small juveniles of <i>H. flavolineatum</i> (Flav) and <i>H. plumieri</i> (Plu) among school groups.....	47
4.2 Recovery data (time, size, location) for large juveniles of <i>H. flavolineatum</i> (Flav). (*) Denotes fish without movement.....	48
4.3 Daily incremental growth (cm/day fork length) of <i>Haemulon flavolineatum</i> from the tagging experiments. Comparisons of growth in Experiment 2 between fish showing and not showing movement exclude individuals at liberty for less than 30 days.....	49

4.4	Length (cm) to weight (g) conversion equations for juvenile <i>Haemulon flavolineatum</i> . Common slopes and intercepts are given when ANCOVA results indicate that the equations are not significantly different. (-) Indicates no data is available. A common equation for FL to TL was not developed because slopes were not equal.....	49
4.5	Estimates of the von Bertalanffy parameters (L_{∞} and k) for <i>Haemulon flavolineatum</i> . Values for W_{∞} were derived from L_{∞} using the conversion equations in Table 4.....	50

List of Figures

<u>Figure</u>	<u>Page</u>
2.1 Growth in mean fork length for Experiments 1 (left) and 2 (right). Experiment 1 ran from March to June 2004 and Experiment 2 ran from September to December 2004.	16
2.2 Incremental growth in mean weight during Experiment 1 (left) and 2 (right). Experiment 1 ran from March to June 2004 and Experiment 2 ran from September to December 2004.	16
2.3 Histogram displaying the starting fork lengths of all tagged fish at the beginning of the experiment (white) and of those recovered at the end of the experiment (black). Experiment 1 is on top and Experiment 2 is on the bottom.	18
3.1 Habitat map of the study area off La Parguera, Puerto Rico (from Kendall et al. 2001). Circles indicate locations for attempted recapture by spearing and trapping of <i>Haemulon flavolineatum</i>	25
3.2 La Parguera, Puerto Rico showing benthic habitats (from Kendall et al. 2001) and the tagging locations of <i>Haemulon flavolineatum</i> located on the three reefs used in the study.	26
3.3 Location of juvenile grunt resting schools monitored for tags at Majimo/Caracoles reef in La Parguera, Puerto Rico. Red numbers and dots are the schools (See Table 1); black numbers are the number of recaptured individuals at each location. Solid blue lines are the confirmed feeding routes, while dashed lines are the extension of those routes. Benthic habitats shown are from Kendall et al. (2001).	27
3.4 Tagging locations on three reefs with the benthic habitats (from Kendall et al. 2001) for La Parguera, Puerto Rico and the subsequent recovery locations and numbers for transitional adults.	31
4.1 La Parguera, Puerto Rico showing benthic habitats (from Kendall et al. 2001) and the tagging locations located on the three reefs used in the study.	43

List of Appendices

<u>Appendix</u>	<u>Page</u>	
A	<p>Mark-recapture data sorted by group for small juvenile movements (Experiment 1) including all captured haemulid species. Tagged is the number of fish tagged, Caught is the total number of fish captured and measured, and Recapture is the number of fish caught in that sample with marks. The numbers before the dash in Group column are the school group (see Chapter 3) and the number after the dash is the sampling event for recovery. Mean, minimum and maximum lengths are cm FL. Species: French = <i>Haemulon flavolineatum</i>, White = <i>H. plumieri</i>, Blue = <i>H. sciurus</i>, Tomtate = <i>H. aurolineatum</i>, Ceasar = <i>H. carbonarium</i>, Sailor = <i>H. parra</i>, Small = <i>H. chrysargyreum</i>, Spanish = <i>H. macrostomum</i>.....</p>	63
B	<p>Geospatial coordinates (decimal degrees) of the 14 sampled grunt-schooling locations at Majimo/Caracoles (Figure 3, Chapter 3).</p>	65
C	<p>Locations sampled for the recovery of tagged haemulids in Experiment 2 (see Chapter 3) studying large-scale juvenile to adult habitat movement. Data are organized by sampling sequence. The first two locations were recovery of dead individuals while tagging. Method code indicates spearing (1), Arrowhead trapping (2), or juvenile net and trap (3). Effort is defined as man-hours of operation (Time*Number of divers). Time indicates hours spent spearing or soak time for traps in days (as indicated). Number of Fish is the number of haemulids recovered (<i>Haemulon flavolineatum</i> or <i>H. plumieri</i>). <i>H. plumieri</i> were only recovered in traps and listed in their own column. C/E is the catch per unit of effort (Number of Fish/Effort) for spear sampling only. Effort and C/E were not calculated for traps as indicated by (-). The three traps with (?) were recorded, but dates and soak time were lost.</p>	66

CHAPTER 1: INTRODUCTION

As in many animals, reef fishes in tropical environments undergo migrations for reproduction (Warner 1995, Aguilar-Perera and Aguilar-Davila 1996, Domeier et al. 1996, Rosario Jimenez and Figuerola Fernandez 2001), feeding (Ogden and Ehrlich 1977), and to minimize the risk of predation (Dahlgren and Eggleston 2000). During migrations, fishes often cross several types of habitats, e.g. reef, seagrass, mangrove, and sand. For many commercially important and managed species, the understanding of how their habitats are connected in relation to their migration is of great importance (Recksiek and Appeldoorn 1998, Nagelkerken 2000, Recksiek et al. 2001). Many studies have documented ontogenetic migrations involving distinct habitat shifts. For example, Appeldoorn et al. (1997) found an increase in median size in the white grunt, *Haemulon plumieri*, progressively moving offshore, inferring an ontogenetic migration from inshore to offshore habitats.

Werner and Gilliam (1984) proposed that the ultimate reason for ontogenetic migrations is to minimize the ratio between mortality and growth. They postulated that habitat selection is determined by an individual's need to remain protected while attempting to maximize growth. Dahlgren and Eggleston (2000) supported this theory by studying juvenile Nassau groupers, *Epinephelus striatus*, in both juvenile and adult habitat. They found that juvenile habitat reduced potential for growth compared to the adult habitat, but minimizes the risks of predation proportionately.

During ontogenetic migrations, fishes migrate to different habitats according to life cycle stage and physical development. Some examples of fishes undergoing ontogenetic migrations are Haemulidae (Appeldoorn et al. 1997, 2003, Nagelkerken 2000, Nagelkerken et al. 2000, Lindeman et al. 2000, Recksiek et al. 2001, and Cocheret de la Morinière 2002, Cocheret de la Morinière et al. 2003a), Lutjanidae (Lindeman et al. 2000, Nagelkerken et al. 2000, Friedlander et al. 2002, Christensen et al. 2003, Cocheret de la Morinière et al. 2003b, Szedlmayer and Lee 2004), Serranidae (Eggleston 1995, Dahlgren 1999, Dahlgren and Eggleston 2000), *Elops saurus* (McBride et al. 2001), and Labridae (Robertson and Foster 1982). These ontogenetic habitat shifts depend upon fish

growth, food utilization and mortality, and can often be predicted by environmental gradients.

In tropical regions, grunts (*Haemulidae*) are of commercial (Appeldoorn and Lindeman 1985) and ecological (Meyer and Schultz 1985) importance, spawn year round, and have variable recruitment on a semi lunar cycle (McFarland et al. 1985). Grunts are among the most numerous species on Atlantic tropical reefs (Rasotto and Sadovy 1995; Lindeman et al. 1998) Aggregations of several hundred juveniles can be found close to mangrove prop roots and patch reefs (Ogden and Ehrlich 1977, Quinn and Ogden 1984, Rooker and Dennis 1991, Nagelkerken 2000, Cocheret de la Morinière 2002), then undergo ontogenetic migrations from these nursery areas to coral reef habitats as they mature (Appeldoorn et al. 1997, 2003, Lindeman et al. 2000, Nagelkerken 2000, Recksiek et al. 2001, and Cocheret de la Morinière 2002). These migrations involve changes in the diet (Dennis 1992) and behavior (Appeldoorn et al. 1997), both of which appear to be linked casually with length (Mateo 1999). Yet, while we know the distribution of grunts, and that they undergo migrations offshore to adult habitats; we do not understand the pathways utilized by these fishes.

The French grunt (*Haemulon flavolineatum*) is perhaps the most abundant and ubiquitous fish in coral reef ecosystems within the region. As juveniles, they are the most numerous of *Haemulon* sp. comprising over 80% of the total catch of daytime resting schools (Hein 1999), are an important invertebrate consumer off the coral reef (Ogden and Erlich 1977, Dennis 1992, Roque et al. unpublished data), contribute to nutrient transport and increased coral growth (Meyer and Schultz 1985), and act as a common source of food for predatory fishes (McFarland et al. 1979). Grunts compromise the majority of the catch in Puerto Rico (Appeldoorn and Lindeman 1985) and contribute up to 7% of Florida's recreational catch. Most notably, French grunts are similar in behavior and ecology to the larger, more commercially important grunt species (Lindeman 1986).

Fish use several physical methods for dispersion, including tides and currents. They have well developed sensory abilities such as vision, olfaction, and hearing for detecting directional cues toward preferred habitats. Despite that, many tropical marine species undergo ontogenetic migrations, there is a lack of studies on the linkages between

habitats and developmental stages (Appeldoorn et al. 2003). The present work targets understanding the migratory pathways used during ontogeny, to what extent these pathways connect habitat and how grunts are able to detect such pathways.

Migration and related underlying factors have long been studied. Unfortunately, the majority of these studies have focused on a few commercially important species of temperate regions, especially the salmonids. Other studies have been conducted with species that are in danger of extinction, such as sturgeons and paddlefish.

There are several ways fishes can detect habitat: olfaction, temperature, magnetism, vision, sound, and physical processes (Kingsford et al. 2002). Olfaction has proven to be a vital sense for homing in salmon (Cooper et al. 1976), being even more accurate than visual cues (Nagiec 1975). Olfaction has also proven to be important in navigation for the European silver eel, *Anguilla anguilla* (Westin 1998). While olfaction is important in these species, it is not the only factor determining successful navigation. Both of these species are born in an area, disperse away, and then return to their natal area to spawn. During juvenile migrations, they develop an imprint of the route, and the reversal of that memory proves to be important to successful homing (Westin 1998). Using sense-impaired and farmed European silver eels, *A. anguilla*, Westin (1998) demonstrated the ability of eels to home in on temperature and smell, but postulated that physical factors in the Baltic Sea prevent and confuse migrating eels from reaching the Sargasso Sea during their return migration. Salmon develop large olfactory bulbs early in their ontogeny, which continue to develop into adult stages. The bulbs detect odors, such as the pheromones of local populations, guiding them to spawning grounds (Baker and Montgomery 2001) and aiding in the avoidance of tributaries contaminated with metals (Goldstein et al. 1999).

Another possible factor is vision, but due to the limited field of vision of a fish's eye and the properties of light in water, vision should play a minor role in migration between juvenile and adult habitat. However, vision may be a factor when migrating between juvenile aggregations (Kingsford et al. 2002). Additionally, during nightly feeding migrations grunts are able to visually distinguish markers along feeding routes in the seagrass, even when displaced from the pathways (Ogden and Erlich 1977).

A more important factor than vision could be sound detection. Fish are known to communicate with each other and are able to differentiate between amplitude and frequency, allowing for the detection of intraspecific calls (Hawkins 1986). In addition, reef larvae can detect reefs by sound from at least one kilometer away (Leis et al. 1996). McCauley (1997) was able to detect reef sounds over the ambient sound levels as far as 4-20 km away from their sources. Furthermore, reef larvae are more attracted to traps emitting reef sounds than pelagic larvae (Tolimieri et al. 2000).

Passive guidance by physical processes (i.e. tidal movements and currents) is another possible mechanism for dispersal. Tidal flows aid in the dispersal (Robertson and Foster 1982), duration, and direction (Takeno and Hamanaka 1994, Aprahamian et al. 1998, Moore 1999) of migration. Many studies have shown the importance of ebb or flood tide transport, through a bay or estuary for silver eels, salmonids (Robertson and Foster 1982, McCleave and Wippelhauser 1987, Lacroix and McCurdy 1996, Aprahamian et al. 1998, Moore et al. 1998, Moore 1999), plaice, *Pleuronectes platessa*, (Metcalf et al. 1994) and menhaden, *Brevoortia tyrannus* (Forward et al. 1999).

Although there are several mechanisms available to guide fish migration, it is still unknown what triggers fish to migrate between habitats. Physiological senses (vision and olfaction) used for migration are developed during ontogeny; hence, most fish migrations depend upon the fish's physiological condition. In salmon, Veselov et al. (1998) studied downstream migration in relation to the development of parrs and smolts. They noted that behavioral changes were associated with development. During the alevin stage, (second stage after the embryo and before the parr stage) when they reside in between the gravel of the streambed, salmon have a negative association with current flow and visual acuity is low. In the parr stage, the ability to swim against the current and visual acuity improve. They then become territorial and maintain station above the gravel bed until winter when they descend to the bed again. In spring, when they smolt, salmon rise out of the gravel bed, but visual acuity and ability to maintain position decrease. At this stage, smolts begin to school and start the migration downstream (Hansen et al. 1995, Moore 1999). In clupeids, migration between habitats is dependent upon the development of auditory and retinal systems (Higgs and Fuiman 1998). In French grunts, timing of the feeding

migrations is dependent upon the level of retinal development (McFarland and Wahl 1996). The large-scale ontogenetic migration of white grunts to offshore habitats has been estimated at 15-18 cm, the approximate size of sexual migration, but location and behavior are more closely related to size, not the state of sexual maturity (Mateo 1999).

Another issue even less studied concerns whether migrations occur as an individual or group event. In salmon, it depends on the lifecycle stage. During the parr stage (the third stage of development), it is territorial and migrates as an individual, but when it develops into the smolt stage (the fourth stage of development as it transitions into the sea), it rises and begins to school (Veselov et al. 1998). Robertson and Foster (1982) documented the departure of juvenile *Epibulus insidator* (Labridae) offshore while mimicking mangrove leaves individually or in groups up to ten individuals. Voellestad et al. (1994) transplanted European silver eels, *Anguilla anguilla*, upriver during their downstream migration and determined that the number of recaptured fish increased with increasing numbers of non-tagged migrants. This suggests that European silver eels prefer to migrate as a group.

In the coral reef ecosystem, juvenile grunts migrate to nightly feeding grounds as a size specific group, and may migrate between juvenile habitats in the same manner. McLean and Herrnkind (1971) observed a schooling group of large transitional sized grunts in a sand flat two kilometers away from the nearest reef. Appeldoorn et al. (1997) postulated that this was an observation of transitional grunts disbursing to adult habitats, although they warned of the possible effects of a turbidity cloud seen behind the migrating grunts. From this, it is possible that grunts were migrating to the reef as a group. Individual schools of grunts may travel together in a preferred direction toward adult habitats, therefore seeing individuals from a school grouped together at discrete reefs.

This thesis utilizes *H. flavolineatum* as an indicator species to elucidate the ontogenetic movements of juveniles in both small short-term interschool movements, and larger long-term offshore movements through a mark recapture program. The study has been divided into three parts. Chapter 2 explores the effects of the tagging methodology on juvenile grunts. Chapter 3 focuses on ontogenetic migrations by examining both short-

term and long-term movements. Finally, in Chapter 4, growth from tagged and recaptured fish was quantified and an overall growth model developed.

CHAPTER 2: VIABILITY OF CODED WIRE TAGGING ON JUVENILE *HAEMULON FLAVOLINEATUM* (FRENCH GRUNT) AS DETERMINED BY GROWTH, SURVIVAL, AND TAG RETENTION UNDER EXPERIMENTAL CONDITIONS.

1.0 Introduction:

Many fishes make ontogenetic migrations, progressively moving from settlement and nursery areas, often inshore, to adult habitats (Beck et al. 2001). Such migrations are characteristic of many species that inhabit coral reefs as adults (Lindeman et al. 2000, Nagelkerken et al. 2002, Cocheret de la Morinière et al. 2002) with seagrass beds and mangroves typically acting as settlement/nursery areas. The common occurrence of juveniles in these habitats, and the clear progression of mean sizes to offshore areas is generally a good indicator of ontogenetic migrations, and given growth information the timing of such migrations can be inferred (Appeldoorn et al. 1997). However, these types of data do not give information on pathways or mechanisms of migration, nor do they identify which habitats, or areas of a single habitat type are most important for the growth and survival of juveniles (Beck et al. 2001).

Grunts (Family: Haemulidae) are commercially (Appeldoorn and Lindeman 1985) and ecologically (Meyer and Schultz 1985) important coral reef fishes that undergo ontogenetic migrations from shallow seagrass beds and mangroves to reef environments (Appeldoorn et al. 1997, 2003, Lindeman et al. 2000, Nagelkerken et al. 2002, Cocheret de la Morinière et al. 2002, Mumby et al. 2004). While these studies have determined the basic patterns of migration, they have not determined the path of migration, except in very constrained circumstances (e.g., Cocheret de la Morinière et al. 2002). One contributing factor has been the difficulty in tracking juveniles over the time frame that ontogenetic migrations occur.

Tagging is the most straightforward way to track individuals or groups of fishes. There are three prerequisites to using tagging methods to study ontogenetic migrations. Because the tagging of juveniles is necessary, tags must be applicable to small fishes without affecting behavior. Given the time frame of ontogenetic migration, tags must be retained over the full course of the migration (potentially years), which also requires that large numbers of juveniles be tagged to account for the large rate of mortality expected in small juveniles (Shulman and Ogden 1987).

Several studies of grunts have employed various methods for tagging. Monroe (personal communication) tagged large juveniles in Jamaica using t-bar anchor tags, but noted little movement over a period of 1.38 years. Appeldoorn and Recksiek (unpublished data), similarly attempted to use these tags to track the movement of large juveniles (10-13 cm TL) in Puerto Rico, but found the tags significantly increase mortality, with marked fish rapidly disappearing. Tank and field observations revealed lesions from rubbing the tag against hard substrata, harassment by conspecifics and other species, and individual acts of predation.

To study site fidelity, Hein (1999) used colored beads sewn to the dorsal musculature next to the soft dorsal fin. His results showed high fidelity over seven days, but also an exponential rate of disappearance. Like Appeldoorn and Recksiek, he suspected that predators singled out tagged fish.

Freeze branding and tattooing were also successfully attempted by Appeldoorn and Recksiek (unpublished data). However, freeze branding large numbers of individuals was difficult in conditions of high humidity, where water vapor would freeze on the brand, thus causing a buffer between the fish and the brand. Large numbers of juveniles can be tattooed with alizarin blue dye using a dental air injector, but this method is best suited for batch processing due to the limited areas where the tattoo sufficiently contrasts with the skin (i.e., the white pigmentation of the caudal and ventral areas). Tattoos can last up to a year, but more generally for a shorter time, while freeze brands tended to fade after six months. Additionally, small individuals (<7 cm) suffered high mortality particularly due to the shock of freeze branding.

In a manner similar to tattooing, Ogden and Ehrlich (1977) painted juveniles with a day-glow fluorescent pigment imbedded in the skin at 100psi. The paint would slough off when immersed in water, but the imbedded particles were detectable under ultraviolet light. Pigments were detectable for 2 months, but longer-term retention is unknown. Mortality also is unknown, but Phinney et al. (1967) reported negligible mortality in young salmonids from this process.

Passive integrated transponder (PIT) tags were successfully used by Appeldoorn and Recksiek (unpublished data) to individually tag large juvenile white grunts (*H. plumieri*). These tags are surgically implanted into the body cavity and have good

retention. However, the tagging is a slow process, and fish less than 10 cm TL show high rates of mortality.

In summary, previous studies have shown external tags to cause high mortality, surface marks to have limited duration, and internal PIT tags to be impractical for either large numbers or small individuals. As a consequence, none of these methodologies met the prerequisites necessary for the study of ontogenetic migration pathways. Coded wire tags (CWTs) are small (1.1 mm) magnetically charged stainless steel wires that are inserted into the fish. Because of their small size, low injury rates, internal implantation, and lowered mortality from intraspecific and predator interactions, CWTs are ideal for tagging small fish. They have been successfully implanted in anchovies (Leary and Murphy 1975), and juvenile salmon (Blankenship and Tipping 1993), catfish, bass, shiners, and bluegills (Heidinger and Cook 1988). With a low per tag cost and an expected high survival of tagged individuals, CWTs represent a potentially viable alternative for tagging large numbers of juvenile grunts.

The purpose of this study was to test the applicability of CWTs to the study of ontogenetic migration pathways of juvenile *H. flavolineatum*. Of principle concern was the method of tagging, the effect of CWTs on survival and growth, and their rate of retention. These factors were studied in a controlled tank environment using juvenile French grunts (*H. flavolineatum*) as the test species.

2.0 Materials and Methods

2.1 Collection of fish for tank studies

Using a trap and net setup similar to Ogden and Ehrlich (1977), juvenile fish were collected from the wild along the known feeding migration paths of specific resting schools of juveniles. This allowed for the collection of targeted size groups. Personnel surveyed the targeted school prior to and during its off-reef migration at dusk and marked the migration pathway. The nets and trap were placed across the migration pathway in such a manner that the nets would guide returning fish at dawn towards the mouth of the trap. The trap was monitored at dawn, and when the fish had been guided into the trap, a door on the trap was closed. Captured fish were placed in a seawater filled container and transferred to the laboratory by boat.

At the laboratory, fish were placed in a 5-meter diameter tank. The tank had a flow through seawater system with a coralline sand bottom acting as a filter. Fish were feed once daily with squid and other marine proteins. Food that was not consumed was removed.

2.2 Experimental preparation

Two tank studies, each 90 days in duration were conducted. The first began in March and the second in September. The first study was preliminary in nature and was conducted to become familiar with the tagging methodology as much as the impact of tagging on the fish. From a tank population of over 200 juvenile *H. flavolineatum* ranging in size from 6.9 to 12.3 cm FL, 50 were tagged. The total population size at the start was not determined due to initial problems in recovering all fish from the large tank (see below).

In the second study, a sample of 183 *H. flavolineatum* were used, ranging in size from 6.5-12 cm FL to represent the full range of juvenile sizes available. Fish were allowed to acclimate to the tank for at least 24 hours. From the 183 selected fish, a subsample of approximately 73 randomly selected fish was tagged.

Measurements of fish size and tag retention were made at six intervals: 0, 7, 14, 30, 60, and 90 days. These periods were selected so that retention values could be compared to other studies. To resample the fish, a net was swept over the bottom of the tank. Initially (Study 1), not all fish were caught. During that experiment the recapture procedure became more efficient and was repeated a number of times until no additional fish were caught. For each fish caught, the fork length (FL) and total length (TL) were measured to the nearest 1 mm and wet weights (g) were obtained for all fish. At the end, fish with tags were sacrificed to retrieve the tags and thus identify individuals, and to measure individual growth rates from beginning to the end of 90 days. Mortality was examined daily during feeding times.

2.3 Tagging

Experimental fish were tagged with Northwest Marine Technology's (NMT) decimal coded wire tags (DCWT) in the nape. This location was based on consultations

with NMT personnel and other published studies showing this location to result in high retention and survival rates. Beukers et al. (1995) tagged juvenile damselfish in the nape musculature and obtained 80% retention of tags with laboratory survival of 90%, while Buckley et al. (1994) tagged juvenile rockfish and had 100% retention. Heidinger and Cook (1988) tested several tagging locations for fingerlings of channel catfish, golden shiners, and bluegills. Nape-tagged fish resulted in tag losses of up to 8% after 6 months, but had no effects on growth or survivorship. In contrast, small juveniles often did not have suitable cheek locations, while fish tagged nasally suffered greater tag loss (Heidinger and Cook 1988).

The DCWTs were 0.25 mm by 1.1 mm stainless steel. In the first study, tags were inserted individually using a syringe injector. In the second study, tags were inserted using a NMT multishot hand injector. To conduct the tagging, fish were first held in a transfer tank, then individually hand-held while the needle was inserted into the nape. The needle penetrated 4 mm (to the edge of the needle support collar when using the multishot injector). Each tag was inserted with the push wire and the push wire was held in place while drawing out the needle to ensure insertion of the tag. Retention was checked using a NMT handheld tag detector. Fish were dipped in a freshwater bath for 20 seconds and then placed back in the tank.

In the first trial, the 50 fish tagged with DCWTs were also double tagged using a colored fluorescent elastomer tag supplied by Northwest Marine Technologies. This aided in assessing the reliability of tag detection. The needle was inserted at a shallow angle into the white underbelly to allow visibility of the colored tags. The elastomer was injected into the puncture and then held down while withdrawing the needle to make a small line about 4 mm long.

2.4 Data analysis

Estimates of survival were calculated from the number of individuals known to survive from one sampling period to the next sampling period, and expressed as percent survival. These values were arcsine transformed for statistical testing (Zar 1996) using a student's T-test of means. In addition, the overall survival pattern through the experiment

was tested using a chi-square matrix on all periods, and again using only the start and end values.

For each sampling period, data on fork length, weight, and tag status were recorded. Mean size data were tested by ANOVA and student's t-test to determine the affect that tags and sampling period had on growth. Incremental growth data were tested by student's t-test for fork length and weight.

Retention was determined for the second tank experiment only (see above). A range of retention was determined based on two assumptions. Under the first, missing tagged fish were assumed to have lost their tags, and only dead fish (N_D) recovered with tags were used to reduce the original number (N_0). Under the second, missing tagged fish (N_{TM}) were assumed to have retained their tags but disappeared from the tank (ie. decayed prior to the next observation time), thus effectively lowering the number of fish tagged at the start of the experiment. Retention (R) was determined by

$$\text{Assumption 1: } R = \frac{N_F}{N_0 - N_D} \quad (1)$$

$$\text{Assumption 2: } R = \frac{N_F}{N_0 - N_D - N_{TM}} \quad (2)$$

Conversion equations for fork length to weight, and total length to weight were calculated assuming allometric growth.

$$W = aL^b \quad (3)$$

where W is weight (g) and L is length (cm). Data for fork length and weight were \log_{10} transformed and the parameters determined by linear regression. A regression between fork length and total length (without transformation) yielded a linear equation for conversion.

3.0 Results

3.1 Survival

Forty-five of 50 fish tagged in Experiment 1 survived to the end of 90 days (cumulative survival = 0.90). Forty-three individuals were identified and two tags were

Table 1. Number, survival, and cumulative survival of tagged and untagged juvenile *Haemulon flavolineatum* held in a 5-m diameter tank for 90 days. Ratio is the number of tagged to untagged fish at each sampling.

Period (Days)	Ratio Tag: Untag	Untagged			Tagged			Total		
		N	Period Survival	Cum Survival	N	Period Survival	Cum Survival	N	Period Survival	Cum Survival
0	0.66	110	-	1.00	73	-	1.00	183	-	1.00
7	0.63	109	0.99	0.99	69	0.95	0.95	178	0.97	0.97
14	0.68	102	0.94	0.93	69	1.00	0.95	171	0.96	0.93
30	0.63	99	0.97	0.90	62	0.90	0.85	161	0.94	0.88
60	0.64	96	0.97	0.87	61	0.98	0.84	157	0.98	0.86
90	0.62	93	0.97	0.85	58	0.95	0.79	151	0.96	0.83

lost in processing. During the second month of the experiment and increasing in the third month, minor sores and fin rot were noted on some individuals. Sores were not associated with the position of tag insertion but were seen on all parts of the body, and in extreme cases, tails were devoured until the bones were exposed.

Table 1 lists survival from Experiment 2. In this experiment, 73 fish were tagged and 64 were recovered over 90 days. Sixty-two fish from the 64 recovered tags were read. Two were lost while preparing the tags for reading. Fifty-eight individuals survived to the end for a cumulative survival of 0.79. Untagged survival was 0.85.

Monthly survivorship averaged 0.92 for tagged fish and 0.95 for untagged fish, and were not statistically different ($t=-0.973$, $p=0.433$). However, survival was not uniform over time. During the first month, survival was lower for both tagged (0.84) and untagged (0.90) fish. The pattern of survivorship (Period Survival, Table 1) between tagged and untagged fish exhibited no difference ($t=-0.0923$, $p=0.930$). Chi-square tests of the overall pattern of survival (tag count and untagged count) showed non-significant differences over the entire period ($\chi^2_3=0.986$) and for counts at the beginning and end ($\chi^2_1=0.783$). Fin rot and sores were noted within 1 week of tagging during the second experiment, although widespread infections were not observed until the second and third months. As in the first study, sores were on all locations of the body, with the majority of loss exposing the tailbones

3.2 Growth

Data for growth during Experiments 1 and 2 can be seen in Table 2. Temperatures during Experiment 1 increased over the study and ranged from 26-29°C. Tagged and untagged fish were not statistically different for fork length at the start ($t_{0.05,98}=0.038$) and end ($t_{0.05,186}=1.048$) in Experiment 1 (Figure 1). During Experiment 1, fork length increased significantly over the study period ($t_{0.05,91}=4.355$). The pattern of growth (FL) between time periods was also similar for tagged and untagged fish ($t=0.74$, $p=0.500$) with growth trends across sampling periods being unaffected by the tags ($F=0.62$, $p=0.684$). Tagged fish grew 1.230 cm over 90 days, averaging 0.01366 cm/day. Untagged fish grew 1.009 cm over the same period and averaged 0.01121 cm/day. Individual growth from recovered tagged fish averaged 0.01074 cm/day (SE = 0.001218). This

Table 2. Fork length (cm) and weight (g) for tagged and untagged *Haemulon flavolineatum* by sampling period during Experiment 1 (a) spanning March to June 2004, and Experiment 2 (b) spanning September to December 2004.

	Tagged						Not Tagged				
	Day	N	Mean	StDev	Min	Max	N	Mean	StDev	Min	Max
Fork Length (a)	0	50	9.35	1.13	6.9	11.5	51	9.357	1.05	7.4	12.0
	7	39	9.43	1.06	7.1	11.5	126	9.32	1.62	6.9	12.3
	14	41	9.61	1.07	7.1	11.6	144	9.36	1.15	7.0	12.1
	30	44	9.70	1.12	7.1	12.2	149	9.38	1.15	6.9	11.8
	60	36	10.16	1.07	7.3	12.1	155	9.73	1.12	7.4	12.2
	90	44	10.58	1.15	8.0	12.8	145	10.36	1.11	7.5	12.9
Weight (a)	0	50	17.54	6.35	6	32	51	17.71	6.09	9	37
	7	39	17.56	6.24	6	32	126	16.87	6.47	6	35
	14	41	19.63	6.48	7	35	144	17.88	6.69	6	37
	30	44	20.27	7.04	7	38	149	18.08	6.56	6	35
	60	36	23.19	7.31	8	39	155	20.41	7.42	7	40
	90	44	26.98	8.94	10	46	145	24.99	8.58	9	49
Fork Length (b)	0	73	9.63	1.02	7.4	11.6	110	9.89	1.10	7.4	12.2
	7	69	9.63	1.00	7.5	11.7	109	9.91	1.10	7.0	11.8
	14	69	9.68	0.94	7.2	11.5	102	9.85	0.99	7.2	11.8
	30	62	9.63	1.00	7.4	11.6	98	9.91	0.97	7.6	11.9
	60	61	10.14	0.97	7.7	12.0	96	10.49	0.94	8.2	12.5
	90	58	10.42	0.93	7.8	12.4	93	10.71	0.86	8.5	12.5
Weight (b)	0	73	16.06	5.77	7	36	110	17.89	6.49	6	35
	7	68	16.13	5.35	6	28	109	17.51	5.93	7	33
	14	69	18.10	5.58	7	32	103	19.14	6.22	6	38
	30	62	18.31	5.75	8	32	98	20.28	6.31	8	39
	60	61	19.84	6.81	7	37	96	22.09	6.85	8	42
	90	58	19.05	6.67	5	38	93	21.81	6.63	9	40

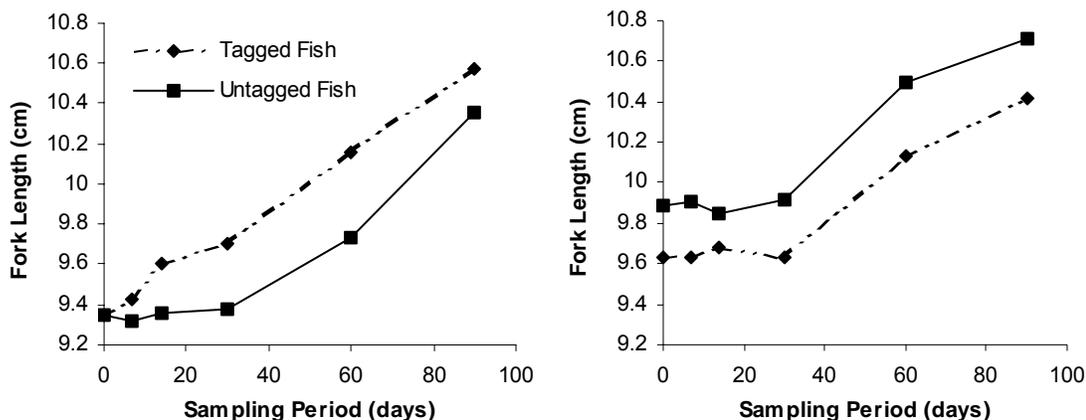


Figure 1. Growth in mean fork length for Experiments 1 (left) and 2 (right). Experiment 1 ran from March to June 2004 and Experiment 2 ran from September to December 2004.

growth rate was not different than the mean growth of tagged fish (above) ($t_{0.05,43}=0.139$) obtained using the mean length difference of all tagged fish at the start and end. Weight increased significantly over the study ($t_{0.05,91}=4.370$), but no significant differences were observed in mean weight between tagged and untagged fish at the start ($t_{0.05,97}=0.140$) and end ($t_{0.05,185}=1.274$) of Experiment 1 (Figure 2). Additionally, patterns of growth

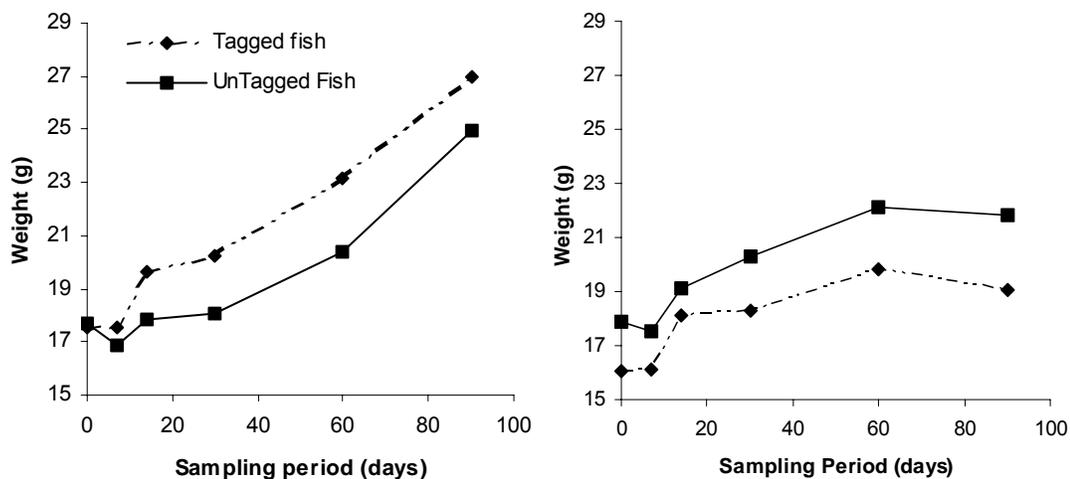


Figure 2. Incremental growth in mean weight during Experiment 1 (left) and 2 (right). Experiment 1 ran from March to June 2004 and Experiment 2 ran from September to December 2004.

(Wt) across time periods for tagged and untagged fish were not significantly different ($t_{0.05,5}=0.917$, $p=0.411$). Tagged fish had a mean growth of 9.44 g (0.10489 g/day), while untagged fish grew by a mean of 7.28 g (0.08088 g/day). Individual recovered tagged fish grew 0.07202 g/day (SE =0.009142) on average, and this was not different from the growth (Wt) interval indicated by the mean difference in weight of all tagged fish ($t_{0.05,43}=0.111$).

Growth in fork length ($t_{0.05,200}=5.863$) and weight ($t_{0.05,200}=4.243$) were significant during Experiment 2. Existing differences in starting mean fork lengths ($t_{0.05,180}=1.601$) and weights ($t_{0.05,180}=1.959$) of tagged and untagged fish were not statistically different, but by the end of the experiment mean fork length ($t_{0.05,148}=1.989$) and weight ($t_{0.05,148}=2.486$) were significantly greater for untagged fish (Figure 1, 2). However, the patterns of incremental growth of fork length ($t_{0.05,4}=0.18172$) and weight ($t_{0.05,4}=0.70323$) indicated that there were no differences in growth between tagged and untagged fish. While growth by sampling period was unaffected by tags in Experiment 2 ($F=0.38$, $p=0.866$), mean fork length of tagged fish increased by 0.788 cm and untagged fish added 0.823 cm. The averages were 0.008755 cm/day and 0.009144 cm/day, respectively. However, the average individual growth (FL) of recovered tagged fish resulted in a mean of 0.0071 cm/day (SE=0.00066). As observed in Experiment 1, this value was not different from the mean growth of the tagged population obtained from the start and end of the experiment ($t_{0.05,59}=0.09455$). Weight increased during the experiment by 2.995 g (0.033278 g/day) and 3.915 g (0.0435 g/day) for tagged and untagged fish, respectively. Mean individual weight growth of recovered tagged fish was 0.058024 g/day (SE =0.00670), which was not different from the weight increase of the tagged population obtained from the mean change in weight at the start and end of the experiment ($t_{0.05,29}=0.685$).

That individual growths of tagged fish was consistently less than that resulting from differences in mean length at the start and end of the experiments implies that smaller fish were not recovered (i.e., selective mortality) or grew slower than larger fish due to competitive differences or food particle size. Histograms (Figure 3) of starting fork lengths and the starting lengths of recovered tagged fish, although skewed to the right

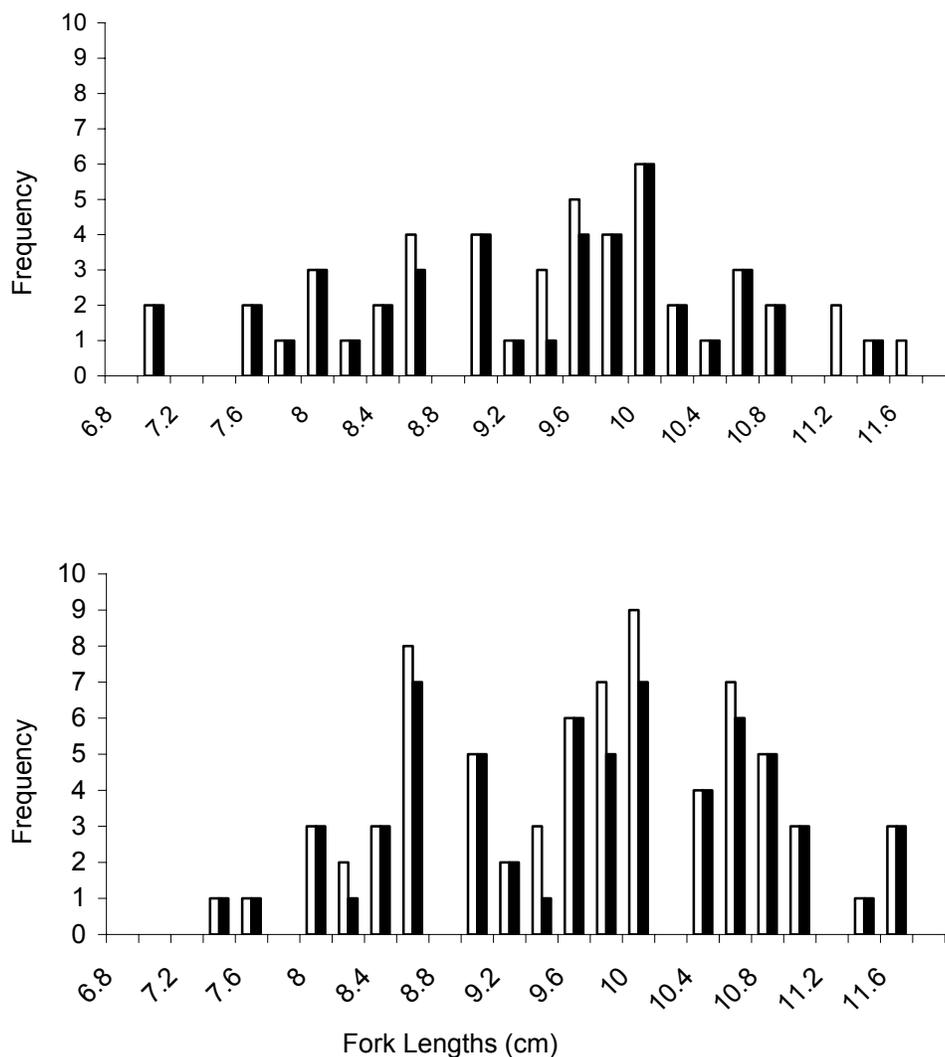


Figure 3. Histogram displaying the starting fork lengths of all tagged fish at the beginning of the experiment (white) and of those recovered at the end of the experiment (black). Experiment 1 is on top and Experiment 2 is on the bottom.

slightly, indicated that fish were lost at all points throughout the curve. Lost fish from Experiment 1 skewed positively (0.051), while recovered fish skewed slightly negatively (-0.356). A t-test of starting fork lengths between missing fish and those recovered indicate that no statistical difference existed ($p=0.657$). The frequency curves of starting fork length during Experiment 2 both skewed negatively. Missing fish (-0.733) were skewed to the left more over recovered fish (-0.146). A t-test revealed that the starting fork lengths for missing and recovered fish continued to be similar ($p=0.062$).

Table 3. Number of live and dead tagged and untagged juvenile *Haemulon flavolineatum* recorded at each sampling period over 90 days during Experiment 2.

Period (days)	Tagged		Untagged	
	Live	Dead	Live	Dead
0	73	0	110	0
7	69	2	109	2
14	69	0	102	4
30	62	5	98	5
60	61	0	96	2
90	58	0	93	0

3.3 Retention

After tag injection, testing showed tag detection to be 100%. The entire girth of the animal passed within the detection field of the wand. Over the study (Experiment 2), two fish were determined to have lost tags, and six tagged fish disappeared from the tank (Table 3). Known tag loss occurred only during the first month. Based upon the two assumptions (Equation 1 & 2), retention ranged from 0.879 to 0.967 (Table 3).

3.4 Length-weight relationships

The slopes of length-weight relationships (Table 4) were compared to determine the similarity between tagged and untagged fish. Data indicated that fish in Experiment 1 began with dissimilar slopes ($F_{1,101}=6.14$), however, both slopes ($F_{1,189}=0.01625$) and intercepts ($t_{0.05,189}=1.14019$) had converged to equality by the end of the study. Slopes ($F_{\text{start},1,183}=0.013086$; $F_{\text{end},1,151}=0.56786$) and intercepts ($t_{\text{start},0.05,183}=0.79836$; $t_{\text{end},1,151}=1.95920$) for tagged and untagged fish during Experiment 2 showed no differences.

During both experiments (1 and 2), the condition index increased substantially during the first month, followed by a steady decline during the last two months. The onset of the decline, in both cases, occurred at the time that evidence of disease was noticeable in the tank-held fish

Table 4. Selected conversion equations for FL (cm) to Wt (g) of *Haemulon flavolineatum*. The parameter (a) in the equation $Wt=a(FL)^b$ is condition index.

Regression Table					
Source	Day	Treatment	Equation	R ²	\bar{a} value
Pooled Lab			Log Wt = 3.2208*Log FL - 1.92413	0.92616	0.01199
Experiment 1					
	0		Log Wt = 3.1139*Log FL - 1.7952	0.97590	0.01605
	7		Log Wt = 3.0764*Log FL - 1.7769	0.91200	0.01682
	14		Log Wt = 3.1015*Log FL - 1.779	0.97520	0.01666
	30		Log Wt = 3.0321*Log FL - 1.7083	0.96590	0.01962
	60		Log Wt = 3.1783*Log FL - 1.8507	0.97840	0.01412
	90		Log Wt = 3.2204*Log FL - 1.8887	0.97210	0.01295
Experiment 2					
	0		Log Wt = 3.2677*Log FL - 2.0249	0.88290	0.00953
	7		Log Wt = 3.1731*Log FL - 1.9349	0.91930	0.01168
	14		Log Wt = 3.1897*Log FL - 1.9001	0.91990	0.01266
	30		Log Wt = 3.1466*Log FL - 1.845	0.93780	0.01434
	60		Log Wt = 3.4308*Log FL - 2.1736	0.90220	0.00674
	90		Log Wt = 3.7088*Log FL - 2.5042	0.83530	0.00316
Experiment 1					
	0	Tagged	Log Wt = 3.17192*Log FL-1.85621	0.98296	0.01394
	0	Untagged	Log Wt = 2.92656*Log FL-1.61180	0.96431	0.02450
	90	Tagged	Log Wt = 3.20056*Log FL-1.87470	0.96770	0.01337
	90	Untagged	Log Wt = 3.19780*Log FL-1.86753	0.97228	0.01359
Experiment 2					
	0	Tagged	Log Wt = 3.21766*Log FL-1.97992	0.87997	0.01055
	0	Untagged	Log Wt = 3.28455*Log FL-2.03880	0.88420	0.00924
	90	Tagged	Log Wt = 3.78215*Log FL-2.59107	0.82073	0.00260
	90	Untagged	Log Wt = 3.57601*Log FL-2.36008	0.84312	0.00440

4.0 Discussion

Over the first 30 days, growth in length was reduced in both experiments and for both groups. However, during this time an increase in the condition index was observed. Figures 1 and 2 show that this occurred because fish added weight slightly during the first 30 days while length growth stalled. The decrease in growth in length may be a response to handling and an acclimation to a change in diet. As fish resumed a normal growth pattern for length, the condition index fell to initial levels as added weight was converted into length growth. Subsequently, condition indexes declined to further levels below those observed for *Haemulon flavolineatum* in Jamaica (Gaut and Munro 1983).

Over both experiments, a presumable bacterial disease affected fish. This disease appears to have affected the condition of the fish, but survivorship during the final two months was stable at approximately 0.96/month. It is possible that the experiments were terminated before the disease was reflected in higher mortality.

During Experiment 1, recovered tagged fish averaged growth of 0.010948 cm (FL)/day. Given that little to no growth occurred during the first month, this value rises to 0.0164 cm/day if the first month is excluded. The adjusted value is a bit higher than growth of similar sized fish released into the wild (Chapter 4). Growth during the second experiment (FL) (0.0071 cm (FL)/day) was less compared to the first experiment. Again, given the apparent experimental effect, this value increases to 0.0107 cm (FL)/day when excluding the first month. The differences between Experiment 1 and 2 may be due to seasonal or temperature differences; however, tagged fish released in the wild during the same period as Experiment 2 averaged 0.0151 cm (FL)/day (Chapter 4), a value closer to Experiment 1.

Tagged fish showed high survival during the preliminary experiment (90% over 90 days), in accordance with other tagging studies of juvenile fish (Beukers et al. 1995, Heidinger and Cook 1988). In the second experiment, both tagged and untagged fish showed a lower 90-day cumulative survival. An experimental effect was evident for both groups, with increased mortality of tagged and untagged fish during the first month. After the first 30 days, survival of both groups increased to a constant monthly survival around 0.96; this was over the period where the effects of the wasting disease became obvious, but without apparent inputs on mortality.

Retention ranged from 0.879 to 0.967 for nape tagged *H. flavolineatum*, depending upon the assumptions used for missing fish. These values are high and typical of results in other species (Heidinger and Cook 1988, Tipping 1993, Buckley et al. 1994, Beukers et al. 1995).

5.0 Implications

The implications from this study are that coded wire tags do not effect the growth and survival of tagged fish compared to untagged fish. Retention in nape tagged *H. flavolineatum* was good and stabilized after 30 days in a fashion similar to other studies

(Heidinger and Cook 1988); indicating that after that period, tags likely are retained until recapture. Tags apparently do not affect growth, but acclimation to the tank and feeding regime took at least 30 days.

For studies involving the release of tagged fish in the wild, data indicated that fish will retain tags over the study period with minimal loss, and mortality should be equal at all times to untagged fish. Growth of released tagged fish will be indistinguishable from untagged fish.

CHAPTER 3: DIRECTIONAL MOVEMENTS OF *HAEMULON FLAVOLINEATUM* (FRENCH GRUNT)

1.0 Introduction

Many coral reef fishes show characteristic habitat shifts during ontogeny (Brothers and McFarland 1981, Appeldoorn et al. 1997, Dahlgren and Eggleston 2000, McBride et al. 2001). Such ontogenetic migrations are thought to minimize the ratio of mortality over growth (Werner and Gilliam 1984). Ontogenetic migrations are well defined in grunts (Haemulidae) and evidenced by the shift in size distributions with progressive offshore locations (Brothers and McFarland 1981, Appeldoorn et al. 1997, 2003).

Grunts are a commercially and ecologically important genus (Meyer and Shultz 1985, Appeldoorn and Lindeman 1985). *Haemulon flavolineatum*, the most numerous of the genus and one of the most ubiquitous fish on the reef, is well studied during its early life history (Environmental tolerance: Sylvester 1973, Hoss et al. 1986; Taxonomy: Konchina 1976; Schooling behavior: Ogden and Ehrlich 1977, Helfman et al. 1982, Hein 1996; Vision: McFarland et al. 1979, McFarland and Wahl 1996; Energy transport: Meyer et al. 1983, Meyer and Schultz 1985; Juvenile ontogeny: McFarland and Kotchian 1982, Lindeman 1986; Orientation: Quinn and Ogden 1984; Recruitment: Shulman 1984, 1985, McFarland et al. 1985, Bortone et al. 1988, Lindeman 1989, Hein 1999, Hill 2001, Lindeman et al. 2001, Cocheret de la Morinière et al. 2002; Diet: Estrada 1986, Dennis 1988, 1992, Heck and Weinstein 1989, Cocheret de la Morinière et al. 2003a,b; Mortality: Shulman and Ogden 1987, Hein 1999; Spatial distribution: Lindeman et al. 1998, Kendall et al. 2003, Adams and Ebersole 2002; Ontogenetic migration: Appeldoorn et al. 1997, 2003, Nagelkerken 2000, Cocheret de la Morinière et al. 2003a,b; Predation: Danilowicz and Sale 1999; Habitat contribution: Nagelkerken et al. 2002, Nagelkerken and Van der Velde 2004).

During ontogeny, juvenile grunts will undergo a series of migrations between habitats (and associated resting schools) (Appeldoorn et al. 1997, 2003, Nagelkerken

2000, Cocheret de la Morinière 2002). These migrations are associated with changes in diet and behavior (Appeldoorn et al. 1997) and appear to be strongly correlated with fish length (Mateo 1999). There are 6 eco-behavioral stages of development reported for *H. flavolineatum* (Appeldoorn et al. unpublished) and *H. plumieri* (Appeldoorn et al. 1997). These stages begin with newly settled fish and proceed through to adult. Newly settled fish start life by settling in seagrass at 1-1.5 cm TL. At this point, they are considered Stage 0 juveniles and settle opportunistically on small isolated structures within seagrass beds while continuing to feed on plankton during the day. Stage 0 fish begin nightly feeding migrations, but do not feed. As juveniles (Stage 1 and 2), they aggregate on patch reefs and size-segregate into schools (Ogden and Erlich 1977). At 3.0 cm TL (Stage 1), individuals form daytime resting schools on structures within the seagrass near the reef. Individuals at this stage are transitional in their feeding ecology and smaller individuals may continue to feed on plankton during the day. From 5.5 to 12 cm TL (Stage 2), *H. flavolineatum* continue to form daytime resting schools. Individuals transition forward on the reef where schools are found in deeper water and along the reef edge (Hill 2001). At 12.0 to 15.0 cm TL (sub-adult), *H. flavolineatum* continue to school during the daytime and migrate to feeding grounds at night. Although they migrate and school, they begin to roam and display more adult like behavior. At 15 cm TL (adult), *H. flavolineatum* mature and migrate offshore (Appeldoorn et al. 1997, 2003).

Inference from school positions and mean size of *H. flavolineatum* give a general indication of the transitional timing and the general areas/habitats involved in ontogenetic migrations, but do not indicate the pathways. Understanding these pathways is critical for protecting essential fish habitat and areas acting as nursery or source areas for adult populations (Beck et al. 2001). Pathways that are bounded by land are simple to understand (e.g., embayments with narrow openings to open reef environments; Nagelkerken 2000, Cocheret de la Morinière 2002); however, it is more difficult to determine pathways, orientation cues, and factors affecting migration in an open coastal environment consisting of mangrove and seagrass beds sheltered by fringing reefs.

Little is known of the actual pathways taken by juveniles to adult habitat. Appeldoorn et al. (2003), commenting on the lack of such studies for tropical marine

fishes, emphasized the need to understand the linkage between habitats and developmental stages. This study aims to ascertain the direction taken by juvenile *H. flavolineatum* and the cues used during ontogenetic migration through a mark and recapture program.

2.0 Materials and Methods

2.1 The study site

The study was conducted at La Parguera (Figure 1) located in southwest Puerto Rico (17.97159° N, 67.04517° W). The embayment at La Parguera consists of three shelf systems (inner, middle, and outer) that parallel the coast (Morelock et al. 1977). These reefs are not subject to fresh water input, except during rain. The average depth of the

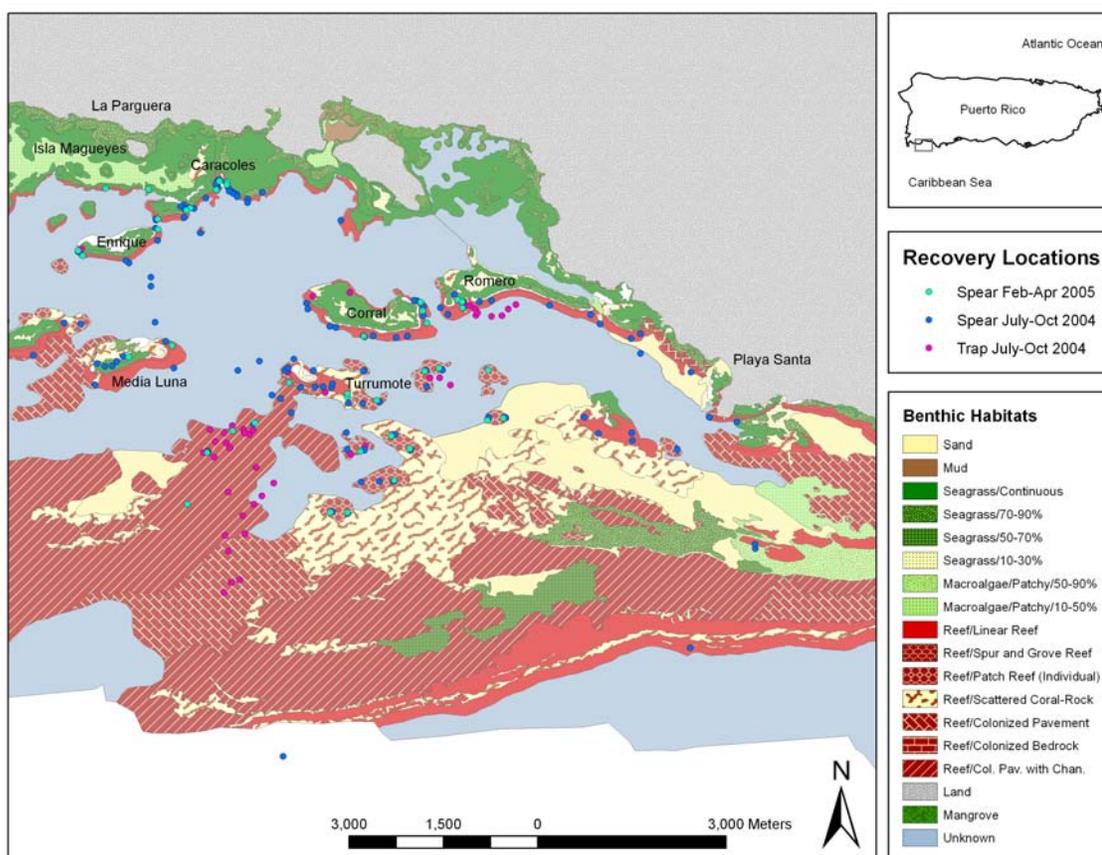


Figure 1. Habitat map of the study area off La Parguera, Puerto Rico (from Kendall et al. 2001). Circles indicate locations for attempted recapture by spearing and trapping of *Haemulon flavolineatum*.

shelf is between 18-20 meters, with the inner shelf averaging 6 meters (Morelock et al. 1994).

Tagging was conducted at three inner shelf reefs: Caracoles, Corral, and Romero (Figure 1, 2). Caracoles proper is covered by mangroves, protecting a shallow lagoon with seagrass. The reef is linear and runs on a northeast axis curving to the east at the northern tip. Depths along the fore reef approach 10 meters at the reef slope. The lagoonal area behind the reef is less than 2 m. The reef is approximately 850 m long and

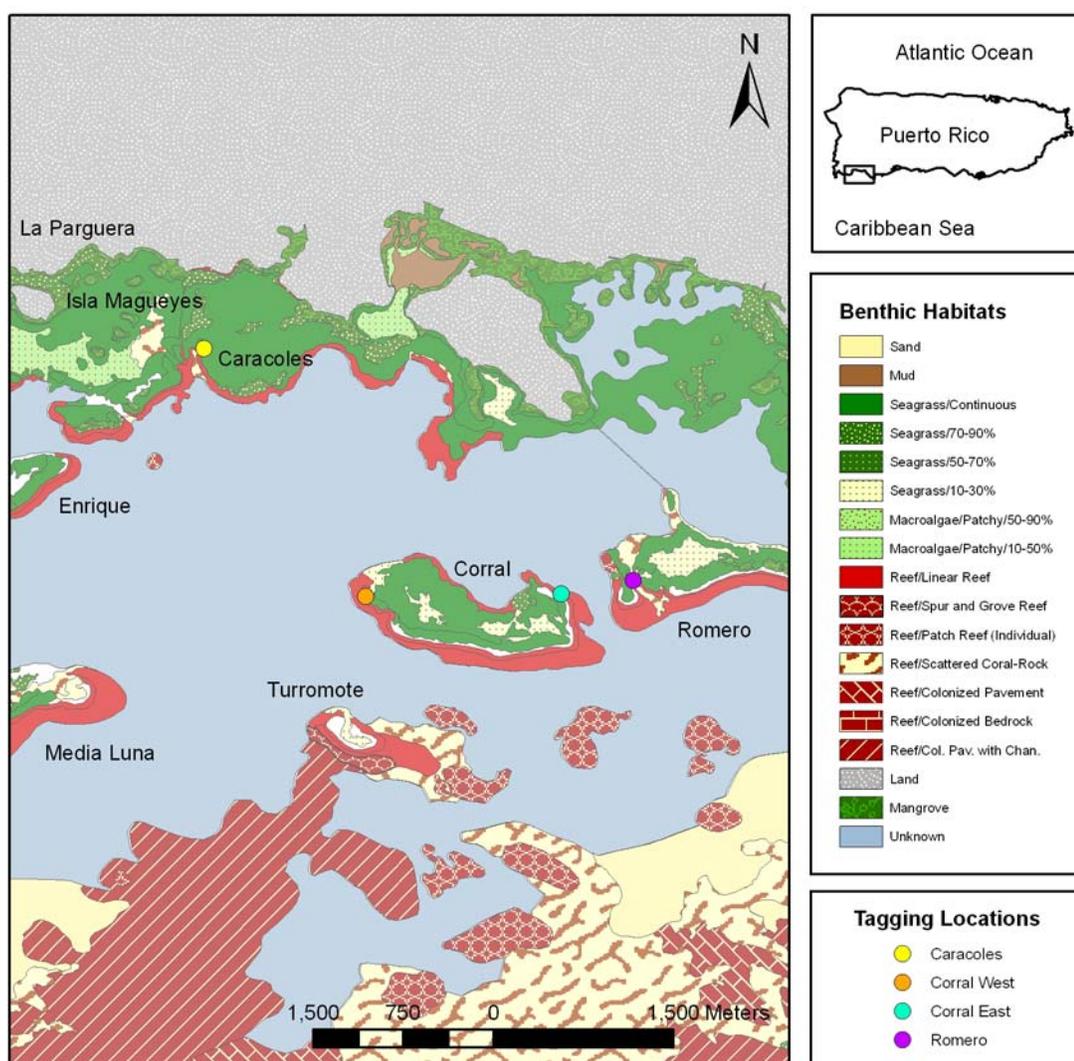


Figure 2. La Parguera, Puerto Rico showing benthic habitats (from Kendall et al. 2001) and the tagging locations of *Haemulon flavolineatum* located on the three reefs used in the study.

has an adjoining submerged reef area called Majimo, which is where tagging and initial recaptures were conducted. Majimo is composed of two patch reefs surrounded by seagrass and patches of gorgonians. A 2-m deep seagrass channel runs between the patch reefs, and a 4-m deep channel that grades from seagrass around the reef halo into sand and rubble near the reef slope further separates Majimo from Caracoles. Twelve daytime resting schools of juvenile *H. flavolineatum* were located at the Caracoles site and grade from small mean sizes to larger sizes toward the reef slope (Figure 3, Table 1). Schools are found within crevices and depressions within the coral structure and also among the braches of *Acropora cervicornis* and *Millipora complanata*.

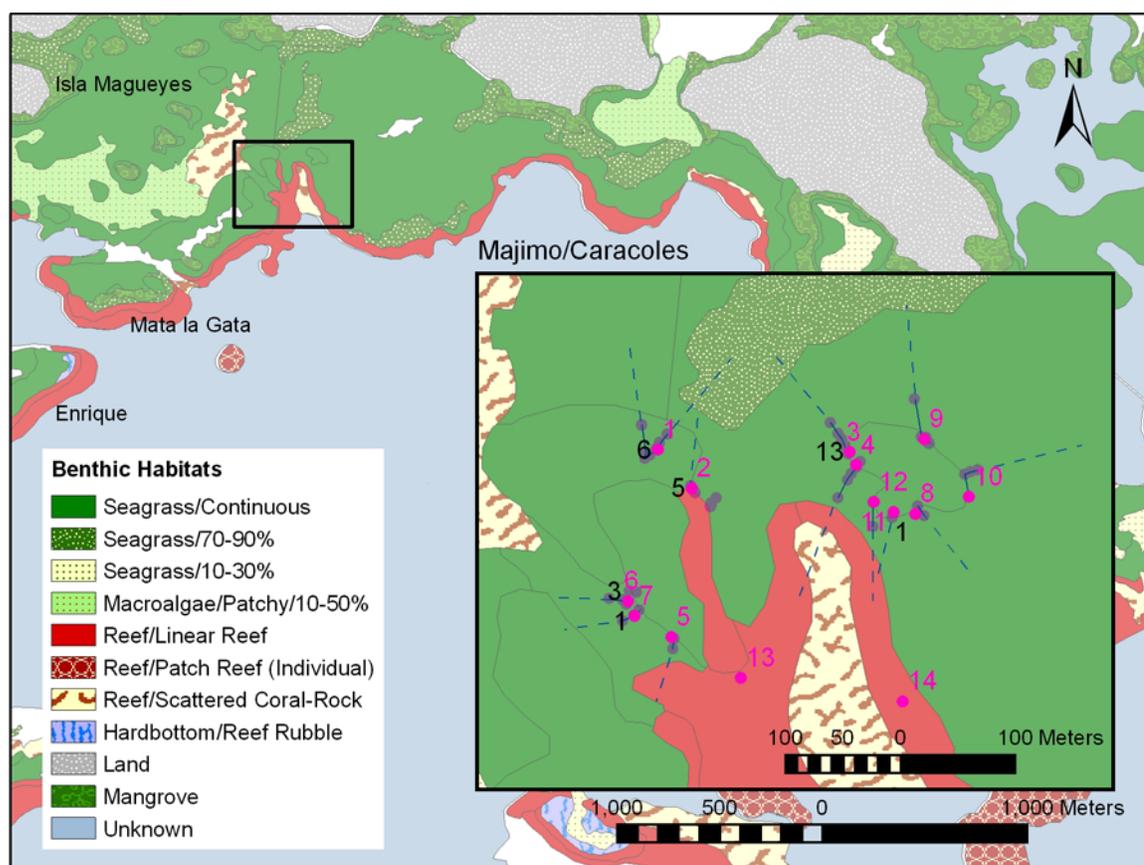


Figure 3. Location of juvenile grunt resting schools monitored for tags at Majimo/Caracoles reef in La Parguera, Puerto Rico. Red numbers and dots are the schools (See Table 1); black numbers are the number of recaptured individuals at each location. Solid blue lines are the confirmed feeding routes, while dashed lines are the extension of those routes. Benthic habitats shown are from Kendall et al. (2001).

Table 1. Descriptive statistics for fork length (cm) by location of juvenile *Haemulon flavolineatum* and *H. plumieri* in resting schools found in the Majimo/Caracoles area of the initial mark-recapture study.

Resting School Site	N	Mean	StDev	Minimum	Maximum
1	698	6.956	1.294	4.7	12.0
2	85	12.254	2.972	7.4	25.8
3	1060	7.867	1.578	5.0	12.2
4	952	7.742	1.709	4.6	12.2
5	580	7.975	1.768	4.5	13.1
6	1577	7.458	1.377	5.0	12.7
7	2138	8.346	1.579	5.1	14.2
8	549	10.218	2.226	5.5	16.1
9	733	8.099	1.903	4.4	13.6
10	931	7.940	2.405	5.1	28.5
11	215	9.784	2.215	5.8	15.4
12	622	8.028	1.718	4.9	14.0
13	9	13.911	1.280	12.8	16.4
14	23	13.739	1.082	11.5	15.2

The reef platform at Corral is 2 km long and 630 m wide (Figure 2). The fore reef is u-shaped and runs east to west. There is a coral rampart on the seaward side with a few mangrove trees established. On the east side is a deep channel (20 m) separating the reef from Romero. This side has no mangroves, and a small coral rampart is formed. A shallow reef terrace, composed of small outcroppings and crevices of coral, extends into a gorgonian plain that drops to 20 m. At the northeast corner of the reef (near the tagging site), water flows over the reef crest. The resting school targeted for tagging sits on a shallow patch of *M. complanata* that is bordered on the lagoonal side by seagrass at 0.5 m. The lagoon is less than 2 m deep and is composed of thick beds of *Thalassia testudinum* and smaller patches of *Syringodium filiforme*; interspersed are alga hummocks. The lagoon side of Corral gradually drops from 2 m down to 20 m toward the mainland. On the western extension of Corral, there is a large emergent patch reef (another tagging site) separated from the main reef by a shallow channel. Interspersed among the various coral heads is a large school of juvenile French grunts. They occupy sheltered areas formed by colonies of *Acropora cervicornis* or that occur around the

bases of *Siderastrea siderea*. Romero is an L-shaped fringing reef covered with mangroves and at its far eastern end is connected to the mainland by a narrow lagoonal channel (Figure 1, 2). The reef is 3.3 km long with a relatively shallow (5 m) short (50 m) terrace composed of gorgonians and reef pavement. The lagoon side of Romero is composed of shallow seagrass beds. At the seaward edge, the slope drops quickly to 20 m. A channel separates the western end of the emergent reef from the main reef. The channel is 6 m at the deepest and is lined with sand. It is deeper at the seaward mouth and shallows less than 2 m at the lagoon side. At the edges, the channel is lined with boulder corals. An extremely large school of juvenile *H. flavolineatum* (targeted for tagging) was located midway on the east side of the channel, residing in large clumps of *Acropora cervicornis*.

2.2 Structural design of the study

The study was designed to investigate ontogenetic movements at two different scales. A small-scale study was designed to test movement among schools within a single reef site. At a larger scale, the movement of individuals targeted the migration pathways and cues used by subadults thought to make larger transitions to off reef locations. Tagging and subsequent recovery locations were specifically selected to reveal potential environmental cues related to choice of migratory pathway.

2.3 Small-scale juvenile movement

The experiment on small juvenile movement occurred at Majimo (Figure 3), where several schools in close proximity were located. The exact positions of each school were determined using a Garmin™ GPS with differential correction, and the approximate size range and quantities at each school were recorded using visual census. For each school, the twilight feeding migrations were observed, and pathways were marked with floats. One school (Site 1, Figure 3 and Table 1) was selected for tagging based on the apparent isolation of its feeding pathway from other schools, the desired median size and abundance of fish, potential sites for recapture, as well as the relative position of the site to factors thought to affect ontogenetic habitat shifts, such as the amount, type and location of surrounding habitats. In addition, observations indicated a general increase in

the mean length of fish in resting schools more seaward of Site 1, indicating the potential of fish leaving Site 1 to move toward these other schools.

Fish from Site 1 were trapped four times using an adaptation of Ogden and Ehrlich's (1977) net and trap method over a 1-month period (August 22, 2003-Sept 24, 2003). The net and trap were placed across the migration pathway in such a manner that the nets guided returning fish toward the trap mouth. The trap was monitored at dawn, and when the fish were corralled into the trap, a gate was closed. The trap was brought to the surface and served as a holding pen.

Fish were removed from the trap in small batches and placed in buckets of fresh seawater for tagging, measuring (FL and TL), and a check for tag retention. Untagged fish were tagged in the nape using decimal coded wire tags, following the procedure developed in Chapter 2. Reference tags were saved in a silicon strip. Saving a reference tag for each fish ensured that each individual could be identified should there be any problems reading the tag upon recapture. Tagged fish were rechecked for retention, placed in a holding pen, and released at the schooling location. Fish were allowed a 1-month period to recover and grow before trapping for recaptures commenced.

Sampling for recaptures ran from October 22, 2003 to March 10, 2004 and occurred at the 12 resting school locations using the same trapping procedure, and at two additional (13 and 14). Fish at the latter locations consisted of larger individuals showing subadult behavior. At these sites, the change in behavior required that spearing be used for recapture sampling. Each location was targeted for monthly sampling. Captured fish were measured (FL and TL) and checked for retention. Tagged fish were retained and brought to the laboratory for tag removal.

At the laboratory, tagged fish were measured (FL and TL) and weighed. Tags were cut out and placed in a labeled beaker. Flesh was dissolved from the tags using a 4% sodium hydroxide solution (Drãno™), rinsed in water, and read under a dissecting microscope. Tags were manipulated with a magnetic tag pencil.

2.4 Large juvenile/adult movement

Four locations were selected to study movements of larger transitional individuals: Caracoles, Corral East, Corral West, and Romero West (Figure 2, 4). These locations were selected due to the abundance of individuals and because their position relative to potential recapture sites may help deduce the cues used by migrating fish. Greater effort was put into tagging juveniles of at least 10 cm (FL) at Romero and Caracoles, while fewer fish were tagged at Corral due to the difficulty of capturing fish. The targeted size was designed to get sufficient numbers of tagged individuals (using the net-trap method), while minimizing the time at large because this is near the suspected transition size from juvenile to adult stages in *H. flavolineatum*.

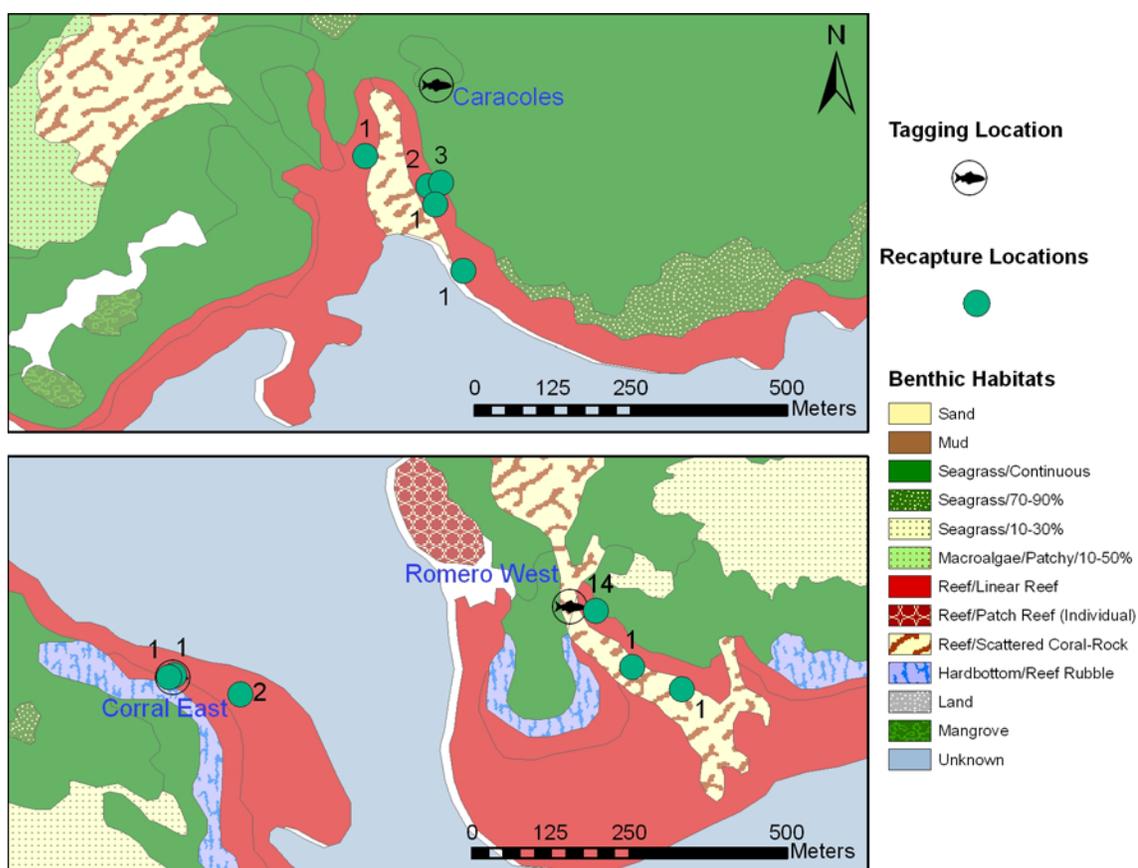


Figure 4. Tagging locations on three reefs with the benthic habitats (from Kendall et al. 2001) for La Parguera, Puerto Rico and the subsequent recovery locations and numbers for transitional adults.

Fish were captured from May 2004 to October 2004. Recovery sampling occurred from February to April 2005. Selection of recovery sampling sites (Figure 1) was based on the NOAA benthic habitat map (Kendall et al. 2001) cross-referenced with depths for likely locations that may contain adult fish. For spearing, dives were planned for 30 to 45 minutes at each site and divers speared fish with Hawaiian slings. Shallower areas were explored by snorkeling. In addition, at some locations, fish were captured using unbaited Caribbean arrow traps soaked for 3-5 days. After hauling, traps were moved to a new location. Laboratory methods followed those of small-scale juveniles.

2.5 Data analysis

For small-scale movements, a difference in the mean length (FL) of fish in schools was tested using ANOVA. This was to confirm the observed relative increase in the mean length of resting schools seaward of Site 1. For recovered tagged fish, fork lengths (beginning and end) were tested (Kruskal-Wallis) to determine if time at liberty or distance moved were a function of length. Additional tests were made on the relationship between time at liberty and tagging date, and time at liberty and distance moved. Finally, recovery location was examined as a function of tagging date. Directionality was tested using a binomial probability that individuals favored seaward migration to the east of the channel (Sites 2, 3, 4, 12, 11, and 8) versus the west side (Sites 6, 7, 5).

3.0 Results

3.1 Small-scale juvenile movement

One hundred and sixty-eight fish were tagged to study small-scale interschool movement within a reef. Eighty percent of tagged fish were *Haemulon flavolineatum* (n=134) and 20% were *H. plumieri* (n=34). Over the 4-month period from October 2004 to January 2005 10,173 *H. plumieri* (13.3%) and *H. flavolineatum* (86.7%) were sampled for recaptures. A total of 29 tagged fish were recovered (Table 2): 3 *H. plumieri* (9% recapture rate) and 26 *H. flavolineatum* (19% recapture rate).

Out of 29 tagged fish recovered, 28 could be read (one tag was lost in the recovery process) (Table 2). Of the 28 recovered tags 18 (64.3%) were from the second

Table 2. Recovery data for ontogenetic movement of small-tagged juveniles of *Haemulon flavolineatum* (Flav) and *H. plumieri* (Plu) among school groups. The numbers before the dash in recovery column are the school group and the number after the dash is the visit.

Species	Date Tagging	Days at Liberty	Recovery Location-Sample	Final Fork Length	Change in Fork Length	Distance Moved
Flav	09/03/03	21	1-1	7.6	0.1	0
Flav	09/03/03	101	1-2	10.2	2.0	0
Flav	09/03/03	101	1-2	9.1	2.4	0
Flav	09/03/03	101	1-2	9.1	1.6	0
Flav	09/03/03	101	1-2	9.9	2.2	0
Flav	09/24/03	80	1-2	9.2	1.5	0
Flav	09/03/03	49	2-1	10.1	1.1	48
Flav	09/24/03	28	2-1	11.1	0.1	48
Flav	09/03/03	92	2-2	9.3	1.0	48
Flav	09/03/03	92	2-2	10.2	1.3	48
Flav	09/24/03	113	2-3	10.6	1.3	48
Flav	09/03/03	55	3-1	8.5	0.6	154
Flav	09/24/03	34	3-1	10.5	0.5	154
Flav	09/24/03	34	3-1	9.2	0.6	154
Flav	?	?	3-1	10.5	?	154
Flav	09/03/03	93	3-2	9.0	1.0	154
Flav	09/03/03	93	3-2	8.6	1.1	154
Flav	09/03/03	93	3-2	9.3	1.2	154
Flav	09/03/03	93	3-2	8.3	0.8	154
Flav	09/03/03	93	3-2	8.5	0.3	154
Flav	09/03/03	135	3-3	10.6	2.5	154
Flav	09/03/03	135	3-3	8.7	1.2	154
Plu	09/19/03	119	3-3	9.4	3.0	154
Plu	09/19/03	119	3-3	9.3	2.7	154
Flav	09/03/03	100	6-2	8.3	0.8	133
Plu	09/19/03	84	6-2	9.0	2.0	133
Flav	09/24/03	79	6-2	7.9	0.9	133
Flav	09/03/03	76	7-1	7.9	0.7	141
Flav	08/22/03	158	8-3	12.1	2.5	216

tagging session and 6 (21.4%) were from the fourth tagging session at Site 1. Their time at liberty ranged 21-158 days.

From those 29 fish migrating from site 1, 12 moved 154 m to Site 3, one moved 141 m to Site 7, three moved 133 m to Site 6, five moved 48 m to Site 2, and finally one moved 216 m to Site 8. The fish recaptured at Site 8 (Figure 3) not only moved the farthest, but also had the longest time at liberty (158 days). This fish was from the first

Table 3. Recovery data for ontogenetic movement of large-tagged juveniles of *Haemulon flavolineatum* (Flav) to adult habitat. Days at liberty with stars (*) denote fish recovered at a location other than the tagging location.

Species	Date Tagging	Days at Liberty	Tagged Location	Final Fork Length (cm)	Change in Fork Length (cm)	Distance Moved
Flav	10/08/2003	7	Corral East	10.9	0.0	0
Flav	10/08/2003	503*	Corral East	14.7	4.8	109
Flav	10/08/2003	503*	Corral East	14.4	3.7	109
Flav	10/16/2003	292*	Corral East	13.5	2.0	0
Flav	01/30/2004	160	Romero West	11.9	0.6	50
Flav	01/30/2004	160	Romero West	11.8	0.6	50
Flav	01/30/2004	160	Romero West	11.3	0.6	50
Flav	01/30/2004	160	Romero West	13.4	1.1	50
Flav	01/30/2004	160	Romero West	11.3	0.5	50
Flav	01/30/2004	160	Romero West	11.0	0.3	50
Flav	01/30/2004	160	Romero West	12.2	0.1	50
Flav	01/30/2004	160	Romero West	11.7	0.9	50
Flav	01/30/2004	160	Romero West	12.2	0.8	50
Flav	01/30/2004	160	Romero West	13.5	0.8	50
Flav	01/30/2004	160	Romero West	13.0	1.2	50
Flav	01/30/2004	160	Romero West	11.5	0.9	50
Flav	01/30/2004	160	Romero West	13.3	1.8	50
Flav	01/30/2004	390	Romero West	14.8	3.7	109
Flav	02/27/2004	14	Romero West	11.6	-0.3	50
Flav	03/17/2004	97*	Caracoles	11.2	0.4	155
Flav	03/17/2004	97*	Caracoles	11.7	0.5	155
Flav	06/15/2004	239*	Caracoles	13.7	3.1	153
Flav	06/24/2004	82*	Caracoles	11.1	0.6	164
Flav	06/30/2004	226*	Caracoles	13.1	2.6	187
Flav	07/01/2004	96*	Caracoles	11.3	0.0	297
Flav	07/01/2004	223*	Caracoles	13.6	2.1	153
Flav	07/01/2004	223*	Caracoles	13.0	2.3	153
Flav	11/21-26/2003	489-494?*	Romero West?	14.9	2.4-5.7	178

batch to be tagged. Of the fish recaptured at the tagging site, one was caught on September 24, 2003 (21 days at liberty). The other five were caught in a single recapture sample; four were free for 101 days, while the remainder was free for 80 days. The four fish recovered were tagged September 3, 2003.

Mean fork length between the 14 schools was statistically different ($p < 0.001$), with schools nearer the reef front having larger mean sizes (Figure 3, Table 1). Tests further indicate that the distance moved was positively correlated to length at both tagging ($p = 0.015$) and recapture ($p = 0.021$). Distance moved was not affected by the time

at liberty ($p=0.374$) nor the growth in fork length ($p=0.081$). Time at liberty of individuals was not significantly related to fork length ($p_{\text{start}}=0.118$ and $p_{\text{end}}=0.160$). Recovery location was unrelated either to the tagging episode ($p=0.308$) or the recovery episode ($p=0.207$). Additionally, neither distance traveled ($p=0.229$) nor days at liberty ($p=0.056$) were related to tagging date. Finally, there were unequal probabilities for the direction taken by migrating fish between two potential pathways ($p=0.018$). There was a significantly greater chance of finding a tagged fish at Sites 3 and 8 along the east side of the seaward channel (Figure 3)

3.2 Large-scale juvenile/adult movement

To study transitional movements to adult habitats, 1,311 fish were tagged (92% *H. flavolineatum*, 7% *H. plumieri*, 1% *H. scirius*; 48 at Corral East, 14 at Coral West, 600 at Romero West, 607 at Caracoles/Majimo). Recapture sampling (Figure 1) consisted of 1,110 fish speared, trapped in Antillean arrow traps, or caught in the nets and trap used for tagging. Nineteen fish were recaptured by October 2004 and 8 more were recovered by April 2005 (Figure 4, Table 3). All were *H. flavolineatum*. One recovered tag was unreadable because it was a half tag, so individual identification was impossible. From the tagging log and recovery location, it is suspected that this fish was tagged at Romero West. Final recovery for tagged fish is 2.06% for all methods of recapture. Of 27 recaptures, 16 showed no displacement from the tagging location. Thirteen were caught along the original pathway at Romero West 160 days later, while an additional fish was caught 14 days after tagging on a return-tagging episode. The other resident fish was recaptured at Corral East only 7 days after tagging. Of the 12 fish that moved, eight came from the last round of tagging at Caracoles (March-July 2004). These fish were found less than 0.5 km from where they were originally tagged moving east along the submerged reef line and adjacent seagrass beds (Figure 4). Two fish at Corral East moved around the corner of the reef toward the fore reef, while movement was not perceived for the other one. Two fish from Romero West moved to an area at the mouth of the canal on Romero's reef front.

Returns ranged from 7-503 days. Two fish caught at Caracoles were tagged the same day and then later caught at the same location. Two fish caught at Corral East had the longest times at liberty of 503 days. These fish moved around the corner toward the reef front and were captured nearby together. The other migrating fish recovered at Corral was tagged one week earlier than the other two fish. It was caught 292 days later, and found in a resting school near to the school where it was tagged. Of the 12 fish that moved, time at liberty ranged from 82 - 503 days. All tagged fish were recovered in resting schools. The fish recovered at Caracoles were in loosely attached schools on the backside of the reef crest, with smaller individuals mixed in. When approached, the fish would disperse individually or in small groups and seek refuge as individuals. Recovered fish at Romero West that moved were found at locations 7-m deep and were loosely aggregated and hidden beneath overhangs and crevices.

4.0 Discussion

4.1 Small-scale juvenile movement

Appeldoorn et al. (1997, 2003) Nagelkerken et al. (2002) and Cocheret de la Morinière et al. (2002) demonstrated with length frequency data from Puerto Rico, Columbia, Florida, Curacao, and the Bahamas that *Haemulon flavolineatum* move ontogenetically. Similarly, in this study, forward movement to the reef front was initially inferred by an increase in the mean size of individuals in schools. The measured general movement of fish in this study from the tagging site toward the reef front is the first direct evidence to support this inference.

The results further indicate that juveniles move by dispersing among the available schools within the general trend toward the reef front, but with a preference for one general pathway over the other. The degree of movement was not affected by individual growth rates, or the time at liberty, but dispersal distance was positively correlated to size at recapture. Furthermore, fish caught together were similarly sized. These observations and other studies (McFarland and Hillis 1982, Mateo 1999) suggest that the progression of fish through the reef system (individually or in small groups) occurs when fish achieve a size transitional between those characterizing the old and new schools. Five of the six

fish recaptured at Site 1 (tagging school) were below the mean size-at-tagging for all recaptured fish, with the sixth only slightly larger than the mean. It is thus possible that these remaining individuals had not yet achieved a size sufficient to transition to another school.

It is not certain how or when fish move from one school to another. In this study there was substantial distance between the various reefs hosting resting schools, so inter-reef transitions require significant movement over open habitat. This situation differs markedly from that of McFarland and Hillis (1982), where various schools, differing in mean length, were found in close proximity (6 schools within a 4-m diameter collapsed coral head). One likely possibility is that reef transition occurs when fish return after nocturnal feeding. In this study, feeding migration pathways off the reef suggest that fish from Sites 1, 2 and 3 head for a common feeding area (Figure 3). The extrapolations of observed feeding pathways for each of these sites join in a seagrass area to the north. This provides both an opportunity and means for individual fish from one reef to encounter other fish and join their migration back to a new reef. Indeed, on several occasions, when monitoring the sunrise migration, I observed what appeared to be fish on one migration pathway turning and following a passing group of fish traveling on a different, intersecting migration pathway. This mechanism may explain why the majority of fish from Site 1 migrated seaward along the eastern margin of the channel.

McFarland and Hillis (1982) suggested that antagonistic behavior among individuals might also be a factor contributing to the transition of fish from one school to another. Antagonistic behavior occurs most commonly during the morning aggregation as fish return to the reef after feeding. As fish come together in small groups, larger juveniles begin mouth pushing, nipping, and chasing. These behaviors increase with the size of the fish. In addition, the largest juveniles may occupy territory on the reef during the day and defend the space through displays and aggressive behavior. Antagonistic behavior may serve to induce individuals to leave the reef in order to reduce the level of antagonism as their length increases. At Site 1, several larger fish at this location were antagonistic and territorial; the largest grunt caught was 12 cm. If these larger fish were indeed resident, they would act to drive others off the reef as they grew. McFarland and

Hillis (1982) actually observed one territorial grunt being ejected by a larger, more aggressive individual, in this case forcing the deposed fish to return to a nearby school of medium sized fish.

4.2 Large-scale juvenile/adult movement

Grunts have ontogenetic eco-behavioral stages (McFarland 1980, Appeldoorn et al. 1997), with sub-adult fish found in loosely knit groups along the reef front. Recovered fish were less than 15 cm and recaptured on the same reefs where they were tagged. No recaptures were found further offshore. Although no fish were found off reef, those fish found to have moved from the tagging location proceeded forward on the reef and entered into loosely knit sub-adult resting schools.

Large-scale movement patterns are hard to generalize, given the limited number of recaptured fish showing movement and the limited movement displayed. However, these data at least suggest that larger juvenile fish move seaward following the distribution of reef habitat. For instance, fish at Corral East moved along reef habitat from the backreef schooling location and around the northeast corner moving forward on the reef. Individuals at Romero West left their juvenile schools and moved into the channel joining schools of sub-adults.

One possible means used for orientation during these movements is vision. It is known that juvenile grunts travel along nightly feeding routes maintained over several months (Ogden and Erlich 1977) using visual cues (McFarland et al. 1979), and juvenile fish are able to encounter the routes when displaced (Quinn and Ogden 1984). Fish at Caracoles followed the reef line to the east and up current, using the nightly feeding migrations as a means of exchange as observed in Figure 3 and 4.

Since the size of an individual fish determined the distance moved at Majimo and size is an indicator of ontogenetic development and school placement (Mateo 1999), it is reasonable to assume that for large-scale migration to occur, fish must grow to some threshold size. This period of residency and growth is much longer than that reported by other studies. Many authors have reported that in 12 months haemulids can grow to maturity and a size at which larger migrations can occur (Hein 1999, Gallardo-Cabello et

al. 2003, Potts and Manooch 2001, Peters et al. 1994). To maximize the probability of detecting large-scale movements in the present study, large juveniles (approximately 10 cm) were tagged, yet some fish in this study were resident for up to 503 days, and all fish showing movement were recaptured in nearby schools on the same reef where tagged. In that time, the greatest growth interval was under 5 cm and the greatest sized reached was 14.9 cm. It is thus possible that the time at liberty was insufficient for growth to the size necessary for large-scale migration. The previous growth studies were based upon otolith readings; however, Brothers and McFarland (1981) determined that daily otolith lines were indistinguishable for *H. flavolineatum* after 100 days, and Shaw (1997) showed daily lines to grossly underestimate age (and hence overestimate growth) of large juvenile *H. plumieri* over 287 days (aged between 149 to 184 days). It is possible that growth rates in previous studies were overestimated (Chapter 4).

5.0 Implications

Fish moved to new schools primarily by the nighttime re-aggregation before they returned the safety of the reef. Short-term movements between schools are assessed by sparring and antagonistic behavior displayed at the home school location and in the feeding grounds. Transfer occurs visually during the morning aggregation. Once individual fish reach sub-adult size, they begin to wander over the reef, encountering other schools visually, chemically, or aurally. Transfer appears to be assessed individually, but small groups do appear together; this maybe due more to the linear placement of more ontogenetically developed schools further along the reef structure than to movement as a group.

Large-scale movements were not obtained during this study, and the question of ontogenetic group movement to offshore habitat cannot be answered at this time. Three things contribute to the lack of data: first, the time of liberty was of a short duration and recoveries could be found with more time; second, the effort was small compared to the size of the area searched and if more manpower was available, more areas could have been searched; third, the number of fish tagged was low for a study of this scale, but the

lack of manpower and the time available for the study demanded a more manageable number of tagged fish.

Finally, grunts are resident upon a reef for about 2 years. Residency and growth rates of recovered fish do not support the premise that grunts mature within 12 month.

CHAPTER 4: GROWTH AND SURVIVORSHIP OF *HAEMULON FLAVOLINEATUM* AS DETERMINED BY MARK AND RECAPTURE STUDIES AT LA PARGUERA, PUERTO RICO WITH COMPARISONS TO LABORATORY RAISED SPECIMENS.

1.0 Introduction

Grunts (Haemulidae) are ubiquitous in the Caribbean and Gulf of Mexico. Being exploited by sport fishers in developed areas and artisan fishers of undeveloped areas, they play a role that is both ecologically (Meyer and Shultz 1985) and commercially (Appeldoorn and Lindeman 1985) important. The French grunt (*Haemulon flavolineatum*) is perhaps the most abundant and ubiquitous fish in coral reef ecosystems within the region. As juveniles, they are the most numerous *Haemulon* species comprising over 80% of the daytime resting schools (Hein 1999), an important invertebrate consumer of the coral reef (Ogden and Erlich 1977, Appeldoorn personal communication) contributing to nutrient transport and increased coral growth (Meyer and Schultz 1985), and act as a common source of food for predatory fishes (McFarland et al. 1979). Haemulids comprised 4% of the total commercial catch in Puerto Rico (Matos-Caraballo 2002) and contribute up to 7% of Florida's recreational catch. Most notably, French grunts are similar in behavior and ecology to the larger more commercially important grunt species (Lindeman 1986).

One of the most versatile measures of a species's life history is that of individual growth. Growth rate is biologically related to such processes as maturation, reproduction, risk of predation, longevity and asymptotic size, and is fundamental to the quantification of stock productivity and surplus production. Simple growth studies are often the basis for more complex assessments of populations. Various studies have reported the growth of grunts in the Caribbean, with most focused on the larger, more commercially important species, such as *H. plumieri* (Peters et al. 1994, Potts and Manooch 2001, Ximenes-Carvalho and Fonteles-Filho 1995). Other species include *H. aurolineatum*, *H. melanurum*, *H. sciurus*, and *Orthopristis chysoptera* (Peters et al. 1994, Ximenes-Carvalho and Fonteles-Filho 1995, 1996). Despite its abundance, ubiquitous distribution, and importance, growth information for the French grunt is lacking. The most definitive study concerns its early life history. Using daily otolith increments, Brothers and McFarland (1981) studied growth of early juveniles to 100 days. Subsequent studies have confirmed this early life growth (Lindeman 1998, Peters et al. 1994, Hein 1999). Studies on adults in Jamaica (Hartsuijker 1982) using

length-frequency analysis have yielded variable results (see Appeldoorn 1993). Similarly, Dennis (1988) studied the growth of commercially caught *H. flavolineatum* using length frequency analysis, but it was determined later that the growth parameters obtained were outliers due to the mixing of other, larger grunts in the commercial data used for the study (Appeldoorn 1993). Thus, the growth for *H. flavolineatum* of sizes larger than early juvenile stages has yet to be adequately described.

The purpose of the study was to determine the growth and survivorship of released *H. flavolineatum* based upon a mark and recapture procedure to elucidate on the complementary study of ontogenetic migration (Chapter 3).

2.0 Materials and Methods

2.1 Study site

The study was conducted at La Parguera, Puerto Rico (Figure 1) located in the southwest coast (17.972° N, 67.045° W). The embayment at La Parguera consists of three shelf systems (inner, middle, and outer), separated by emergent reef lines that parallel the coast (Morelock et al. 1977). These reefs are not subject to fresh water input, except from runoff from the nearby slopes during rain. The average depth of the mid and outer shelves is between 18-20 m, with the inner shelf averaging 6 m (Morelock et al. 1994).

Tagging locations were located at three inner shelf reefs: Caracoles, Corral, and Romero (Figure 1). Caracoles is covered by mangroves and protects a shallow lagoon with seagrass. The reef is linear and runs on a northeast axis curving to the east at the northern tip. Depths along the reef approach 10 m at the reef slope. The lagoonal area behind the reef is approximately 2 m. The reef is approximately 850 m long and has an adjoining submerged reef area called Majimo. Majimo is composed of two patch reefs surrounded by seagrass and patches of gorgonians. A 2-m deep seagrass channel runs between the patch reefs of Majimo and a 4-m deep channel that grades from seagrass around the reef halo into sand and rubble near the reef slope further separates Majimo from Caracoles. Twelve daytime resting schools of *Haemulon flavolineatum* are located at Majimo and grade from small to large toward the reef slope. Schools are found within crevices and depressions within the coral structure and are further found among the branches of *Acropora cervicornis* and *Millepora complanata*.

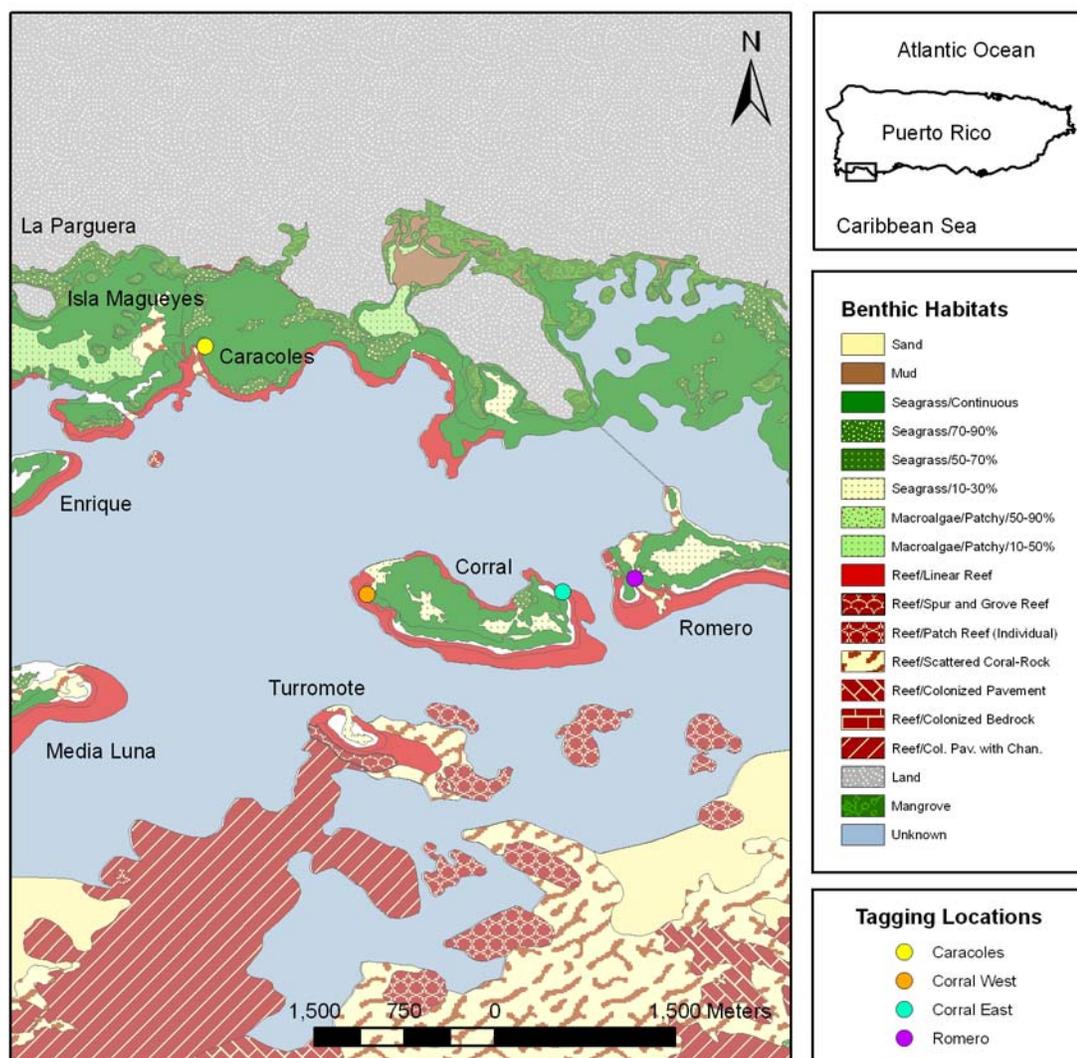


Figure 1. La Parguera, Puerto Rico showing benthic habitats (from Kendall et al. 2001) and the tagging locations located on the three reefs used in the study.

Corral is 2 km long and 630 m wide. The linear reef is u-shaped and runs east to west (Figure 1). There is a coral rampart on the seaward side with a few mangrove trees established. On the east side is a deep channel (20 m) separating the reef from Romero. This side has no mangroves, and a small coral rampart is formed. A shallow reef terrace, composed of small outcroppings of coral, extend into a gorgonian plain that drops to 20 m. At the northeast corner of the reef, water flows over the reef crest, and the resting school where tagging was conducted is located nearby. The school sits on a shallow patch of *M. complanata* that is bordered on the lagoonal side by seagrass at 0.5 m. The entire lagoon is

less than 2 m deep and is composed of thick beds of *Thalassia testudinum* and smaller patches of *Syringodium filiforme*. Interspersed are alga hummocks. The lagoon side of Corral gradually drops from 2 m down to 20 m toward the mainland. On the western extension of Corral, there is a large emergent patch reef that is separated from the main section by a shallow channel. Interspersed among the various coral heads is a large school of grunts. They occupy sheltered areas found within *Acropora cervicornis* or around the bases of *Siderastrea siderea*.

Romero is an L-shaped fringing reef covered with mangroves and is connected to the mainland by a narrow lagoonal channel. The reef is 3.3 km long and composed of two parts separated by a channel near the western end. Both sections have a relatively shallow (5 m) short terrace (50 m) composed of gorgonians and reef pavement. The lagoon side of Romero is composed of shallow seagrass beds. At the seaward edge, the slope drops quickly to 20 m. An extremely large school (used for tagging) is located midway on the east side of the channel (Figure 1) and resides in large clumps of *Acropora cervicornis*. The channel is 6 m at the deepest and is lined with sand. It is deeper at the seaward mouth and shallows to less than 2 m at the lagoon side. At the edges, the channel is lined with boulder corals.

2.2 Tagging

Fish were tagged using sequentially coded decimal wire tags (DCWT Northwest Marine Technologies, NMT). The tags are advantageous to the study of smaller fish due to decreased mortality and greater retention in small fish compared to larger tags (Guy et al. 1996). Beukers et al. (1995) tagged juvenile damselfish in the nape musculature and obtained 80% retention with laboratory survival of 90%, while Buckley et al. (1994) tagged juvenile rockfish and had 100% retention. Retention in *H. flavolineatum* was between 88% and 97% (Chapter 2). Additionally, cost is advantageous because substantial amounts of individually identified fish can be tagged. Finally, insertion is quick compared to other internal tags requiring surgery (Appeldoorn, personal communication).

Individuals were captured as small juveniles (6-12 cm FL) at Majimo, the extension of Caracoles reef, and as large juveniles (>10 cm) at Caracoles, Corral, and Romero. Tagging at each location was over a period from September 2003 to July 2004. Using a trap and net setup similar to Ogden and Ehrlich (1977), juvenile fish were collected from known feeding migration paths of specific juvenile resting schools, allowing for the collection of targeted

size groups. Personnel surveyed the targeted school prior to and during its off-reef migration at dusk and marked the migration pathway. The net and trap were placed across the migration pathway, in such a manner that the nets would guide returning fish at dawn towards the mouth of the trap. The trap was monitored at dawn, and when the fish had been guided into the trap, a door on the trap was closed. The trap was brought to the surface as a holding pen and fish were removed in groups to be tagged.

Retrieved fish were measured (fork length and total length) and checked for retention from previous tagging episodes. For untagged fish the tag was implanted in the nape musculature (Heidinger and Cook 1988, Chapter 2). A reference tag for each fish was saved in a silicon strip on the data sheet. Fish were rechecked for retention and released into a secondary holding pen until they could be released en masse to the reef. They were left at liberty for at least a month before tag recovery commenced.

Recovery operations began October 2003 for smaller fish (Experiment 1) and ended March 2004. Larger fish (Experiment 2) were captured from May 2004 to October 2004. Recovery began in February 2005 and ended April 2005. Selection of recovery sites were based on the NOS benthic habitat map cross-referenced with depths for likely locations in the area that may contain adult fish. Dives were planned for 30 to 45 minutes at each point, and divers speared fish with Hawaiian slings. Shallower areas were explored by snorkeling. In addition, some locations were trapped using unbaited Caribbean arrow traps soaked for 3-5 days in the water, recovered, and moved to a new location. Recovered fish in all locations were put into labeled location bags for transport back to the laboratory.

At the laboratory, fish were measured (fork length, total length) and weighed, then tested for tag retention. Fish with tags were set aside and labeled to their sequence in the data; untagged fish were discarded. Tags were cut out of marked fish and placed in a labeled beaker. A 4% sodium hydroxide solution (Drāno™) was used to dissolve the flesh from the tags, then washed in water and read under a dissecting microscope using a NMT supplied magnetic tag pencil.

2.3 Data analysis

Fork lengths (start and end), weights (start and end), and average daily growth increment data were compared using ANOVA. Conversion equations for fork length to weight and total length to weight were obtained via linear regression using all available log

transformed data and tested for differences using ANCOVA, while equations for fork length to total length were developed without transformation. Finally, von Bertalanffy growth parameters from tagging data were estimated by non-linear regression using Solver in Excel™. Growth and time at liberty were entered into the von Bertalanffy growth equation for increment data,

$$I = (L_{\infty} - L_1) (1 - e^{-kd}) \quad (1)$$

where I is the increment of growth between tagging and recapture, L_1 is the length at tagging, and d is the time increment between marking and recapture. The equation was set to zero, and the growth parameters L_{∞} and k were estimated. Limits for each run were set for 300 sec, 10000 iterations, or within 5% tolerance until the sum of the values did not change.

3.0 Results

3.1 Recovery

Twenty-nine fish were recovered during the study period for the small juveniles tagged at Caracoles (Table 1). One tag was lost. Fork lengths at recovery ranged in size from 7.6 to 12.1 cm, and fish were at liberty from 21 days to 153 days. The mean size of returned fish was 9.3 cm, while the median time at liberty was 93 days.

During the large-scale movement study, 28 fish were recovered (Table 2). Two fish were recovered at less than 30 days, of which one showed negative growth for the time at liberty. The average fish recovered was 12.6 cm and free for 198 days, while growing 1.3 cm. However, there was a distinct difference in growth between those fish showing displacement and those caught at the initial site of tagging. Fish showing no movement had an average length at tagging of 11.38 cm and grew an average of 0.0049 cm/day while fish that moved had an average initial length of 10.86 cm but grew 0.0078 cm/day (Table 2).

3.2 Growth Increments

The two tagging experiments clearly broadened the range of sizes for which growth data became available. In the first experiment, fish displayed a smaller mean starting size (7.92 cm), with a range of 6.4-10 cm at the beginning of the study and with fish growing to

Table 1. Recovery data for ontogenetic movement of small juveniles of *H. flavolineatum* (Flav) and *H. plumieri* (Plu) among school groups.

Species	Date Initial	Days at Liberty	Final Fork Length	Change in Fork Length
Flav	09/03/03	21	7.6	0.1
Flav	09/03/03	101	10.2	2.0
Flav	09/03/03	101	9.1	2.4
Flav	09/03/03	101	9.1	1.6
Flav	09/03/03	101	9.9	2.2
Flav	09/24/03	80	9.2	1.5
Flav	09/03/03	49	10.1	1.1
Flav	09/24/03	28	11.1	0.1
Flav	09/03/03	92	9.3	1.0
Flav	09/03/03	92	10.2	1.3
Flav	09/24/03	113	10.6	1.3
Flav	09/03/03	55	8.5	0.6
Flav	09/24/03	34	10.5	0.5
Flav	09/24/03	34	9.2	0.6
Flav	?	?	10.5	?
Flav	09/03/03	93	9.0	1.0
Flav	09/03/03	93	8.6	1.1
Flav	09/03/03	93	9.3	1.2
Flav	09/03/03	93	8.3	0.8
Flav	09/03/03	93	8.5	0.3
Flav	09/03/03	135	10.6	2.5
Flav	09/03/03	135	8.7	1.2
Plu	09/19/03	119	9.4	3.0
Plu	09/19/03	119	9.3	2.7
Flav	09/03/03	100	8.3	0.8
Plu	09/19/03	84	9.0	2.0
Flav	09/24/03	79	7.9	0.9
Flav	09/03/03	76	7.9	0.7
Flav	08/22/03	158	12.1	2.5

an average size of 9.34 cm. By contrast, in the second experiment, fish displayed a mean size of 11.13 cm, and the average size of recovered fish increased to 12.57 cm. Experiment 1 fish had a daily growth rate of 0.0151 cm/day, while Experiment 2 fish showed significantly slower growth (0.0063 cm/day) over the period of release ($p < 0.001$, $F = 42.3$).

Growth of daily increments varied throughout the season (Table 3). Experiment 1 fish were tagged during October and grew during the fall months. Experiment 2 fish were tagged

Table 2. Recovery data (time, size, location) for large juveniles of *H. flavolineatum* (Flav). (*) Denotes fish without movement.

Species	Date Initial	Days at Liberty	Tagged Location	Final Fork Length (cm)	Change in Fork Length (cm)
Flav	10/08/2003	7*	Corral East	10.9	0.0
Flav	10/08/2003	503	Corral East	14.7	4.8
Flav	10/08/2003	503	Corral East	14.4	3.7
Flav	10/16/2003	292	Corral East	13.5	2.0
Flav	01/30/2004	160*	Romero West	11.9	0.6
Flav	01/30/2004	160*	Romero West	11.8	0.6
Flav	01/30/2004	160*	Romero West	11.3	0.6
Flav	01/30/2004	160*	Romero West	13.4	1.1
Flav	01/30/2004	160*	Romero West	11.3	0.5
Flav	01/30/2004	160*	Romero West	11.0	0.3
Flav	01/30/2004	160*	Romero West	12.2	0.1
Flav	01/30/2004	160*	Romero West	11.7	0.9
Flav	01/30/2004	160*	Romero West	12.2	0.8
Flav	01/30/2004	160*	Romero West	13.5	0.8
Flav	01/30/2004	160*	Romero West	13.0	1.2
Flav	01/30/2004	160*	Romero West	11.5	0.9
Flav	01/30/2004	160*	Romero West	13.3	1.8
Flav	01/30/2004	390	Romero West	14.8	3.7
Flav	02/27/2004	14*	Romero West	11.6	-0.3
Flav	03/17/2004	97	Caracoles	11.2	0.4
Flav	03/17/2004	97	Caracoles	11.7	0.5
Flav	06/15/2004	239	Caracoles	13.7	3.1
Flav	06/24/2004	82	Caracoles	11.1	0.6
Flav	06/30/2004	226	Caracoles	13.1	2.6
Flav	07/01/2004	96	Caracoles	11.3	0.0
Flav	07/01/2004	223	Caracoles	13.6	2.1
Flav	07/01/2004	223	Caracoles	13.0	2.3
Flav	11/21-26/2003	489-494?	Romero West?	14.9	2.4-5.7

in January and February primarily with tagging in late spring/early summer for Caracoles. Recoveries occurred in late summer and late winter.

3.3 Conversion Equations

Comparisons between fork length to total length showed unequal slopes ($F=10.393$) (Table 4). The fork length to weight regressions were determined to have both a common slope ($F=2.903$) and a common elevation ($t=1.855$). The combined slope is 3.0252 and the

Table 3. Daily incremental growth (cm/day fork length) of *Haemulon flavolineatum* from the tagging experiments. Comparisons of growth in Experiment 2 between fish showing and not showing movement exclude individuals at liberty for less than 30 days.

	Exp. 1	Exp. 2			Pooled Exp. 1 & 2
		All	Movement	No Movement	
Mean	0.0151	0.0063	0.0078	0.0049	0.0108
Std Err	0.0012	0.0007	0.001	0.0007	0.0009
Min	0.0032	0	0	0.0006	0
Max	0.0252	0.0130	0.0130	0.0113	0.0252
n	26	25	12	13	51

elevation is -1.7462. Equations for total length to weight also resulted in equal slopes ($F=1.84$) and elevations ($t=1.935$). The pooled total length to weight slope for the wild periods is 3.0193 and the intercept is -1.8845.

Table 4. Length (cm) to weight (g) conversion equations for juvenile *Haemulon flavolineatum*. Common slopes and intercepts are given when ANCOVA results indicate that the equations are not significantly different. (-) Indicates no data is available. A common equation for FL to TL was not developed because slopes were not equal.

	Slope	Std Err	Intercept	R ²	n
Experiment 1					
FL to TL	1.1255	0.0010	-0.0666	0.994	8774
FL to Wt	3.3029	0.1325	-2.0430	0.954	32
TL to Wt	3.2296	0.1545	-2.1391	0.936	32
Experiment 2					
FL to TL	1.1353	0.0026	0.0167	0.996	821
FL to Wt	3.0219	0.0181	-1.7123	0.973	787
TL to Wt	3.0167	0.0172	-1.8742	0.975	787
Common					
FL to TL	-	-	-	-	-
FL to Wt	3.0252	-	-1.7462	-	-
TL to Wt	3.0193	-	-1.8845	-	-

Table 5. Estimates of the von Bertalanffy parameters (L_{∞} and k) for *Haemulon flavolineatum*. Values for W_{∞} were derived from L_{∞} using the conversion equations in Table 4.

Group	L_{∞} (cm FL)	W_{∞} (g)	k (yr ⁻¹)
Experiment 1	26.00	342.31	0.248
Experiment 2	28.00	458.00	0.126
Pooled Exp. 1 and 2	28.32	443.27	0.166

3.4 von Bertalanffy Growth Parameters

Estimates of von Bertalanffy's growth parameter (Table 5) L_{∞} (cm) were 26.00 (Experiment 1) and 28.00 (Experiment 2), with a pooled value of 28.323. Similarly, the estimates of the growth value k (yr⁻¹) were 0.248 (Experiment 1) and 0.126 (Experiment 2), respectively. The pooled k was estimated at 0.166.

4.0 Discussion

Individual growth is plastic and dependent upon several factors, such as food intake, proper environment, temperature, health, and age. Brothers and McFarland (1981) investigated the early growth of *H. flavolineatum* to 100 days. Fish grew to a size of 4 cm over the first 100 days, averaging growth of 1.2 cm per month. Saksena and Richards (1975) obtained similar results (1.6 cm/mo) rearing *H. plumieri* for the first 40 days, which matched Shaw's (1997) back calculated rates from otoliths. If these rates prevail, juveniles might grow to 12 cm within one year, the size at which fish may leave juvenile resting schools and take on subadult behavior (Chapter 3). However, growth rates are expected to decline with increasing size. In this study, the two experiments tagged individuals of *H. flavolineatum* of different mean sizes. Experiment 1 represented the smallest individuals on average with faster growth reflecting their younger status. Fork length growth exhibited in Experiment 2 was lower, as expected in older and larger fish. Unlike earlier studies of growth, data here covered a wide range of sizes well defining the growth curve at the time when juveniles approach maturity and the slower somatic growth that characterizes the reproductive stage. When the two data sets are considered together, the resulting growth curve gives a more robust interpretation than when considered separately. Even at the highest average monthly growth rates obtained in this

study (Experiment 1: 0.453 cm/mo, Experiment 2: 0.189 cm/mo), *H. flavolineatum* are estimated to reach 12 cm in over 2 years.

Several authors have reported more rapid growth potential of 12 cm within one year for haemulids (Shaw 1997, Hein 1999, Potts and Manooch 2001, Gallardo-Cabello et al. 2003). Several of these studies aged fish by otoliths and estimated growth from the resulting intervals (Shaw 1997, Hein 1999, Potts and Manooch 2001), but Brothers and McFarland (1981) warned that daily growth rings were hard to differentiate beyond 100 days. Shaw (1997) studied the daily deposition of lines in *H. plumieri* sagittae by video processed light microscopy and found that interpretation of lineal depositions beyond 150 days was likely to underestimate true age. For five *H. plumieri* (13.5 –15.3 cm) maintained for 287 days, only 149-184 otolith increments were counted. This would certainly put into question the results of otolith-based studies, particularly that of Hein (1999) who, like Shaw, observed “daily” otolith increments through video processed light microscopy.

Only two reliable values for von Bertalanffy growth parameters are available from the literature, both from Jamaica. Gaut and Munro (1983) reported the largest fish recovered in Jamaica was 27.0 cm FL from Pedro Bank, and using Pauly’s (1980) method where $L_{\infty} = L_{\max} / 0.95$, L_{∞} is estimated at 28.4 cm. This is almost identical to that obtained in the present study (28.32 cm, pooled data) as well as the value (converted from W_{∞}) from Hartsuijker (1982) (in Appeldoorn 1993). The latter study also reported a k value (0.18) comparable to that found in the present study, but Billings and Munro (1974) (in Appeldoorn 1993) found a much higher value of k (0.35), although a lower value of L_{∞} (25 cm). Their parameters would result in growth to 12 cm in 1.85 years, faster but still within the relative time frame found in this study. Growth curves derived from tagging data do not have absolute time associated with them, thus the third von Bertalanffy parameter (t_0) cannot be estimated. This parameter does not affect the shape of the curve and hence the rate of growth, but it does determine the absolute age for any corresponding estimate of growth at size. Values for t_0 typically are negative; some by several years (e.g., see Appendix 6.2 in Claro et al. 2001), and this shift may resolve differences among studies.

Nevertheless, the variations in growth time to 12 cm for *H. flavolineatum* reported remain to be resolved. While it is unlikely that the fish grow as rapidly as reported in short-term studies of small juveniles, it is also unclear whether the growth results here represent real growth. While tank studies (Chapter 2) showed no effect of tagging on growth, there is considerable variability in the growth data that may affect overall results in unexpected ways that cannot be partitioned without a larger sample size. Possible factors include variability in days at liberty, seasons of tagging and growth, and behavior. Regarding the latter, it is interesting that in Experiment 2 there was significantly greater growth observed among fish that showed net migration. Werner and Gilliam (1984) hypothesized that fish act to minimize the ratio of mortality over growth, and that ontogenetic migration occurs when growth benefits at a new location outweigh the risk of mortality. It is tempting to speculate that this greater growth indicates that growth rates increased after migrating out of the original habitat, but this observation is confounded by the fact that all but two non-migrating fish were from one school, of a larger mean size, tagged in winter and recovered on the same day.

Both experimental groups were similar in their total length to weight curves, indicating that individuals grew equally over the range sampled. The common total length to weight slope shows that growth for *H. flavolineatum* is isometric. The fork length to weight slopes for both experimental groups were similar as well. Fork length to total length while not statistically equal due to the large sample size of Experiment 2 fish, all revolve around a slope of 1.1. The conversions calculated in this study are similar to the ones published in Gaut and Munro (1983) and Dennis (1992) for *H. flavolineatum*.

CHAPTER 5.0 CONCLUSIONS AND RECOMMENDATIONS

Three components were examined over the course of this study: the effectiveness of coded wire tags in grunts, growth of tagged juvenile *Haemulon flavolineatum* in the wild, and movements associated with small and large-scale ontogenetic migrations of *H. flavolineatum*. Results of these studies led to the following conclusions and recommendations.

Retention of coded wire tags in nape-tagged juvenile *H. flavolineatum* was good, and stabilized after 30 days, similar to other fishes (Heidinger and Cook 1988). Coded wire tags did not affect the survival of tagged juvenile *H. flavolineatum* when compared to untagged fish. Tags apparently do not affect growth, but in the laboratory study there was a 30-day acclimation period to the handling procedures.

Growth interval data covered a broader range of sizes than previous studies and refined the growth curve for *H. flavolineatum*. Results indicate growth is slower and age is greater than interpretations based on daily deposition lines in otoliths.

The combined L_{∞} from this study is 28.3 cm. This value is close to the estimated L_{∞} from Pauly's (1980) method of estimation based on the largest captured individual, and L_{∞} and k are comparable estimates from Hartsuijker (1982).

When making ontogenetic habitat shifts, small juveniles independently move toward the reef front by transiting through size static schools. Movement is not necessarily toward the nearest school, but follows a general pathway. Fish appear to move to new schools primarily by the nighttime re-aggregation before returning to the safety of the reef. Short-term movements between schools may be preceded by sparing and antagonistic behavior displays at the home school location and in the feeding grounds. Transfer occurs visually during the morning aggregation.

No recaptures were made off the reefs where tagging occurred. If a larger-scale migration to more offshore adult habitats occurs at 15 cm (FL) (*H. plumieri*) as suggested by Appeldoorn et al. (1997, 2003), then 1.5 years at liberty would be needed for grunts to obtain sufficient size for departure when tagged at 10 cm.

LITERATURE CITED

- Adams, A.J. and J.P. Ebersole. 2002. Use of back reef and lagoon habitats by coral reef fish. *Marine Ecology Progress Series*. 228: 213-226.
- Aguilar Perera, A. and W. Aguilar-Davila. 1996. A spawning aggregation of Nassau grouper *Epinephelus striatus* (Pisces: Serranidae) in the Mexican Caribbean. *Environmental Biology of Fishes*. 45(4): 351-361.
- Appeldoorn, R.S. 1993. Interspecific relationships between growth parameters, with application to haemulid fishes. *Proceedings of the 7th International Coral Reef Symposium, Guam 22-27 June 1992*. 2: 899-904.
- Appeldoorn, R.S., A. Friedlander, J. Sladek Nowlis, P. Ussegilo and A. Mitchell-Chui. 2003. Habitat connectivity in reef fish communities and marine reserve design in Old Providence – Santa Catalina, Colombia. *Gulf and Caribbean Research*. 14(2): 61-77.
- Appeldoorn, R.S., C.W. Recksiek, R.L. Hill, F.E. Pagan and G.D. Dennis. 1997. Marine protected areas and reef fish movements: The role of habitat in controlling ontogenetic migration. *Proceedings of the 8th International Coral Reef Symposium*. 2: 1917-1922.
- Appeldoorn, R.S. and K.C. Lindeman. 1985. Multispecies assessment in coral reef fisheries using higher taxonomic categories as unit stocks, with an analysis of an artisanal Haemulid fishery. *Proceedings of the 5th International Coral Reef Congress, Tahiti 27 May - 1 June 1985, Vol. 5: Miscellaneous papers (A)*. 5: 507-514.
- Aprahamian, M.L., G.O. Jones, and P.J. Gough. 1998. Movement of adult Atlantic salmon in the Usk estuary, Wales. *Journal of Fish Biology*. 53: 221-225.
- Baker, C.F. and J.C. Montgomery. 2001. Species-specific attraction of migratory banded Kokopu juveniles to adult pheromones. *Journal of Fish Biology*. 58: 1221-1229.
- Beck, M.W., K.L. Heck Jr., K.W. Able, D.L. Childers, D.B. Eggleston, B.M. Gillanders, B. Halpern, C.G. Hays, K. Hoshino, T.J. Minello, R.J. Orth, P.F. Sheridan, and M.P. Weinstein. 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience*. 51(8): 633-641.
- Beukers, J.S., G. P. Jones, and R.M. Buckley. 1995. Use of implant micro tags for studies on populations of small reef fish. *Marine Ecology Progress Series*. 125: 61-66.

- Billings, V.C. and J.L. Munro. 1974. The biology, ecology, exploitation, and management of Caribbean reef fishes. Part Ve. The biology, ecology, and bionomics of Caribbean reef fishes: Pomadasyidae (Grunts). Science Report ODA/UWI Fish Ecology Research Project: 1969-1973. Jamaica. 128 p.
- Blankenship, H.L. and J.M. Tipping. 1993. Evaluation of visible implant and sequentially coded wire tags in sea run cutthroat trout. North American Journal of Fisheries Management. 13: 391-394.
- Bortone, S.A., R.L. Shipp, W.P. Davis, and R.D. Nester. 1988. Artificial reef development along the Atlantic coast of Guatemala. Northeast Gulf Science. 10(1): 45-48.
- Brothers, E.B. and W.N. McFarland. 1981. Correlation between otolith microstructure, growth, and life history transitions in newly recruited French grunts [*Haemulon flavolineatum* (Desmarest), Haemulidae]. Rapp. P. -v Réunion. Cons. Int. Explor. Mer. 178: 369-374.
- Buckley, R.M., J.E. West, and D.C. Doty. 1994. Internal micro tag systems for marking juvenile reef fishes. Bulletin of Marine Science. 55: 848-857.
- Christensen, J.D., C. Jeffrey, M.E. Monaco, C. Caldow, M. Kendall, and R. Appledorn. 2003. Cross-shelf habitat utilization patterns of reef fishes in southwestern Puerto Rico. Gulf and Caribbean Research 14: 9-27.
- Claro, R., K.C. Lindeman, and L.R. Parenti. 2001. Ecology of marine fishes of Cuba. Smithsonian Institution Press. Washington, D.C. 219 pp.
- Cocheret de la Morinière, E. 2002. Post settlement life cycle migration of reef fish in the mangrove sea grass coral reef continuum. PhD. Thesis University of Nijmegen. The Netherlands. 168 pp.
- Cocheret de la Moriniere, E., B.J. Pollux, I. Nagelkerken, and G. van der Velde. 2002. Post-settlement Life Cycle Migration Patterns and Habitat Preference of Coral Reef Fish That Use Seagrass and Mangrove Habitats as Nurseries Estuarine, Coastal and Shelf Science. 55(2): 309-321.
- Cocheret de la Morinière, E., B.J.A. Pollux, I. Nagelkerken, and G. van der Velde. 2003a. Diet shifts of Caribbean grunts (Haemulidae) and snappers (Lutjanidae) and the relation with nursery to coral reef migrations. Estuarine, Coastal and Shelf science. 57(5-6): 1079-1089.

- Cocheret de la Morinière, E., B.J.A. Pollux, I. Nagelkerken, M.A. Hemminga, A.H.L. Hiskes, and G. van der Velde. 2003b. Ontogenetic dietary changes of coral reef fishes in the mangrove-seagrass-reef-continuum: stable isotopes and gut content analysis. *Marine Ecology Progress Series*. 246: 279-289.
- Cooper, J.C., A.T. Scholz, R.M. Horrall, A.D. Hasler and D.M. Madison. 1976. Experimental confirmation of the olfactory hypothesis with homing artificially imprinted Coho salmon (*Oncorhynchus kisutch*). *Journal of Fisheries Research Board of Canada*. 33: 703-710.
- Danilowicz, B.S. and P.F. Sale. 1999. Relative intensity of predation on the French grunt, *Haemulon flavolineatum*, during diurnal, dusk, and nocturnal periods on a coral reef. *Marine Biology*. 133: 337-343.
- Dahlgren, C.P. 1999. Population dynamics of early juvenile Nassau grouper: An integrated modeling and field study. PhD Dissertation. North Carolina State University. Raleigh, North Carolina. 145 pp.
- Dahlgren, C.P. and D.B. Eggleston. 2000. Ecological process underlying ontogenetic habitat shifts in a coral reef fish. *Ecology*. 81(8): 2227-2244.
- Dennis, G.D. 1988. Commercial catch length-frequency data as a tool for fisheries management with an application to the Puerto Rico trap fishery. *Memoria Sociedad de Ciencias Naturales La Salle*. 48(s3): 289-310.
- Dennis, G.D. 1992. Resource utilization by members of a guild of benthic feeding coral reef fish. PhD Dissertation. University of Puerto Rico, Mayagüez. Puerto Rico. 224 pp.
- Domeier, M.L., C. Koenig, and F. Coleman. 1996. Reproductive biology of the gray snapper (*Lutjanus griseus*), with notes on spawning for other western Atlantic snappers (Lutjanidae). *Biology, fisheries, and culture of tropical groupers and snappers*. ICLARM Conference Proceeding. 48: 189-201.
- Eggleston, D.B. 1995. Recruitment in Nassau grouper, *Epinephelus striatus*: post-settlement abundance, microhabitat features, and ontogenetic shifts. *Marine Ecology Progress Series*. 124: 9-22.
- Estrada, R.M. 1986. Feeding habits of fishes of the genus *Haemulon* (Pisces: Haemulidae) from the reefs of Santa Marta region, Colombia. *Anales del Instituto de Investigaciones Marinas de Punta de Betin*. 15-16: 49-66.

- Forward Jr., R.B., M.C. De Vries, R.A. Tankersley, D. Rittschof, W.F. Hettler, J.S. Burke, J.M. Welch, and D.E. Hoss. 1999. Behaviour and sensory physiology of Atlantic menhaden larvae. *Brevoortia tyannus*, during horizontal transport. *Fisheries Oceanography*. 8: 27-56.
- Friedlander, A.M., J.D. Parrish, and R.C. Defelice. 2002. Ecology of the introduced snapper *Lutjanus kasmira* (Forsskal) in the reef fish assemblage of a Hawaiian bay. *Journal of Fish Biology*. 60(1): 28-48.
- Gallardo Cabello, M., E. Espino Barr, F. Gonzalez Orozco, and A. Garcia Boa. 2003. Age determination of *Anisotremus interruptus* (Perciformes: Haemulidae) by scale reading, in the coast of Colima, Mexico. *Revista de Biología Tropical*. 51(2): 519-528.
- Gaut, V.C. and J.L. Munro. 1983. Chapter 10: The biology, ecology, and bionomics of the grunts, Pomadasyidae. In Munro, J.L. (ed). *Caribbean Coral Reef Fishery Resources*. ICLARM Studies and Reviews 7. pp. 110-141. International Center for Living Aquatic Resources Management. Manila, Philippines.
- Goldstein, J.N., D.F. Woodward, and A.M. Farag. 1999. Movements of adult Chinook salmon during spawning migration in a metals contaminated system, Coeur d'Alene River, Idaho. *Transactions of the American Fisheries Society*. 128: 121-129.
- Guy, C.S., R.D. Schultz, and C.P. Clouse. 1996. Coded wire tag loss from paddlefish: a function of study location. *North American Journal of Fisheries Management*. 16: 931-934.
- Hansen, L.P., N. Jonsson, and B. Jonsson. 1995. Factors affecting upstream and downstream migration in anadromous European salmonids and catadromous eel. Copenhagen-Denmark ICES. 26 pp.
- Hartsuijker, L. 1982. Trap fishing survey of Pedro Bank (Jamaica), 2nd phase: A re-assessment of the stocks of reef fish on Pedro Bank, Jamaica. Fisheries Division, Technical Report 4. 43 pp.
- Hawkins, A.D. 1986. Underwater sound and fish behaviour. In Pitcher, T.J. (ed.) *The Behavior of Teleost Fishes*. pp. 114-151. Johns Hopkins University Press. Baltimore, Maryland.
- Heck, Jr. K.L. and M.P. Weinstein. 1989. Feeding habits of juvenile reef fishes associated with Panamanian seagrass meadows. *Bulletin of Marine Science*. 45(3): 629-636.

- Heidinger, R.C. and S.B. Cook. 1988. Use of coded wire tags for marking fingerling fishes. *North American Journal of Fisheries Management*. 8: 268-272.
- Hein, R.G. 1996. Mobbing behavior in juvenile French grunts (*Haemulon flavolineatum*). *Copeia* 1996(4): 989-991.
- Hein, R.G. 1999. Age, growth and factors controlling post settlement habitat of juvenile French grunts (*Haemulon flavolineatum*) near Tobacco Caye, Belize, Central America. PhD Dissertation University of Rhode Island. 216 pp.
- Helfman, G.S., J.L. Meyer, and W.M. McFarland. 1982. The ontogeny of twilight migration patterns in grunts (Pisces: Haemulidae). *Animal Behaviour*. 30(2): 317-326.
- Higgs, D.M. and L.A. Fuiman. 1998. Associations between sensory development and ecology in three species of clupeoid fish. *Copeia* 1998. 1: 133-144.
- Hill, R.L. 2001. Post settlement processes and recruitment dynamics in the white grunt, *Haemulon plumieri* Lacepede (Pisces: Haemulidae). PhD Dissertation University of Puerto Rico Mayagüez. 152 pp.
- Hoss, D.E., D.S. Peters and W.F. Hettler. 1986. Effects of lowered water temperature on the survival and behaviour of juvenile French Grunt, *Haemulon flavolineatum*. *Bulletin of Marine Science*. 39: 134-138.
- Kendall, M.S., J.D. Christensen, and Z.H. Starr. 2003. Multiscale data used to analyze the spatial distribution of French grunts, *Haemulon flavolineatum*, relative to hard and soft bottom in a benthic landscape. *Environmental Biology of Fishes*. 66: 19-26.
- Kendall, M.S., M.E. Monaco, K.R. Buja, J.D. Christensen, C.R. Kruer, M. Finkbeiner, and R.A. Warner. 2001. (On-line). Methods Used to Map the Benthic Habitats of Puerto Rico and the U.S. Virgin Islands URL: <http://biogeo.nos.noaa.gov/projects/mapping/caribbean/startup.htm>. Also available on U.S. National Oceanic and Atmospheric Administration. National Ocean Service, National Centers for Coastal Ocean Science Biogeography Program. 2001. (CD-ROM). Benthic habitats of Puerto Rico and the U.S. Virgin Islands. Silver Spring, MD: National Oceanic and Atmospheric Administration.
- Kingsford, M.J., J.M. Leis, A. Shanks, K.C. Lindeman, S.G. Morgan and J.Pineda. 2002. Sensory environments, larval abilities and local self-recruitment. *Bulletin of Marine Science*. 70: 309-340.
- Konchina, Y.V. 1976. The systematics and distribution of the grunts family (Pomadasyidae). *Journal of Ichthyology*. 16(6): 883-900.

- LaCroix, G.L. and P. McCurdy. 1996. Migratory behaviour of post-smolt Atlantic salmon during initial stages of seaward migration. *Journal of Fish Biology*. 49: 1086-1101.
- Leary, D.F. and G.I. Murphy. 1975. A successful method for tagging the small fragile Engraulid, *Stolephorus purpureus*. *Transactions of the American Fisheries Society*. 1: 53-55.
- Leis, J.M., P.A. Sweatman, and S.E. Reader. 1996. What pelagic stages of coral reef fishes are doing in blue water: daytime field observation of larval behavioral capabilities?. *Marine Freshwater Research*. 47: 401-412.
- Lindeman, K.C. 1986. Development of larvae of the French grunt, *Haemulon flavolineatum*, and comparative development of twelve species of western Atlantic Haemulon (Percoidei, Haemulidae) *Bulletin of Marine Science*. 39: 673-716.
- Lindeman, K.C. 1989. Coastal construction, larval settlement, and early juvenile habitat use in grunts, snappers and other coastal fishes of southeast Florida. *Bulletin of Marine Science*. 44(2): 1068-1089.
- Lindeman, K.C. 1998. Development of grunts and snappers of southeast Florida: Cross-shelf distributions and effects of beach management alternatives. PhD. Dissertation. University of Miami, Coral Gables, Florida. 419 pp.
- Lindeman, K.C., G.A. Diaz, J.E. Serafy, and J.S. Ault. 1998. A spatial framework for assessing cross-shelf habitat use among newly settled grunts and snappers. *Proceedings of the Gulf and Caribbean Fisheries Institute*. 50: 385-416.
- Lindeman, K.C., R. Pugliose, G.T. Waugh, and J.S. Ault. 2000. Developmental patterns within a multispecies reef fishery: management applications for essential fish habitats and protected areas. *Bulletin of Marine Science*. 66: 929-956.
- Lindeman, K.C., T.N. Lee, W.D. Wilson, R. Claro, and J.S. Ault. 2001. Transport of larvae originating in South West Cuba and the Dry Tortugas: Evidence for partial retention in grunts and snappers. *Proceedings of the Gulf and Caribbean Fisheries Institute*. 52: 732-747.
- Mateo, J. 1999. Función de la madurez sexual en el control de las migraciones ontogénicas de la cachicata blanca, *Haemulon plumieri*, (Pices: Haemulidae) en La Parguera, Puerto Rico. M.S. Thesis University of Puerto Rico Mayagüez. 88 pp.

- Matos Caraballo, D. 2002. Overview of Puerto Rico's small-scale fisheries statistics 1998-2001. Proceedings of the Gulf and Caribbean Fisheries Institute. 55: 103-118.
- McBride, R.S., T.C. MacDonald, R.E. Matheson Jr., D.A. Rydene, and P.B. Hood. 2001. Nursery habitats for ladyfish, *Elops saurus*, along salinity gradients in two Florida estuaries. Fishery Bulletin 99: 443-458.
- McCauley, R.D. 1997. Aspects of marine biological sound in northern Australia IV: Fish choruses in the Great Barrier Reef, spatial extant and temporal patterns. Defense Sci. Tech. Org. Sydney, Australia.
- McCleave, J.D. and G.S. Wippelhauser. 1987. Behavioral aspects of selective tidal stream transport in juvenile American eels. Common strategies of anadromous and catadromous fishes. Proceedings of an international symposium held in Boston, Massachusetts, USA, March 9-13, 1986. 1: 138-150.
- McFarland, W.N. 1980. Observations on recruitment in haemulid fishes. Proceedings of the Gulf and Caribbean Fisheries Institute. 32: 132-138.
- McFarland, W.N. and C.M. Wahl. 1996. Visual constraints on migration behavior of juvenile French grunts. Environmental Biology of Fishes. 46: 109-122.
- McFarland, W.N., E.B. Brothers, J.C. Ogden, M.J. Shulman, E.L. Bermingham, and N.M. Kotchin-Prentiss. 1985. Recruitment patterns in young French grunts, *Haemulon flavolineatum* (Family Haemulidae), at St. Croix, Virgin Islands. Fishery Bulletin. 83: 413-426.
- McFarland, W.N., J.C. Ogden, and J.N. Lythgoe. 1979. The influence of light on the twilight migrations of grunts. Environmental Biology of Fishes. 4(1): 9-22.
- McFarland, W.N. and N.M. Kotchian. 1982. Interaction between schools of fish and mysids. Behavioral Ecology and Sociobiology. 11(2): 71-76.
- McFarland, W.N. and Z. M. Hillis. 1982. Observations on agnostic behavior between members of juvenile French and white grunts – family Haemulidae. Bulletin of Marine Science. 32(1): 255-268.
- McLean, R. and W.F. Herrnkind. 1971. Compact schooling during a mass movement by grunts. Copeia 1971. 328-330.
- Metcalfe, J.D., G.P. Arnold, and B.H. Holford. 1994. The migratory behavior of plaice in the North Sea as revealed by data storage tags. Copenhagen-Denmark ICES 1994. 13 pp.

- Meyer, J. L. and E.T. Shultz. 1985. Migrating haemulid fishes as a source of nutrients and organic matter on coral reefs. *Limnology and Oceanography*. 30: 146-156.
- Meyer, J. L., E.T. Shultz, and G.S. Helfman. 1983. Fish schools: An asset to corals. *Science*. 220(4601): 1047-1049.
- Moore, A. 1999. The riverine, estuarine, and coastal migratory behaviour of wild Atlantic salmon smolts. In: McCormick, S. and D. MacKinlay (eds.). *Smolt physiology, ecology, and behavior*. pp. 145-148. International Congress on the Biology of Fish. Towson University, Baltimore Maryland July 27-30, 1998.
- Moore, A., M. Ives, M. Scott, and S. Bamber. 1998. The migratory behavior of wild sea trout (*Salmo trutta* L.) smolts in the estuary of the River Conwy, North Wales. *Aquaculture*. 168: 57-68.
- Morelock, J., N. Schneidermann, and W.R. Bryant. 1977. Shelf reefs, southwestern Puerto Rico. *Reefs and Related Carbonates - Ecology and Sedimentology*. In: Stanley H. Frost, Malcolm P. Weiss, and John B. Saunders (eds.) *Studies in Geology* 4. 17-25 pp. Tulsa, Oklahoma: American Association Petroleum Geologists.
- Morelock J., E.A. Winget, and C. Goenaga. 1994. Geologic maps of the Southwestern Puerto Rico Parguera to Guánica insular shelf. Scale 1:40,000. Map I-2387. *Miscellaneous Investigations Series*. Published by U.S. Department of the Interior. U.S. Geological Survey. 6 pp.
- Mumby, P.J., A.J. Edwards, J.E. Arias Gonzalez, K.C. Lindeman, P.G. Blackwell, A. Gall, M.I. Gorczyńska, A.R. Harborne, C.L. Pescod, H. Renken, C.C.C. Wabnitz, and G. Llewellyn. 2004. Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature*. 427(6974): 533-536.
- Nagelkerken, I. 2000. Importance of shallow water bay biotopes as nurseries for Caribbean fishes. PhD. Thesis University of Nijmegen. The Netherlands. 168 pp.
- Nagelkerken, I., C.M. Roberts, G. van der Velde, M. Dorenbosch, M.C. van Riel, E. Cocheret de la Morinière, and P.H. Nienhuis. 2002. How important are mangroves and seagrass beds for coral reef fish? The nursery hypothesis tested on an island scale. *Marine Ecology Progress Series*. 244: 299-305.
- Nagelkerken, I. and G. van der Velde. 2004. Are Caribbean mangroves important feeding grounds for juvenile reef fish from adjacent seagrass beds? *Marine Ecology Progress Series*. 274: 143-151.

- Nagelkerken, I., M Dorenbosch, W.C.E.P. Verberk, E. Cocheret de la Morinière, G. van der Velde. 2000. Day-night shifts of fishes between shallow water biotopes of a Caribbean bay, with emphasis on the nocturnal feeding of Haemulidae and Lutjanidae. *Marine Ecology Progress Series*. 194: 55-64.
- Nagiec, M. 1975. Some mechanisms underlying fish migration. *Wiad Ekol.* 21: 201-212.
- Ogden, J.C. and P.R. Ehrlich. 1977. The behavior of heterotypic resting schools of juvenile grunts (Pomadasyidae). *Marine Biology*. 273-280.
- Pauly, D. 1980. A new methodology for rapidly acquiring basic information on tropical fish stocks: growth, mortality, and stock recruitment relationships. In Saila, S.B. and P.M. Roedel. (eds) *Stock Assessment for Tropical Small-scale Fisheries*. pp. 154-172. ICMRD. University of Rhode Island. Kingston, Rhode Island.
- Peters, D.S., L. Settle, J. Burke, and E. Laban. 1994. Comparative utilization of Florida Bay as a nursery area by juvenile grunts. *Bulletin of Marine Science*. 54(3)
- Phinney, D., D. Miller, and M. Dahlberg. 1967. Mass-marking of young salmonids with fluorescent pigment. *Transactions of the American Fisheries Society*. 96(2): 157-162.
- Potts, J.C. and C.S. Manooch III. 2001. Differences in the age and growth of white grunt (*Haemulon plumieri*) from North Carolina and South Carolina compared with Southeast Florida. *Bulletin of Marine Science*. 68(1): 1-12.
- Quinn, T.P. and J.C. Ogden. 1984. Field evidence of compass orientation in migrating juvenile grunts (Haemulidae). *Journal of Experimental Marine Biology and Ecology*. 81: 181-192.
- Rasotto, M.B. and Y. Sadovy. 1995. Peculiarities of the male urogenital apparatus of two grunt species (Teleostei: Haemulidae). *Journal of Fish Biology*. 46: 936-948.
- Recksiek, C.W., B.R. Murphy, R.S. Appeldoorn, and K.C. Lindeman. 2001. Integrating fish fauna and habitat assessments: a fundamental step in developing fishery reserve design criteria. *Proceedings of the Gulf and Caribbean Fisheries Institute*. 52: 654-666.
- Recksiek, C.W. and R.S. Appeldoorn. 1998. In pursuit of design criteria for marine fisheries reserves. *Proceedings of the Gulf and Caribbean Fisheries Institute*. 50: 372-384.
- Robertson, D.R. and S.A. Foster. 1982. Off reef emigration of young adults of the labrid fish *Epibulus sinisdiator*. *Copeia* 1982. 1: 229-232.

- Rooker, J.R. and G.D. Dennis. 1991. Diel, lunar and seasonal changes in a mangrove fish assemblage off southwestern Puerto Rico. *Bulletin of Marine Science*. 49(3): 684-698.
- Rosario Jimenez, A. and M. Figuerola Fernandez. 2001. Tag and recapture study of the red hind and coney at three spawning aggregation sites off the west coast of Puerto Rico. *Proceedings of the Gulf and Caribbean Fisheries Institute*. 52: 15-25.
- Saksena, V.P. and W. J. Richards. 1975. Description of eggs and larvae of laboratory reared white grunt, *Haemulon plumieri* (Lacepede)(Pices, Pomadasyidae). *Bulletin of Marine Science*. 25(4): 523-536.
- Shaw II, J. C. 1997. Otolith age validation and growth of the white grunt, *Haemulon plumieri* (Lacipede, 1801) in southwestern Puerto Rico. M.S. Thesis University of Rhode Island. 98 pp.
- Shulman, M.J. 1984. Resource limitation and recruitment patterns in a coral reef fish assemblage. *Journal of Experimental Marine Biology and Ecology*. 74: 85-109.
- Shulman, M.J. 1985. Variability in recruitment of coral reef fishes. *Journal of Experimental Marine Biology and Ecology*. 89: 205-219.
- Shulman, M.J. and J.C. Ogden. 1987. What controls tropical reef fish populations: recruitment or benthic mortality? An example in the Caribbean reef fish *Haemulon flavolineatum*. *Marine Ecology Progress Series*. 39: 233-242.
- Sylvester, J.R. 1973. A note on the upper lethal temperature of juvenile *Haemulon flavolineatum* from the Virgin Islands. *Journal of Fish Biology*. 5: 305-307.
- Szedlmayer, S.T. and J.D. Lee. 2004. Diet shifts of juvenile red snapper (*Lutjanus campechanus*) with changes in habitat and fish size. *Fishery Bulletin*. 102(2): 366-375.
- Takeno, K. and Y. Hamanaka. 1994. Migration of Japanese flounder, *Paralichthys olivaceus*, around Wakasa Bay estimated by means of releasing with tags. *Bulletin of Kyoto Institute of Ocean Fisheries Science*. 17: 66-71.
- Tipping, J.M. 1993. Use of magnetic wire tag locations to mark tiger muskellunge. *North American Journal of Fisheries Management*. 13: 190-193.
- Tolimieri, N., A. Jeffs, and J.C. Montgomery. 2000. Ambient sound as a cue for navigation by the pelagic larvae of reef fish. *Marine Ecological Progress Series*. 207: 219-224.

- Veselov, A.E., R.V. Kazakov, M.I. Sysoyeva, and I.N. Bahmet. 1998. Ontogenesis of rheotactic and optomotor responses of juvenile Atlantic salmon. *Aquaculture*. 168: 17-26.
- Voellestad, L.A., B. Jonsson, N.A. Hvidsten, and T.F. Naesje. 1994. Experimental test of environmental factors influencing the seaward migration of European silver eels. *Journal of Fish Biology*. 45: 641-651.
- Warner, R.R. 1995. Large mating aggregations and daily long distance spawning migrations in the bluehead wrasse, *Thalassoma bifasciatum*. *Environmental Biology of Fishes*. 44: 337-345.
- Werner, E.E. and J.F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. *Ann. Rev. Ecol. Syst.* 15: 393-423.
- Westin, L. 1998. The spawning migration of European silver eel (*Anguilla anguilla* L.) with particular reference to stocked eel in the Baltic. *Fisheries Research*. 38: 257-270.
- Ximenes Carvalho, M.O. and A.A. Fonteles Filho. 1995. Age and growth of fishes of genus *Haemulon* (Pisces: Pomadasyidae), in Ceara State, Brazil. *Arquivos de Ciencias do Mar. Fortaleza*. 29(1-2): 14-19.
- Ximenes Carvalho, M.O. and A.A. Fonteles Filho. 1996. Age and growth of the tomtate, *Haemulon aurolineatum* (Pisces: Pomadasyidae), from Ceará State, Brazil. *Arquivos de Ciencias do Mar. Fortaleza*. 30(1-2): 73-77.
- Zar, H. 1996. *Biostatistical Analysis*. Prentice Hall, New Jersey. 918 pp.

Appendix A

Mark-recapture data sorted by group for small juvenile movements (Experiment 1) including all captured haemulid species. Tagged is the number of fish tagged, Caught is the total number of fish captured and measured, and Recapture is the number of fish caught in that sample with marks. The numbers before the dash in Group column are the school group (see Chapter 3) and the number after the dash is the sampling event for recovery. Mean, minimum and maximum lengths are cm FL. Species: French = *Haemulon flavolineatum*, White = *H. plumieri*, Blue = *H. sciurus*, Tomtate = *H. aurolineatum*, Ceasar = *H. carbonarium*, Sailor = *H. parra*, Small = *H. chrysargyreum*, Spanish = *H. macrostomum*.

Date	Group	Min	Max	Mean	Tagged	Caught	Recapture	French	White	Blue	Tomtate	Caesar	Sailor	Small	Spanish
08/22/03	1-1	6.4	9.6	7.4	11	34	0	10	24	0	0	0	0	0	0
09/03/03	1-1	6.5	11.6	8.4	83	83	0	77	6	0	0	0	0	0	0
09/19/03	1-1	6.1	7.5	6.9	23	25	1	4	21	0	0	0	0	0	0
09/24/03	1-1	6.5	12.0	8.4	51	94	41	79	15	0	0	0	0	0	0
12/13/03	1-2	5.1	10.2	6.9	0	140	5	134	1	0	10	0	0	0	0
01/29/04	1-3	4.7	10.3	6.3	0	396	0	304	23	0	65	1	0	0	0
10/22/03	2-1	7.4	27.8	13.0	0	38	2	33	3	2	0	2	0	0	0
12/04/03	2-2	8.1	25.8	13.1	0	27	2	23	2	3	0	0	0	1	0
01/15/04	2-3	9.8	18.4	13.0	0	27	1	24	0	1	0	0	0	3	0
10/28/03	3-1	5.8	12.1	9.0	0	123	4	91	30	0	5	1	0	0	0
12/05/03	3-2	5.0	11.4	7.9	0	325	5	269	48	0	12	0	0	1	0
01/16/04	3-3	5.3	13.9	7.6	0	660	4	443	179	0	38	4	0	0	0
10/29/03	4-1	6.4	12.3	9.5	0	183	0	142	6	0	33	0	0	2	0
12/17/03	4-2	4.6	12.2	7.8	0	438	0	343	67	0	24	0	0	4	0
01/17/04	4-3	5.0	11.0	7.1	0	440	0	301	93	0	43	1	0	2	0
11/05/03	5-1	6.6	12.7	9.8	0	53	0	37	15	0	1	0	0	0	0
12/19/03	5-2	4.5	12.5	8.1	0	204	0	167	36	0	0	0	0	1	0

Date	Group	Min	Max	Mean	Tagged	Caught	Recapture	French	White	Blue	Tomtate	Caesar	Sailor	Small	Spanish
01/28/04	5-3	5.3	13.1	7.6	0	327	0	253	72	0	1	1	0	0	0
11/12/03	6-1	5.0	12.5	7.1	0	147	0	144	1	1	1	0	0	0	0
12/12/03	6-2	5.0	16.0	7.8	0	669	3	518	124	4	24	1	0	1	0
01/22/04	6-3	5.1	11.9	7.3	0	894	0	703	87	0	100	4	0	0	0
11/18/03	7-1	6.1	13.0	9.0	0	699	1	665	0	0	35	0	0	0	0
12/22/03	7-2	5.2	13.5	8.1	0	600	0	582	3	3	2	2	0	8	0
01/21/04	7-3	5.1	14.2	8.0	0	903	0	875	13	0	1	6	0	8	0
11/20/03	8-1	6.0	15.6	12.3	0	95	0	90	0	0	0	0	0	5	0
12/20/03	8-2	5.5	15.6	9.6	0	199	0	194	0	0	0	3	0	2	0
01/27/04	8-3	6.0	16.1	10.0	0	269	1	265	0	0	0	5	0	0	0
11/22/03	9-1	6.1	13.0	9.5	0	154	0	106	47	0	0	0	0	1	0
12/23/03	9-2	4.4	13.6	7.7	0	242	0	191	48	1	1	1	0	0	0
02/04/04	9-3	5.0	12.8	7.7	0	344	0	235	106	0	0	3	0	0	0
11/23/03	10-1	5.1	28.5	8.8	0	279	0	141	125	3	0	1	1	8	0
12/24/03	10-2	5.3	21.5	8.5	0	264	0	170	90	3	0	1	0	0	0
02/03/04	10-3	5.2	14.3	7.1	0	405	0	344	61	0	0	0	0	0	0
12/03/03	11-1	7.3	16.3	11.3	0	66	0	58	0	1	0	1	0	6	0
01/14/04	11-2	6.7	14.1	9.7	0	83	0	75	2	0	0	3	0	2	1
02/18/04	11-3	5.8	15.4	8.7	0	46	0	45	0	0	0	1	0	0	0
12/30/03	12-1	4.9	14.0	7.7	0	323	0	304	2	0	10	7	0	0	0
02/13/04	12-2	5.9	13.1	8.4	0	177	0	171	2	0	1	3	0	0	0
03/10/04	12-3	5.8	14.0	8.3	0	145	0	143	0	0	0	2	0	0	0
02/05/04	13-1	12.8	16.4	13.9	0	9	0	9	0	0	0	3	0	0	0
02/05/04	14-1	11.5	15.2	13.7	0	23	0	23	0	0	0	3	0	0	0

Appendix B

Geospatial coordinates (decimal degrees) of the 14 sampled grunt-schooling locations at Majimo/Caracoles (Figure 3, Chapter 3).

School	Latitude (°N)	Longitude (°W)
1	17.96655	67.03298
2	17.96625	67.03272
3	17.96653	67.03148
4	17.96643	67.03143
5	17.96508	67.03288
6	17.96537	67.03322
7	17.96525	67.03317
8	17.96605	67.03097
9	17.96663	67.03090
10	17.96618	67.03055
11	17.96606	67.03114
12	17.96614	67.03129
13	17.96477	67.03233
14	17.96458	67.03107

Appendix C

Locations sampled for the recovery of tagged haemulids in Experiment 2 (see Chapter 3) studying large-scale juvenile to adult habitat movement. Data are organized by sampling sequence. The first two locations were recovery of dead individuals while tagging. Method code indicates spearing (1), Arrowhead trapping (2), or juvenile net and trap (3). Effort is defined as man-hours of operation (Time*Number of divers). Time indicates hours spent spearing or soak time for traps in days (as indicated). Number of Fish is the number of haemulids recovered (*Haemulon flavolineatum* or *H. plumieri*). *H. plumieri* were only recovered in traps and listed in their own column. C/E is the catch per unit of effort (Number of Fish/Effort) for spear sampling only. Effort and C/E were not calculated for traps as indicated by (-). The three traps with (?) were recorded, but dates and soak time were lost.

Location	Latitude (°N)	Longitude (°W)	Date	Time (hrs)	Number of Divers	Number of Fish	Number w/Tag	Method Code	Number of <i>H. plumieri</i>	Effort	C/E	Size Range (cm FL)
Corral east	17.94769	67.00273	10/16/2003	1 day	N/A	1	1	3	0	-	-	10.9
Romero	17.94860	66.99672	02/27/2004	1 day	N/A	1	1	3	0	-	-	11.6
Turromote	17.93916	67.02075	05/10/2004	0.5	2	7	0	1	0	1.000	7.000	13.7-17.7
Media Luna	17.93783	67.03880	05/11/2004	0.6	2	0	0	1	0	1.100	0.000	0.0
Romero	17.94570	66.99765	05/11/2004	0.6	2	1	0	1	0	1.200	0.833	13.6
Turromote	17.93516	67.01635	05/11/2004	0.6	2	4	0	1	0	1.233	3.243	14.5-18.6
Enrique	17.95621	67.04133	05/12/2004	0.8	2	6	0	1	0	1.500	4.000	12.1-14.5
Caracoles	17.96083	67.03583	05/13/2004	0.8	2	8	0	1	0	1.633	4.898	12.2-17.9
Corral	17.94636	67.01868	05/13/2004	0.8	2	1	0	1	0	1.500	0.667	w/o Head
Corral	17.94680	67.00135	05/13/2004	0.6	2	3	0	1	0	1.267	2.368	11.0-14.5
Buoy	17.89777	66.96111	05/17/2004	0.8	1	8	0	1	0	0.750	10.667	12.6-17.7
Pt 40	17.92622	67.00318	05/17/2004	0.6	2	6	0	1	0	1.100	5.455	15.5-17.8
Pt 48	17.91270	66.95140	05/17/2004	0.8	2	18	0	1	0	1.533	11.739	11.1-18.6
Pt 49	17.95736	67.03492	05/17/2004	0.5	2	2	0	1	0	0.900	2.222	15.0-15.4
Pt 34	17.92857	67.01283	05/18/2004	0.4	2	0	0	1	0	0.833	0.000	0.0
Pt 41	17.92756	66.96986	05/18/2004	0.5	2	3	0	1	0	1.067	2.813	14.7-16.1
Enrique Pt 2	17.95293	67.04557	05/19/2004	0.8	2	1	0	1	0	1.533	0.652	15.4
Godo's Pt	17.88194	67.02222	05/19/2004	0.7	1	6	0	1	0	0.700	8.571	16.0-18.0

Location	Latitude (°N)	Longitude (°W)	Date	Time (hrs)	Number of Divers	Number of Fish	Number w/Tag	Method Code	Number of <i>H. plumieri</i>	Effort	C/E	Size Range (cm FL)
Media Luna Pt 20	17.93537	67.05067	05/19/2004	0.5	2	2	0	1	0	1.033	1.935	15.5
Pt 47	17.91700	67.01261	05/19/2004	0.4	2	2	0	1	0	0.733	2.727	15.1-17.8
Playa Santa Pt 19	17.93742	66.96111	05/24/2004	0.3	1	0	0	1	0	0.267	0.000	0.0
Pt 32	17.93095	66.95837	05/24/2004	0.4	1	0	0	1	0	0.367	0.000	0.0
Pt 33	17.93028	66.95420	05/24/2004	0.4	1	1	0	1	0	0.433	2.308	9.3
Romero Pt 07	17.94665	66.99880	05/25/2004	0.5	2	4	0	1	0	1.000	4.000	14.2-15.4
Turromote Pt 15	17.93750	67.01022	05/25/2004	0.5	2	1	0	1	0	1.033	0.968	14.4
Turromote Pt 21	17.93509	67.01977	05/25/2004	0.6	2	2	0	1	0	1.200	1.667	13.8-16.7
Mata la Gata	17.95956	67.03729	05/26/2004	0.8	2	6	0	1	0	1.500	4.000	12.0-14.1
Pt 18	17.93750	67.01029	05/26/2004	0.5	2	1	0	1	0	1.067	0.938	16.2
Turromote Pt 28	17.93299	67.00792	05/26/2004	0.7	2	3	0	1	0	1.300	2.308	12.4-17.1
Pt 30	17.93088	66.98895	05/27/2004	0.6	2	4	0	1	0	1.100	3.636	14.0-18.0
Pt 46	17.91729	67.01492	05/27/2004	0.6	2	4	0	1	0	1.267	3.158	14.9-17.2
Pt 36	17.92856	66.97499	05/27/2004	0.5	2	2	0	1	0	1.000	2.000	13.7-15.5
Pt 9	17.94414	67.05280	05/28/2004	0.8	2	11	0	1	0	1.500	7.333	12.6-16.0
Laurel Pt 13	17.93960	67.05990	05/28/2004	0.5	2	7	0	1	0	1.067	6.563	11.7-16.1
Media Luna	17.94168	67.04000	05/28/2004	0.5	2	3	0	1	0	0.933	3.214	14.4-16.1
Pt 17	17.93763	66.99845	06/02/2004	0.6	1	8	0	1	0	0.567	14.118	11.0-15.2
Pt 42	17.92633	66.96315	06/02/2004	0.5	1	5	0	1	0	0.517	9.677	14.6-17.4
Pt 45	17.92165	67.00580	06/02/2004	0.4	1	1	0	1	0	0.383	2.609	16.7
Godó's Pt 2	17.88194	67.02222	06/04/2004	0.7	1	5	0	1	0	0.700	7.143	16.3-17.0
Pt 42	17.92156	67.01064	06/04/2004	0.3	2	0	0	1	0	0.500	0.000	0.0
Turromote	17.93754	67.01785	06/04/2004	0.6	1	4	0	1	0	0.600	6.667	12.2-13.6
Laurel Pt 8	17.94424	67.05527	06/09/2004	0.6	1	10	0	1	0	0.617	16.216	12.2-15.2
Pt 37	17.92868	66.96998	06/09/2004	0.5	1	0	0	1	0	0.500	0.000	0.0
Pt 44	17.92163	67.00784	06/09/2004	0.6	1	1	0	1	0	0.550	1.818	15.6
Pt 12	17.94227	66.97012	06/10/2004	0.6	1	1	0	1	0	0.600	1.667	14.1

Location	Latitude (°N)	Longitude (°W)	Date	Time (hrs)	Number of Divers	Number of Fish	Number w/Tag	Method Code	Number of <i>H. plumieri</i>	Effort	C/E	Size Range (cm FL)
Pt 31	17.93091	66.97718	06/10/2004	0.5	1	0	0	1	0	0.533	0.000	0.0
Pt 35	17.92831	67.00555	06/10/2004	0.8	1	8	0	1	0	0.750	10.667	15.2-18.0
Pt 39	17.92615	67.01013	06/10/2004	0.5	1	2	0	1	0	0.500	4.000	17.3-17.4
S 11	17.94437	66.97482	06/14/2004	0.6	1	5	0	1	0	0.600	8.333	11.1-14.4
S 16	17.93759	67.00085	06/14/2004	0.6	1	5	0	1	0	0.583	8.571	10.6-17.3
S 29	17.93083	66.99149	06/14/2004	0.6	1	4	0	1	0	0.600	6.667	12.9-16.9
Pt 104	17.94749	66.99546	06/15/2004	1.0	1	8	0	1	0	1.000	8.000	11.0-16.7
Pt 22	17.93517	67.01759	06/15/2004	0.9	1	2	0	1	0	0.933	2.143	15.3-15.7
Pt 38	17.92619	67.01276	06/15/2004	0.4	1	0	0	1	0	0.367	0.000	0.0
Pt R01	17.94659	66.99537	06/15/2004	0.7	1	2	0	1	0	0.700	2.857	13.6-15.5
Pt 1	17.96233	67.03410	06/17/2004	1.4	1	3	0	1	0	1.400	2.143	12.4-15.3
Pt 24	17.93522	67.00079	06/17/2004	0.5	2	0	0	1	0	0.900	0.000	0.0
Pt 27	17.93279	67.01040	06/17/2004	0.5	2	0	0	1	0	1.033	0.000	0.0
Pt c01	17.96389	67.03223	06/17/2004	0.5	1	10	0	1	0	0.517	19.355	10.7-15.5
Pt 23	17.93511	67.01510	06/22/2004	0.7	2	11	0	1	0	1.333	8.250	13.5-17.1
Pt 26	17.93282	67.01262	06/22/2004	0.5	2	2	0	1	0	1.033	1.935	17.0-18.1
Pt c02	17.96458	67.03107	06/22/2004	1.2	2	23	2	1	0	2.367	9.718	11.1-15.0
Pt 14	17.93750	67.02210	06/23/2004	0.5	1	3	0	1	0	0.517	5.806	12.1-16.8
Pt c03	17.96297	67.02946	06/23/2004	1.0	1	16	0	1	0	1.000	16.000	10.8-14.8
Pt c04	17.96488	67.03227	06/30/2004	1.0	1	15	0	1	0	1.000	15.000	10.1-15.3
Pt c05	17.96424	67.03250	06/30/2004	0.8	1	5	0	1	0	0.783	6.383	12.4-16.0
Pt c06	17.96324	67.03008	06/30/2004	0.5	1	9	0	1	0	0.533	16.875	11.0-13.9
Pt c07	17.96225	67.02779	06/30/2004	0.5	1	2	0	1	0	0.450	4.444	13.8-14.6
Pt c08	17.96139	67.03741	06/30/2004	1.0	1	9	0	1	0	1.033	8.710	9.8-14.2
Pt c09	17.96321	67.02562	06/30/2004	0.5	1	0	0	1	0	0.467	0.000	0.0
Pt c10	17.96114	67.03781	07/01/2004	0.8	1	6	0	1	0	0.750	8.000	10.0-13.9
Pt c11	17.95919	67.04155	07/01/2004	0.8	1	15	0	1	0	0.817	18.367	10.1-14.8

Location	Latitude (°N)	Longitude (°W)	Date	Time (hrs)	Number of Divers	Number of Fish	Number w/Tag	Method Code	Number of <i>H. plumieri</i>	Effort	C/E	Size Range (cm FL)
Pt c12	17.95798	67.04166	07/01/2004	0.8	1	8	0	1	0	0.800	10.000	11.5-13.6
Pt e1	17.95496	67.05271	07/07/2004	1 day	N/A	0	0	3	0	-	-	0.0
Pt e2	17.95456	67.05321	07/07/2004	1.0	1	11	0	1	0	1.000	11.000	11.2-14.6
Pt e3	17.95330	67.04607	07/07/2004	0.3	1	1	0	1	0	0.300	3.333	15.5
Pt ml1	17.93841	67.05033	07/07/2004	1.0	1	14	0	1	0	0.983	14.237	10.5-15.9
Pt ml2	17.93805	67.04913	07/07/2004	0.7	1	2	0	1	0	0.650	3.077	11.4-12.2
Pt ml3	17.93809	67.04803	07/07/2004	0.8	1	13	0	1	0	0.783	16.596	8.2-16.5
Pt ml4	17.93872	67.04738	07/07/2004	0.7	1	12	0	1	0	0.683	17.561	11.2-15.9
Pt ml5	17.93946	67.04636	07/07/2004	1.1	1	21	0	1	0	1.100	19.091	11.0-16.2
Pt rom	17.94860	66.99672	07/08/2004	1 day	N/A	13	13	3	0	-	-	11.0-13.5
Pt cor1	17.94761	67.00228	07/23/2004	0.5	1	2	0	1	0	0.517	3.871	11.3-13.9
Pt phos 1	17.95921	67.01378	07/23/2004	0.8	1	2	0	1	0	0.833	2.400	10.4-13.5
Pt cor 3	17.94769	67.00273	08/03/2004	0.9	2	17	1	1	0	1.800	9.444	9.9-16.8
Pt m1	17.96374	67.03061	08/03/2004	0.6	2	10	0	1	0	1.100	9.091	10.8-16.3
Pt m2	17.96307	67.03002	08/03/2004	0.7	2	9	0	1	0	1.300	6.923	12.1-15.6
Pt 11 a	17.94572	66.97622	08/10/2004	1.3	2	19	0	1	0	2.667	7.125	11.2-17.6
Pt 12 a	17.94296	66.96873	08/10/2004	1.6	2	19	0	1	0	3.200	5.938	11.6-16.0
Pt cor 4	17.94724	67.01893	08/11/2004	1.4	2	14	0	1	0	2.800	5.000	10.5-17.3
Pt cor 5	17.94549	67.00133	08/11/2004	1.5	2	15	0	1	0	3.000	5.000	10.0-17.7
Pt 105	17.92552	67.01216	08/13/2004	2 days	N/A	0	0	2	0	-	-	0.0
Pt 106	17.92670	67.01001	08/13/2004	2 days	N/A	0	0	2	0	-	-	0.0
Pt 107	17.92167	67.00784	08/13/2004	2 days	N/A	0	0	2	0	-	-	0.0
Pt 108	17.92165	67.00562	08/13/2004	2 days	N/A	0	0	2	0	-	-	0.0
Pt 109	17.94961	67.04228	08/13/2004	0.5	2	0	0	1	0	1.033	0.000	0.0
Pt 110	17.92135	67.02374	08/17/2004	4 days	N/A	0	0	2	0	-	-	0.0
Pt 111	17.91950	67.02553	08/17/2004	4 days	N/A	0	0	2	0	-	-	0.0
Pt 112	17.91663	67.02840	08/17/2004	4 days	N/A	0	0	2	0	-	-	0.0

Location	Latitude (°N)	Longitude (°W)	Date	Time (hrs)	Number of Divers	Number of Fish	Number w/Tag	Method Code	Number of <i>H. plumieri</i>	Effort	C/E	Size Range (cm FL)
Pt 113	17.91377	67.03106	08/17/2004	4 days	N/A	0	0	2	0	-	-	0.0
Pt 114	17.93149	67.02115	08/13/2004	0.5	2	0	0	1	0	1.033	0.000	0.0
Pt 115	17.93394	67.02406	08/17/2004	0.6	2	0	0	1	0	1.233	0.000	0.0
Pt 116	17.95089	67.04228	08/17/2004	0.4	2	0	0	1	0	0.767	0.000	0.0
Pt 117	17.93347	67.02273	08/18/2004	0.6	2	1	0	1	0	1.200	0.833	13.5
Pt 118	17.92359	67.02641	08/23/2004	6 days	N/A	3	0	2	3	-	-	16.5-20.5
Pt 119	17.91828	67.02673	08/23/2004	6 days	N/A	0	0	2	0	-	-	0.0
Pt 120	17.91404	67.02804	08/23/2004	6 days	N/A	0	0	2	0	-	-	0.0
Pt 121	17.90739	67.02883	08/23/2004	6 days	N/A	1	0	2	0	-	-	14.0
Pt 122	17.94442	67.04167	08/18/2004	0.2	2	0	0	1	0	0.467	0.000	0.0
Pt 123	17.90703	67.03006	08/31/2004	7 days	N/A	1	0	2	1	-	-	19.1
Pt 124	17.90553	67.03114	08/31/2004	7 days	N/A	0	0	2	0	-	-	0.0
Pt 125	17.91154	67.03049	08/31/2004	7 days	N/A	0	0	2	0	-	-	0.0
Pt 126	17.92002	67.03059	08/31/2004	7 days	N/A	0	0	2	0	-	-	0.0
Pt 127	17.93435	67.01607	09/03/2004	3days	N/A	0	0	2	0	-	-	0.0
Pt 128	17.93730	67.02163	09/03/2004	3days	N/A	0	0	2	0	-	-	0.0
Pt 129	17.92893	67.03333	09/03/2004	3days	N/A	0	0	2	0	-	-	0.0
Pt 130	17.92582	67.03362	09/03/2004	3days	N/A	1	0	2	0	-	-	17.5
Pt 131	17.92573	67.03362	09/07/2004	4 days	N/A	4	0	2	0	-	-	16.2-16.9
Pt 132	17.94826	67.01795	09/07/2004	4 days	N/A	0	0	2	0	-	-	0.0
Pt 133	17.93652	67.00032	09/08/2004	4 days	N/A	0	0	2	0	-	-	0.0
Pt 134	17.94737	66.99524	09/07/2004	4 days	N/A	0	0	2	0	-	-	0.0
Pt 135	17.94880	67.01237	09/10/2004	2days	N/A	0	0	2	0	-	-	0.0
Pt 136	17.94695	66.99442	09/10/2004	2days	N/A	0	0	2	0	-	-	0.0
Pt 137	17.93748	67.02916	09/08/2004	0.6	2	0	0	1	0	1.167	0.000	0.0
Pt 138	17.93656	66.99888	09/10/2004	2days	N/A	0	0	2	0	-	-	0.0
Pt 139	17.94253	67.00373	09/08/2004	0.5	2	3	0	1	0	1.000	3.000	12.0-15.1

Location	Latitude (°N)	Longitude (°W)	Date	Time (hrs)	Number of Divers	Number of Fish	Number w/Tag	Method Code	Number of <i>H. plumieri</i>	Effort	C/E	Size Range (cm FL)
Pt 140	17.94230	67.00542	09/08/2004	0.5	1	2	0	1	0	0.500	4.000	11.7-16.2
Pt 141	17.94255	67.00886	09/08/2004	0.5	1	2	0	1	0	0.500	4.000	15.0-16.4
Pt 142	17.94554	66.99347	09/14/2004	4days	N/A	1	0	2	1	-	-	20.7
Pt 143	17.93549	66.99722	09/14/2004	4days	N/A	0	0	1	0	-	-	0.0
Pt 144	17.92976	67.02679	09/14/2004	0.6	2	29	0	1	0	1.100	26.364	12.0-17.5
Pt 145	17.94650	66.99364	09/21/2004	7days	N/A	0	0	2	0	-	-	0.0
Pt 146	17.91274	66.95144	09/21/2004	7days	N/A	15	0	2	15	0.000	9.375	16.0-20.0
Pt 147	17.96502	67.03198	09/14/2004	0.8	1	8	1	1	0	0.817	9.796	11.1-13.6
Pt 148	17.94593	66.99318	09/24/2004	4days	N/A	0	0	2	0	-	-	0.0
Pt 149	17.92889	67.02683	09/21/2004	7days	N/A	1	0	2	1	-	-	18.7
Pt 150	17.92826	67.02744	09/24/2004	4days	N/A	0	0	2	0	-	-	0.0
Pt 151	17.92638	67.03037	09/24/2004	4days	N/A	7	0	2	5	-	-	15.6-18.5
Pt 152	17.92897	67.02833	09/27/2004	4days	N/A	4	0	2	1	-	-	16.1-17.3
Pt 153	17.92701	67.03086	09/27/2004	4days	N/A	1	0	2	0	-	-	15.9
Pt 154	17.94541	66.99111	09/27/2004	4days	N/A	1	0	2	0	-	-	21.8
Pt 155	17.93886	67.02596	09/27/2004	0.3	2	0	0	1	0	0.633	0.000	0.0
Pt 156	17.94553	66.98952	10/01/2004	4days	N/A	0	0	2	0	-	-	0.0
Pt 157	17.92847	67.02818	09/30/2004	3days	N/A	3	0	2	0	-	-	15.5-16.2
Pt 158	17.92721	67.03255	09/30/2004	3days	N/A	1	0	2	0	-	-	17.0
Pt 159	17.92582	67.03373	09/27/2004	0.8	2	23	0	1	0	1.533	15.000	12.0-18.0
Pt 160	17.94238	67.01020	09/28/2004	0.5	1	4	0	1	0	0.500	8.000	11.6-16.8
Pt 161	17.94373	67.01453	09/28/2004	1.0	2	17	0	1	0	2.000	8.500	12.1-15.8
Pt 162	17.94388	67.01543	09/28/2004	1.0	2	11	0	1	0	2.000	5.500	11.5-16.0
Pt 164	17.93564	67.01496	09/30/2004	1.1	2	13	0	1	0	2.100	6.190	11.0-16.8
Pt 165	17.93786	67.02160	09/30/2004	1.3	2	18	0	1	0	2.500	7.200	11.4-18.0
Pt 166	17.92847	67.03117	09/30/2004	6days	N/A	1	0	2	0	-	-	17.1
Pt 167	17.92572	67.03434	09/30/2004	6days	N/A	0	0	2	0	-	-	0.0

Location	Latitude (°N)	Longitude (°W)	Date	Time (hrs)	Number of Divers	Number of Fish	Number w/Tag	Method Code	Number of <i>H. plumieri</i>	Effort	C/E	Size Range (cm FL)
Pt 168	17.94648	66.98862	10/01/2004	5days	N/A	0	0	2	0	-	-	0.0
Pt 169	17.94010	66.96870	10/01/2004	0.3	1	1	0	1	0	0.333	3.000	16.4
Pt 170	17.94705	66.98240	10/01/2004	0.3	2	2	0	1	0	0.667	3.000	14.3-15.1
Pt 171	17.94769	66.99109	10/01/2004	0.3	1	1	0	1	0	0.333	3.000	15.1
Pt 172	17.94752	66.99294	10/01/2004	0.3	1	1	0	1	0	0.333	3.000	14.0
Pt 173	17.96471	67.03225	10/05/2004	0.8	2	10	0	1	0	1.633	6.122	10.4-14.5
Pt 174	17.96336	67.03056	10/05/2004	1.1	2	10	1	1	0	2.100	4.762	10.0-15.2
Pt 175	17.96258	67.02936	10/05/2004	0.9	2	30	0	1	0	1.833	16.364	10.0-14.5
Pt 176	17.96172	67.02782	10/05/2004	0.6	2	4	0	1	0	1.167	3.429	11.7-14.6
Pt 177	17.94713	66.98746	?	?	N/A	0	0	2	0	-	-	0.0
Pt 178	17.92953	67.03000	?	?	N/A	0	0	2	0	-	-	0.0
Pt 179	17.92510	67.03271	?	?	N/A	0	0	2	0	-	-	0.0
Pt 180	17.96435	67.03255	10/06/2004	1.0	2	12	0	1	0	2.000	6.000	11.7-15.7
Pt 181	17.96098	67.03663	10/06/2004	0.6	2	14	0	1	0	1.267	11.053	11.0-15.2
Pt 182	17.96073	67.03719	10/07/2004	0.6	2	6	0	1	0	1.200	5.000	11.8-14.0
Pt 183	17.95930	67.04160	10/07/2004	1.1	2	12	0	1	0	2.200	5.455	11.2-15.9
Pt 184	17.93377	67.01275	02/07/2005	0.9	2	11	0	1	0	1.700	6.471	13.4-17.1
Pt 185	17.93577	67.02148	02/07/2005	0.9	2	2	0	1	0	1.700	1.176	12.9-15.9
Pt 186	17.92880	67.02995	02/07/2005	0.3	2	0	0	1	0	0.500	0.000	0.0
Pt 187	17.91827	67.03668	02/08/2005	0.7	2	2	0	1	0	1.333	1.500	14.5-15.6
Pt 188	17.94105	67.03908	02/08/2005	0.8	2	11	0	1	0	1.567	7.021	13.4-17.2
Pt 189	17.93942	67.04558	02/08/2005	0.8	2	26	0	1	0	1.667	15.600	10.1-16.6
Pt 190	17.96482	67.03203	02/09/2005	0.9	2	7	0	1	0	1.700	4.118	11.2-12.8
Pt 191	17.96463	67.03088	02/09/2005	0.9	2	13	3	1	0	1.767	7.358	10.8-16.0
Pt 192	17.96432	67.03097	02/11/2005	1.0	2	8	1	1	0	2.000	4.000	11.9-15.9
Pt 193	17.96227	68.69900	02/11/2005	0.8	2	16	0	1	0	1.667	9.600	11.5-15.0
Pt 194	17.96353	67.03253	02/11/2005	0.9	2	5	0	1	0	1.867	2.679	11.2-16.3

Location	Latitude (°N)	Longitude (°W)	Date	Time (hrs)	Number of Divers	Number of Fish	Number w/Tag	Method Code	Number of <i>H. plumieri</i>	Effort	C/E	Size Range (cm FL)
Pt 195	17.96087	67.03643	02/11/2005	0.6	2	5	0	1	0	1.100	4.545	11.7-13.5
Pt 196	17.96057	67.03698	02/18/2005	0.7	2	5	0	1	0	1.333	3.750	12.2-14.2
Pt 197	17.95933	67.04127	02/18/2005	1.1	2	8	0	1	0	2.133	3.750	11.8-15.8
Pt 198	17.95782	67.04122	02/18/2005	0.8	2	5	0	1	0	1.600	3.125	11.5-14.9
Pt 199	17.95473	67.05325	02/18/2005	0.5	1	1	0	1	0	0.500	2.000	12.9
Pt 200	17.95397	67.05253	02/22/2005	0.5	1	14	0	1	0	0.483	28.966	10.8-16.0
Pt 201	17.96370	67.04913	02/22/2005	0.8	2	15	0	1	0	1.533	9.783	11.4-15.9
Pt 202	17.96360	67.04268	02/22/2005	0.2	2	0	0	1	0	0.333	0.000	0.0
Pt 203	17.94620	67.00143	02/22/2005	0.5	2	6	0	1	0	1.033	5.806	11.3-15.1
Pt 204	17.94742	67.00178	02/22/2005	0.6	2	20	2	1	0	1.267	15.789	10.0-15.3
Pt 205	17.94445	67.00085	02/22/2005	0.5	2	5	0	1	0	1.000	5.000	12.0-16.6
Pt 206	17.94780	66.99620	02/23/2005	0.9	2	11	1	1	0	1.800	6.111	11.9-16.1
Pt 207	17.91713	67.01263	03/04/2005	0.5	2	0	0	1	0	1.000	0.000	0.0
Pt 208	17.92182	67.00569	03/04/2005	0.5	2	2	0	1	0	1.000	2.000	14.5-15.8
Pt 209	17.92637	67.00333	03/04/2005	0.8	2	7	0	1	0	1.500	4.667	14.2-17.1
Pt 210	17.91716	67.01519	03/15/2005	0.6	2	1	0	1	0	1.233	0.811	16.5
Pt 211	17.92594	67.01075	03/15/2005	0.5	2	1	0	1	0	0.900	1.111	16.3
Pt 212	17.93767	66.99158	03/15/2005	0.6	2	1	0	1	0	1.267	0.789	16.8
Pt 213	17.92810	67.00612	03/16/2005	0.7	2	3	0	1	0	1.333	2.250	15.0-16.1
Pt 214	17.93072	66.98926	03/16/2005	0.6	2	2	0	1	0	1.167	1.714	15.6-16.1
Pt 215	17.93326	67.00829	03/16/2005	0.7	2	7	0	1	0	1.400	5.000	13.8-17.1
Pt 216	17.93039	66.99169	03/23/2003	0.6	2	4	0	1	0	1.167	3.429	15.7-16.4
Pt 217	17.94658	66.99544	03/23/2003	0.8	2	7	0	1	0	1.500	4.667	11.0-15.1
Pt 218	17.94749	66.99549	03/29/2005	0.8	3	13	1	1	0	2.500	5.200	12.8-17.4
Pt 219	17.93417	67.01272	03/29/2005	0.8	3	12	0	1	0	2.500	4.800	12.3-15.8
Pt 220	17.93795	66.99899	03/31/2005	0.7	2	1	0	1	0	1.300	0.769	16.2
Pt 221	17.92993	67.02657	03/31/2005	1.0	1.5	13	0	1	0	1.500	8.667	12.6-18.0

Location	Latitude (°N)	Longitude (°W)	Date	Time (hrs)	Number of Divers	Number of Fish	Number w/Tag	Method Code	Number of <i>H. plumieri</i>	Effort	C/E	Size Range (cm FL)
Pt 222	17.94253	67.01035	03/31/2005	0.6	1	5	0	1	0	0.617	8.108	12.9-15.0
Pt 223	17.93747	67.00110	04/12/2005	0.8	2	0	0	1	0	1.500	0.000	0.0
Pt 224	17.94248	67.01028	04/12/2005	0.9	2	8	0	1	0	1.767	4.528	13.5-17.0
Pt 225	17.92570	67.03372	04/12/2005	0.8	2	26	0	1	0	1.567	16.596	13.1-17.2