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The effects of trawling and habitat use on red snapper and the associated community

Robert Joseph David Wells

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THE EFFECTS OF TRAWLING AND HABITAT USE ON RED SNAPPER AND THE
ASSOCIATED COMMUNITY

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Oceanography and Coastal Sciences

by
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May 2007

DEDICATION

This piece of work is dedicated to the most important and influential people in my life. My wife, Janel Wells, my son, Caden Wells, and my parents, Joe and Sue Wells.

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I sincerely want to express my thanks to my major advisor, Dr. James H. Cowan, Jr., who provided the utmost intellectual stimulation throughout my time at LSU. His open door policy, excitement for research, and hands off approach are all qualities that I greatly appreciate. His breadth of knowledge and ability to concurrently discuss both research and LSU sports not only enhanced the success of the overall project, but enhanced my overall Ph.D. experience as well.

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ABSTRACT

The primary impediment to the recovery of Gulf of Mexico (GOM) red snapper is believed to be high levels of bycatch of age 0 and age 1 individuals in shrimp trawls. Thus, conservation of GOM red snapper involves evaluating both habitat-specific function and effects of shrimp trawls on red snapper and the associated benthic ecosystem. The two goals of this study were to evaluate the effects commercial shrimp trawls have on juvenile red snapper life history parameters, on associated fish and invertebrate communities and their habitat, and to identify essential fish habitat (EFH) for red snapper by applying all four data quality levels specified by the National Marine Fisheries Service. Sampling with a suite of gear types occurred during quarterly cruises over a two-year period on the northern Gulf of Mexico continental shelf. Presence of commercial shrimp trawls had negative impacts on the benthic ecosystem at large. Red snapper were found to have truncated size distributions, slower growth rates in the fall, higher mortality rates, lower production potential, and different feeding dynamics, as revealed by differences in $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$, over habitats exposed to trawling. Differences in biotic communities, diversity indices, size structure, and habitat characteristics were also found between similar habitats in trawled versus non-trawled areas. Ontogenetic habitat shifts from low to higher relief habitats with increasing size and age were found for red snapper. Shell-rubble and reef habitats may be important for red snapper by providing protection from predators; however, the sand and mud habitat appears to be the most important for enhancing production and early life survival of age 0 fish based upon faster daily growth rates and higher production potential. Results of this study indicate the presence of commercial shrimp trawling negatively impacts the benthic ecosystem and post-settlement processes acting on age 0 red snapper. All habitats sampled in this

study are important during some portion of the life history of red snapper. Thus, if shrimp closures are proposed in the GOM to enhance survival of age 0 and age 1 red snapper, then all habitat types sampled in this study will need to be protected.

GENERAL INTRODUCTION

Estimates of biological reference points indicate Gulf of Mexico (GOM) red snapper (*Lutjanus campechanus*) are overfished and are currently experiencing overfishing (GMFMC 2005). The primary impediment to the recovery of GOM red snapper is believed to be high levels of bycatch of age 0 and age 1 individuals in shrimp trawls (Goodyear 1995, Schirripa and Legault 1999). An estimated 25-30 million age 0 and age 1 red snapper are caught annually in shrimp trawls (Ortiz et al. 2000) and shrimp trawl bycatch may account for as much as 90% of juvenile red snapper mortality (Goodyear and Phares 1990, Goodyear 1995). To decrease bycatch of juvenile red snapper by shrimp trawlers, bycatch reduction devices (BRDs) became mandatory in the shrimp fishery of the western GOM (1998) and in the exclusive economic zone in the eastern GOM (2004). Bycatch reduction devices were expected to reduce bycatch mortality by more than 50% (GMFMC 1996), and assumed 100% survival of excluded juveniles. However, concerns about the effectiveness of BRDs have arisen due to low numbers of red snapper individuals excluded (10-20%) (Foster and Scott-Denton 2004) and high post-exclusion mortality of juveniles (Gallaway et al. 1998). Low survival of excluded juvenile fishes is attributed to increased predation by larger fishes and marine mammals, physiological stress, embolism, and species displacement from their habitat (Main and Sangster 1988, DeAlteris and Reifsteck 1993, Broadhurst 1998, UGA Marine Extension Service and National Marine Fisheries Service (NMFS) Harvesting Branch 2003).

The development of BRD technology assumed that juvenile red snapper were randomly distributed over benthic habitat in the GOM. However, studies characterizing habitat preferences of age 0 red snapper indicate that juveniles are not randomly

distributed on shrimp grounds, and that age 0 red snapper prefer low-relief structure, such as shell-rubble habitat (Workman and Foster 1994, Szedlmayer and Howe 1997, Szedlmayer and Conti 1999). In addition, natural hard bottom habitats, such as reef pinnacles, shelf-edge banks, and ledges, have been shown to be important habitat for adult red snapper and other reef fishes (Parker et al. 1983, Schroeder et al. 1988). Little information exists regarding these natural reefs due to misconceptions that little natural hard bottom habitat exists on the shallow (<40 m) northern GOM shelf. As a result, most studies have focused on mud, sand, shell, and artificial reefs as habitat for red snapper (Moseley 1966, Bradley and Bryan 1975, Holt and Arnold 1982, Workman and Foster 1994, Szedlmayer and Howe 1997, Szedlmayer and Conti 1999, Rooker et al. 2004, Patterson et al. 2005). Despite the potential importance of natural reef habitat for red snapper in the northern GOM, no studies have adequately addressed the role these habitats play in the life history of red snapper.

To increase the spawning stock biomass of adult red snapper, reductions in juvenile bycatch by shrimp trawls appear to be necessary. It has been proposed that a technological solution to bycatch reduction may not exist and that the addition of either shrimp non-trawl areas or time closures may need to be implemented by fisheries managers to provide additional protection for juvenile red snapper from trawls (Gallaway et al. 1999). However, before management strategies can be implemented, studies addressing the functional importance of different habitats (i.e., do they convey higher growth rates and offer increased production potential?) for juvenile red snapper are warranted.

Habitat-mediated processes in the post-settlement survival of continental shelf fish species have received increasing attention (Eggleston 1995, Tupper and Boutilier

1995, Thrush et al. 2002, Rooker et al. 2004). Habitat selection has been shown to be influenced by predation pressure and prey availability (Hixon and Beets 1989, Auster et al. 1997), physiological constraints (Allen and Baltz 1997, Kupschus and Tremain 2001), and physical processes (Boehlert and Mundy 1988). Habitat quality can be a function of the growth of organisms when natural mortality is size, hence growth-rate, dependent (Houde 1987, Sogard 1997). An assumption in my approach is faster growing juveniles have lower mortality rates due to reduced exposure time to predators (Cowan et al. 1996). Therefore, it is advantageous to utilize high quality habitats that provide greater foraging and growth opportunities, resulting in an enhanced probability of survival. Thus, habitats that support a disproportionately high number of rapidly growing juveniles and contribute to higher potential survivorship (i.e., high instantaneous growth:instantaneous mortality ratios) need to be identified and perhaps protected.

Reductions in habitat complexity by trawling affect target and non-target species and can ultimately influence recruitment to harvestable stocks (Auster et al. 1996, NRC 2002). Of particular importance in my study is the threat posed by habitat degradation to juvenile red snapper survival in the GOM. The GOM trawl fishery targets shrimp in soft sediment habitat that is assumed to be of low structural complexity and species diversity. However, these habitats support a high diversity of organisms that play key roles in the trophic dynamics of the ecosystem (Arreguin-Sanchez et al. 2004) and provide important prey resources for red snapper and other upper-level consumers (Bradley and Bryan 1975, Davis 1975, Futch and Bruger 1976, Lee 1998, McCawley 2003). Additionally, trawling in the northern GOM is not confined to soft sediments and often affects more complex habitats. Auster (1998) identified habitats such as biogenic structures and shell aggregates as some of the most susceptible to severe adverse impacts of trawling. Thus,

there is a need to identify the habitat-specific effects shrimp trawls have on the life history parameters of bycatch species, including red snapper.

The Sustainable Fisheries Act, an amendment to the Magnuson-Stevens Fishery Conservation and Management Act in 1996, defined essential fish habitat (EFH) as those waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity (Benaka 1999). Specifically, the Act called for the identification and description of EFH, of the adverse impacts on EFH, and of the necessary measures for proper conservation and enhancement of EFH. The NMFS, in response to a mandate from Congress to identify and protect EFH, specified four levels of analysis that, depending on data available, could be implemented to provide qualitative to quantitative assessments of habitat quality: 1) presence and absence, 2) density, 3) growth, reproduction, or survival, and 4) production (Minello 1999). This shift toward an EFH management approach through habitat-mediated processes is needed for the conservation of GOM red snapper, whose overfished status stems from an EFH issue.

The primary goals of this study were twofold: 1) to evaluate the effects commercial shrimp trawls have on juvenile red snapper life history parameters, on the associated fish and invertebrate communities and their habitat, and 2) to identify EFH for red snapper on the northern GOM continental shelf applying all four levels of analyses specified by NMFS. Effects of trawling were evaluated over both sand and shell rubble, while identification of EFH was investigated over sand, shell rubble, and natural reef habitats.

Proper gear selection for the specific objectives of a study remains one of the most important considerations in any sampling design (Rozas and Minello 1997). As such, appropriate gear selection must account for both deployment and processing time to

aid in a sufficient sample size, while attaining adequate precision. Thus, Chapter 1 is devoted to comparing the different gear types that I used, and their ability to collect red snapper over natural reef habitats. I was specifically interested in determining the size selectivity associated with each gear and comparing the relative catchability (q-ratio) between gears that collected similar sizes of red snapper. Chapter 2 is focused on estimating the relative abundance and size-specific habitat use of red snapper and associated fish assemblages over different habitat types with a non-invasive underwater video methodology. The goal of Chapter 3 is to characterize habitat use patterns and to assess the effects of trawling on demersal fish and invertebrate communities on the northern GOM continental shelf. In Chapter 4, I specifically focus on red snapper and investigate habitat use and the habitat-specific effects that shrimp trawling has on red snapper distribution, densities, size, and vital rates, such as growth rate, mortality rate, and production potential. Lastly, the goal of Chapter 5 is to investigate the role of ontogeny, habitat, and exposure to shrimp trawling on the feeding habits of red snapper, with a combined stable isotope and stomach contents approach.

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CHAPTER 1: A COMPARISON OF MULTIPLE GEAR TYPES IN SAMPLING RED SNAPPER ON NATURAL LOW-RELIEF REEFS

Introduction

Proper gear selection for the specific objectives of a study is one of the most important considerations in any sampling design. Employing multiple sampling gears has increased, both for characterizing fish communities and for evaluating the relative abundance of single species across multiple habitat types, due to the size-selectivity and bias associated with individual gears (Willis et al. 2000, Diaz et al. 2003). As such, appropriate gear selection must account for deployment and processing time to aid in a sufficient sample size, while attaining adequate precision.

Characterization of habitat use patterns by organisms associated with reef habitats is difficult due to habitat complexity, the mobility and cryptic nature of many species, and ontogenetic habitat shifts (Sale and Douglas 1981, Bortone et al. 1989). Individual sampling techniques each have their own strengths and weaknesses when targeting specific species or size ranges. Otter trawls are a common technique for sampling demersal species, and providing relative abundance estimates of small, cryptic, and burrowing species (Harmelin-Vivien and Francour 1992, Hayes et al. 1996). However, low and highly variable catch efficiencies are associated with towed nets (e.g., seines, trawls), and can greatly reduce the success of these mobile gear types (Orth and van Montfrans 1987, Rozas and Minello 1997). Collection devices, such as fish traps, can also be useful for targeting specific species associated with structurally complex habitats, such as coral and rocky reefs (Whitelaw et al. 1991, Newman and Williams 1996); however, the inability to define a sampling area and the influence of environmental parameters (e.g., currents, bait plume) can affect gear performance, yet are difficult to quantify.

Underwater video camera arrays have become an increasingly common tool for characterizing marine fish assemblages (Gledhill et al. 1996, Willis et al. 2000, Cappo et al. 2004), and for indexing abundances of single species over a particular habitat type (Ellis and DeMartini 1995). This technique, and other video methods, is particularly desirable for estimating fish abundance when depth constraints and physical complexity of bottom topography exist (Bortone et al. 1986, Greene and Alevizon 1989). However, difficulties associated with video censuses are evident, such as biased estimates due to poor visibility, difficulty in species identification, fish movement that results in double counting, or avoidance and under-representation of small, cryptic species (Sale and Douglas 1981, Bohnsack and Bannerot 1986). Nevertheless, video methods offer unique advantages over more traditional methods (e.g., otter trawls, diver counts) of assessing relative fish abundance as they are non-destructive and the equipment can be deployed and retrieved rapidly from depth. Thus, the use of both trawling and visual counts has been suggested to provide a good representation of the relative abundance of fishes due to the high capture success of small, benthic, and cryptic species by trawls, while large, mid-water, and more mobile species are better estimated with visual techniques (Harmelin-Vivien and Francour 1992).

Natural low-relief reef habitats in the form of reef pinnacles, banks, and ledges, as well as many artificial reefs, exist on the inner shelf of the northern Gulf of Mexico (GOM), and have been suggested to be important reef habitat for red snapper and other reef fishes (Parker et al. 1983, Schroeder et al. 1988, Szedlmayer and Shipp 1994, Patterson et al. 2005). However, the structural heterogeneity of these reef habitats makes it difficult to adequately sample a wide size range of the species of interest. Despite the potential importance of natural and artificial reef habitats in the northern GOM for red

snapper, to date no studies have adequately addressed the effectiveness and size selectivity of different gear types on red snapper.

The goals of this study were to compare different gear types and their ability to collect red snapper over natural low-relief reef habitats. I was specifically interested in determining which gears sampled the highest catch per unit area (A). As fish grow, their vulnerability to a particular gear changes, which can affect gear efficiency. Different-sized fish are caught with varying efficiencies due to gear selectivity, catchability, or to differences in fish distribution or habitat. Thus, my objective was not to assess gear efficiency across all four gears, but rather to determine the size selectivity associated with each gear and to compare the relative catchability (q-ratio) between gears that collected similar sizes of red snapper.

Methods and Materials

Study Site

Two natural low-relief reef habitats on the northern GOM inner continental shelf, located approximately 20 km south of Mobile Bay, Alabama, were chosen for this study. These reefs have been characterized as reef-like outcrops of rock rubble and shell hash supporting a diverse epifaunal assemblage, and are identified by the names Southeast Banks and 17 Fathom Hole on navigation charts (Schroeder et al. 1988).

Gear Types

Four different gear types were used to sample red snapper quarterly in 2004 and 2005 on the R/V *Caretta*, an 18-m research vessel operated by the National Marine Fisheries Service (NMFS) Pascagoula, Mississippi laboratory. Gear types included an otter trawl, a small fish trap, a chevron trap, and a stationary 4-camera underwater video array. Standard NMFS Fall Groundfish Survey trawl gear was used (FGS; SEAMAP

Information System, NMFS, Pascagoula, MS), which included a single 12.8-m wide net with 4 cm mesh size, towed at approximately 4.6 km h^{-1} for 10 min, adjacent to the reef structure. An addition to the standard trawl was a 0.7cm mesh cod end lining that was added to increase gear selectivity for smaller individuals. The small fish trap (dimensions: 64 cm width x 60 cm length x 43 cm height, mesh: 2.2 cm plastic coated wire) and the chevron trap (dimensions: 150 cm width x 180 cm length x 60 cm height, opening: 10 cm x 5 cm, mesh: 3.8 cm plastic coated wire) were each soaked on a reef for a two hour period. The camera array consisted of four Sony DCR-VX1000 digital video camcorders housed in aluminum underwater housings (Figure 1.1). Cameras were positioned orthogonal to one another at a height of 25 cm above the bottom of the camera rig to provide a nearly 360° view. Each camera had a 72.5° viewing angle with an approximate viewing distance of 5 m, resulting in an estimated viewing volume of 70.4 m³ (Rademacher and Render 2003). In addition, two parallel-beam lasers placed 10 cm apart were attached below each camera to aid in estimating lengths of observed fish to the nearest cm. The camera array was deployed for a 30-min period and was baited with a single Atlantic menhaden (*Brevoortia tyrannus*), which was replaced after each deployment. All sampling was performed during daylight hours (30 minutes after sunrise to 30 minutes before sunset). Trawl surveys were conducted three to six days prior to traps and the underwater video array, which were concurrently deployed on the same day.

Data Analysis

Estimates of catch per unit area (A) were calculated for each gear type (g:, where i=trawl, small fish trap, chevron trap, and video) at each survey station. Sampling areas were calculated for each gear type and resulted in an estimated 9,813 m² covered by each trawl sample, and 7,854 m² by each trap and underwater video sample. I calculated the

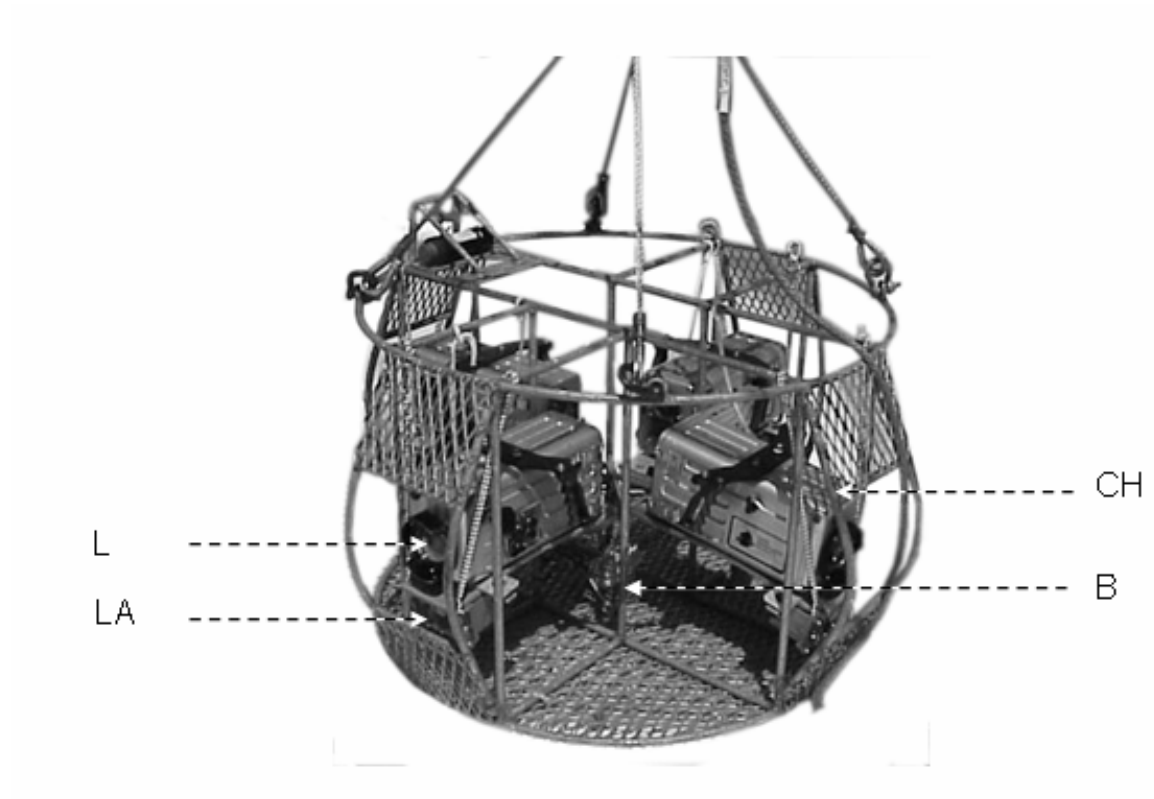


Figure 1.1. Baited camera array used to collect underwater video of red snapper and the fish community. Cameras were mounted inside aluminum underwater camera housings (CH) and positioned orthogonal to one another. Lenses (L) and laser arrays (LA) were positioned to provide nearly 360° of coverage. A single Atlantic menhaden (*Brevoortia tyrannus*) was placed in the bait box (B) during each deployment.

area sampled by the traps and video array using an estimate of 50 m as a radius of influence (Lokkeborg et al. 1995), using the area of a circle (πr^2). Catch per unit area (A_i) was calculated as the percent catch for each gear type divided by the percent area covered by each gear using the following equation:

$$A_i = ((\text{catch}_i / \Sigma \text{ catch}) * 100) / ((\text{area}_i / \Sigma \text{ area}) * 100)$$

Gear-specific vulnerability of red snapper was compared using length-frequency distributions. Red snapper length-frequency data were binned by 10 mm size classes for each gear type and were compared with Kolmogorov-Smirnov (KS) two-sample tests (Sokal and Rohlf 1995). Red snapper also were grouped according to their corresponding age class estimated from length with a von Bertalanffy growth function developed using red snapper from this study (Chapter 4). In addition, size distributions of the fish community (excluding red snapper) were compared to red snapper sizes by each gear type to assess if the size bias was gear or species-specific.

Relative catchability (q-ratio) estimates were compared between gears that targeted similar sizes of red snapper over the same habitat, thus sampling the same operative population. Catchability estimates were obtained using the average catch of each gear type during all quarters. Specifically, catchability comparisons were made between the trawl and small fish trap, and between the underwater video and chevron trap, using the following equation from Arreguin-Sanchez and Pitcher (1999):

$$C_i = q_i s E_i N$$

where C_i is the total catch by gear type i , q_i is the catchability coefficient of gear type i , s is the probability of gear selection, E_i is the effort (area sampled) of gear type i , and N is the operative population the gear is sampling. I assumed the operative population (N) and the selectivity (s) were equal between gears that targeted similar sizes of red snapper

on the same habitat. Thus, for gear i , $C_i = q_i s E_i N$, and for gear j , $C_j = q_j s E_j N$. Therefore solving for the relative catchability (q-ratio) gives the following equation:

$$q_i/q_j = C_i E_j / C_j E_i$$

Results

Data from the six sampling cruises were used to compute gear comparison statistics. A total of 756 red snapper was collected or observed using the four gear types during the study. The total number of red snapper sampled varied by gear type, with the highest percentage of red snapper sampled with trawls (69.3%), followed by the chevron trap (19.3%), the video array (6.8%), and the small fish trap (4.6%).

Estimates of A were greatest with trawls compared to other gear types for both red snapper and other members of the fish community (Figures 1.2 and 1.3). The high A calculated from the trawl catches was consistent between reef sites. In addition, estimates of A showed similar patterns when analyzing only red snapper, or the fish community (excluding red snapper) (Figures 1.2 and 1.3). The second highest A was calculated from the chevron trap, but the number of red snapper collected per unit of area between reef sites ranged from nearly equal (Southeast Banks) to over 6-fold fewer (17 Fathom Hole) than the corresponding trawl samples. Overall, the small fish trap and underwater video had the lowest estimates of A .

Red snapper length distributions were significantly different among gears, regardless of the sampling location (KS tests: $P < 0.05$; Figures 1.2 and 1.3). The smallest red snapper were collected using the trawl (primarily between 30-250 mm TL), followed by the small fish trap (150-250 mm TL), the underwater video array (100-150 and 300-350 mm TL), and the largest red snapper were consistently collected using the chevron trap (150-440 mm TL) (Figures 1.2 and 1.3). Further, age 0 red snapper were most

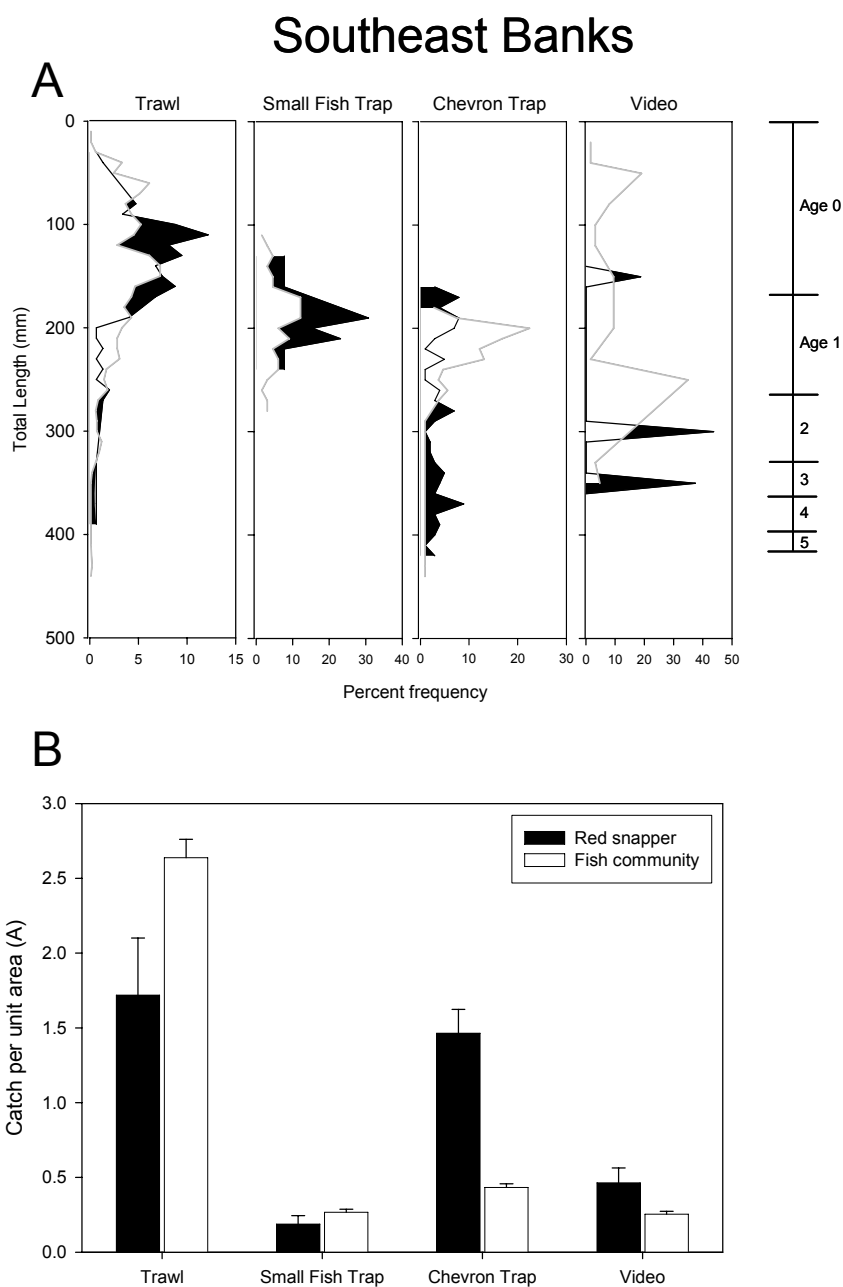


Figure 1.2. (A) Size frequency distributions of red snapper and the fish community (excluding red snapper) collected by each gear type at Southeast Banks. Age-at-size bins are shown for red snapper and were based upon a von Bertalanffy model from otolith microstructure analysis. (B) Relative catch per unit area (A_i) by gear type at Southeast Banks for red snapper and for the fish community (excluding red snapper) (± 1 SE).

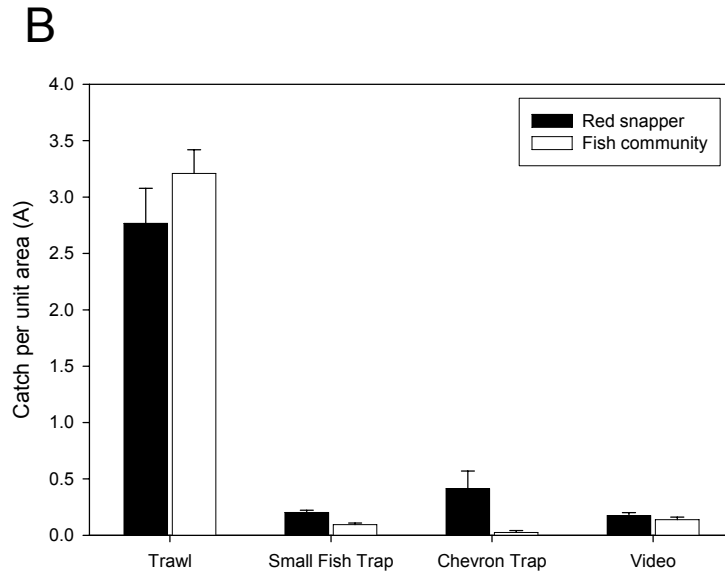
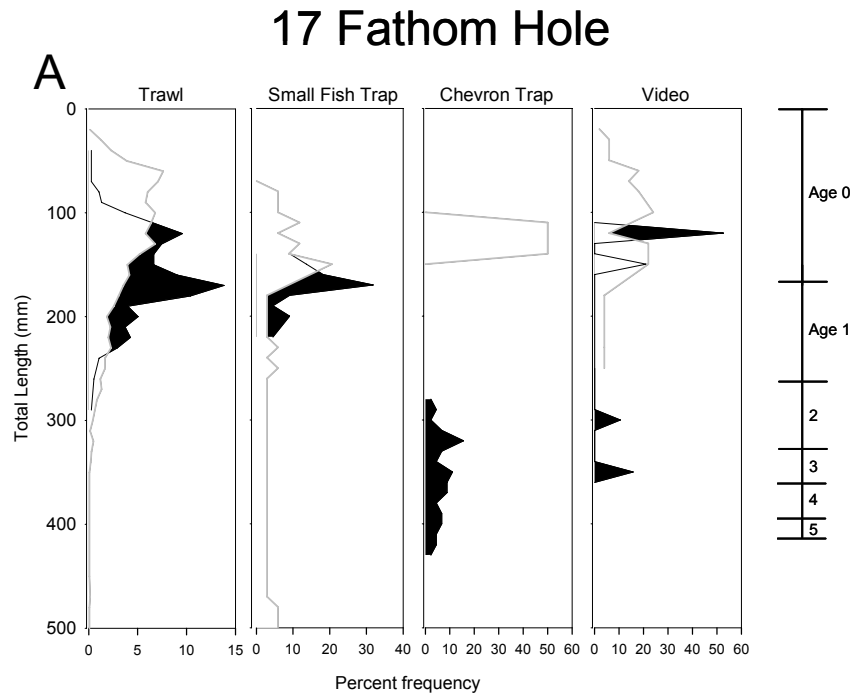


Figure 1.3. (A) Size frequency distributions of red snapper and the fish community (excluding red snapper) collected by each gear type at 17 Fathom Hole. Age-at-size bins are shown for red snapper and were based upon a von Bertalanffy model from otolith microstructure analysis. (B) Relative catch per unit area (A_i) by gear type at 17 Fathom Hole for red snapper and for the fish community (excluding red snapper) (± 1 SE).

abundant in the trawl, and both age 0 and age 1 red snapper were abundant in the small fish trap. Red snapper observed using the underwater video ranged from age 0 to age 3, and the chevron trap sampled red snapper primarily between ages 1 and 5. The trawl sampled the widest size-at-age range of all gears, while the small fish trap appeared to be the most size selective (Figures 1.2 and 1.3). Qualitatively, size distributions between red snapper and all other fishes showed high overlap by gear type (Figures 1.2 and 1.3); however, non-significant size differences were observed only with the small fish trap at each sampling location (KS tests: SEB: $P=0.2798$, 17FH: $P=0.1744$).

Relative catchability (q-ratio) comparisons between gears that target similar sizes of red snapper indicate that the trawl and chevron trap have high catchabilities for juvenile (ages 0-1) and adult (ages 2-5) red snapper, respectively. The q-ratio of the trawl to the small fish trap was 5.6 at Southeast Banks and 2.9 at 17 Fathom Hole, indicating the trawl was between three to five times more effective at sampling juvenile red snapper than the small fish trap (ages 0-1). In addition, the q-ratio of the chevron trap to the underwater video was 3.5 at Southeast Banks and 2.7 at 17 Fathom Hole, thus the chevron trap was approximately three times more effective at sampling larger, older red snapper (ages 2-5).

Discussion

My results show that trawls numerically sample the most red snapper per unit area when compared to the small fish trap, chevron trap, and underwater video array on natural low-relief reefs in the northern GOM. However, each gear type is size-selective, with the trawl capturing the smallest red snapper and the chevron trap capturing the largest red snapper. Thus, the overall effectiveness of a gear for collecting red snapper over natural low-relief reefs is size dependent. Trawling has the highest catchability for

sampling juvenile red snapper, while the chevron trap best estimates the relative abundance of larger red snapper.

The gear-dependent size selectivity in my study is consistent with similar studies that have used multiple gear types (Willis et al. 2000). Otway et al. (1996) found demersal trawls caught 65% of the entire catch of snapper, *Pagrus auratus*, off Sydney, Australia; however, these fish were significantly smaller than those collected with concurrent longline sampling. In my study, trawls collected the widest size range of red snapper, and appeared effective at collecting the smallest individuals associated with the reef habitat. These results are likely a function of the relative availability of many age 0 red snapper versus the fewer older fish that survive to older ages (age 2 and older). In addition, despite significant differences between the red snapper and fish community size distributions by gear type (except small fish traps), the size distributions demonstrated good concordance in most cases, thus indicating that these gear types are size-selective across species. This finding makes my estimates more robust for the entire fish community.

Assumptions about the operative area sampled by the stationary gear types affects my catchability estimates. I assumed that my stationary gears sampled a 50 m radius, but my estimates would have underestimated red snapper densities if smaller areas were effectively sampled, and overestimated the counts if effective areas were larger. In addition, I assumed a circular sampling area, but a semicircular area may be more realistic due to the bait plume being affected by directional currents. Thus, studies that aim to compare across mobile and stationary gears need to incorporate the operative sampling area. In addition, studies need to account for the effects that baited gears have

on fish behavior and the associated environmental parameters that may influence fish detectability (Stoner 2004).

The use of multiple gear types in this study has shown that a wide size spectrum of red snapper utilize natural low-relief reef habitat on the GOM inner continental shelf. Previous studies investigating red snapper habitat use have shown that sub-adult and adult red snapper are associated with reef habitat, while smaller conspecifics are found over mud, sand, and shell-rubble (Moseley 1966, Bradley and Bryan 1975, Rooker et al. 2004, Patterson et al. 2005). In addition, differences in age-specific habitat use may be attributed to the agonistic behavior by adults toward younger conspecifics (Bailey et al. 2001). Workman et al. (2002) reported that age 0 red snapper preferred reef structures, but recruitment to these structures was limited by the presence of older age 1 conspecifics. The trawls were likely sampling small red snapper adjacent to the reef structure that were either displaced or precluded from the reef by older red snapper; nevertheless, the use of multiple gear types has provided a more complete image of red snapper habitat use than if only one gear type had been used. The use of multiple gear types is therefore essential to understand life histories of species that utilize different habitats.

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CHAPTER 2: VIDEO ESTIMATES OF RED SNAPPER AND ASSOCIATED FISH ASSEMBLAGES ON SAND, SHELL, AND NATURAL REEF HABITATS IN THE NORTHCENTRAL GULF OF MEXICO

Introduction

Underwater video camera arrays have become an increasingly common tool for characterizing marine fish assemblages (Gledhill et al. 1996, Willis and Babcock 2000, Willis et al. 2000, Gledhill 2001, Rademacher and Render 2003, Capo et al. 2004) and indexing abundances of a single species over a particular habitat type (Ellis and DeMartini 1995). This technique, and other video methods, are particularly desirable for estimating fish abundance when depth constraints and physical complexity of the bottom make other types of surveys difficult (Bortone et al. 1986, Greene and Alevizon 1989). However, problems associated with video sampling exist, such as biased estimates due to poor visibility, difficulty in species identification, fish movement, and under-representation of small, cryptic species (Sale and Douglas 1981, Bohnsack and Bannerot 1986). Nevertheless, video methods offer unique advantages over more traditional methods (e.g., otter trawls, SCUBA surveys) of assessing relative fish abundance as they are non-destructive and the equipment can be deployed and retrieved rapidly from depth.

Effectively sampling the fish community on the northcentral Gulf of Mexico (GOM) inner continental shelf would require several complimentary gear types due to the variety of habitat types that exist. The inner shelf is composed primarily of sand, mud, and silt with little or no vertical relief (Ludwick 1964, Kennicutt et al. 1995). Several studies have characterized fish assemblages over low-relief mud and sand habitats (Moore et al. 1970, Franks et al. 1972, Chittenden and McEachran 1976) while others have characterized shelf-edge bank fish assemblages from the western GOM Flower Garden Banks (Dennis and Bright 1988, Rooker et al. 1997, Gledhill 2001), the Pinnacles

Reef Tract in the northern GOM (Weaver et al. 2001), and the eastern GOM Florida Middle Grounds (Smith et al. 1975, Gledhill 2001). However, extensive low-relief (cm to m) shell ridges at 20 to 40 m depths exist in the northcentral GOM as the result of alternating periods of sea level during the Holocene transgression (Schroeder et al. 1995, McBride et al. 1999, Dufrene 2005). In addition, natural hard bottom habitats in the form of reef banks and ledges exist on the shallow inner-shelf; these have been suggested as important reef habitat for red snapper and other reef fishes (Parker et al. 1983, Schroeder et al. 1988, Weaver et al. 2001). However, little information exists regarding the function of these shell ridges and inner shelf natural reefs due to long held misconceptions that little or no natural hard bottom reef habitat existed on the shallow (<40 m) northcentral GOM shelf.

Red snapper, *Lutjanus campechanus*, is a demersal reef fish predominately found along the continental shelf out to the shelf edge from North Carolina to the Yucatan Peninsula, including the GOM, but not the Caribbean Sea (Hoese and Moore 1998). Studies characterizing habitat preference of age 0 red snapper have found that they are not randomly distributed on low-relief mud and sand habitats, rather age 0 red snapper have an affinity for low-relief structure such as shell-rubble habitat (Szedlmayer and Howe 1997, Szedlmayer and Conti 1999, Patterson et al. 2005). Older sub-adult and adult red snapper are found in association with mid- to high-relief shelf features such as coral reefs, shelf-edge banks, and rock outcroppings, as well as artificial structures such as artificial reefs, petroleum platforms, and submerged wreckage (Bradley and Bryan 1975, Moseley 1966, Szedlmayer and Shipp 1994). To date, most studies investigating habitat use of red snapper have focused on mud, sand, shell, and artificial structures (Moseley 1966, Bradley and Bryan 1975, Holt and Arnold 1982, Workman and Foster

1994, Szedlmayer and Howe 1997, Szedlmayer and Conti 1999, Rooker et al. 2004, Patterson et al. 2005). However, no studies have examined habitat use patterns of juvenile and adult red snapper and the associated fish assemblages over natural hard bottom reefs in the shallow northcentral GOM.

The objective of this study was to estimate relative abundances of red snapper and associated fish assemblages over different habitat types with underwater video methodology. Specifically, I sought to assess the efficacy of using the video methodology to investigate abundance and size-specific habitat use of red snapper among sand, shell, and natural hard bottom reef habitats. My goal was to then delineate the relative importance of these habitats to different life stages of red snapper and the associated fish assemblage.

Methods and Materials

Study Area

Video observations were conducted at sand, shell, and natural reef habitats in the northcentral GOM on the Alabama and Mississippi inner continental shelf (Figure 2.1). Seabed characterization of the region was recently performed with digital side-scan sonar and with sediment box cores to ground truth habitat type (Dufrene 2005, Strelcheck et al. 2005). Eight sampling sites were chosen for this study; these included two low-relief (cm) sand sites, four low- to high-relief (cm to m) shell-ridge sites (2 low-relief shell (0.5 to 1 m) and 2 high-relief shell (1 to 3 m)), and two high-relief (2 to 4 m) natural hard bottom reef sites (Figure 2.1).

Video Estimation

Sampling was conducted quarterly during 2004 and 2005 with a 4-camera underwater video array (Chapter 1, Figure 1.1). The camera array consisted of four Sony

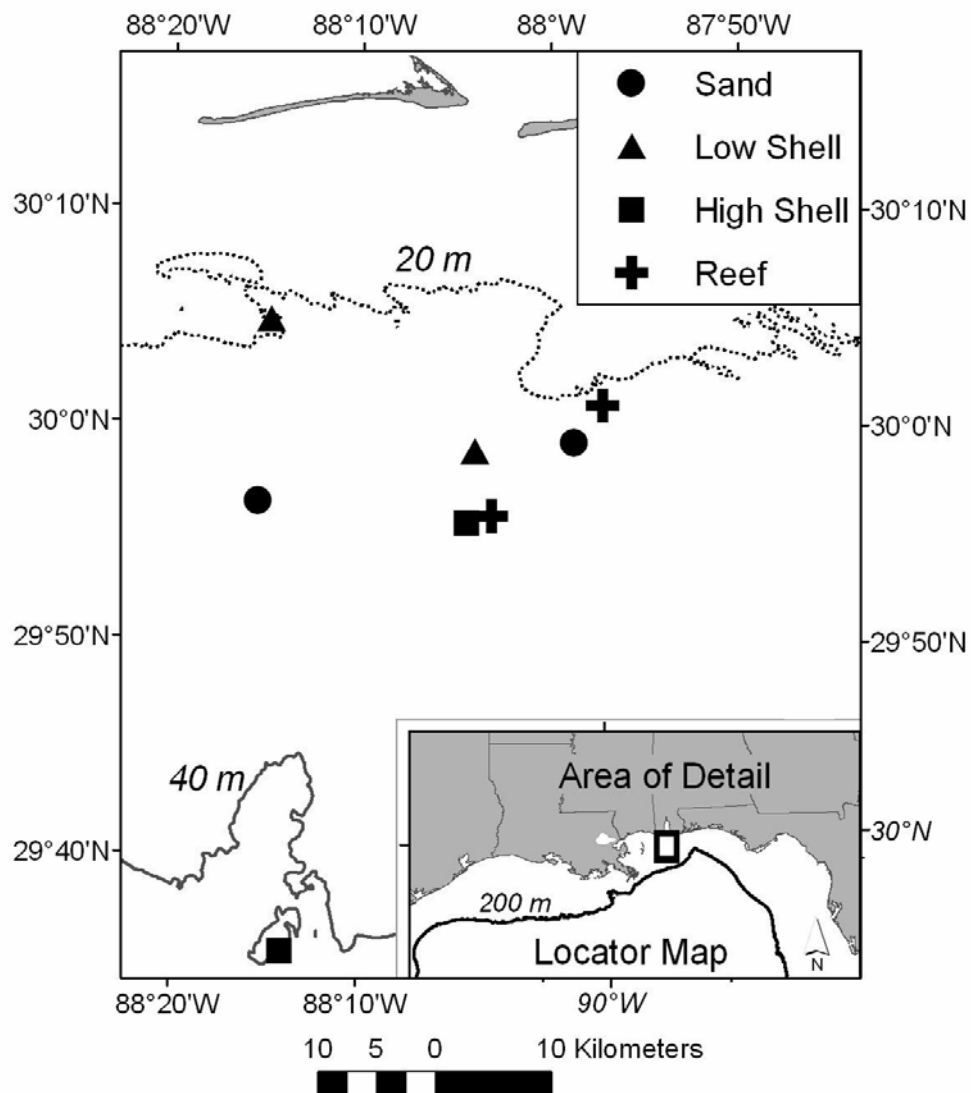


Figure 2.1. Map of the video study site locations in the northcentral GOM. The 20- and 40-m depth contours are shown with the 200-m depth contour within the locator map representing the shelf edge.

DCR-VX1000 digital video camcorders housed in aluminum underwater housings. Cameras were positioned orthogonally to one another at a height of 25 cm above the bottom of the camera rig to provide a nearly 360° view. Each camera had a 72.5° viewing angle with an approximate viewing distance of 5 m (Gledhill and Lyckowski-Shultz 1994), resulting in an estimated viewing volume of 70.4 m³ (Rademacher and Render 2003). Two parallel beam lasers placed 10 cm apart were attached below each camera to aid in estimating lengths of observed fish to the nearest cm. The array was deployed for a 30-min period and was baited with a single Atlantic menhaden (*Brevoortia tyrannus*), which was replaced after each deployment. All video samples were taken during daylight hours (30 minutes after sunrise to 30 minutes before sunset). Profiles of the water column were measured at each deployment with a Sea-Bird SBE-25 CTD. Parameters measured included temperature, salinity, depth, dissolved oxygen content, and optical backscatter (or transmissivity) to gain an estimate of visibility.

Trawl sampling was also conducted adjacent to all video sites several days before or after the video surveys to obtain habitat-specific relative abundance estimates of juvenile red snapper and associated fish assemblages. Therefore, video data were compared to concomitant trawl data to obtain size selectivity by gear type using the ratio of length-specific abundance estimates from the trawls relative to the video (Lauth et al. 2004). In addition, similar length-specific abundance estimates from the trawls relative to the video were made for those species that most contributed to the fish assemblages over each habitat type, and no differences in my fish assemblage results were detected between gears over different habitats.

Statistical Analysis

A continuous 20 min segment of one tape was examined for fish abundances at each deployment (Gledhill 2001). Tapes were chosen based upon the optimal view of the habitat of interest combined with the best visibility (i.e. in focus, good orientation relative to the current). Start time began once the camera array was on the bottom and after sufficient time elapsed for the water column to clear of sediments disturbed by the camera array.

All fish were identified to the lowest possible taxonomic level and counted. The minimum count (*MIN*), the maximum number of a species observed at any one time on the tape, was used for all statistical comparisons (Ellis and DeMartini 1995, Willis and Babcock 2000, Cappo et al. 2004). Estimates of total length (TL) were made only at *MIN* counts to eliminate repeated measurements of the same fish. Maximum counts (*MAX*) were also made to obtain total counts of each fish species seen over the 20 min segment of the tape analyzed.

Video counts of red snapper were modeled with a Poisson distribution. Specifically, a log-linear fixed effects model was computed with the GENMOD procedure in SAS to predict red snapper numbers, with season and habitat as factors (Willis and Babcock 2000, Willis et al. 2000) (SAS Institute, Inc. 2002). Model fit was evaluated with a maximum likelihood method and analysis of deviance. In addition, red snapper length comparisons among seasons and habitats were evaluated separately with a Kruskal-Wallis one-way analysis of variance on the ranks due to violations of normality and homogeneity of variance assumptions required by ANOVA (Systat software, Inc. 2004). Dunn's test was used to determine *a posteriori* differences among means ($\alpha=0.05$).

Fish assemblage data were analyzed using procedures within the PRIMER (Plymouth Routines in Multivariate Ecological Research) statistical package (Clarke and Warwick 2001). Fish that were not identified to species and those with a total count of one were excluded from all statistical analyses. Twenty-five species representing 85% of the overall fish assemblage were included in the statistical analyses. First, a Bray-Curtis similarity matrix was computed to examine similarities among all samples. A non-metric multi-dimensional scaling (MDS) model was computed to map sample similarities in a two-dimensional ordination. A two-factor Analysis of Similarity (ANOSIM) permutation procedure was computed to test for significant differences of fish assemblages among habitats and seasons (Warwick et al. 1990a).

To assess species-specific contributions, Similarity Percentages (SIMPER) was used as the *post-hoc* analysis to estimate the contribution of a particular species to the overall fish assemblage similarity (within season or habitat) and dissimilarity (among seasons and habitats) (Clarke 1993). A cutoff percentage of 90% was used to determine those species accounting for 90% of the total similarities and dissimilarities.

Additionally, a stepwise data reduction procedure, BV-STEP, was used to determine which group of species accounted for the observed patterns in the fish assemblage (Clarke and Warwick 1998). This procedure used a Spearman rank correlation coefficient of 95% as a cutoff to determine which group of species together explained most of the variability in the assemblage.

Patterns of species diversity among habitats and seasons were investigated with a series of species diversity indices computed with DIVERSE (Warwick et al. 1990b).

Indices included the Shannon diversity (H') and Pielou's evenness (J'). Diversity measures were estimated with the following equations:

$$H' = -\sum_i p_i \log(p_i)$$

where p_i is the proportion of the total count from the i^{th} species,

$$J' = H'/\log S$$

where S (species richness) is the total number of species present in the sample. Effects of habitat and season on the diversity indices were analyzed with a two-factor analysis of variance (ANOVA) (Systat software, Inc. 2004).

Species abundances and environmental correlations were investigated with canonical correspondence analysis (CCA) with the CANOCO program (ter Braak and Smilauer 2002). This analysis is designed to maximally correlate environmental variables with fish assemblage data with a non-linear weighted averaging method. A global permutation test with Monte Carlo permutations was used to investigate the statistical significance between the species abundances and environmental variables. Temperature, salinity, depth, and dissolved oxygen were the continuous environmental variables used, and habitat types were coded as nominal variables (sand, shell, and reef). Relative importance of environmental variables was evaluated based on inter-set correlations between environmental variables and the axes. These correlations are the correlation coefficients between the environmental variables and the species-derived sample scores, and are more robust to collinearity than are canonical coefficients (ter Braak and Smilauer 2002). Inter-set correlation coefficients with absolute values greater than or equal to 0.4 were interpreted as ecologically important (Hair et al. 1984, Rakocinski et al. 1996). In addition, the same 25 species used for previous fish assemblage analyses were used in the CCA to reduce the bias associated with rare taxa.

Results

Forty-two (12 sand, 17 shell, and 13 reef) of 64 possible video sampling opportunities were achieved over the two year study period; the 2005 winter cruise was cancelled due to inclement weather.

Red Snapper

Relative abundance estimates of red snapper from the *MIN* index showed significant differences in abundances among habitat types ($\chi^2=6.90$, $P=0.0318$) (Figure 2.2). Higher abundance estimates were observed over reef habitat than over either shell or sand habitats. In contrast, there was no seasonal difference in abundance ($\chi^2=2.44$, $P=0.4854$), nor was the interaction between habitat and season significant ($\chi^2=9.97$, $P=0.1260$). Nevertheless, a general trend of higher abundance estimates over the reef was observed in the winter and spring followed by a decline in the summer and fall.

Differences in red snapper size were observed both spatially and temporally. Red snapper observed over reef habitats were significantly longer than conspecifics observed over sand (Dunn's Method; $P<0.05$) (Table 2.1). Shell habitats supported intermediate-sized red snapper, but no size differences were observed when compared to red snapper collected over sand and reef habitats (Table 2.1). Due to insufficient numbers of red snapper observed on sand and shell habitats over all seasons, only the reef habitat was investigated for a seasonal size effect. A significant seasonal size difference existed, with the largest red snapper observed over the reef during the summer season (Kruskal-Wallis, $P=0.002$) (Table 2.1). Progressively smaller red snapper were seen over subsequent seasons in the fall, winter, and spring (Table 2.1).

Size selectivity of the video gear was observed for red snapper. Numbers of small red snapper were under-represented using the video method (see Chapter 1 for more

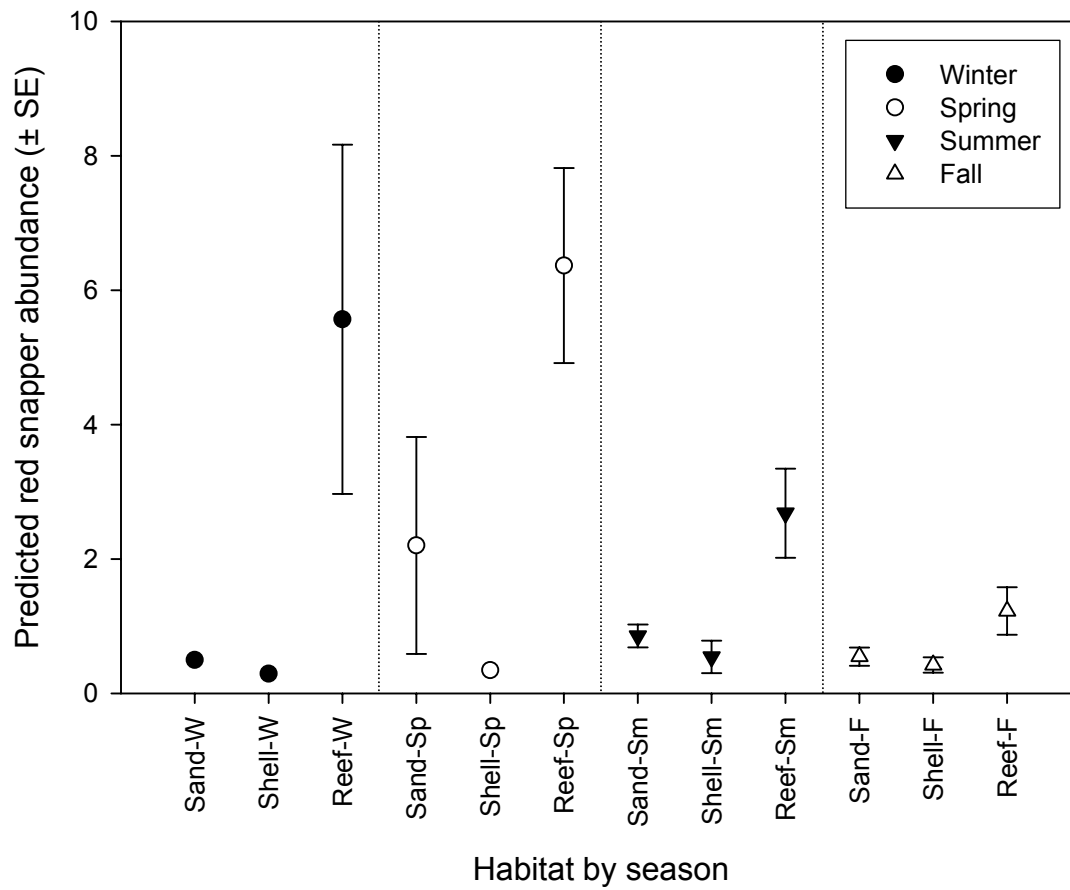


Figure 2.2. Relative abundance estimates of red snapper, *Lutjanus campechanus*, (± 1 SE) predicted by using a log-linear model over sand, shell, and reef habitats by season. Relative abundance is expressed as the *MIN* count of red snapper 20 min⁻¹ deployment.

Table 2.1. Average sizes (TL in mm \pm 1 SE) of red snapper observed over sand (n=14), shell (n=7), and reef (n=51) habitats. Average seasonal lengths are displayed for the reef habitat. Habitats and seasons with significantly different sizes are represented by different letters (Dunn's test, $P < 0.05$).

		Average size	Differences
Habitat	Sand	12.3 (0.30)	A
	Shell	15.0 (0.20)	AB
	Reef	25.0 (0.43)	B
Season (Reef)	Winter	25.0 (1.34)	A
	Spring	19.2 (1.67)	B
	Summer	31.5 (0.76)	A
	Fall	28.3 (6.67)	A

details). The gear size selectivity ratio of small red snapper collected in trawls relative to video estimates indicated that on average 10.5 (<100 mm TL) and 1.4 (101-200 mm TL) red snapper were collected in trawls relative to one red snapper observed using the video method (Figure 2.3). In contrast, large red snapper were more abundant in the video estimates compared to the trawled counts with 0.4 (201-300 mm TL) and 0.04 (> 300 mm TL) red snapper collected in trawls relative to one red snapper seen with the video method (Figure 2.3).

Fish Assemblage

Thirty-three species representing 16 families were identified in this study (Table 2.2). Unidentifiable taxa were distributed among seven families and an unidentified fish category. A group of seven species best characterized the observed fish assemblage patterns shown with the BV-STEP procedure: *Caranx crysos*, *Centropristis ocyurus*, *Diplectrum bivittatum*, *D. formosum*, *L. campechanus*, *Stenotomus caprinus*, and *Syacium papillosum*. These accounted for 95.0% of the correlation among species and the observed patterns detected in fish assemblages.

Fish assemblages showed significant differences among the three habitat types (ANOSIM; Global R=0.230, P=0.008) (Figure 2.4). Further examination indicated that fish assemblages over the reef and shell habitats differed significantly (ANOSIM; Global R=0.312, P=0.006). However, there were no seasonal differences in fish assemblages within habitats during my two-year study period (ANOSIM; Global R=0.039, P=0.299).

Table 2.3 shows the SIMPER results for species that contributed most to the overall similarity within habitat type. The longspine porgy accounted for 73.1% of the cumulative species similarity among samples within the sand habitat, the dwarf sand

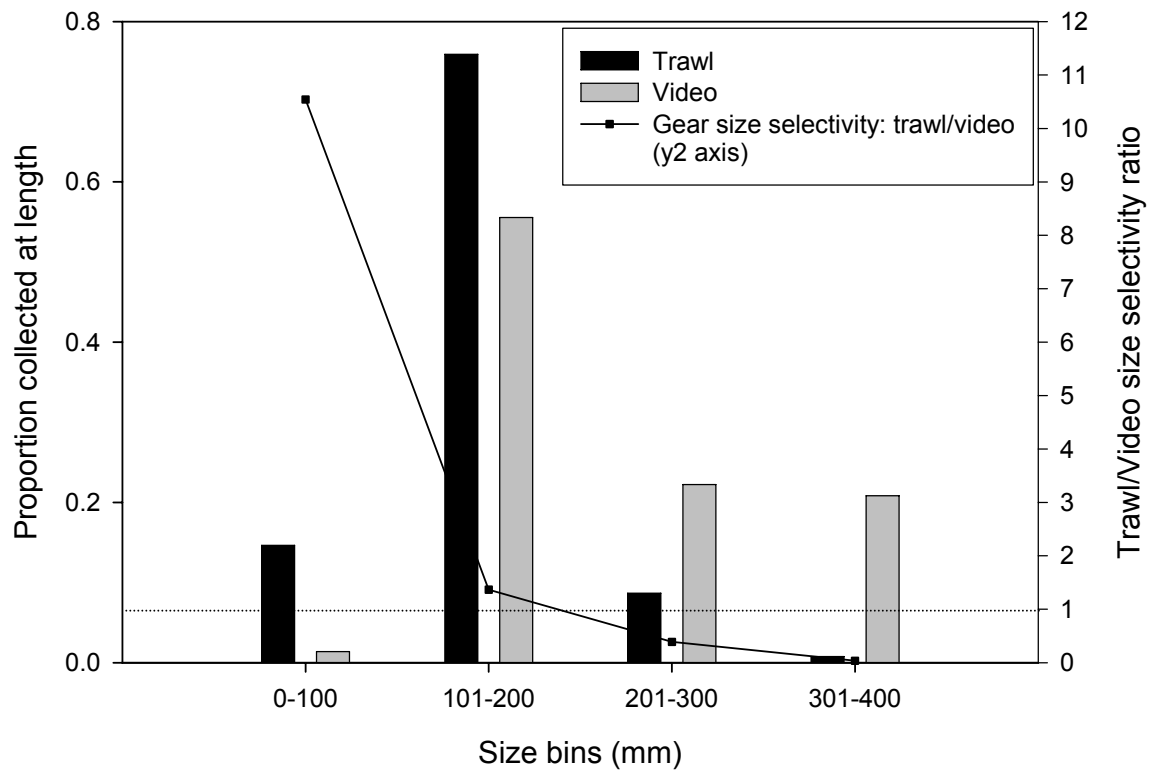


Figure 2.3. Size selectivity of red snapper, *Lutjanus campechanus*, collected with trawl and observed with underwater video methodology. The left ordinate represents the proportion-at-length of red snapper collected using each gear type. The right ordinate represents the ratio of the proportion-at-length collected from the trawl relative to the video gear using four size bins (<100 mm, 101-200 mm, 201-300 mm, and >300 mm TL). The dotted line represents a 1:1 ratio of red snapper observed in trawls relative to the video method, which would indicate no gear bias.

Table 2.2. Total number of fish observed from video estimates arranged in order of decreasing abundance by *MIN*. *MIN* is the maximum number observed at any one time, *MAX* is the total number observed over the entire tape, *n* is the frequency of occurrence (out of 42 camera deployments), and total length TL (\pm SE) is the average size of each species. Sizes were not estimated for unidentified fish, thus NA (not applicable).

Taxon	Common name	MIN	MAX	n	TL (\pmSE)
<i>Stenotomus caprinus</i>	Longspine porgy	141	2699	24	9.3 (0.2)
<i>Diplectrum bivittatum</i>	Dwarf sand perch	78	889	26	5.8 (0.3)
<i>Lutjanus campechanus</i>	Red snapper	72	1206	18	21.6 (1.1)
Carangidae	Family Carangidae	44	116	4	9.6 (0.6)
<i>Haemulon aurolineatum</i>	Tomtate	28	187	7	22.3 (0.9)
<i>Caranx crysos</i>	Blue runner	27	64	5	26.2 (2.2)
<i>Micropogonias undulatus</i>	Atlantic croaker	25	654	6	10.5 (0.5)
<i>Trachurus lathami</i>	Rough scad	25	132	5	7.4 (0.7)
<i>Diplectrum formosum</i>	Sand perch	22	83	15	8.1 (0.7)
Bothidae	Family Bothidae	16	26	14	17.9 (1.6)
<i>Centropristis ocyurus</i>	Bank sea bass	14	102	12	11.1 (1.0)
<i>Syacium papillosum</i>	Dusky flounder	13	62	8	14.8 (2.0)
<i>Lutjanus synagris</i>	Lane snapper	10	27	5	21.0 (2.1)
Unidentified fish	Unidentified fish	7	26	7	NA
<i>Menticirrhus americanus</i>	Southern kingfish	6	25	3	12.2 (1.3)
<i>Eucinostomus gula</i>	Silver jenny	5	28	4	10.4 (1.0)
<i>Rhomboplites aurorubens</i>	Vermilion snapper	5	22	1	15.0 (0.0)
<i>Xyrichtys novacula</i>	Pearly razorfish	4	47	3	3.3 (1.0)
<i>Balistes capriscus</i>	Gray triggerfish	4	14	3	23.8 (1.3)
Sciaenidae	Family Sciaenidae	4	12	4	15.0 (2.9)
<i>Leiostomus xanthurus</i>	Spot	4	6	2	13.3 (1.8)
<i>Halichoeres radiatus</i>	Puddingwife	3	13	3	15.0 (2.9)
<i>Centropristis philadelphica</i>	Rock sea bass	3	7	3	8.7 (4.1)
<i>Orthopristis chrysoptera</i>	Pigfish	3	5	3	10.7 (2.3)
<i>Ophichthus puncticeps</i>	Palespotted eel	3	3	2	4.7 (0.3)
<i>Mycteroperca microlepis</i>	Gag grouper	2	15	1	35.0 (0.0)
<i>Chloroscombrus chrysurus</i>	Atlantic bumper	2	6	2	15.0 (5.0)
<i>Decapterus punctatus</i>	Round scad	2	5	1	10.0 (0.0)
Ophidiidae	Family Ophidiidae	2	5	1	15.0 (0.0)
Ophichthidae	Family Ophichthidae	2	3	2	6.0 (4.0)
Triglidae	Family Triglidae	2	3	2	15.0 (5.0)
<i>Archosargus probatocephalus</i>	Sheepshead	2	2	1	33.0 (0.0)
<i>Prionotus rubio</i>	Blackwing searobin	1	8	1	35.0 (0.0)
<i>Brevoortia patronus</i>	Gulf menhaden	1	7	1	15.0 (0.0)
<i>Sphoeroides parvus</i>	Least puffer	1	4	1	1.0 (0.0)
<i>Calamus leucosteus</i>	Whitebone porgy	1	3	1	10.0 (0.0)
<i>Serranus phoebe</i>	Tattler	1	3	1	2.0 (0.0)
<i>Gymnothorax nigromarginatus</i>	Blackedge moray	1	2	1	15.0 (0.0)
<i>Halichoeres bivittatus</i>	Slippery dick	1	2	1	5.0 (0.0)
Carcharhinidae	Family Carcharhinidae	1	1	1	60.0 (0.0)
<i>Sphyrna guachancho</i>	Guaguanche	1	1	1	20.0 (0.0)

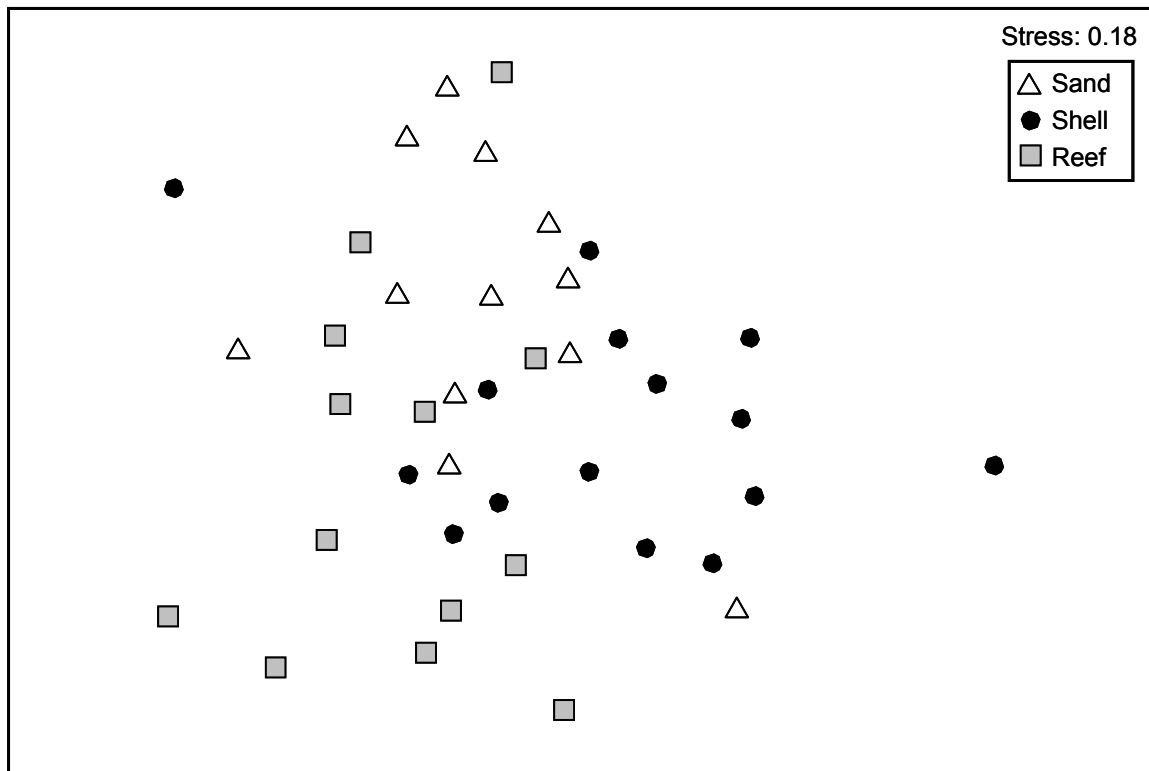


Figure 2.4. Multi-dimensional scaling (MDS) plot of all samples over the two-year study period. Each sample represents the 25 species analyzed for the fish assemblage.

Table 2.3. SIMPER results of the species that most contributed to the within-habitat similarity for each of the three habitat types: sand, shell, and reef; shown are mean abundance of important species within habitat type, the contribution (SIM) to the average within similarity, and the average within similarity/standard deviation (SIM/SD) ratio. A 90% cut-off was used for the cumulative % contribution of species.

Habitat	Species	Mean	SIM	SIM/SD	% contribution	% cumulative contribution
Sand	Longspine porgy	7.42	20.26	1.15	73.12	73.12
	Dwarf sand perch	0.75	3.19	0.51	11.52	84.64
	Sand perch	0.50	1.36	0.39	4.92	89.56
	Red snapper	1.17	0.81	0.31	2.93	92.49
Shell	Dwarf sand perch	3.60	11.63	1.02	58.51	58.51
	Sand perch	0.80	2.26	0.43	11.37	69.88
	Longspine porgy	1.07	2.25	0.42	11.31	81.19
	Dusky flounder	0.47	1.06	0.26	5.32	86.51
	Lane snapper	0.60	0.74	0.21	3.72	90.23
Reef	Red snapper	3.92	15.23	1.11	58.71	58.71
	Longspine porgy	2.77	5.72	0.47	22.05	80.77
	Dwarf sand perch	1.15	2.44	0.40	9.40	90.16

perch accounted for 58.5% for the shell habitat, and the red snapper represented 58.7% of the similarity within the reef habitat. The longspine porgy, dwarf sand perch, and red snapper SIM/SD values were 1.15, 1.02, and 1.11, respectively. The SIM/SD ratios exceeding 1.0 indicates that each of the three species consistently contributed to the within habitat similarity among samples (Clarke and Warwick 2001). These three species were also important in discriminating fish assemblages between reef and shell habitats. For example, the three dominant species together accounted for 50% of the overall dissimilarity (Table 2.4). The red snapper contribution was the highest at 19.7%, followed by that for dwarf sand perch (15.8%), and longspine porgy (14.5%). The red snapper most consistently contributed to these dissimilarity differences based upon the DIS/SD value of 1.22.

Diversity indices varied by habitat, with highest species richness, evenness, and diversity associated with the reef fish assemblage (Table 2.5). Species evenness and diversity were lowest for the sand fish assemblage; values increased over the shell habitat. However, no significant differences were detected among habitat-specific indices. Similar trends were observed over the reef by season, with the lowest values of all three indices observed during winter. Species richness increased to a stable maximum over the remaining seasons, while species evenness and diversity peaked in the fall (Table 2.5). Similarly, no significant seasonal effects were detected among indices for reef habitat.

Environmental variables were significantly correlated with species from the fish assemblages (CCA axis 1, $P=0.002$; all axes combined, $P=0.002$) (Table 2.6, Figure 2.5). The first two CCA axes accounted for 62.5% of the cumulative percentage of the species-environment relationship. Shell and reef habitats correlated well with CCA axis 1, while

Table 2.4. SIMPER results of the species that most contributed to the dissimilarity between shell and reef habitats; shown are mean abundance of important species within habitat type, the contribution (DIS) to the average dissimilarity, and the average dissimilarity/standard deviation (DIS/SD) ratio. A 90% cut-off was used for the cumulative % contribution of species.

Species	Mean _{shell}	Mean _{reef}	DIS	DIS/SD	% contribution	% cumulative contribution
Red snapper	0.47	3.92	16.65	1.22	19.69	19.69
Dwarf sand perch	3.60	1.15	13.35	0.90	15.78	35.47
Longspine porgy	1.07	2.77	12.27	0.98	14.51	49.98
Tomtate	0.07	2.08	6.13	0.53	7.25	57.23
Blue runner	1.40	0.31	5.27	0.42	6.23	63.46
Rough scad	0.53	0.69	4.16	0.37	4.92	68.38
Sand perch	0.80	0.31	4.05	0.76	4.79	73.17
Dusky flounder	0.47	0.31	3.95	0.49	4.67	77.84
Atlantic croaker	0.07	1.15	3.23	0.32	3.82	81.66
Lane snapper	0.60	0.08	2.57	0.56	3.05	84.70
Bank sea bass	0.33	0.38	2.43	0.72	2.88	87.58
Vermilion snapper	0.00	0.38	1.66	0.28	1.96	89.54
Southern kingfish	0.00	0.31	1.61	0.35	1.90	91.44

Table 2.5. Average species richness (S), Pielou evenness (J'), and Shannon diversity (H') indices for sand, shell, and reef habitats. Seasonal diversity indices are displayed for the reef habitat.

		S	J'	H'
Habitat	Sand	4.0	0.608	0.941
	Shell	3.9	0.741	1.046
	Reef	4.3	0.780	1.151
Season (Reef)	Winter	3.6	0.544	0.827
	Spring	4.2	0.767	1.122
	Summer	4.3	0.640	1.004
	Fall	4.2	0.888	1.231

Table 2.6. Canonical correspondence analysis (CCA) statistics and inter-set correlations relating environmental variables with CCA axes. Bold values denote variables with absolute value correlations ≥ 0.4 .

Statistics	Axis 1	Axis 2	Axis 3	Axis 4	Total inertia
Eigenvalues	0.491	0.380	0.214	0.141	
Species-environment correlations	0.887	0.821	0.765	0.713	
Cumulative percentage variance					
of species data	9.5	16.8	21.0	23.7	
of species-environment relation	35.2	62.5	77.8	87.9	
Sum of all eigenvalues					5.18
Sum of all canonical eigenvalues					1.39
Inter-set correlations					
Environmental variables					
Depth	0.2685	-0.5518	0.0566	0.0588	
Temperature	0.3581	0.1259	0.0660	-0.3304	
Salinity	0.1244	0.2233	0.5389	0.0075	
Dissolved oxygen	-0.1395	-0.2579	0.0021	-0.1429	
Sand	0.0582	-0.5508	0.3537	0.3094	
Shell	0.5365	0.5891	0.0154	0.0291	
Reef	-0.5609	-0.0323	-0.3503	-0.3212	

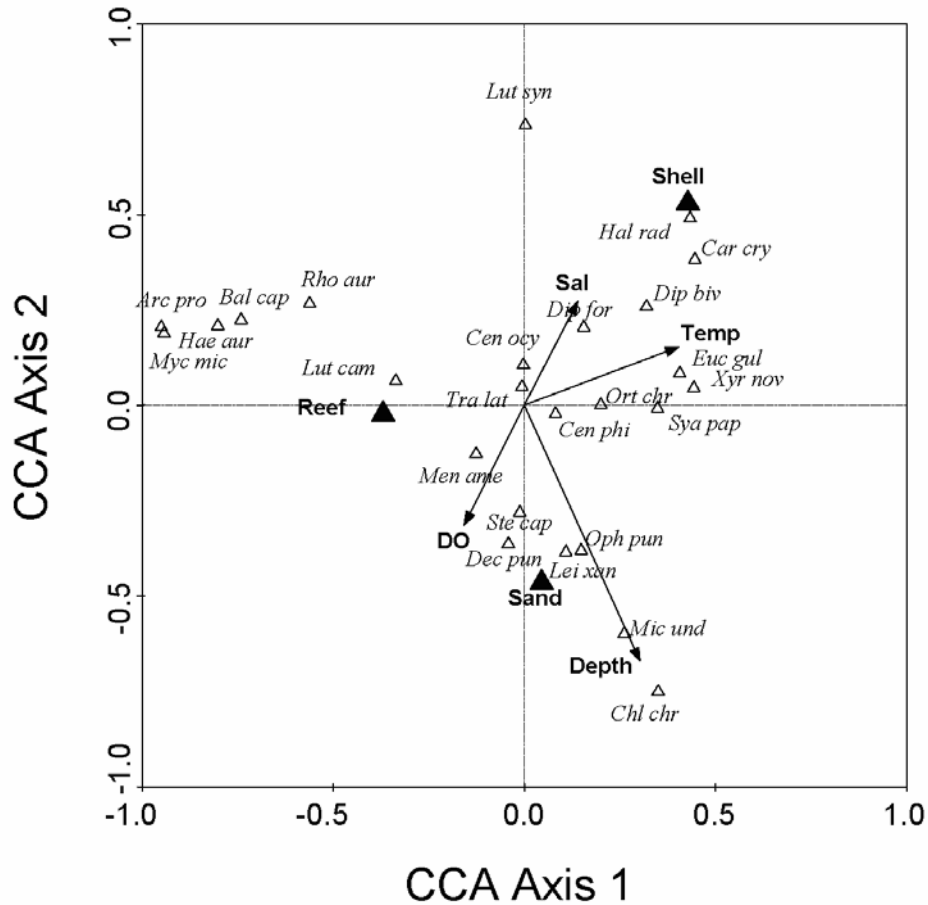


Figure 2.5. Biplot of axes 1 and 2 from canonical correspondence analysis of fish species and environmental variables. Environmental variables include Depth (m), Temp = water temperature ($^{\circ}\text{C}$), Sal = salinity (ppt), DO = dissolved oxygen (mg/L), Sand, Shell, and Reef. Species codes: Sheepshead (*Arc pro* = *Archosargus probatocephalus*), gray triggerfish (*Bal cap* = *Balistes capriscus*), blue runner (*Car cry* = *Caranx crysos*), bank sea bass (*Cen ocy* = *Centropristis ocyurus*), rock sea bass (*Cen phi* = *Centropristis philadelphica*), Atlantic bumper (*Chl chr* = *Chloroscombrus chrysurus*), round scad (*Dec pun* = *Decapterus punctatus*), dwarf sand perch (*Dip biv* = *Diplectrum bivittatum*), sand perch (*Dip for* = *Diplectrum formosum*), silver jenny (*Euc gul* = *Eucinostomus gula*), tomtate (*Hae aur* = *Haemulon aurolineatum*), puddingwife (*Hal rad* = *Halichoeres radiatus*), pearly razorfish (*Xyr nov* = *Xyrichtys novacula*), spot (*Lei xan* = *Leiostomus xanthurus*), red snapper (*Lut cam* = *Lutjanus campechanus*), lane snapper (*Lut syn* = *Lutjanus synagris*), southern kingfish (*Men ame* = *Menticirrhus americanus*), Atlantic croaker (*Mic und* = *Micropogonias undulatus*), gag (*Myc mic* = *Mycteroperca microlepis*), palespotted eel (*Oph pun* = *Ophichthus puncticeps*), pigfish (*Ort chr* = *Orthopristis chrysoptera*), vermilion snapper (*Rho aur* = *Rhomboplites aurorubens*), longspine porgy (*Ste cap* = *Stenotomus caprinus*), dusky flounder (*Sya pap* = *Syacium papillosum*), rough scad (*Tra lat* = *Trachurus lathami*).

depth, sand, and shell correlated strongly with CCA axis 2 (Table 2.6). Caution should be applied when interpreting nominal habitat variables in relation to CCA axes because the inter-set correlation coefficients are not useful (ter Braak and Smilauer 2002). Thus, nominal habitat variables were used to convey species-specific habitat use information. Species that displayed a specific habitat affinity appeared to correlate well with the corresponding nominal habitat variable (Figure 2.5). Red snapper and other reef-associated species were highly correlated with reef habitat type with a high negative score on axis 1. Species primarily found on shell corresponded with increasing salinity and temperature and had high positive scores on axes 1 and 2. Species that were found in association with the sand habitat showed a correlation with increased depth and high dissolved oxygen, and loaded negatively on CCA axis 2.

Discussion

This study highlights the efficacy of using video methodology to assess habitat use by red snapper and associated fish assemblages in the northcentral GOM. The method has its inherent biases (e.g. larger fishes were observed while smaller cryptic fishes were likely missed, effects of bait plumes on abundance estimates); however, it appears to be a practical method to characterize adult red snapper habitat use over a variety of substrate types. Structurally complex habitat types with high relief, such as natural and artificial reefs, rock outcrops, and petroleum platforms, should be sampled by using non-invasive sampling techniques to avoid habitat destruction. In addition, the logistical simplicity of dropping the camera array for a 30 min period makes this an appropriate method if multiple deployments over distant sites are needed, as was the case in this study.

My study found similar habitat-specific results as others with small, intermediate, and large sized red snapper over sand, shell, and reef habitats, respectively. Juvenile red snapper were predominately collected over low-relief sand habitats, which is consistent with the findings of Rooker et al. (2004) and Patterson et al. (2005). In contrast, both sub-adult and adult red snapper were found over higher relief habitats such as the shell-rubble and natural hard bottom reef habitats. These findings are consistent with previous studies that have found adult red snapper over high relief habitats such as shelf-edge banks, mid-shelf banks, rock outcrops, coral reefs, and artificial structures (Moseley 1966, Bradley and Bryan 1975, Dennis and Bright 1988, Stanley and Wilson 2000, Gledhill 2001). It has been suggested that red snapper recruit to these high-relief habitats by about 18 months of age, or 20 cm TL (Gallaway et al. 1999). Nieland and Wilson (2003), using a fishery independent survey design, found red snapper first recruited to petroleum platforms at age 2 and between 27.5 and 37.5 cm TL. The largest red snapper observed in the current study (mean = 25 cm TL) were associated with the hard bottom reef habitats, but seasonal differences in length ranged from 19.2 to 31.5 cm TL in the spring and summer, respectively. Therefore, these natural hard bottom reef habitats on the shallow inner shelf may be functionally important for sub-adult and adult red snapper in the northcentral GOM.

Seasonal size differences at the reef habitats were likely attributed to emigration and immigration of red snapper. Moseley (1966) observed changes in red snapper abundance at reefs and attributed these movement patterns to passing cold fronts, while Bradley and Bryan (1975) found similar trends and suggested the offshore movement of prey as a potential mechanism. Recent studies have found red snapper exhibit low site fidelity and moderately high dispersal from artificial reefs in the northern GOM

(Patterson et al. 2001a, Patterson and Cowan 2003). Moreover, Strelcheck et al. (2005) concluded that site fidelity could be affected by reef spacing, with the lowest fidelity occurring on the reefs that were located in close proximity to other reefs.

Authors of other tagging studies reported high site fidelity with little movement from artificial reefs in the northern GOM (Szedlmayer and Shipp 1994, Szedlmayer 1997, Szedlmayer and Schroepfer 2005). In particular, Szedlmayer and Schroepfer (2005) found no seasonal movements and long average residence times (218 d when excluding caught fish from analysis) for red snapper on artificial reefs in my study area. However, their study was conducted over a 4 year period and they interpreted long-term residence as any time greater than 117 d. My interpretation of their telemetry data, excluding caught fish, indicated only 15.6% of tagged red snapper had residency times greater than 12 months. In addition, 65.6, 43.8, 34.4, and 21.9% of tagged red snapper in their study had residence times less than 9, 6, 3, and 1 month, respectively. Nevertheless, the large size range of red snapper in their study (43.5-84 cm TL), combined with the use of large artificial structures, such as army tanks and cars, may negate a direct comparison to my results.

In this study, the largest red snapper were observed over the reef habitat during the summer season, with progressively smaller fish over the following seasons, suggesting larger fish were either moving away or being caught by hook-and-line. The summer samples were the first after the recreational fishing season opened on April 21st of both years, and the reef sites sampled in this study are known to local fisherman and are identified on navigation charts as Southeast Banks and 17 Fathom Hole (Schroeder et al. 1988). By spring, the smallest red snapper were observed over the reef, and when combined with previous size-at-age data, suggests these fish were age 1 individuals that

recruited from adjacent low-relief habitats (e.g. sand, mud, shell ridges) (Szedlmayer and Shipp 1994, Patterson et al. 2001b, Wilson and Nieland 2001).

Red snapper abundance estimates at the reefs did not significantly change with season, suggesting large fish may have been replaced by smaller conspecifics. Bailey et al. (2001) performed laboratory studies on the cohabitation of juvenile and of sub-adult red snapper and found smaller fish were not allowed to occupy the reef when larger fish were present. Moreover, Workman et al. (2002) found increased numbers of age 0 red snapper occupied reefs when age 1 specimens were absent. The general trend of decreasing sizes with little change in relative abundance in this study indicates smaller fish were likely replacing larger conspecifics as the latter emigrated off the reef due either to natural movements or to fishing mortality. However, my results are based upon low sample sizes ranging from two reef samples in winter to four reef samples in both spring and summer seasons. In addition, a large amount of variability was observed both in my winter and spring estimates, which may influence the lack of any detectable seasonal patterns. Thus, studies that aim to look at fish movement on and off a reef using underwater video methods need to incorporate more replication to gain insight into fish movement patterns.

The longspine porgy, dwarf sand perch, and red snapper were collected over all habitat types; nevertheless, they each appeared to show affinities to sand, shell, and reef habitats, respectively. The longspine porgy is reported to be one of the most abundant fish species collected over sand and mud habitats off Texas, Louisiana, and Mississippi (Moore et al. 1970, Franks et al. 1972, Chittenden and McEachran 1976, Geoghegan and Chittenden 1982). However, this species is not restricted to these habitats as Parker et al. (1979) found it to be one of the most abundant species on artificial reefs off South

Carolina. The longspine porgy was the most widespread species in this study because it was the dominant taxa contributing to the sand assemblage and was one of the most important contributing species to characterize the reef and shell assemblages. Little information exists on the habitat preference of the dwarf sand perch, but limited studies have reported this species on low-relief sand and mud areas (Fraser 1971, Bortone et al. 1981). This study was the first to document the potential importance of shell habitat to the dwarf sand perch based upon its relative importance to characterization of the shell habitat fish assemblage.

The red snapper was numerically the most dominant reef-associated species in this study. Many studies characterizing both natural and artificial reef fish assemblages in the northern GOM have found red snapper to be abundant (Stanley and Wilson 2000, Gledhill 2001, Rademacher and Render 2003); however, no studies have shown red snapper to be the most important species to contribute to the structure of the reef fish assemblage.

The CCA technique is useful in delineating habitat associations by species and characterizing fish assemblages based upon habitat type. Species that correlated with the sand habitat type have been previously characterized as utilizing sand habitats. These include Atlantic croaker, Atlantic bumper, spot, round scad, southern kingfish, and palespotted eel (Moore et al. 1970, Chittenden and McEachran 1976, Hale 1987, Hoese and Moore 1998, Pierce and Mahmoudi 2001). Additional species, other than dwarf sand perch, that displayed an affinity for the shell habitat included sand perch, blue runner, and puddingwife, all of which have been previously documented over a variety of habitat types (Hastings and Bortone 1976, Bortone et al. 1981, Pierce and Mahmoudi 2001). A mutualistic foraging association between the puddingwife and the bar jack, *Caranx ruber*,

has been observed (Baird 1993). This social facilitation was also observed with several other species suggesting the blue runner, a close relative of the bar jack, could co-occur with the puddingwife over shell habitats for foraging purposes.

All species that showed an affinity to reef habitat type in the CCA biplot also were reef associated. These species included the red snapper, vermillion snapper, sheepshead, gag grouper, gray triggerfish, and tomtate (Caldwell 1965, Smith et al. 1975, Parker et al. 1979, Sedberry and van Dolah 1984, Moran 1988; Kellison and Sedberry 1998). Bortone et al. (1997) found the vermillion snapper to be the best representative species for offshore artificial reef fish assemblages in the northern GOM. In addition, tomtate has been found to be the most abundant species over rock outcrops at mid-shelf depths of 25-38 m off the South Carolina coast (Sedberry and Van Dolah 1984).

The abundance of several species correlated with environmental variables and these variables may have influenced fish assemblage structure. Depth was the only measured environmental variable that had a correlation coefficient ≥ 0.4 , and both the Atlantic croaker and Atlantic bumper correlated strongly with depth. However, both species are regularly found in shallow inshore waters (< 20 m) and are not limited to deeper offshore waters (Moore et al. 1970, Chittenden and McEachran 1976, Pierce and Mahmoudi 2001). In addition, several species were correlated with temperature, salinity, and dissolved oxygen content. Of notable importance were correlations of longspine porgy with high dissolved oxygen levels and dwarf sand perch, sand perch, and bank sea bass with high temperature and salinity. The association of sand perch and bank sea bass with high salinity is consistent with similar analyses investigating species-environmental relationships (Bortone et al. 1997). However, the largest differences in temperature, salinity, and dissolved oxygen within any season during my video sampling were 4.75

°C, 1.80 ppt, and 2.53 mg/L, respectively. These narrow differences likely contributed to the minimal impacts that water mass characteristics had on the species distributions and abundances.

The highest diversity indices were associated with the reef fish assemblage. Similar studies using trawl methodology found higher diversity and biomass over hard bottom habitats than over sand bottom (Wenner 1983, Sedberry and Van Dolah 1984). Higher vertical relief, with more structural complexity, likely provides greater microhabitat space for a suite of different species to occupy. However, my diversity indices were lower than other studies characterizing fish assemblages over natural reef habitats in the GOM (Smith et al. 1975, Dennis and Bright 1988, Rezak et al. 1990, Rooker et al. 1997). Differences in gear type likely contributed to the observed trends as these studies used SCUBA techniques that are capable of better identifying smaller cryptic species and sampling a larger area. Gledhill (2001) used a similar camera array to characterize reef fish assemblages on offshore shelf-edge banks and found much higher diversity indices; differences are likely due to the location and scale of reef habitats. My reef sites were located on the inner continental shelf at depths between 25 and 32 m and total reef area is estimated to have ranged from m² to several km² in size. In contrast, the offshore banks Gledhill (2001) analyzed were in average water depths of 63.5 m with areal sizes in the hundreds of km².

The goal of this study was to use a non-destructive method to characterize fish assemblages, with an emphasis on red snapper, over distinct habitat types. Results indicated the underwater video method was a useful tool to identify fish assemblages over different habitat types in the northcentral GOM. Specifically, this study revealed

habitat use patterns of the largest red snapper utilizing these sand, shell, and reef habitats, while excluding the smallest individuals that the trawl gear was capable of collecting.

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CHAPTER 3: HABITAT USE AND THE EFFECTS OF SHRIMP TRAWLING ON FISH AND INVERTEBRATE COMMUNITIES

Introduction

Characterization of habitat use by the biotic community is an essential first step in identifying community structure and providing baseline information for ecosystem-based management. Fish and invertebrate communities can be successfully described with a suite of properties such as numerical abundance, biomass, species evenness, richness, and diversity (Bloomfield and Gillanders 2005, Ley 2005). Habitat characteristics can then be related to community structure to provide a framework for assessing relative habitat value (Friedlander and Parrish 1998, Willis and Anderson 2003). Once the framework is identified, the impacts of activities such as trawling and dredging on benthic habitats and their associated communities can be assessed to provide information on ecosystem effects these activities have on the benthic community.

Habitat disturbance by trawling is one of the greatest threats to marine biodiversity due to substrate modifications such as the reduction of habitat complexity, benthic community disturbance, removal of non-target species, and reduction in habitat productivity (Hammer et al. 1993, Auster and Langton 1998, Jennings et al. 2001, NRC 2002). The physical damage caused by trawls destroys critical biogenic and sedimentary habitat structure for benthic species, and can potentially alter the structure of habitat-specific biological communities (Auster et al. 1996, Collie et al. 1997, Freese et al. 1999; Koenig et al. 2000). In addition, indirect negative impacts occur to species that use either the habitat created by infaunal and epifaunal organisms (e.g. ecosystem engineers) or depend upon these species as food resources (Auster et al. 1996, Auster 1998, Coleman and Williams 2002).

The Gulf of Mexico (GOM) trawl fishery targets penaeid shrimps in soft-sediment habitats that are assumed to be of low structural and species diversity. However, these habitats play an important role in transferring carbon to higher trophic levels, as well as serving as important nursery areas for many species (Snelgrove 1999, Thrush et al. 2001, Rooker et al. 2004, Patterson et al. 2005). Moreover, trawling in the northern GOM is not confined solely to soft-sediments, but also to a suite of different habitat types such as low relief shell-rubble reefs. Auster (1998) identified biogenic structures and shell aggregates as some of the most susceptible to adverse impacts by trawling activities.

Shrimp trawling in the GOM directly affects many fish and invertebrate species via bycatch mortality. Harrington et al. (2005) found the highest discard to landings ratio in U.S. marine fisheries was from the GOM shrimp trawl fishery. Further, declines of commercially and recreationally important finfish, elasmobranchs, endangered sea turtles, and negative impacts on the benthic ecosystem have been attributed to the shrimp trawl fishery (Henwood and Stuntz 1987, Goodyear and Phares 1990, Martinez et al. 1996, Shephard and Myers 2005). In an attempt to reduce excessive bycatch of fish and invertebrates, bycatch reduction devices (BRDs) in shrimp trawls were required in western GOM federal waters by 1998. However, recent estimates have indicated that only 16.5% of all species are successfully being excluded by BRDs (Foster and Scott-Denton 2004). Thus, a technological solution to bycatch reduction may not exist, and the addition of shrimp no-trawl areas or time closures may be needed to supplement the BRD program (Gallaway et al. 1999, Patterson et al. 2005). However, before additional management strategies can be implemented, species-specific habitat use patterns, and the effects of trawling on benthic ecosystems need to be quantified. Aside from simply

characterizing the bycatch, alterations of seafloor habitats by trawling and resulting effects on post-settlement processes of fishes and invertebrates in the GOM has received little attention.

The continental shelf of the northern GOM is primarily characterized by low relief sand bottoms interspersed with areas of mud and silt (Ludwick 1964, Kennicutt et al. 1995). These habitats support a large number of fishes and benthic invertebrates that are assumed to play a vital role in the trophic dynamics of the ecosystem (Arreguin-Sanchez et al. 2004). Several studies have characterized the distribution and abundance of fish and invertebrates inhabiting benthic communities in the GOM (Moore et al. 1970, Franks et al. 1972, Chittenden and McEachran 1976, Chittenden and Moore 1977). In addition, two extensive low-relief (cm to m) shell-rubble ridges at the 20 m and 40 m isobaths exist in the northern-central-GOM on the MAFLA sand sheet (Schroeder et al. 1995, Dufrene 2005). The large size of these shell ridges suggests they may be important to the fish and invertebrate communities utilizing these areas (Szedlmayer and Howe 1997, Rooker et al. 2004, Patterson et al. 2005). Higher relief natural hard bottom reef habitats in the form of reef pinnacles, banks, and ledges also exist on the shallow inner-shelf; these have been suggested as important reef habitats for red snapper, *Lutjanus campechanus*, and other reef fishes (Parker et al. 1983, Schroeder et al. 1988). To date, no studies have investigated the effects of trawling on the biotic community of these shell-rubble ridge and hard bottom reef systems on the northern GOM shallow (<40 m) inner shelf.

The goal of this study was to characterize habitat use patterns and to assess the effects of trawling on demersal fish and invertebrate communities on the northern GOM continental shelf. Specifically, sand, shell-rubble, and natural hard bottom reef habitats

were selected for habitat-specific community comparisons. In addition, sand and shell-rubble habitats were compared inside and outside an extensive artificial reef permit area off Alabama, which served as a *de facto* non-trawl area, to assess the impacts of shrimp trawling on habitat characteristics and the associated biological communities.

Methods and Materials

Sampling Site

Sampling was conducted on the continental shelf in the northern GOM (Figure 3.1). The largest artificial reef permit area in the United States, which covers over 4,000 km², exists in this region (Shipp 1999). These reef zones serve as *de facto* non-trawl areas (Link 1997) that are in close proximity to sampling locations exposed to trawling. Seabed characterization of the region inside and outside of the permit areas was recently performed with digital sidescan sonar and box core sediment analysis during previous studies (Dufrene 2005, Patterson et al. 2005). Four different habitat types were examined: sand sites with interspersed mud, low relief (<1 m) shell-rubble sites (<40% CaCO₃), high relief (1-3 m) shell-rubble sites (>40% CaCO₃) and natural hard bottom high-relief (>2 m) reef sites (Figure 3.1). One approximately 8 km² study area of each habitat type was selected inside the reef permit area (non-trawled sites) and outside of the permit area (trawled sites) to compare the effect of trawling on habitat characteristics and fish and invertebrate communities.

Sampling Methodology

Trawl sampling was conducted quarterly in 2004 and 2005 onboard the R/V *Caretta*, an 18-m research vessel operated by the National Marine Fisheries Service (NMFS) Pascagoula, Mississippi laboratory. Each of the 8 km² habitat areas were divided into ten stations measuring approximately 1 km in length and 200 m in width.

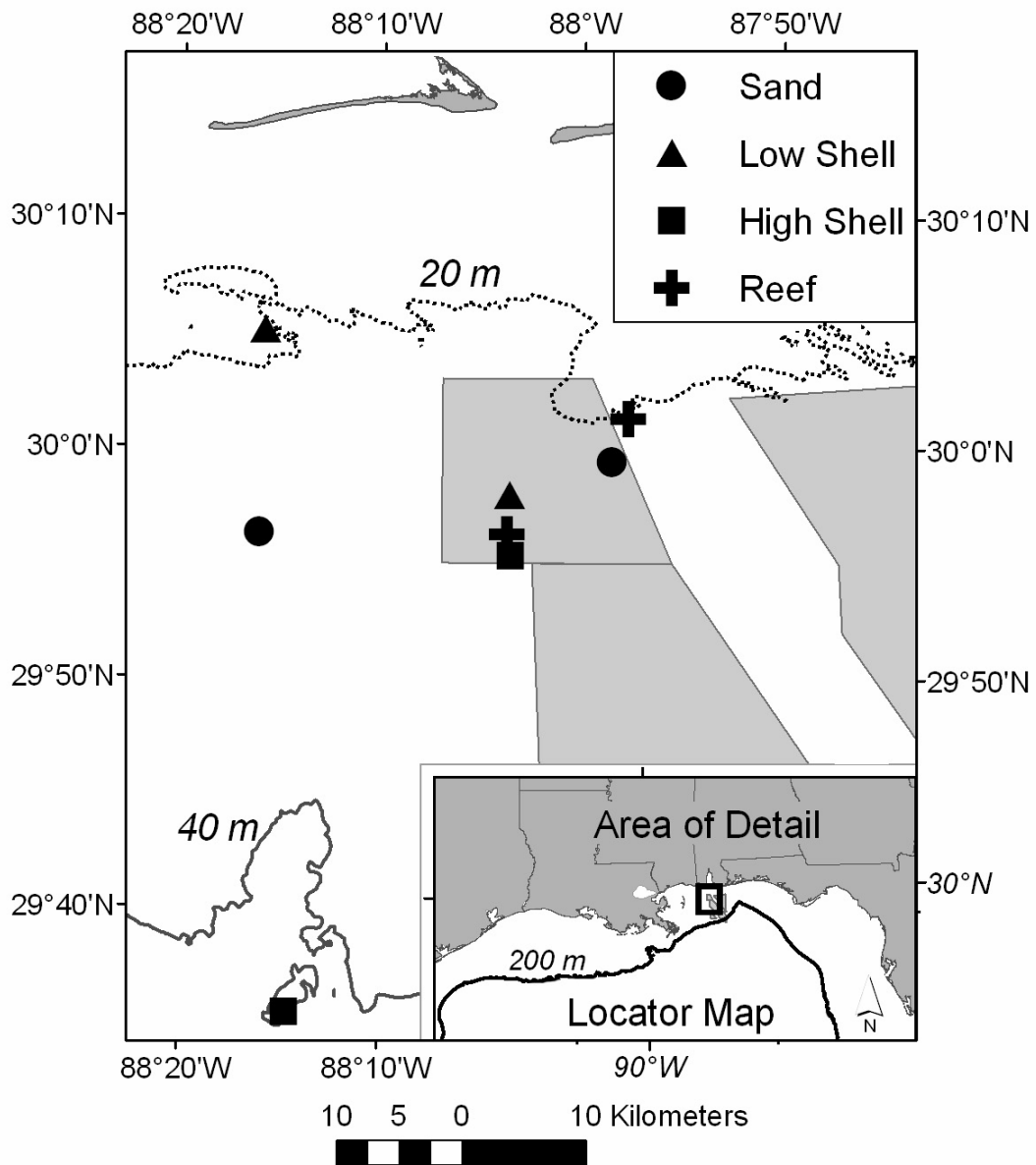


Figure 3.1. Map of the study site locations in the northcentral GOM. The 20- and 40-m depth contours are shown with the 200-m depth contour representing the shelf edge. Shaded regions indicate the Alabama artificial reef permit areas I used as my *de facto* non-trawl areas.

Three of the ten stations in each area were randomly selected for trawl samplings; stations were fixed for the duration of the study. All stations were trawled in a northwest to southeast direction in an effort to remain in the habitat of interest. Sampling was conducted with standard NMFS Fall Groundfish Survey (FGS) trawl gear (FGS; SEAMAP Information System, NMFS, Pascagoula, MS), which included a single 12.8-m wide otter trawl with 4 cm mesh size, towed at approximately 4.6 km h⁻¹ for 10 min sample⁻¹. In addition, a 0.7 cm cod end lining was added to the NMFS standard gear type to increase capture efficiencies for smaller individuals. Trawl sampling occurred only during daylight hours (30 min after sunrise and 30 min before sunset). Trawls were towed along the edges of the natural hard bottom reefs to avoid damaging the habitat or hanging the net. During all trawl sampling, vessel position was overlain on sidescan mosaics in ArcPad 6.0 for continuous GPS tracking of trawl position and to aid in proper navigation.

All fishes and invertebrates from the trawl collections were weighed, sorted and identified to the lowest possible taxon. The entire catch was first weighed to the nearer 0.1 kg and each fish was then measured and weighed to the nearer mm total length (TL) and total weight (g), respectively. Each invertebrate was measured to the nearer mm in a manner consistent with body shape. If more than ten individuals of the same species were collected, a random sub-sample of ten were selected to be measured (all red snapper were measured). All habitat structural items were weighed to the nearer g; these included alga, coral, shell, sponge, and wood. The entire catch then was discarded, except for the red snapper, which were saved for additional analysis.

Water mass characteristics (salinity, temperature, depth, dissolved oxygen, and optical backscatter) were measured at each site with a SeaBird SBE-25 conductivity-

temperature-depth (CTD) instrument. Habitat characteristics were quantified with a video-equipped remotely operated vehicle (ROV); transect locations were randomly chosen near my trawl survey areas on similar habitat types, but not directly along my trawl transects. Once chosen, these same transect locations were used throughout the two year study period for ROV sampling. A VideoRay Pro II ROV was used to perform two-consecutive 50-m transects at each site. The ROV was equipped with GPS to aid in navigation and to estimate distance covered. Each of the two ROV transects started at the same point of origin and ran in opposite directions to prevent the re-sampling of transect survey areas. Analysis of ROV data was performed in the laboratory by estimating percent coverage of habitat categories (see below) from 25 equally sized squares overlain on digital images of individual video frames. One digital image (frame) was analyzed every 10 m per transect, resulting in ten total observations per site. The near-field half of each observation was first enumerated, and then forwarded to view the far-field half to prevent bias of the percent cover due to the oblique angle of the camera (Auster et al. 1996). Percent cover was divided among five categories including: 1) sessile biological features (e.g., alga, anemone, bryozoan, coral, sponge, worm tube); 2) mobile biota (e.g., fish, invertebrate); 3) sediment type (e.g., sand and mud, sandstone, shell, rock); 4) sediment characteristics by sediment type (e.g., flat, hole, mound, ridge, ripple); and, 5) miscellaneous features (e.g. wood). In addition, a maximum vertical relief estimate (the maximum height (cm) of any geological or biological structure within view) was made at each observation. Height was estimated in reference to the 10 cm width of the ROV arms.

Data Analysis

Fish and invertebrate community data were analyzed with the PRIMER (Plymouth Routines in Multivariate Ecological Research) statistical package (Clarke and Warwick 2001). First, fish and invertebrate densities were computed for each taxon in each trawl sample by dividing the total number of individuals collected by the total area swept by the trawl. Densities of fish and invertebrates were transformed by using $\log(x+1)$ to downweight the abundant species and to retain information regarding some of the less abundant species. A Bray-Curtis similarity matrix then was computed among all samples with density data. A stepwise data reduction procedure in PRIMER, BV-STEP, was performed with a Spearman rank correlation coefficient of 95% as the cutoff to determine which group of species together explained most of the variability in the fish and invertebrate communities (Clarke and Warwick 1998).

Two-factor non-metric multi-dimensional scaling (MDS) models were computed for each sampling season to visualize similarities within and dissimilarities among habitats and areas exposed to trawling versus those that were not. Stress (residual modeling error) coefficients were used to assess the degree of correspondence in the data as goodness-of-fit criteria for each seasonal model. A stress value of 0.2 was treated as a critical value to test goodness-of-fit of a given MDS model in two dimensions (Clarke 1993).

The analysis of similarities (ANOSIM) permutation procedure was used to test for differences in fish and invertebrate communities among habitats, seasons, and the exposure to trawling (Warwick et al. 1990a). A percent habitat distinctness value for each habitat type in the trawled and non-trawled area was calculated by taking the number of significant pairwise differences divided by the total number of pairwise

comparisons possible and multiplying by 100. To assess species-specific contributions, SIMPER (Similarity Percentages) was used as the *post-hoc* analysis to indicate the contribution of a particular species to the overall fish and invertebrate community similarity (within season or habitat) and dissimilarity (among seasons and habitats) (Clarke 1993). A cutoff percentage of 90% was used to determine those species accounting for 90% of the total similarities and dissimilarities. Species with both high similarity or dissimilarity values and with low standard deviations (e.g. >1.0) consistently contributed to the similarity or dissimilarity among samples (Clarke and Warwick 2001). An alpha level of 0.05 was set for all statistical analyses.

The total number of species, the total number of individuals, the Pielou's evenness (J'), and the Shannon diversity (H') indices were all calculated with the DIVERSE procedure in PRIMER (Warwick et al. 1990b) (see Chapter 2 for details and equations). Diversity indices were analyzed with a randomized block design, three-factor analysis of variance (ANOVA) with year as the block effect and habitat, presence of trawling, and season as the main effects (Blanchard et al. 2004). The equal variance assumption was assessed by examining the plot of the residuals versus the predicted values. Normality was tested with a Shapiro-Wilk test, and by examining a normal probability plot of the residuals versus the expected values.

Sizes of abundant fish species that most contributed to the community structure were analyzed by habitat and the presence of trawling. Length-frequency distributions were compared with Kolmogorov-Smirnov two-sample tests (Sokal and Rohlf 1995) and differences in location were tested by the median linear rank test (Gibbons and Chakraborti 1992).

Habitat characteristics from the ROV surveys were analyzed with PRIMER and canonical correlation analysis (CCA) (ter Braak and Smilauer 2002). Bray-Curtis similarity matrices were used to compare habitat characteristics. Habitat characteristic data were quantified as a percent area (except vertical relief), thus the data were square root transformed. Analysis of Similarity and SIMPER were performed to describe differences, and to identify the most important habitat characteristics discriminating among habitat type and between trawled and untrawled habitats. Habitat characteristics were combined with near-bottom water mass characteristics in the CCA to determine if environmental data were correlated with species density. Habitat type and the presence of trawling were entered as nominal variables (sand, shell, reef, trawl or non-trawl). In addition, the same 28 species used for community analyses were used in the CCA to reduce bias associated with rare taxa. Inter-set correlation coefficients with absolute values greater than or equal to 0.4 were interpreted as ecologically important (Hair et al. 1984, Rakocinski et al. 1996). A biplot with the species and the environmental scores was produced, as this shows the species scores regressed on the environmental variables.

Trawling Exposure

The potential exposure to shrimp trawling in my study area was estimated using annual commercial shrimp trawling effort data. My trawled sites were between the depths of 18 and 40 m and located within subareas 10 and 11, of the 21 NMFS statistical subareas used to calculate shrimp catch per unit of effort. Patella (1975) estimated the bottom surface area between 18 and 55 m depth within subareas 10 and 11 to be 10,444.7 km². Shrimp effort data between 18 and 55 m depth within subareas 10 and 11, during 2004 and 2005, were 4860.9 and 4570.8 days fished (24 h), respectively (per. com. James Nance, NOAA/NMFS, Galveston, TX). I based my calculations of the area swept by a

commercial shrimp vessel using the standard NMFS gear specifications (12.8-m wide net, 4.6 km h⁻¹ tow speed) (FGS; SEAMAP Information System, NMFS, Pascagoula, MS). I used a conservative estimate of two nets towed per fishing vessel, as most vessels tow between two and four nets at a time (NRC 2002). Thus, a total bottom area of 2.826 km² was swept by trawls per day fished. Therefore, taking the total number of days fished multiplied by the total bottom area swept per day, yielded an estimated area of 13,736.9 and 12,917.1 km² that was swept during 2004 and 2005, respectively. These conservative calculations indicate that sufficient fishing effort was performed to cover the entire area at least once per year between the depths of 18 and 55 m within subareas 10 and 11, although I have no direct way to determine if my sites had actually been trawled.

Life History Strategy

The conceptual model proposed by Winemiller and Rose (1992) was used to ordinate the representative species collected from trawled versus non-trawled habitats on a tri-lateral continuum of life history strategy. Winemiller and Rose (1992) defined opportunistic strategists as those with an early age at maturity, short generation time (T), high net replacement rate (R₀), and low juvenile survivorship. In contrast, periodic strategists have later ages at maturity, higher fecundity, longer generation times (T), lower net replacement rates (R₀), and low juvenile survivorship. The intrinsic rate of natural increase (r) incorporates both the generation time and replacement rate by $r = \ln R_0/T$.

Results

A large number of species (n=214; 144 fishes and 70 invertebrates) and individuals (n=83,226) were collected in trawl samples over the GOM continental shelf during the two year study period. Species sampled represented 11 classes, 33 orders, and

90 families. Results from the BV-STEP procedure in PRIMER indicated 15 fish and 13 invertebrate (28 total) species accounted for 90% of the variance in community structure (Table 3.1). Therefore, all statistical analyses of community structure were computed with those 28 species.

The community structure and habitat characteristics analyzed with ANOSIM indicated no differences between the low shell-rubble and high shell-rubble content sites either within the non-trawled area or within the trawled area (ANOSIM; Global $R=0.076$, $P=0.280$). I therefore collapsed these two levels of the habitat factor into a single shell-rubble level for the non-trawled area and one for the trawled area. In addition, year differences (2004 and 2005) as a main effect were not significant (ANOSIM; Global $R=0.073$, $P=0.120$); therefore samples were combined across years to increase power.

Habitat-specific Communities

Significant differences existed in the fish and invertebrate community among habitat types (ANOSIM; Global $R=0.436$, $P<0.001$) and sampling seasons (ANOSIM; Global $R=0.342$, $P<0.001$), as well as between trawled and non-trawled areas (Global $R=0.128$, $P<0.001$). Plots of MDS results demonstrate the similarities within and dissimilarities among habitats and seasons with respect to the exposure to trawling (Figure 3.2). The sand, shell, and reef communities in the trawled and non-trawled areas showed differences in community structure. Specific pair-wise comparisons among habitat types by season within both the trawled and non-trawled areas indicate that significant differences existed 50% and 67% of the time, respectively (Table 3.2).

The community over the sand habitat was the most distinct when compared to the shell and reef communities in the trawled area (Table 3.2). Results of the SIMPER analysis indicate that seven species most contributed to the community over the trawled

Table 3.1. Classification and habitat-specific abundance of the 28 most abundant species used for all analyses. Total numbers represent the total number of all 214 species collected in the study.

				Sand Trawl	Sand Non- Trawl	Shell Trawl	Shell Non- Trawl	Reef Trawl	Reef Non- Trawl
Class	Order	Family	Species						
Ascidiacea	Paxillosida	Luidiidae	<i>Luidia clathrata</i>	20	20	2	63	6	27
Asterozoa	Ophiurida	Ophiidermatidae	<i>Ophioderma appressum</i>	2	0	6	34	1	1
		Ophiolepididae	<i>Ophiolepis elegans</i>	1284	68	30	175	59	132
Echinoidea	Arbacioida	Arbaciidae	<i>Arbacia punctulata</i>	2	1	57	23	32	8
Malacostraca	Decapoda	Dromiidae	<i>Dromidia antillensis</i>	3	0	1	14	1	6
		Inachidae	<i>Podochela sidneyi</i>	11	13	7	25	7	16
		Panaeidae	<i>Farfantepeneaeus aztecus</i>	212	25	17	0	0	7
			<i>Parapeneaeus politus</i>	4	2	210	1	0	0
		Parthenopidae	<i>Parthenope granulata</i>	20	6	5	13	5	6
		Portunidae	<i>Callinectes similus</i>	60	1	3	1	1	3
			<i>Ovalipes floridanus</i>	12	1	35	2	7	3
			<i>Portunus spinimanus</i>	51	7	32	21	7	9
		Sicyoniidae	<i>Sicyonia brevirostris</i>	84	25	64	29	10	12
Osteichthyes	Aulopiformis	Synodontidae	<i>Saurida brasiliensis</i>	2836	978	424	184	49	1099
			<i>Synodus foetens</i>	561	255	171	244	133	332
	Clupeiformes	Engraulidae	<i>Anchoa hepsetus</i>	302	7905	533	0	617	0
	Perciformes	Haemulidae	<i>Orthopristis chrysoptera</i>	1	2	87	173	21	8
		Lutjanidae	<i>Lutjanus campechanus</i>	245	79	158	438	154	403
			<i>Lutjanus synagris</i>	19	6	43	89	14	20
		Sciaenidae	<i>Cynoscion nothus</i>	191	3	228	0	2	39
			<i>Micropogonias undulatus</i>	5214	78	146	7	0	978
		Serranidae	<i>Centropristis ocyurus</i>	8	8	11	191	30	69
			<i>Diplectrum bivittatum</i>	295	122	324	35	19	64
		Sparidae	<i>Lagodon rhomboides</i>	217	37	201	205	67	86
			<i>Stenotomus caprinus</i>	7685	21482	1512	1702	2266	3760
		Stromateidae	<i>Peprilus burti</i>	1333	60	711	4	9	11
	Pleuronectiformes	Paralichthyidae	<i>Syacium papillosum</i>	682	423	276	930	130	951
	Scorpaeniformes	Triglidae	<i>Prionotus roseus</i>	65	5	50	148	1	32
Total of all species			Total numbers (n=83,226)	23,965	32,614	6,611	6,167	4,307	9,562
			Total number of trawls	21	24	33	48	21	24

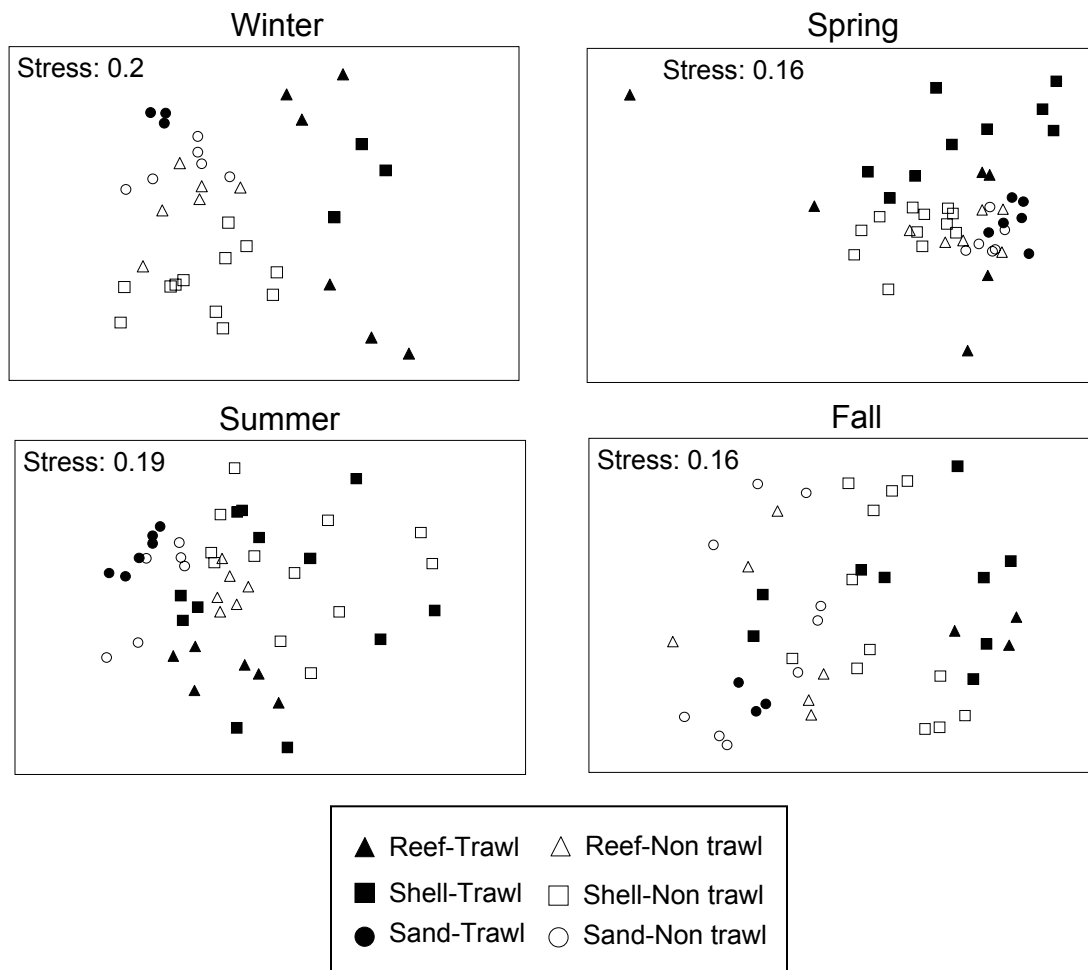


Figure 3.2. Multi-dimensional scaling (MDS) plots of habitat-specific trawl samples by season over the two-year study period. Each sample represents the 28 species analyzed for the habitat-specific fish and invertebrate community. Stress coefficients represent goodness-of-fit criteria.

Table 3.2. Dissimilarity matrix showing the quarterly community differences of each habitat relative to the other habitat-specific communities. Letter coding indicates a significant difference ($p < 0.05$) (W=Winter, Sp=Spring, Sm=Summer, F=Fall).

	Reef-trawl	Reef-non trawl	Shell-trawl	Shell-non trawl	Sand-trawl	Sand-non trawl
Reef-trawl	-	W,Sp,Sm,F	Sp	W,Sp,Sm,F	W,Sp,Sm	W,Sp,Sm,F
Reef-non trawl	W,Sp,Sm,F	-	W,Sp,F	W,F	W,Sm	Sp,Sm
Shell-trawl	Sp	W,Sp,F	-	W,Sp,F	Sp,F	W,Sp,F
Shell-non trawl	W,Sp,Sm,F	W,F	W,Sp,F	-	W,Sp,Sm,F	W,Sp,Sm,F
Sand-trawl	W,Sp,Sm	W,Sm	Sp,F	W,Sp,Sm,F	-	W,Sp,Sm
Sand-non trawl	W,Sp,Sm,F	Sp,Sm	W,Sp,F	W,Sp,Sm,F	W,Sp,Sm	-

sand habitat (Table 3.3). In order of decreasing importance, these included the longspine porgy (*Stenotomus caprinus*), largescale lizardfish (*Saurida brasiliensis*), Atlantic croaker (*Micropogonias undulatus*), gulf butterfish (*Peprilus burti*), dwarf sand perch (*Diplectrum bivittatum*), inshore lizardfish (*Synodus foetens*), and dusky flounder (*Syacium papillosum*). In contrast, pinfish (*Lagodon rhomboides*) was an important member of the shell community, while red snapper and striped anchovy (*Anchoa hepsetus*) were important to the reef community in the trawled area (Table 3.3).

The shell and sand habitats supported the most unique communities within the non-trawled area (Table 3.2). The bank sea bass (*Centropristis ocyurus*) was the most important contributor to the shell community and the largescale lizardfish, red snapper, and dusky flounder most distinguished the reef community (Table 3.4). The species that most contributed to the sand community in the non-trawled area by order of importance were the longspine porgy, brittle star (*Ophiolepis elegans*), dwarf sand perch, and Atlantic croaker (Table 3.4).

Trawl Versus Non-trawl Communities

The fish and invertebrate communities occupying the trawled and non-trawled sand and shell habitats each differed in three of the four seasons (Table 3.2, Figure 3.2). The sand trawled and non-trawled communities significantly differed in the winter, spring, and summer, while the shell trawled and non-trawled communities differed in the winter, spring, and fall. Several species emerged as general representative species for trawled versus non-trawled locations, regardless of habitat type (Table 3.5). The species more commonly found in trawled areas included the longspine porgy, Atlantic croaker, largescale lizardfish, gulf butterfish, brown shrimp (*Farfantepenaeus aztecus*), dwarf

Table 3.3. SIMPER results of the species that most contributed to the dissimilarity between sand, shell, and reef communities exposed to trawling. Mean densities of important species within habitat type, the contribution (DS) to the average dissimilarity, and the average dissimilarity/standard deviation (DS/SD) ratio. A 90% threshold was used for the cumulative % contribution of species, but only species with a 5.0% contribution and above are shown.

Sand vs. Shell Species	Sand	Shell	DS	DS/SD	% contribution	% cumulative contribution
Longspine porgy	409.00	45.82	7.69	1.48	12.22	12.22
Largescale lizardfish	157.56	12.85	6.10	1.40	9.70	21.92
Atlantic croaker	119.56	4.42	5.17	1.00	8.21	30.13
Gulf butterflyfish	56.61	21.55	4.31	1.20	6.85	36.98
Inshore lizardfish	29.44	5.18	3.54	1.62	5.62	42.60
Dwarf sand perch	12.17	9.82	3.36	1.53	5.35	47.95
Dusky flounder	35.17	8.36	3.33	1.41	5.29	53.24

Sand vs. Reef Species	Sand	Reef	DS	DS/SD	% contribution	% cumulative contribution
Longspine porgy	409.00	107.90	8.07	1.59	12.12	12.12
Largescale lizardfish	157.56	2.33	6.54	1.48	9.81	21.93
Atlantic croaker	119.56	0.00	5.54	0.98	8.31	30.24
Gulf butterflyfish	56.61	0.43	4.45	1.17	6.68	36.92
Dwarf sand perch	12.17	0.90	3.95	1.87	5.93	42.84
Dusky flounder	35.17	6.19	3.71	1.68	5.58	48.42
Inshore lizardfish	29.44	6.33	3.71	1.40	5.57	53.99

Shell vs. Reef Species	Shell	Reef	DS	DS/SD	% contribution	% cumulative contribution
Longspine porgy	45.82	107.90	8.39	1.13	13.21	13.21
Red snapper	4.79	7.33	4.64	1.11	7.30	20.51
Largescale lizardfish	12.85	2.33	4.28	0.95	6.74	27.25
Inshore lizardfish	5.18	6.33	4.20	1.11	6.61	33.86
Pinfish	6.09	3.19	3.85	1.01	6.07	39.92
Dusky flounder	8.36	6.19	3.80	1.09	5.99	45.91
Dwarf sand perch	9.82	0.90	3.60	1.20	5.68	51.59
Striped anchovy	16.15	29.38	3.40	0.55	5.35	56.94

Table 3.4. SIMPER results of the species that most contributed to the dissimilarity between sand, shell, and reef communities that are not exposed to trawling (non-trawl). Mean densities of important species within habitat type, the contribution (DS) to the average dissimilarity, and the average dissimilarity/standard deviation (DS/SD) ratio. A 90% threshold was used for the cumulative % contribution of species, but only species with a 5.0% contribution and above are shown.

Sand vs. Shell Species	Sand	Shell	DS	DS/SD	% contribution	% cumulative contribution
Longspine porgy	807.59	35.46	8.52	1.30	14.63	14.63
Largescale lizardfish	36.22	3.83	5.37	1.25	9.21	23.84
Red snapper	5.37	9.13	3.65	1.22	6.28	30.12
Dusky flounder	17.48	19.38	3.65	1.02	6.27	36.39
Dwarf sand perch	7.33	0.73	3.29	1.47	5.65	42.03
Brittle star	40.81	3.65	3.22	1.04	5.52	47.56

Sand vs. Reef Species	Sand	Reef	DS	DS/SD	% contribution	% cumulative contribution
Largescale lizardfish	36.22	45.46	4.75	1.31	10.13	10.13
Red snapper	5.37	16.79	3.74	1.26	7.98	18.11
Dusky flounder	17.48	39.63	3.73	1.06	7.95	26.06
Atlantic croaker	116.30	40.75	3.60	0.85	7.69	33.74
Longspine porgy	807.59	156.67	3.49	1.20	7.46	41.20
Brittle star	40.81	5.50	3.09	1.21	6.60	47.80
Dwarf sand perch	7.33	2.67	2.51	1.35	5.35	53.15

Shell vs. Reef Species	Shell	Reef	DS	DS/SD	% contribution	% cumulative contribution
Longspine porgy	35.46	156.67	6.03	1.17	11.77	11.77
Largescale lizardfish	3.83	45.46	4.99	1.25	9.74	21.52
Red snapper	9.13	16.79	4.11	1.35	8.02	29.54
Dusky flounder	19.38	39.63	4.04	1.16	7.89	37.43
Inshore lizardfish	5.08	13.83	3.00	1.36	5.85	43.28
Brittle star	3.65	5.50	2.92	1.18	5.70	48.98
Bank sea bass	3.98	2.88	2.72	1.24	5.30	54.28
Atlantic croaker	0.15	40.75	2.63	0.57	5.14	59.42

Table 3.5. SIMPER results of the species that most contributed to the dissimilarity between sand and shell trawl and non-trawl communities. Mean densities of important species within habitat type, the contribution (DS) to the average dissimilarity, and the average dissimilarity/standard deviation (DS/SD) ratio. A 90% threshold was used for the cumulative % contribution of species, but only species with a 5.0% contribution and above are shown.

Sand						
Species	Sand-trawl	Sand-non trawl	DS	DS/SD	% contribution	% cumulative contribution
Atlantic croaker	119.56	116.30	4.75	1.11	10.23	10.23
Largescale lizardfish	157.56	36.22	4.64	1.34	9.98	20.21
Gulf butterfish	56.61	13.85	3.64	1.23	7.83	28.03
Brittle star	13.89	40.81	2.96	1.16	6.36	34.39
Brown shrimp	8.89	2.85	2.72	1.42	5.84	40.24
Red snapper	9.94	5.37	2.52	1.20	5.43	45.66
Dusky flounder	35.17	17.48	2.41	0.98	5.18	50.84
Dwarf sand perch	12.17	7.33	2.38	1.30	5.12	55.96

Shell						
Species	Shell-trawl	Shell-non trawl	DS	DS/SD	% contribution	% cumulative contribution
Longspine porgy	45.82	35.46	7.02	1.31	11.39	11.39
Red snapper	4.79	9.13	4.38	1.16	7.12	18.51
Dusky flounder	8.36	19.38	4.22	1.25	6.85	25.36
Largescale lizardfish	12.85	3.83	4.10	0.96	6.66	32.02
Pinfish	6.09	4.27	3.30	0.93	5.36	37.38
Dwarf sand perch	9.82	0.73	3.28	1.15	5.33	42.71
Bank sea bass	0.33	3.98	3.18	1.20	5.16	47.87

sand perch, and pinfish. In contrast, the brittle star and bank sea bass were found over non-trawled habitat types in greater abundances. In addition, red snapper and dusky flounder showed mixed habitat-specific preferences with greater numbers observed over sand trawled and shell non-trawled habitats.

Life History Strategy

The representative species collected from trawled and non-trawled habitats lie on the continuum between opportunistic and periodic life history strategists (Table 3.6). Based upon the criteria outlined by Winemiller and Rose (1992), four species (longspine porgy, largescale lizardfish, gulf butterfish, silver seatrout) that were abundant over trawled areas are opportunistic strategists; attaining small sizes, early maturation, and high intrinsic rates of natural increase. In contrast, the two species (bank sea bass, red snapper) that were more abundant over the non-trawled area (specifically the non-trawled shell) are periodic strategists; attaining larger sizes, delayed maturation, and lower intrinsic rates of natural increase.

Faunal Diversity

Diversity and evenness indices were highest for shell communities while species richness and the total number of species were highest for sand communities (Table 3.7). Significant habitat x trawl x season interactions occurred among indices indicating the magnitude of the differences varied over time relative to habitat type and the exposure to trawling. Nevertheless, least square means indicated similar trends of highest diversity and evenness indices for both non-trawled and trawled shell communities, followed by reef and then sand communities (Table 3.7). Differences in the diversity indices were also found between sand and shell communities exposed and not exposed to trawling. Higher diversity and evenness indices were observed for the non-trawled versus the

Table 3.6. Life history information of the most important fish species discriminating between trawled and non-trawled communities. Lengths are in total length (TL). I used www.fishbase.org to obtain life history information for two species due to limiting information in the literature, and for all intrinsic rates of natural increase.

Common Name	Scientific Name	Size at maturity	Age at maturity	Maximum size	Maximum age	Intrinsic rate of increase (r)	Reference
Longspine porgy	<i>Stenotomus caprinus</i>	90-125 mm	12 months	200 mm	2.5-3 yr	3.94 yr ⁻¹	Geoghegan and Chittenden 1982
Largescale lizardfish	<i>Saurida brasiliensis</i>	157 mm	9 months	250 mm	3 yr	3.82 yr ⁻¹	Froese and Pauly 2006
Gulf butterfish	<i>Peprilus burti</i>	134-215 mm	9-16 months	269 mm	2-2.5 yr	4.90 yr ⁻¹	Murphy and Chittenden 1991
Silver seatrout	<i>Cynoscion nothus</i>	162-197 mm	12 months	220 mm	2 yr	2.04 yr ⁻¹	DeVries and Chittenden 1982
Bank sea bass	<i>Centropristis ocyurus</i>	185 mm	2 yr	300 mm	8 yr	2.08 yr ⁻¹	Froese and Pauly 2006
Red snapper	<i>Lutjanus campechanus</i>	295-482 mm	2-5 yr	1039 mm	59 yr	1.06 yr ⁻¹	Wilson and Nieland 2001 Woods et al. 2003

trawled shell community, while higher diversity and evenness indices were observed for the trawled versus non-trawled sand communities (Table 3.7). Likewise, the trawled sand community had higher species richness, but the total number of individuals was higher for non-trawled sand. In contrast, species richness was higher for the non-trawled shell community, while trawled shell supported a higher total number of individuals (Table 3.7).

Size Structure

Truncated size distributions and smaller median sizes were observed for eight of the nine fish species that most contributed to the community structure between trawled and non-trawled areas of similar habitat type (Figure 3.3). Differences were habitat-specific, except for red snapper, which showed significantly truncated size distributions and smaller median sizes over trawled sand (Kolmogorov-Smirnov test: $P=0.001$, median test: $P=0.0004$) and trawled shell (Kolmogorov-Smirnov test: $P<0.0001$, median test: $P<0.0001$), compared to similar non-trawled habitat types. Habitat-specific shell comparisons showed seven species with smaller sizes over trawled shell habitats compared to non-trawled shell, and five of the seven species showed significant differences. Similarly, habitat-specific sand comparisons indicated that seven species were smaller over trawled sand, with four showing significant differences. In contrast, the inshore lizardfish and gulf butterfish showed larger median sizes and size distributions over trawled sand, with gulf butterfish being significantly larger than conspecifics collected over the non-trawled sand habitat (Kolmogorov-Smirnov test: $P<0.0001$, median test: $P=0.0038$).

Table 3.7. Least square mean (± 1 standard error) estimates of diversity, evenness, richness, and total abundance of individuals collected from each habitat exposed and not exposed to trawling, over the two-year study period. Asterisk (*) indicates a significant habitat effect and plus sign (+) indicates a significant trawl effect ($P < 0.05$).

Trawled					Non-Trawled			
Habitat	Diversity	Evenness	Richness	Abundance	Diversity	Evenness	Richness	Abundance
Sand	1.72 (± 0.10) +	0.52 (± 0.04) +	28.12 (± 1.46)*+	1097 (± 174)*	1.03 (± 0.09)*+	0.39 (± 0.04)*+	17.25 (± 1.33) +	1359 (± 156)*
Shell	1.85 (± 0.09)	0.69 (± 0.04)	16.76 (± 1.31)	185 (± 152)	2.07 (± 0.07)*	0.73 (± 0.04)*	18.92 (± 1.03)	128 (± 110)
Reef	1.77 (± 0.09)	0.65 (± 0.04)	16.51 (± 1.34)	245 (± 156)	1.64 (± 0.10)*	0.55 (± 0.04)*	19.79 (± 1.46)	382 (± 174)

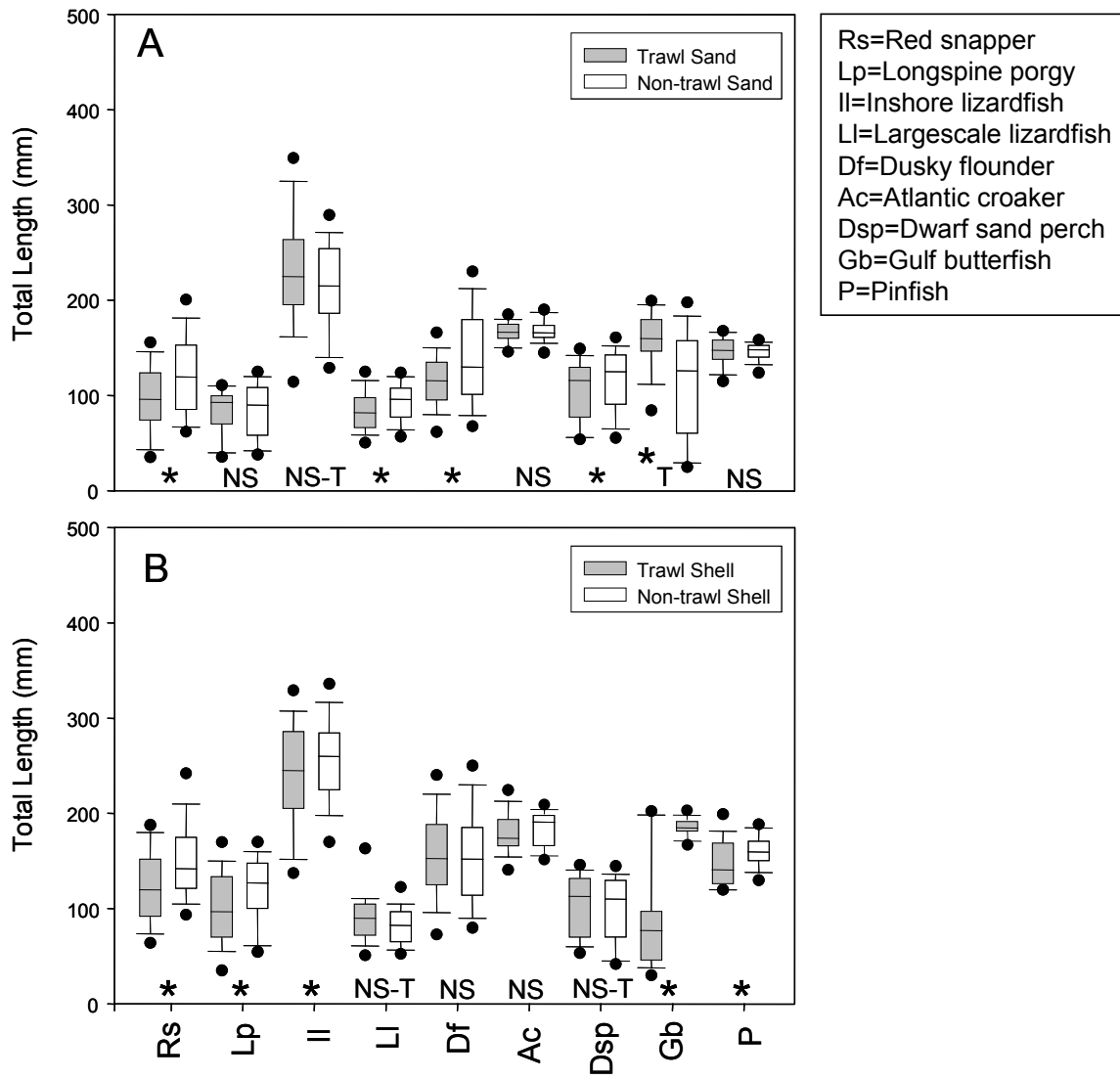


Figure 3.3. Habitat-specific size comparisons of the nine most abundant and influential fish species between sand trawl and non-trawl (A) and shell trawl and non-trawl (B). Ends of the boxes define the 25th and 75th percentiles, line at the median, error bars defining the 10th and 90th percentiles and outlier points represent the 5th and 95th percentiles. Asterisks indicate a significant size distribution difference (Kolmogorov-Smirnov test) and median difference (median rank test) with larger non-trawl sizes ($p < 0.05$). NS indicates no significant differences, but non-trawl average sizes were larger. *T indicates significant differences with larger trawl sizes and NS-T indicates trawl average sizes were larger, but no significant difference.

Habitat Characteristics

Habitat characteristics between sand and shell trawled and non-trawled habitats showed significant differences, regardless of season (Sand: ANOSIM; Global $R=0.252$, $P=0.048$; Shell: ANOSIM; Global $R=0.263$, $P=0.028$). Table 3.8 shows the SIMPER results of the habitat variables that most differentiated between the trawled and non-trawled areas of similar habitat type. The trawled sand habitat contained more shell flats and holes in the sand, while the non-trawled sand habitat had more mounds and wood on the seafloor. Together, these four variables contributed to over 90% of the overall dissimilarity between the sand habitats exposure to trawling. Shell habitat variables indicated sand flats were abundant on trawled shell areas while shell ridges, bryozoans, and tubeworms were more abundant over non-trawled shell habitats (Table 3.8). Seasonal differences were not detected (ANOSIM; Global $R=0.048$, $P=0.281$), indicating these habitat characteristics were stable over time.

Habitat characteristics among sand, shell, and reef habitats within the trawled and non-trawled areas also showed differences (ANOSIM; Global $R=0.302$, $P=0.001$). Sand flats were the most important variable characterizing sand habitats, shell flats for shell habitats, and a mixture of shell and sand flats, sandstone, and rock for characterizing the reef habitat types both within and outside of the non-trawled area. Overall seasonal differences in habitat characteristics among habitats were negligible (ANOSIM; Global $R=0.044$, $P=0.074$); however, shell habitats during the spring surveys had a high percentage of bryozoans.

Fish and Habitat Associations

A mixture of habitat types, habitat characteristics, the presence of trawling, and water mass characteristics was responsible for structuring fish and invertebrate

Table 3.8. SIMPER results of the habitat characteristics that most contributed to the dissimilarity between sand and shell trawl and non-trawl habitats. Mean densities of important habitat variables within habitat type, the contribution (DS) to the average dissimilarity, and the average dissimilarity/standard deviation (DS/SD) ratio. A 90% threshold was used for the cumulative % contribution of habitat variables, but only variables with a 5.0% contribution and above are shown.

Sand Habitat variables	Sand- trawl	Sand- non trawl	DS	DS/SD	% contribution	% cumulative contribution
Sand mounds	2.80	4.60	7.98	1.54	32.76	32.76
Shell flats	6.25	3.50	5.88	1.23	24.13	56.89
Sand holes	4.50	1.54	4.44	1.16	18.23	75.12
Wood	0.00	0.88	3.67	0.95	15.04	90.16

Shell Habitat variables	Shell- trawl	Shell- non trawl	DS	DS/SD	% contribution	% cumulative contribution
Sand flats	34.88	24.06	11.23	1.08	23.34	23.34
Shell ridges	4.47	8.40	7.39	0.91	15.35	38.69
Bryozoans	0.08	6.75	6.00	0.83	12.47	51.16
Tubeworms	0.13	3.73	4.90	0.78	10.19	61.35
Shell flats	55.95	55.33	3.74	1.36	7.78	69.13
Algae	0.68	0.21	3.05	0.67	6.33	75.47
Wood	0.23	0.16	2.42	0.69	5.04	80.50

communities in this study. The CCA biplot of species scores shows the weighted average of a species with the corresponding water mass variables and with the mean values of species within a habitat (as the nominal variables). The most important variables for CCA axis 1 were the presence of trawling, temperature, sand habitat, and shell habitat (Figure 3.4). In addition, three of the same four variables (temperature, sand habitat, and shell habitat) were the most important variables for CCA axis 2 (Figure 3.4). The variables that loaded highly positive on CCA axis 1 are inversely related to those that loaded negatively on CCA axis 1. Thus, the presence of trawling was inversely correlated with estimates of habitat vertical relief and almost all of the percent composition differences among the structural habitat variables. These included, in order of their correlation coefficients relative to CCA axis 1, tubeworms, bryozoans, anemones, wood, rock, coral, sandstone, and algae. In addition, temperature and dissolved oxygen were important positive water mass characteristics on axis 2, while salinity and depth loaded negatively on axis 2.

Mobile invertebrate species loaded positively on CCA axis 1 and were positively correlated to trawling. These include species such as the lesser blue crab (*Callinectes similus*), blotched swimming crab (*Portunus spinimanus*), and brown shrimp. In addition, fish species that were found to be more abundant over trawled areas and sand habitats loaded positively on CCA axis 1. These include striped anchovy, Atlantic croaker, silver seatrout (*Cynoscion nothus*), gulf butterfish, and dwarf sand perch. In contrast, less mobile invertebrates such as the urchin (*Arbacia punctulata*), brittlestar (*Ophioderma appressum*), starfish (*Luidia clathrata*), sponge crab (*Dromidia antillensis*), and shortfinger neck crab (*Podochela sidneyi*) correlated with structural variables. Additionally, red snapper, lane snapper (*Lutjanus synagris*), and bank sea bass were more

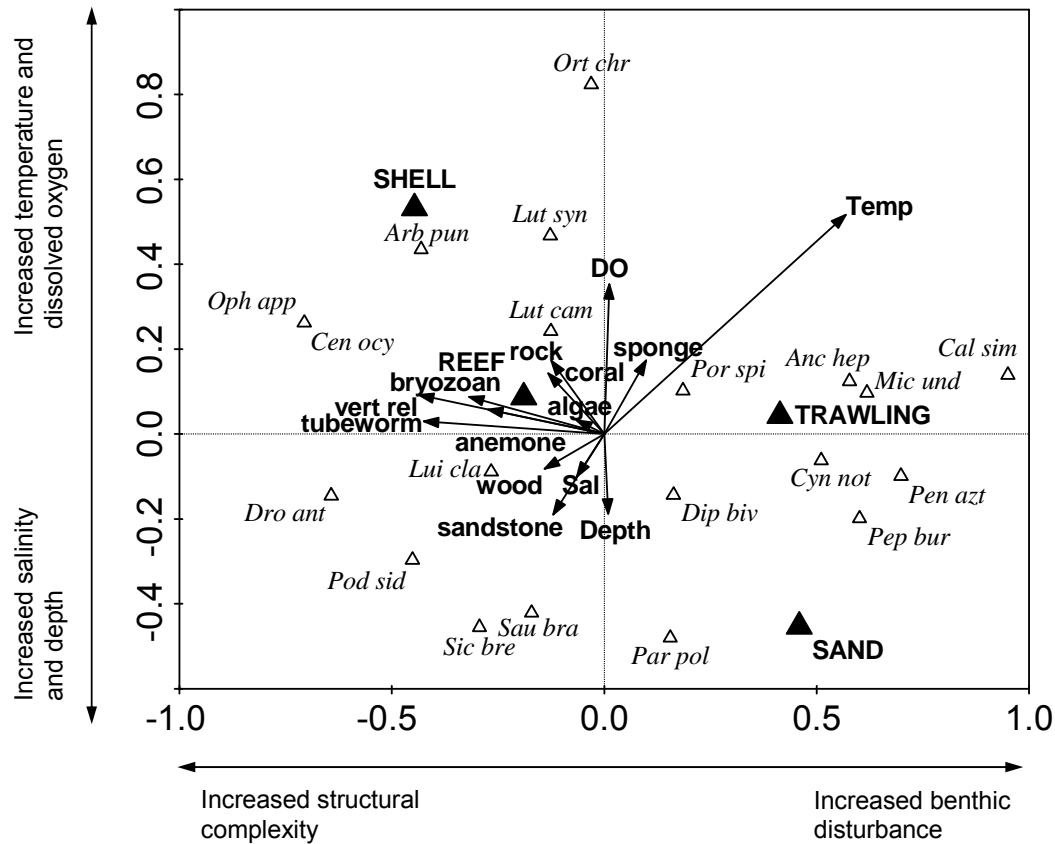


Figure 3.4. Biplot of axes 1 and 2 from canonical correspondence analysis of the abundant fish and invertebrate species (*italics*), habitat characteristics (**bold**), and water mass variables (**bold**). Nominal variables (Trawling, Sand, Shell, Reef) are in **bold** and all capital letters. Only 20 of the 28 species are included for visual simplification. The eight excluded species loaded weakly on both CCA axes. Species codes: *Anc hep* = *Anchoa hepsetus* (striped anchovy), *Arb pun* = *Arbacia punctulata* (urchin), *Cal sim* = *Callinectes similus* (lesser blue crab), *Cen ocy* = *Centropristis ocyurus* (bank sea bass), *Cyn not* = *Cynoscion nothus* (silver sea trout), *Dip biv* = *Diplectrum bivittatum* (dwarf sand perch), *Dro ant* = *Dromidia antillensis* (hairy sponge crab), *Lui cla* = *Luidia clathrata* (sea star), *Lut cam* = *Lutjanus campechanus* (red snapper), *Lut syn* = *Lutjanus synagris* (lane snapper), *Mic und* = *Micropogonias undulatus* (atlantic croaker), *Oph app* = *Ophioderma appressum* (brittlestar), *Ort chr* = *Orthopristis chrysoptera* (pigfish), *Par pol* = *Parapenaeus politus* (rose shrimp), *Far azt* = *Farfantepenaeus aztecus* (brown shrimp), *Pep bur* = *Peprilus burti* (gulf butterflyfish), *Pod sid* = *Podochela sidneyi* (shortfinger neck crab), *Por spi* = *Portunus spinimanus* (blotched swimming crab), *Sau bra* = *Saurida brasiliensis* (largescale lizardfish), *Sic bre* = *Sicyonia brevirostris* (brown rock shrimp).

common over structured habitats and were correlated with shell, reef, and structural variables.

Discussion

Results from this study identify differences among sand, shell, and reef communities over the inner continental shelf of the GOM. In addition, differences in biotic communities, diversity indices, size structure, and habitat characteristics between similar habitats in trawled and non-trawled areas indicates that the presence of trawling significantly impacts the benthic ecosystem.

Differences in habitat use by fishes and invertebrates over sand, shell, and reef habitats indicate that these habitats provide unique qualities to their associated communities. Several species showed consistent habitat use patterns regardless of exposure to trawling. The longspine porgy, dwarf sand perch, and Atlantic croaker were more abundant over sand habitat, both outside and within the non-trawled area. The longspine porgy and Atlantic croaker have been characterized previously as the most abundant demersal fish species over sand and mud habitats on the northern GOM continental shelf (Moore et al. 1970, Chittenden and McEachran 1976, Chittenden and Moore 1977). In addition, dwarf sand perch collections in previous studies suggest this species primarily occupies sand and mud habitats (Fraser 1971, Bortone et al. 1981). The pinfish and bank sea bass displayed an affinity toward shell habitats in both the trawled and non-trawled areas. Juvenile pinfish are primarily found in estuarine habitats, but larger adults are found in offshore waters (Nelson 2002). Information pertaining to the habitat preferences of pinfish on the continental shelf is limited; however, Jordan et al. (1996) found habitat selection by pinfish of structurally complex seagrass beds was a function of behaviorally mediated predator avoidance. Thus, structural complexity of

shell rubble may explain the abundance of pinfish on the shallow GOM shelf. This may also be true of bank sea bass that have a preference for hard bottom habitats, such as shell rubble (Robins and Ray 1986, Hoese and Moore 1998). Numerically, red snapper displayed an affinity for reef habitats both outside and within the non-trawled areas. The reef located outside of the non-trawled area also was likely not exposed to trawling; nevertheless, my results support other studies demonstrating the affinity of red snapper for structured habitats at the sizes such as those sampled during my study (average 155.1 mm TL \pm 2.0) (Moseley 1966, Bradley and Bryan 1975).

The effects of trawling on benthic communities affected the species composition over sand and shell habitats. Several representative species consistently abundant over trawled areas share similar life history characteristics of small sizes, short life spans, high mortalities, and rapid biomass turnover (DeVries and Chittenden 1982, Geoghegan and Chittenden 1982, Murphy and Chittenden 1991, McEachran and Fechhelm 1998). These species included longspine porgy, silver seatrout, largescale lizardfish, and gulf butterfish. My findings are consistent with Chittenden (1977) in that these abundant species found over brown and white shrimp grounds in the GOM exhibit life history characteristics that are typical of species that are adapted to environments that exhibit frequent perturbations. In addition, disturbance theory predicts short-lived, highly motile species, with high rates of reproduction will recover faster than long-lived, sessile, and low dispersal species (Pickett and White 1995). As such, my results are consistent with life-history theory and further define the effects of trawling on fish community dynamics.

Differences in the invertebrate community were defined by the combination both of habitat type and the effects of exposure to trawling. Several of the species frequently collected over non-trawled areas of shell and reef habitat with more structural complexity

were sedentary and sessile species relative to those collected over trawled areas. Two brittlestars (*O. appressum* and *O. elegans*), a sea star (*L. clathrata*), urchin (*A. punctulata*), hairy sponge crab (*D. antillensis*), shortfinger neck crab (*P. sidneyi*), and the brown rock shrimp (*Sicyonia breverostris*) were more abundant over the structurally complex non-trawled areas. The brittlestars, sea star, and urchin are common over flat sand habitats, but were likely in low abundance in trawled areas due to their high vulnerability to active fishing gears that sweep the bottom. The hairy sponge crab is commonly found in offshore reef habitat with sponges attached to the carapace, the shortfinger neck crab is found in association with reefs and rocky outcroppings, and the rock shrimp is found over shell bottom habitats (Williams 1984). In contrast, two portunid crabs (*C. similis* and *P. spinimanus*) and the brown shrimp (*F. aztecus*) were more commonly observed in areas exposed to trawling. The portunid crabs mobility may enable these species to escape from active fishing gears. In addition, the life history characteristics of the brown shrimp are similar to the finfish that were abundant over trawled areas; short life spans, high mortalities, and rapid biomass turnover (St. Amant et al. 1966, Lassuy 1983), which may explain their abundance over trawled sand habitat.

The use of an artificial reef permit area as a *de facto* non-trawl area required two assumptions. First, that trawling did not occur within this area, which is supported by both Link (1997), who suggested that these reef permit areas added a significant amount of untrawable area to the northern GOM shelf, and by the distributional shrimp trawl effort, which shows the extensive effort in the trawled area and little to no effort in the non-trawled area (NRC 2002). Second, the presence of the artificial reefs did not directly affect the fish and invertebrate communities in my study. The 28 species analyzed for

community comparisons were not composed of reef-dependent species; rather the species I selected for analysis were found over all habitat types, albeit in different densities.

Patterns observed in this study are consistent with conceptual models that contend that fishing disturbance reduces species diversity, evenness, and richness, and leads to an increase in one or a few numerically dominant small and fast growing species (Hall 1999). These patterns were temporally consistent over more complex shell rubble habitat type, whereas the sand habitat showed opposite trends in the diversity indices. My results are thus consistent with the findings that more complex habitats are more sensitive to effects of fishing activities and result in reductions in habitat complexity which can lead to increased predation on species relying on the structure, or indirectly on other organisms that create the structures (e.g. ecosystem engineers) (Auster et al. 1996, Auster 1998, Coleman and Williams 2002, NRC 2002). Sainsbury et al. (1997) found that a loss of the structural epibenthic community resulted in a shift from snapper (Lutjanidae) and emperor (Lethrinidae) fishes toward one dominated by lizardfish (Synodontidae) and bream (Nemipteridae). The reduction in bryozoans, tubeworms, and the shell ridge features in the trawled shell area I studied likely contributed to the differences I observed between trawled and non-trawled shell habitats. In addition, Collie et al. (2000) reported that sandy bottom communities were much more resilient to disturbance events and concluded that 2-3 physical disturbance events per year could occur without any major changes in the community composition. Based upon my calculation of trawling effort, at least one disturbance event per year was possible in my study sites, which may explain the diversity of the trawled sand community.

Diversity indices in this study indicate shell habitats support diverse fish and invertebrate communities over the shallow inner continental shelf of the northern GOM.

My comparisons among sand, shell, and reef were chosen because these habitats comprise the majority of habitats on the northern GOM inner shelf (Ludwick 1964, Parker et al. 1983, Schroeder et al. 1988, Kennicutt et al. 1995, Dufrene 2005). My diversity estimates are similar to other studies that have investigated benthic communities in the northern GOM. Chittenden and McEachran (1976) found diversity and evenness values over sand habitats on the NW GOM inner shelf ranging from 0.892 to 2.586 and 0.293 to 0.937, respectively. In addition, Chittenden and Moore (1977) found an average diversity of 2.616 over the 110-m bathymetric contour of the NW GOM. The diversity estimates from this study are likely a function of gear type because reef habitat was found to have the highest diversity, evenness, and richness in the same areas studied using an underwater video camera array (Chapter 2). However, other studies characterizing offshore reef fish communities in the GOM have reported higher values than the indices reported in this study (Smith et al. 1975, Dennis and Bright 1988, Rezak et al. 1990, Rooker et al. 1997, Gledhill 2001). The use of otter trawls to sample the reef community influenced my results because I sampled along the edges of the reef structure in an attempt to minimize trawling impacts on sensitive members of the reef community, such as corals and sponges. Thus, the combination of using multiple gear types such as underwater video and otter trawls to identify the large mobile species as well as the small cryptic species may provide the best estimate of species diversity.

My results suggest that trawling also is size-selective, which could further exacerbate negative impacts on the GOM fish community. Truncated size distributions and reduced median sizes of the species in this study suggest differential mortality of larger individuals due to the size selectivity of the fishing gear. Smaller individuals are likely pushed aside by the pressure wave created by the trawl or passed through the mesh

of the net, thereby experiencing reduced trawl induced mortality (Gilkinson et al. 1998, Blanchard et al. 2004). Decreases in the biomass of demersal fish and invertebrate fauna have been attributed to trawling and dredging in other studies (Bianchi et al. 2000, Zwanenburg 2000, Duplisea et al. 2002). However, this study was unique in that differences existed in the length distributions for 8 of the 9 species selected because of their numerical abundance as bycatch. These species are among the most abundant species collected as bycatch in the shrimp trawl fishery in the GOM (Chittenden and McEachran 1976, Nichols et al. 1990). Additionally, some of these species have short lifespans (see Table 3.6), and fishing induced size truncation may favor genotypes with slower growth, earlier age at maturity, and an overall decrease in population productivity (Conover and Munch 2002).

The Atlantic croaker was the only species that did not show a size difference between trawled and non-trawled areas, regardless of habitat. These results are consistent with Diamond et al. (1999) who showed severe declines in the abundance of GOM Atlantic croaker have occurred since the 1930s, but no changes have been found in life history parameters, such as the size distribution, maximum size, and size at maturity. In contrast, Atlantic croaker have declined in abundance in the Atlantic and life history parameter changes have occurred, including a reduction in maximum size, size at maturity, and size distribution. These changes were attributed both to the effects of bycatch on the juveniles and the intense fishing pressure on adults (Diamond et al. 1999). Currently, there are no directed commercial or recreational fisheries for Atlantic croaker in the GOM, although they are landed in small numbers by recreational anglers targeting other species.

Alternative management strategies such as area closures over shell rubble and surrounding sand habitats in the northern GOM may have species-specific and ecosystem wide benefits. My results describe the effects that trawling has on epibenthos (i.e. tubeworms, bryozoans, anemones, corals, and algae) and associated fish and invertebrate community compositions, diversities, and size distributions. Of the 21 statistical subareas in the GOM, as defined by the NMFS, there are 11 million hectares of seafloor with depths less than 64 m. Of this area, only 185,000 hectares, or 1.68% has been estimated as untrawable bottom due to hangs, petroleum platforms, and artificial reef permit areas (Link 1997). To date, no habitats exposed to trawling have been closed in the GOM to assess the impacts on the benthic ecosystem. Studies in the North Atlantic, North Pacific, and the North Sea over closed areas have been valuable in quantifying the effects of fishing on the benthic communities (Auster et al. 1996, Freese et al. 1999, Piet and Jennings 2005). Similar studies in the GOM would prove beneficial to provide management with knowledge of the ecosystem effects of fishing, beyond single-species effects. I acknowledge that using only area closures may be insufficient as a management tool, and that effort reductions (bycatch quotas) will also be needed to offset the effects of displaced fishing efforts in open fishing areas.

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CHAPTER 4: TRAWLING EFFECTS AND HABITAT SELECTION ON LIFE HISTORY PARAMETERS OF GULF OF MEXICO RED SNAPPER

Introduction

Estimates of biological reference points (e.g. B_{CUR}/B_{MSY} , F_{CUR}/F_{MSY}) indicate that Gulf of Mexico (GOM) red snapper (*Lutjanus campechanus*) are overfished and are currently experiencing overfishing (GMFMC 2005). The primary impediment to the recovery of GOM red snapper is high levels of bycatch of age 0 and age 1 individuals in shrimp trawls (Goodyear 1995, Schirripa and Legault 1999). An estimated 25-30 million age 0 and age 1 red snapper are caught annually in shrimp trawls (Ortiz et al. 2000) and estimates indicate shrimp trawl bycatch may account for as much as 90% of juvenile red snapper mortality (Goodyear and Phares 1990, Goodyear 1995). As a result, bycatch reduction devices (BRDs) became mandatory in the western GOM in 1998, and extended to the eastern GOM in 2004, to decrease bycatch of juvenile red snapper by shrimp trawlers. Bycatch reduction devices were expected to reduce bycatch mortality by more than 50% (GMFMC 1996) with survival of excluded juveniles assumed to be 100%. However, concerns about the effectiveness of BRDs have arisen due to low numbers of individuals excluded (10-20%) (Foster and Scott-Denton 2004), and high post-exclusion mortality of juveniles (Gallaway et al. 1998). Low survival of excluded juvenile fishes is attributed to increased predation by larger fishes and marine mammals, physiological stress, embolism, and species displacement from their habitat (Main and Sangster 1988, DeAlteris and Reifsteck 1993, Broadhurst 1998, UGA Marine Extension Service and NMFS Harvesting Branch 2003).

Studies characterizing habitat preferences of age 0 red snapper indicate juveniles are not randomly distributed on shrimp grounds, and that age 0 red snapper prefer low-relief structure, such as shell-rubble habitat (Workman and Foster 1994, Szedlmayer and

Howe 1997, Szedlmayer and Conti 1999). In addition, natural hard bottom habitats such as reef pinnacles, shelf-edge banks, and ledges have been shown to be important habitat for adult red snapper and other reef fishes (Parker et al. 1983, Schroeder et al. 1988). Little information exists regarding these natural reefs due to misconceptions that little natural hard bottom habitat exists on the shallow (<40 m) northern GOM shelf. As a result, most studies have focused upon mud, sand, shell, and artificial reefs as habitat for red snapper (Moseley 1966, Bradley and Bryan 1975, Holt and Arnold 1982, Workman and Foster 1994, Szedlmayer and Howe 1997, Szedlmayer and Conti 1999, Rooker et al. 2004, Patterson et al. 2005). Despite the potential importance of natural reef habitat for red snapper in the northern GOM, no studies have adequately addressed the role these habitats play in the life history of red snapper.

Habitat-mediated processes in the post-settlement survival of continental shelf fish species have received increasing attention (Eggleston 1995, Tupper and Boutilier 1995, Thrush et al. 2002, Rooker et al. 2004). Habitat selection has been shown to be influenced by predation pressure and prey availability (Hixon and Beets 1989, Auster et al. 1997), physiological constraints (Allen and Baltz 1997, Kupschus and Tremain 2001), and physical processes (Boehlert and Mundy 1988). Habitat quality can be indexed as a function of the growth of organisms when natural mortality is size, hence growth-rate, dependent (Houde 1987, Sogard 1997). An assumption in my approach is that faster growing juveniles have lower mortality rates due to reduced exposure time to predators (Cowan et al. 1996). Therefore, it is advantageous to utilize high quality habitats that provide greater foraging and growth opportunities, resulting in an enhanced probability of survival. Thus, habitats that both support a disproportionately high number of rapidly

growing juveniles and contribute to higher potential survivorship (i.e. high G:Z ratios) need to be identified, and perhaps protected.

Reductions in habitat complexity by trawling affects target and non-target species and can ultimately influence recruitment to harvestable stocks (Auster et al. 1996, NRC 2002). Of particular importance is the threat to the survival of juvenile red snapper in the GOM. The GOM trawl fishery targets shrimp on soft-sediment habitats that are assumed to be of low structural complexity and species diversity. However, these habitats both support a high diversity of organisms that play key roles in the balance of the ecosystem (Arreguin-Sanchez et al. 2004) and provide important prey resources for red snapper (Bradley and Bryan 1975, Davis 1975, Futch and Bruger 1976, Lee 1998, McCawley 2003). Additionally, trawling in the northern GOM is not confined to soft-sediments, and often affects more complex habitats. Auster (1998) identified habitats such as biogenic structures and shell aggregates as some of the most susceptible to severe adverse impacts of trawling. Thus, there is a need to identify the habitat-specific effects shrimp trawls have on the life history parameters of bycatch species, including red snapper.

To increase the spawning stock biomass of adult red snapper, reductions in juvenile bycatch by shrimp trawls appears to be warranted. It has been proposed that a technological solution to bycatch reduction may not exist, and the addition of shrimp non-trawl areas or time closures may be needed to be implemented by fisheries management to provide additional protection for juvenile red snapper from trawls (Gallaway et al. 1999, Patterson et al. 2005). However, before these management strategies can be implemented, studies addressing the functional importance of different habitats (i.e., differential growth rates and production potential) for juvenile red snapper are necessary.

The purpose of this study was to characterize ontogenetic habitat use of red snapper utilizing natural substrates on the GOM inner continental shelf in areas that have historically supported high concentrations of red snapper. Specifically, I investigated habitat use over sand, low shell-rubble, high shell-rubble, and natural hard bottom reefs. In addition, my goal was to assess habitat-specific effects shrimp trawling has on red snapper density, demographics and vital rates, such as size, growth rate, mortality rate, and production potential. I focused on sand and low shell-rubble habitats to quantify the effects of trawling.

Methods and Materials

Study Sites

My study region lies on the northern GOM continental shelf, where the largest artificial reef complex in the United States exists, covering over 4,000 km² (Shipp 1999) (Figure 4.1). These reef zones also serve as *de facto* non-trawl areas (Link 1997) that are in close proximity to sampling locations exposed to trawling. While limited trawling may occur within the artificial reef zones, sampling effort outside the zones is orders of magnitude greater (NRC 2002).

Seabed characterization of the region inside and outside of the permit areas was recently performed with digital sidescan sonar and box core sediment analysis during previous studies (Dufrene 2005, Patterson et al. 2005, Strelcheck et al. 2005). Four different habitat types were examined: sand sites with interspersed mud, low relief (<1 m) shell-rubble sites (<40% CaCO₃), high relief (1-3 m) shell-rubble sites (>40% CaCO₃) and natural hard bottom high-relief (>2 m) reef sites (Figure 4.1). One approximately 8 km² study area of each habitat type was selected inside the reef permit area (non-trawled sites) and outside of the permit area (trawled sites) to compare the effect of trawling.

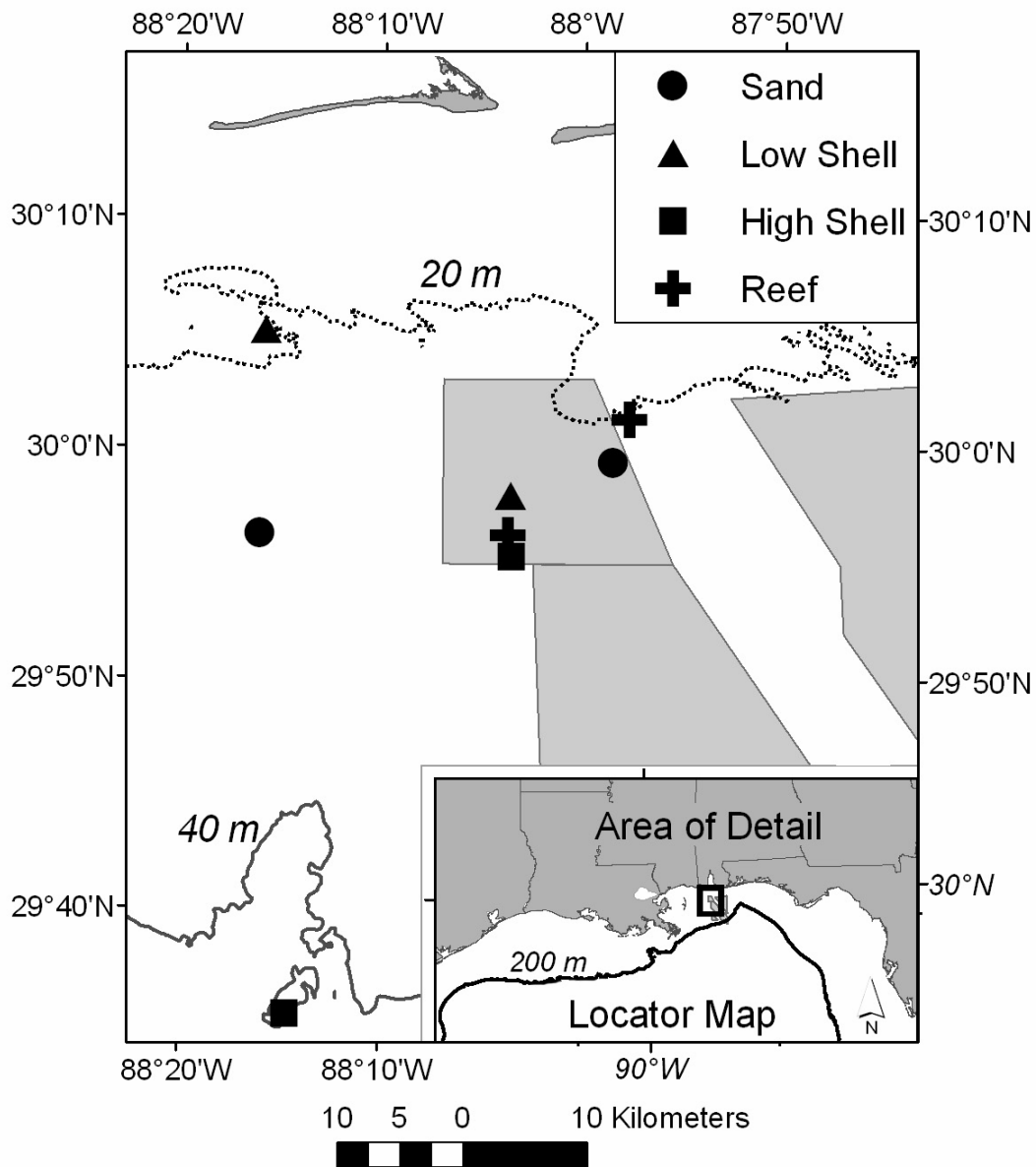


Figure 4.1. Map of the study site locations in the northcentral GOM. The 20- and 40-m depth contours are shown with the 200-m depth contour representing the shelf edge. Enclosed shaded regions indicate the *de facto* non-trawl areas inside the Alabama artificial reef permit areas. The Hugh Swingle Artificial Reef Permit Area represents the shaded region my study sites are enclosed within.

However, due to the lack of trawling that takes place on the hard bottom reef sites, my trawl comparisons were limited to sand and shell-rubble habitats. Lastly, shrimp trawling effort was conservatively calculated for my study area and showed sufficient trawling effort occurred during each year of my study to sweep the entire area at least once per year (Chapter 3).

Shell-rubble ridges in my study area were relict oyster reefs formed prior to the Holocene transgression (Schroeder et al. 1988, Dufrene 2005). Ridges were oriented in a northwest to southeast direction, and extended for several kilometers in length with widths averaging 100 m (Dufrene 2005) (Figure 4.2). The distances between the ridges within each sidescanned 8 km² area varied from 100s of m to over a km and are thought to be part of the Perdido shoals on the eastern Alabama-Florida continental shelf (Dufrene 2005). McBride et al. (1999) described the Perdido shoals over the mid-shelf as two long (30-120 km) and relatively narrow (<6 km) parallel shore features.

Field Sampling

Trawl sampling was conducted quarterly in 2004 and 2005 onboard the R/V *Caretta*, an 18-m research vessel operated by NOAA Fisheries Pascagoula, Mississippi laboratory (hereafter NMFS). Each of the 8 km² area sites was divided into ten stations measuring approximately 1 km in length and 200 m in width. Three of the ten stations in each area were randomly selected for trawl samplings; stations were fixed for the duration of the study and were towed at slightly different positions to avoid repeatedly sampling the same transect. All stations were trawled in a northwest to southeast direction and remained on the habitat of interest. Trawls were towed along the edges of the natural hard bottom reefs so that damage to the immobile biological fauna (i.e. corals) was minimized. In addition, the vessel position was overlain onto bathymetric

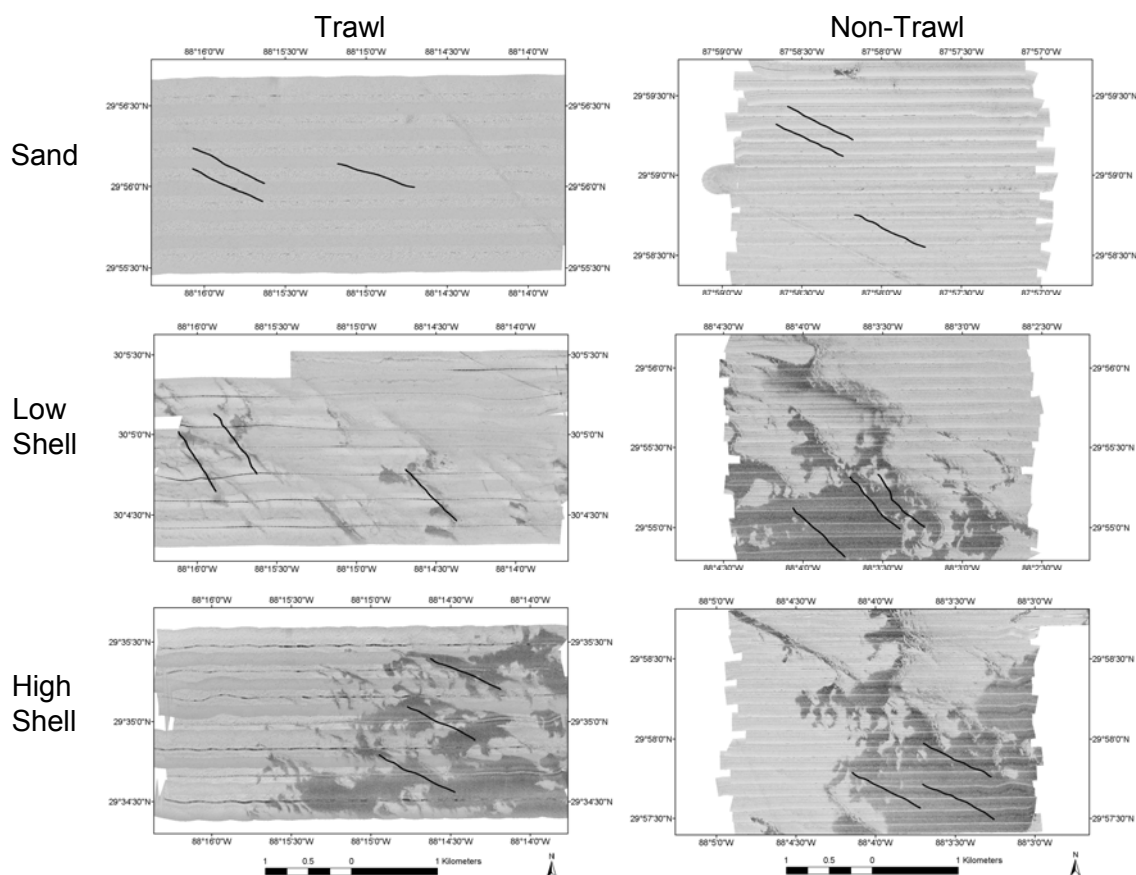


Figure 4.2. Sidescan mosaics with bathymetry overlaid for the sand, low shell-rubble, and high shell-rubble sites both within the area exposed to trawling and in the *de facto* non-trawl area. Track lines from trawls are shown as black lines. Darker areas of the mosaics with high reflectance represent shell substrate while lighter areas represent sand and mud.

sidescan mosaics in ArcPad 6.0 for continuous GPS tracking of trawl position, and to aid in navigation. Standard NMFS Fall Groundfish Survey trawl gear was used (FGS; SEAMAP Information System, NMFS, Pascagoula, MS), which included a single 12.8-m wide otter trawl with 4 cm mesh size, towed at approximately 4.6 km h^{-1} for 10 min sample⁻¹. An addition to the standard SEAMAP trawl was a 0.7 cm cod end lining to increase capture efficiencies for smaller individuals. Trawl sampling occurred only during daylight hours (30 min after sunrise and 30 min before sunset). Baited traps also were used to collect red snapper over all habitats, particularly the reef, since trawling directly over the reef structure itself was not possible. A chevron trap (dimensions: 150 cm width x 180 cm length x 60 cm height, opening: 10 cm x 5 cm, mesh: 3.8 cm plastic coated wire) designed to capture large individuals and two small fish traps (dimensions: 64 cm width x 60 cm length x 43 cm height, mesh: 2.2 cm plastic coated wire) that targeted juveniles were soaked at a fixed location at each site for a two hour period. Traps were deployed adjacent to my trawl locations and were randomly chosen within the same 8 km^2 area that was sidescanned at each site. All red snapper were immediately frozen and taken back to the laboratory. Fish were measured to the nearest mm total length (TL) and weighed to the nearest g. Water mass characteristics (salinity, temperature, depth, dissolved oxygen, and optical backscatter) were measured at each site with a SeaBird SBE-25 conductivity-temperature-depth (CTD) instrument.

Otolith Analysis

Sagittal otoliths of red snapper collected at each habitat were used for age estimates. A subsample ($n=25$ if available) from each habitat during each quarter was selected so that the entire size range from trawl and trap surveys were included in my age estimates. Due to the large size range of red snapper collected, either daily or annual

increment analysis was performed depending on fish size and time of year. Left or right sagittal otoliths were randomly selected and measured to the nearest 0.001 mm and weighed to the nearest 0.0001 g. Otoliths for daily age estimates were mounted in epoxy resin and transversely cut with a low-speed Isomet saw. Thin sections of the otoliths were then attached to slides with thermoplastic cement, polished to the core with 600- and 400-grit sandpaper, and then polished with type A alumina powder (0.3 μ m). Daily ages were determined by counting growth increments along the sulcus from the core to the outer margin on an Olympus BH-2 microscope with Image-Pro Plus 4.5.1 analysis software. Due to the difficulty in estimating daily ages of red snapper larger than 150 mm TL, only red snapper less than this size were used for daily increment analysis. Two readers independently counted increments of a random subsample of red snapper otoliths. Subsamples represented 27% and 20% of year 2004 and 2005 daily otoliths, respectively.

Annual age estimates were determined by counting the number of opaque rings from the core to the outer margin. Otoliths were processed and read following the methods of Cowan et al. (1995). The red snapper birthdate was assumed to be July 1, and age was determined following Patterson et al. (2001). A large number of red snapper ages were classified as 0.5+, representing six months to one year of age. These fish were too old to obtain accurate daily ages but were not yet 365 days old; thus, 0.5+ represents an age between 180 days and 1 year.

Growth and Mortality

Growth rates of age 0 red snapper were estimated from slopes of linear regressions using daily otolith-derived ages. Habitat-specific growth comparisons were performed from winter and fall samples because sufficient sample sizes of age 0 red snapper were collected over most habitats. Growth analyses were not made across

seasons due both to the seasonal temperature differences and the disproportionate numbers of red snapper collected over different seasons and habitat types. Mortality estimates of red snapper were derived from regressions of \log_e -transformed abundance at age in a catch curve. Instantaneous daily mortality rates of juvenile red snapper were estimated by using an exponential model of decline in numbers at age (Rooker et al. 1999, Wells and Rooker 2004). Mortality estimates were based upon 5-day cohort groupings over the age range in which a descending catch curve was observed. An ascending catch curve was observed for young red snapper (<140 d) and only a small number of older red snapper (>200 d) were collected due to both gear avoidance and emigration. Thus, red snapper between 140 and 200 days of age from sand and low shell-rubble sites were used to obtain mortality estimates. Red snapper mortality estimates over the sand were based upon 2005 trawl survey data and red snapper mortality estimates over the low shell-rubble were based upon 2004 trawl data due to sufficient sample sizes over the age range examined. Survival estimates were obtained using survival (S) = $1 - e^{(-Zt)}$, where t is the 61-day period that mortality rates were calculated.

Mortality estimates were based upon the assumptions that equal immigration and emigration took place on the habitats of interest, and that the only difference between sites was the presence of trawling. The age range used for mortality estimates was most frequently observed over the sand and low shell-rubble habitat types suggesting that these were the preferred habitats at this life stage, and that size-based gear avoidance was negligible. In addition, I limited my comparisons to similar habitat types (sand and low shell-rubble) that were and were not likely exposed to trawling, and did not compare among habitat types due to habitat-specific life stage utilization. Red snapper mortality

rates over high shell-rubble trawled and non-trawled areas were not estimated due to the small number of red snapper collected at my trawled site.

Production Potential

The ratio of the weight-specific growth coefficient (G) to the instantaneous mortality coefficient (Z) was used to index habitat-specific and life-stage-specific production potential. The incorporation of both G and Z allows these to be used to assess stage-specific productivity. Cohorts of red snapper with G:Z ratios less than one lose biomass whereas those with G:Z ratios greater than one gain biomass and have higher survivorship and production potential (Cowan and Houde 1990, Houde 1996, Rooker et al. 1999). In addition, my habitat-specific G and Z estimates were incorporated into the Ricker (1975) production model to calculate production to biomass ratios (P:B ratios).

Production and biomass relationships were calculated using the following:

$$\bar{B} = \frac{(B_o [e^{(G-Z)} - 1])}{G - Z}$$

$$P = G \bar{B}$$

where \bar{B} is the mean biomass over the time interval, B_o is the initial biomass, and P is the production estimate. Habitat-specific biomass estimates were derived from red snapper weight per unit area calculations.

The G:Z and P:B ratios were calculated for red snapper collected over trawled and non-trawled sand and low shell-rubble habitats to assess differences in the production potential that may be attributable to trawling.

Data Analysis

Differences in densities of red snapper from the trawl surveys were assessed with a block designed four-way factorial analysis of variance (ANOVA) with habitat, season,

the presence or absence of trawling, and age group as the factors, and year (2004 and 2005) as the block. Age 0 fish were classified as individuals less than 180 d, age 0.5+ were between 180 and 364 d, age 1 were 365-729 d, age 2 were 730-1094, and age 3+ fish were equal to or greater than 1095 d. Similarly, trap surveys were analyzed with a four-way factorial ANOVA including habitat, season, the presence or absence of trawling, and trap type as the fourth factor. Red snapper abundances were $\log_e (x+1)$ transformed to normalize data and to reduce heteroscedasticity. *A posteriori* differences among means were detected with Tukey's (HSD) test with an alpha level at 0.05.

Daily growth was modeled for all aged red snapper with a von Bertalanffy growth equation with Proc NLIN (SAS Institute, Inc. 2006). This equation was used to estimate ages of all red snapper that were not aged with otolith based techniques so that age-specific density differences and mortality estimates based on an exponential model of decline could be obtained. Length-at-age data were also fit with other models (i.e. linear, logistic), but the percent variation in length explained by age was maximized with the von Bertalanffy.

Length differences among habitats and between trawled and non-trawled areas of similar habitats (using only the otter trawl data) were analyzed with a two-factor analysis of covariance (ANCOVA) (factors: habitat, presence of trawling), with collection date as the covariate.

Analysis of covariance models were also used to test for differences in growth and mortality of age 0 red snapper, with age as the covariate. Growth rates (slope) and initial size-at-age (y-intercept) were used to test for growth differences, and mortality rates (slope) were used to compare mortality differences of fish collected from trawled versus non-trawled sand and low shell-rubble.

Results

Water mass characteristics were similar among habitats, and did not vary due to exposure to trawling within each quarter sampled (Table 4.1). Low dissolved oxygen (1.76 mg/L, which is characterized as hypoxic (<2mg/L)) was observed during the summer cruise in 2004.

A total of 1,712 red snapper was collected by trawl and trap methodology over the two year study period. These methods were successful in collecting red snapper between 23 and 435 mm TL, with ages ranging from 28 days to 5 years.

Density

Red snapper densities increased with age over higher relief habitats (e.g. high relief shell-rubble and reef), and were higher over non-trawled areas; however, differences were age-specific (Figure 4.3). Red snapper densities were significantly affected by habitat type (ANOVA; $F_{3,711}=6.56$, $P=0.0002$), the exposure to trawling (ANOVA; $F_{1,710}=6.53$, $P=0.0108$), and age group (ANOVA; $F_{4,710}=30.25$, $P<0.0001$). Seasonal differences were not significantly different (ANOVA; $F_{3,708}=2.20$, $P=0.0866$), thus age-specific *post-hoc* density comparisons were analyzed with both habitat and the exposure to trawling as factors. A significant habitat effect was observed for age 1 red snapper (ANOVA; $F_{3,166}=3.71$, $P=0.0128$) (habitat x trawl interaction $P=0.176$), with significantly higher densities associated with reef (2.65 fish ha⁻¹) versus sand (0.16 fish ha⁻¹) habitat ($P=0.0135$). In addition, a significant trawling effect was observed for age 0.5+ red snapper (ANOVA; $F_{1,165}=6.63$, $P=0.0109$) (habitat x trawl interaction $P=0.2352$) with higher densities over non-trawled areas (5.41 fish ha⁻¹) relative to areas exposed to trawling (2.69 fish ha⁻¹). However, pairwise density differences of red snapper collected from trawled versus non-trawled areas of similar habitats were not significant.

Table 4.1. Bottom water mass characteristics at each site on quarterly surveys during 2004 and 2005. Variables include temperature, salinity, and dissolved oxygen (DO). NT=non-trawl. T=trawl.

		Winter 2004	Spring 2004	Summer 2004	Fall 2004	Winter 2005	Spring 2005	Summer 2005	Fall 2005
<u>Temperature (°C)</u>									
Habitat	NT Sand	18.62	21.08	22.34	25.78	19.25	20.38	25.81	24.21
	T Sand		19.91	22.85	23.11	20.10	20.20	26.28	25.47
	NT Shell-low	17.92	20.55	22.56	27.04	20.76	20.47	26.13	25.23
	T Shell-low		22.21	23.46	25.98	20.10	20.20	25.92	24.18
	NT Shell-high	18.05	20.74	22.90	26.74	20.76	20.20	25.83	24.74
	T Shell-high		19.52	20.72	28.13			26.06	
	NT Reef	17.98	20.56	22.51	26.48	19.80	20.55	25.92	25.02
	T Reef	18.72	24.38	24.01	25.95	18.10	20.31	25.99	
<u>Salinity (ppt)</u>									
Habitat	NT Sand	35.73	35.01	36.18	35.80	35.21	35.91	35.50	34.65
	T Sand		35.18	36.34	36.27	35.61	36.28	35.76	35.43
	NT Shell-low	35.51	35.17	36.11	36.33	35.68	35.94	35.45	35.33
	T Shell-low		34.20	35.98	35.52	35.61	36.28	35.44	34.70
	NT Shell-high	35.49	35.13	36.06	36.29	35.68	36.28	35.47	35.01
	T Shell-high		35.73	36.39	36.24			35.77	
	NT Reef	35.50	35.15	36.13	36.27	35.47	35.98	35.46	35.25
	T Reef	35.56	34.63	35.95	35.32	34.45	35.47	35.47	
<u>DO (mg/L)</u>									
Habitat	NT Sand	7.78	7.45	1.76	4.65	6.37	3.57	4.53	6.15
	T Sand		6.54	4.18	4.92	5.93	3.67	5.30	5.91
	NT Shell-low	7.82	7.25	3.35	5.73	5.94	3.97	4.92	6.01
	T Shell-low		7.02	3.30	3.85	5.93	3.67	4.82	6.15
	NT Shell-high	7.79	7.13	3.61	5.20	5.94	3.67	4.41	6.09
	T Shell-high		6.33	5.01	5.82			5.44	
	NT Reef	7.94	7.29	2.93	5.16	6.30	4.10	4.65	6.09
	T Reef	7.85	6.92	4.56	5.35	6.72	3.90	4.87	

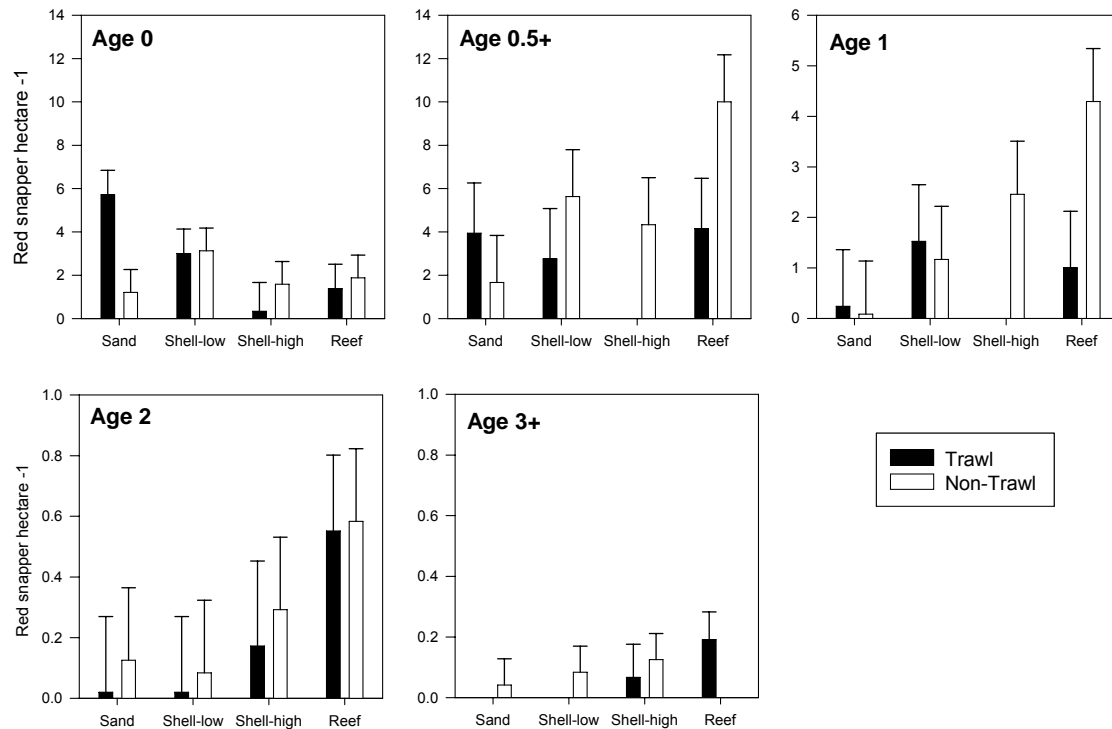


Figure 4.3. Age-specific density estimates (± 1 SE) of red snapper collected using trawls. Black bars represent habitats exposed to trawling and white bars represent habitats not exposed to trawling. Note that the magnitude of the ordinate differs with age due to the low number of older individuals collected using trawls.

Numbers of red snapper collected with traps varied as a function of habitat, exposure to trawling, season, and trap type. Significant interactions occurred among main effect variables (habitat x trawl x season x trap: $P=0.0052$). Significant differences also existed for main effects: habitat (ANOVA; $F_{3,47}=11.37$, $P<0.0001$), trawl (ANOVA; $F_{1,48}=6.00$, $P=0.0180$), and trap (ANOVA; $F_{2,47}=3.75$, $P=0.0309$). Highest red snapper numbers were collected with the chevron trap over the reef habitat in the trawled area. The average reef x trawl x chevron trap density was 9.4 fish hr^{-1} soak period (ranging from 0 in the winter to 20.3 in the fall).

Size

Red snapper size frequency distributions correlated well with age-specific density estimates, indicative of an ontogenetic habitat shift from low relief to higher relief habitats with size and age. Habitat-specific size-frequency distributions varied among seasons (Figure 4.4). A significant habitat effect was detected (ANCOVA; $P<0.0001$), with the smallest red snapper observed over sand habitat (LS mean= 111.9 ± 3.5 mm TL), particularly during summer and fall. *Post-hoc* differences among habitats indicated red snapper were significantly smaller over trawled sand (LS mean= 96.1 ± 3.3 mm TL) than over trawled low shell-rubble ($P<0.0001$; LS mean= 127.0 ± 4.3 mm TL) and reef habitats ($P<0.0001$; LS mean= 172.3 ± 7.9 mm TL). Red snapper collected over non-trawled sand (LS mean= 127.8 ± 6.1 mm TL) were significantly smaller than those over non-trawled high shell-rubble ($P<0.0001$; LS mean= 166.0 ± 3.2 mm TL) and reef habitats ($P<0.0001$; LS mean= 158.1 ± 2.3 mm TL). Red snapper between 50 and 200 mm TL (LS mean= 133.5 ± 2.6 mm TL) were consistently collected over the low shell-rubble in all seasons, while the 100-250 mm TL (LS mean= 143.4 ± 11.8 mm TL) size range was collected over the high shell-rubble. The largest red snapper were found over reef

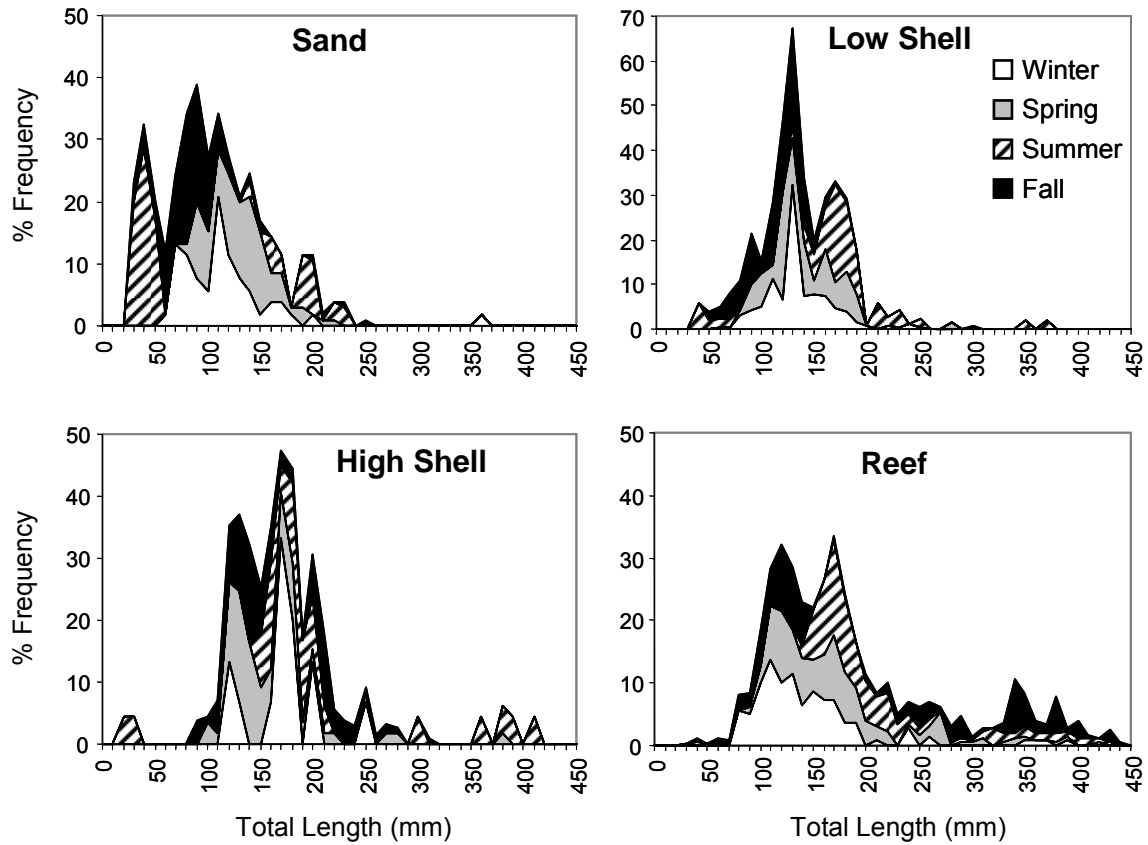


Figure 4.4. Cumulative size-frequency distributions of red snapper collected using trawls by habitat and season.

habitat, where red snapper above 300 mm TL (LS mean=165.2 \pm 4.1 mm TL) were frequently captured (Figure 4.4). Pairwise comparisons among habitats indicated that red snapper were significantly larger on reefs than over both sand and low shell-rubble habitats in the trawled and non-trawled areas ($P < 0.0001$).

Red snapper were significantly larger on non-trawled habitats than over similar trawled habitats (ANCOVA; $P = 0.0119$) (Figure 4.5). Specifically, sand and low shell-rubble were the two habitats investigated for *post-hoc* trawl effects, and both were significant (sand: $P < 0.0001$; low shell: $P = 0.0120$). Average TL (\pm SE) of red snapper collected over non-trawled and trawled sand were 127.8 \pm 6.1 and 96.1 \pm 3.3, respectively, and those over non-trawled and trawled low shell-rubble were 140.1 \pm 2.9 and 126.9 \pm 4.3, respectively. The average TL of red snapper collected over non-trawled high shell-rubble was larger than in the trawled area, but the low sample size ($n = 12$) collected in the trawled area precluded statistical significance ($P = 0.5375$).

Age and Growth

A total of 942 (55%) red snapper collected in my study was aged; daily ages were obtained for 377 (40% of aged fish) and annual age estimates were obtained for 565 red snapper (60% of aged fish). Agreement between readers of red snapper daily otolith counts was high (2004: Reader 1 age = 0.95 x Reader 2 age + 12.72, $r^2 = 0.91$; 2005: Reader 1 age = 0.93 x Reader 2 age + 5.16, $r^2 = 0.93$). In addition, annual age estimates differed for only 4.4% of the readings. Differences in the annulus counts were evaluated by the coefficient of variation (CV), index of precision (D), and average percent error (APE). Due to the low variability between reader counts (CV=0.011, D = 0.008, APE=0.500), annulus counts by reader one were used. Thus, the more experienced reader (reader one) was used to age the remaining otoliths and all counts were repeated at least twice to

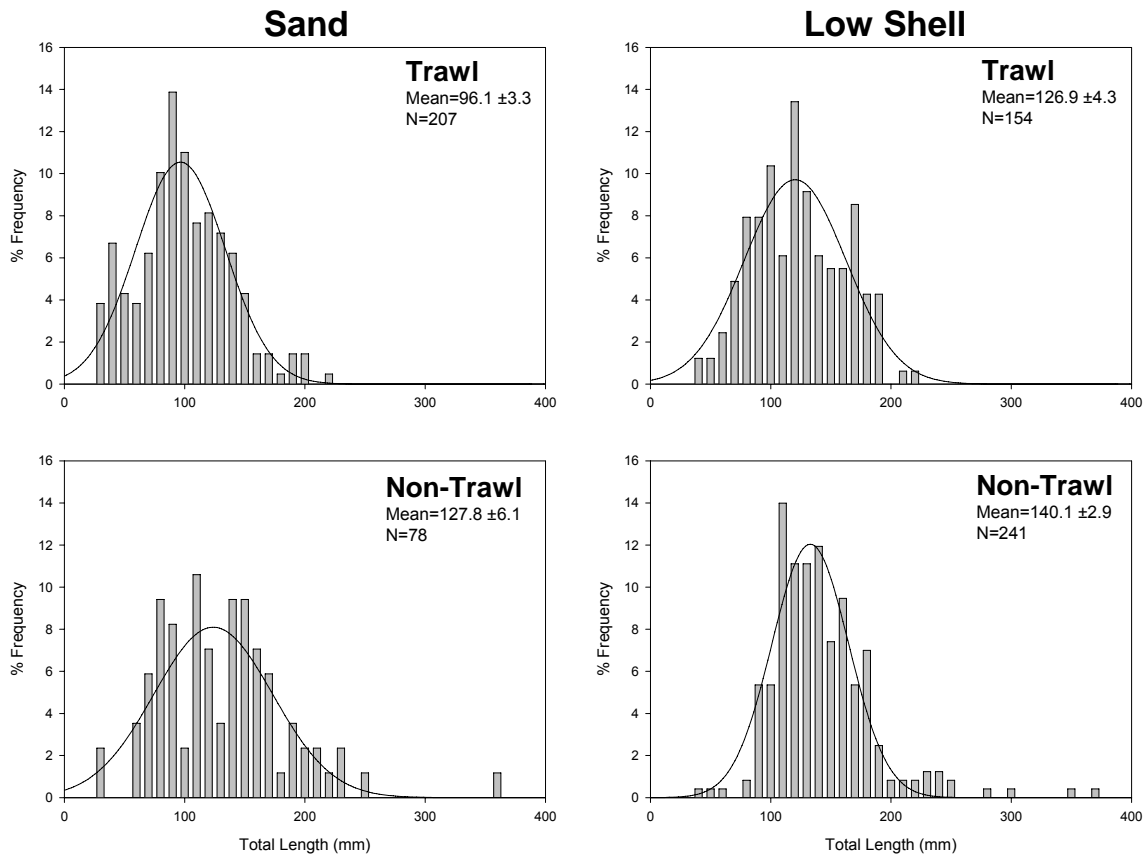


Figure 4.5. Size-frequency distributions of red snapper collected using trawls relative to the exposure to trawling over sand and low shell-rubble habitats. Mean sizes (\pm SE) and sample sizes (N) are included.

ensure high precision. The von Bertalanffy growth equation for all fish was $TL=410.2(1-e^{-0.00156(\text{age})})$ ($F_{2,940}=10,872$, $P<0.0001$, $r^2=0.96$).

Habitat-specific growth rates of age 0 red snapper showed differences among habitats during winter and fall, with highest growth rates over sand habitat (Figure 4.6). A significant growth rate difference was detected for red snapper collected among habitats exposed to trawling during the winter, with the highest growth rates of $1.03 \text{ mm}^{-\text{d}}$ over the sand habitat (ANCOVA slopes: $P=0.0466$; ANCOVA y-intercepts: $P=0.0217$). No significant winter growth differences were detected for red snapper residing among habitats that were not exposed to trawling (ANCOVA slopes: $P=0.1156$; ANCOVA y-intercepts: $P=0.1245$). However, trends in habitat-specific growth rates were similar, as red snapper collected over the sand habitat had the highest average growth rates ($1.01 \text{ mm}^{-\text{d}}$), followed by the reef ($0.74 \text{ mm}^{-\text{d}}$), and the low shell-rubble ($0.72 \text{ mm}^{-\text{d}}$) (Figure 4.6). Red snapper collected over non-trawled sand habitat had significantly higher growth rates ($0.84 \text{ mm}^{-\text{d}}$) than conspecifics among other non-trawled habitats in the fall (ANCOVA slopes: $P=0.2072$; ANCOVA y-intercepts: $P=0.0473$). No significant growth rate differences were detected for red snapper collected over different habitats exposed to trawling in the fall (ANCOVA slopes: $P=0.5751$; ANCOVA y-intercepts: $P=0.0739$); however, habitat-specific growth rate patterns were consistent with my other growth estimates, and showed highest growth rates of $0.65 \text{ mm}^{-\text{d}}$ over the trawled sand habitat (Figure 4.6).

In general, red snapper collected on habitats not exposed to trawling grew faster than their counterparts on trawled habitats (3 of 4 comparisons, Figure 4.7). Red snapper collected over non-trawled sand habitats in the fall grew significantly faster (slope effect) than conspecifics collected over similar sand habitats exposed to trawling (ANCOVA

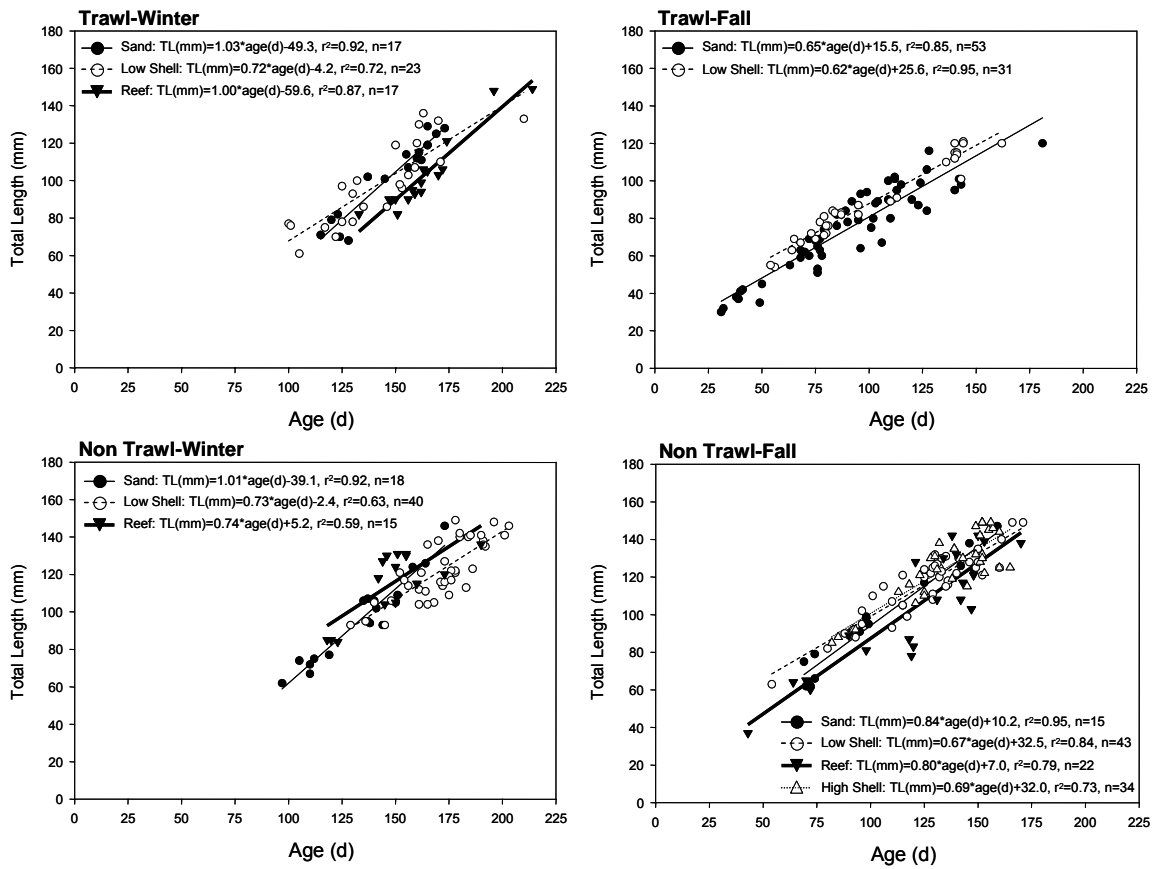


Figure 4.6. Size-at-age relationships of age 0 red snapper collected during the winter and fall trawl cruises determined with linear growth curves for habitat-specific comparisons. Habitats consist of sand, low shell-rubble, high shell-rubble, and reefs.

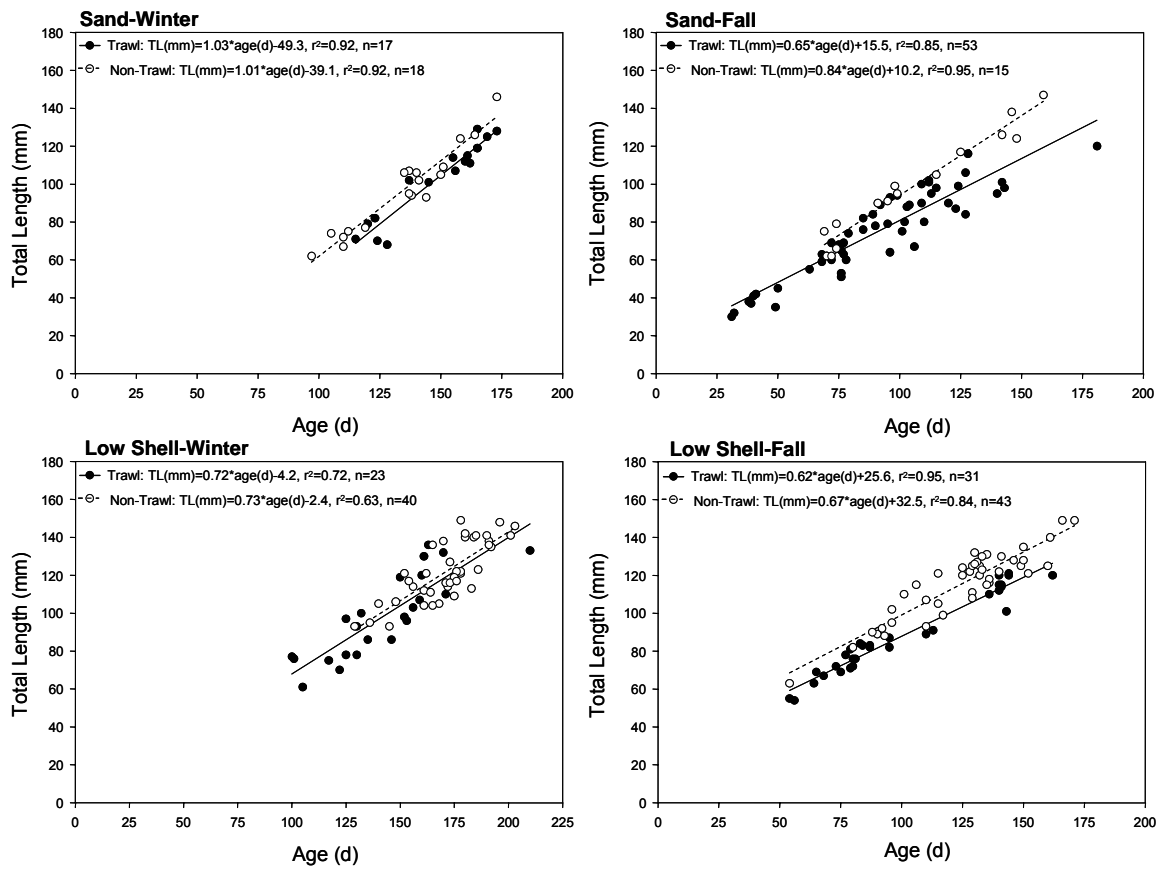


Figure 4.7. Size-at-age relationships of age 0 red snapper collected during the winter and fall surveys over sand and low shell-rubble habitats in trawled and non-trawled areas.

slopes: $P=0.0223$; ANCOVA y-intercepts: $P=0.5337$). Average fall daily growth rates of red snapper over non-trawled sand were $0.84 \text{ mm}^{-\text{d}}$, in contrast to red snapper collected on trawled sand that had average growth rates of $0.65 \text{ mm}^{-\text{d}}$. A similar trawl related difference in the fall was observed over the low shell-rubble habitat, with faster growth rates of red snapper over the non-trawled low shell-rubble ($0.67 \text{ mm}^{-\text{d}}$) than red snapper on similar trawled habitat ($0.62 \text{ mm}^{-\text{d}}$); however, differences were not significant (ANCOVA slopes: $P=0.4253$; ANCOVA y-intercepts: $P=0.2803$). Winter growth rates were similar, regardless of the exposure to trawling. Red snapper growth was slower over non-trawled sand and higher over non-trawled low shell-rubble when compared to red snapper collected over similar habitats exposed to trawling (Figure 4.7)

Mortality

Mortality rate estimates over the size ranges examined show red snapper in trawled areas suffered higher mortality rates than those in similar non-trawled areas (Figure 4.8). Red snapper collected over trawled sand habitats had average mortality rates of $5.9\%^{-\text{d}}$ ($Z=0.0609^{-\text{d}}$) compared to red snapper collected over non-trawled sand $2.2\%^{-\text{d}}$ ($Z=0.0224^{-\text{d}}$) (ANCOVA slopes: $P=0.0025$; ANCOVA y-intercepts: $P=0.0014$). Similar trends were observed for red snapper collected over low shell-rubble habitats, with red snapper mortality rates of $4.1\%^{-\text{d}}$ ($Z=0.0419^{-\text{d}}$) on trawled areas, and $3.2\%^{-\text{d}}$ ($Z=0.0329^{-\text{d}}$) on similar non-trawled areas, but results were not significant (ANCOVA slopes: $P=0.3150$; ANCOVA y-intercepts: $P=0.5875$). Thus, an expected increase of $0.51\%^{-\text{d}}$ and $0.11\%^{-\text{d}}$ red snapper survived over the non-trawled sand and low shell-rubble habitats over the 61-day period, respectively. Differences in mortality rates between similar habitat types exposed or not exposed to trawling provided a trawl-related estimated increase of $3.8\%^{-\text{d}}$ ($Z=0.0385^{-\text{d}}$) over sand, and $0.9\%^{-\text{d}}$ ($Z=0.009^{-\text{d}}$) over the

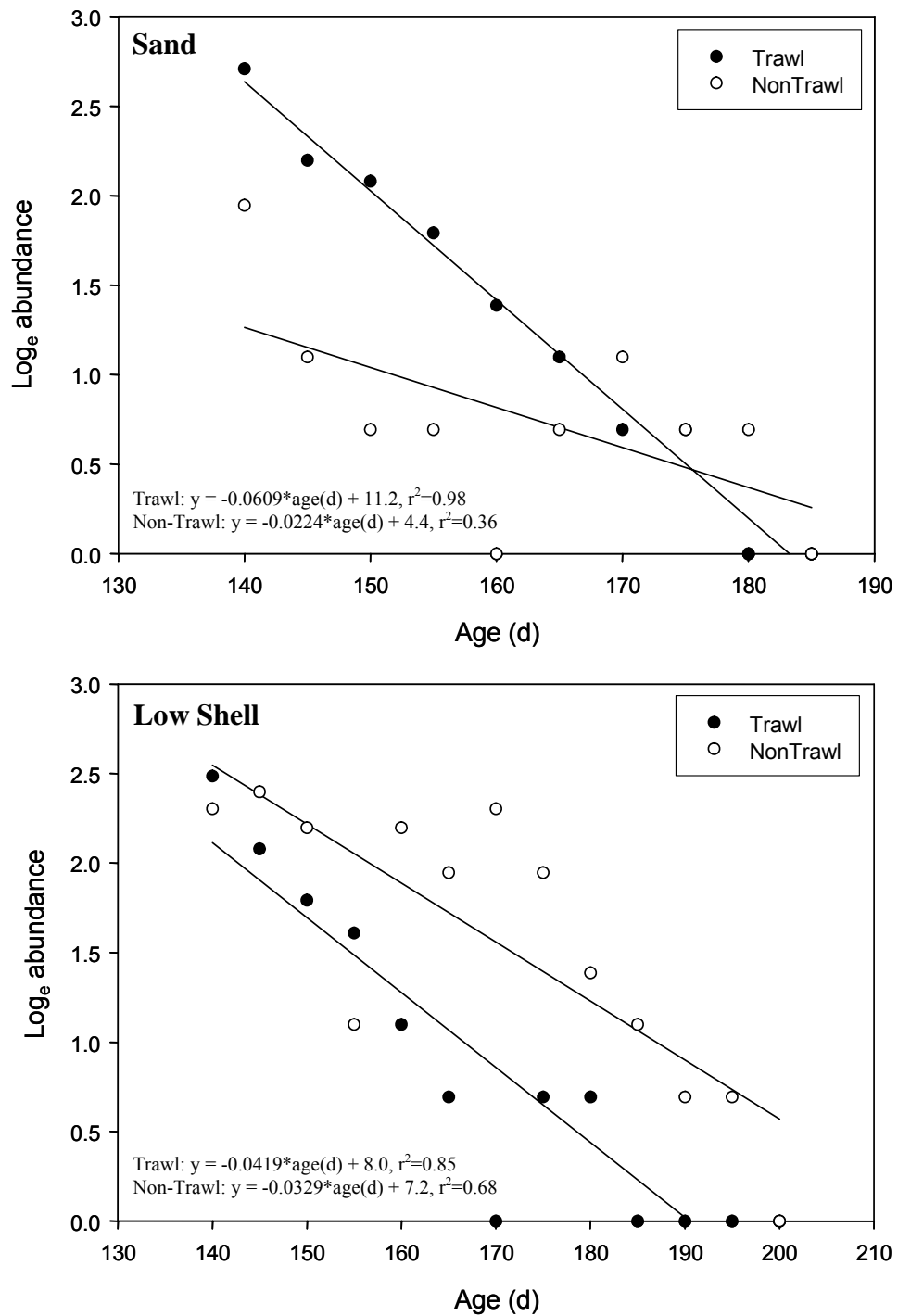


Figure 4.8. Mortality estimates of red snapper based upon age-specific catch curves using regression plots of \log_e abundance on age for 5-day cohorts. Sand estimates were based upon 2005 data and low shell-rubble estimates were based upon 2004 data.

low shell-rubble. A trawl-related survival difference of 1.87%^{-d} of red snapper was therefore observed on shell relative to sand habitat.

Production Potential

Habitat-specific G:Z ratios indicated that red snapper collected from habitats exposed to trawling had lower G:Z ratios than those collected from similar non-trawled habitats (Figure 4.9). The highest G:Z ratio of 1.09 was observed for red snapper over non-trawled sand, while similar trawled sand areas had a ratio of 0.38, indicating over a two-fold difference in biomass production and survival potential between habitats. The G:Z ratio of red snapper collected on non-trawled low shell-rubble habitats was 0.50, in contrast to 0.37 for red snapper residing on similar trawled habitat. In addition, the average G:Z ratios of red snapper collected from sand (0.74) were higher than those collected from low shell-rubble habitat (0.44).

Similar trends of higher P:B ratios of red snapper collected from non-trawled relative to similar trawled habitats were observed. The P:B ratios of red snapper collected from non-trawled and trawled sand habitats were 0.025 and 0.023, respectively. Similarly, the P:B ratios of red snapper collected from non-trawled and trawled low shell-rubble habitats were 0.016 and 0.015, respectively.

Discussion

The apparent effects of shrimp trawls on red snapper density and associated life history parameters were observed in this study. Higher densities of age 0.5+, combined with larger sizes, faster growth rates in the fall, lower mortality estimates, and higher G:Z and P:B ratios suggest juvenile red snapper residing over non-trawled areas may have a higher probability of survival than juvenile red snapper in areas exposed to commercial shrimp trawling.

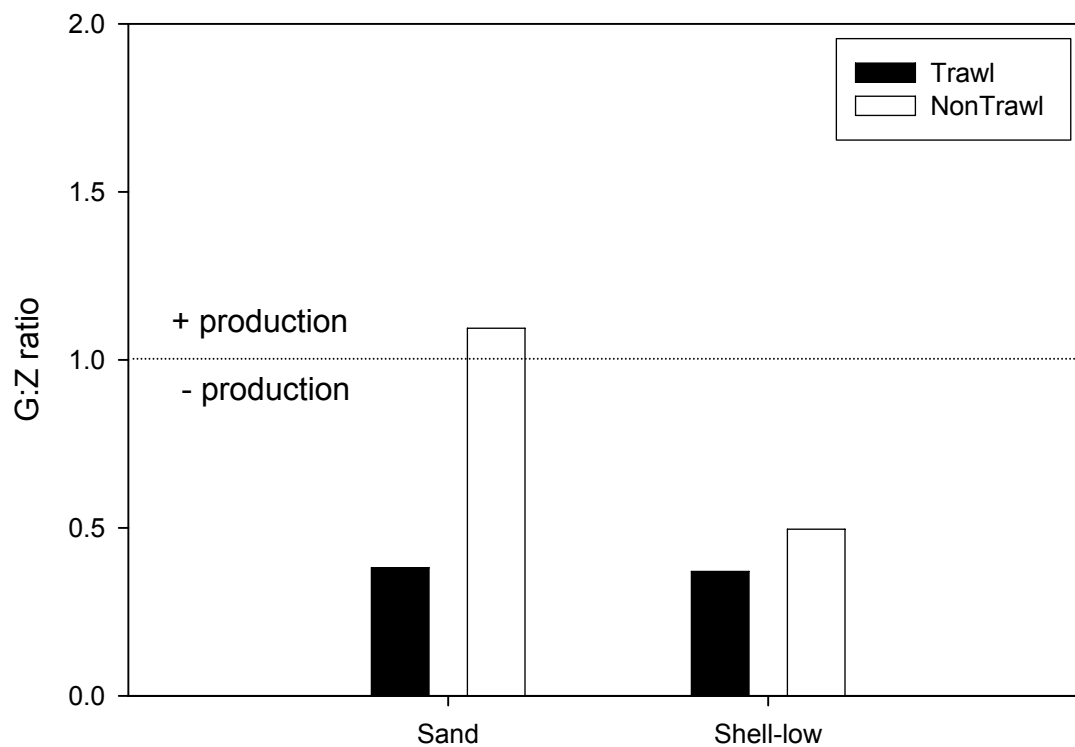


Figure 4.9. Production potential (G:Z ratios) of red snapper collected over trawl and non-trawl sand and low shell-rubble habitats. Weight specific growth rates (G) and total daily instantaneous mortality rates (Z) from the 5-day cohorts used to estimate mortality.

Based upon my results, post-settlement processes acting on age 0 red snapper are negatively affected by trawling. Higher selectivity for larger individuals may be attributable to size selectivity of the fishing gear. Smaller individuals were likely deflected by the pressure wave created by the trawl, or passed through the mesh of the net (Gilkinson et al. 1998, Blanchard et al. 2004). Decreases in the biomass of demersal fish and invertebrate fauna have been attributed to trawling and dredging in other studies (Bianchi et al. 2000, Zwanenburg 2000, Duplisea et al. 2002). In addition, large declines of small coastal elasmobranchs in the northern GOM have been documented where shrimp effort was highest (Shephard and Myers 2005). My findings are also consistent with those of Diamond et al. (2000) who showed that bycatch mortality has a large negative impact on population growth rates of GOM Atlantic croaker, *Micropogonias undulatus*, a common fish species collected as shrimp trawl bycatch in the GOM. However, Diamond et al. (1999) also found that life history parameters such as the size distribution, the number of large fish, and the size at maturity of Atlantic croaker in the GOM has not changed since the 1930s, despite major declines in abundance. This is the first study to document changes in the life history parameters of juvenile red snapper that may be attributable to shrimp trawls.

The greater habitat complexity and absence of commercial shrimp trawling over non-trawled habitats in my study may contribute to the faster growth rates and decreased mortality rates of age 0 red snapper. Habitat complexity as a result of decreased fishing activities has been shown to enhance the survivorship of age 0 Atlantic cod, *Gadus morhua*, at both the microhabitat (Lindholm et al. 1999) and landscape (Lindholm et al. 2001) levels by reducing the vulnerability of fish to predation. The epibenthic community (i.e. tubeworms, bryozoans, anemones, corals, and algae) and vertical relief

estimates in my study were greater over non-trawled habitats, and may therefore provide additional protection from predators (Chapter 3). This concept of habitat-mediated survivorship has been well documented in tropical and temperate reef systems (Carr 1991, Connell and Jones 1991, Sale 1991), but has not been well studied for red snapper. However, an estimated 15,000 artificial reefs exist within the permit areas off of Alabama (Patterson et al. 2001), and these reefs may have an effect on the distribution and abundance of red snapper, and co-occurrence of predators and prey. Differences in the predation pressure between sites exposed and not exposed to trawling may have existed. Large piscivorous fishes and sharks that would increase the predation potential within the non-trawled area are frequently found over highly structured habitats (i.e. artificial reefs) that aggregate large quantities of potential prey (Simpfendorfer and Milward 1993, Rademacher and Render 2003). However, if true, this would likely increase the mortality rates of age 0 red snapper over non-trawled areas.

Movement between trawled and non-trawled areas or to different habitats, such as the artificial reefs within the permit area, may have occurred during my study. An assumption in my approach was that the presence or absence of commercial shrimp trawling was the primary factor responsible for the observed differences between similar habitat types within and outside of the *de facto* non-trawl permit area. To date, no studies have investigated the movement of juvenile red snapper; however, Workman et al. (2002) concluded that juvenile red snapper display site fidelity and may have homing capabilities. In addition, Bailey et al. (2001) found that juvenile (age 0) red snapper were not allowed to occupy the reef when sub-adult (age 1) and adult (age 2+) red snapper were present. My study is consistent with Patterson et al. (2005) that red snapper habitat

use is age-specific, but similar ages overlapped among different habitat types, and dispersion between areas is therefore possible.

Production and mortality estimates are both species- and life-stage specific (Chapman 1978, Houde 1996). My growth, mortality, and production results were age-specific, in that I focused on juvenile red snapper between the ages of 140 and 200 d. Wang and Houde (1995) found annual P:B ratios of bay anchovy (*Anchoa mitchilli*) in Chesapeake Bay decreased from 8.07 to 0.97, after excluding the larval and youngest juvenile stages (3 months posthatch), and to 0.19 for new age 1+ anchovy. To date, most studies have used G:Z ratios on larvae (Cowan and Houde 1990, Houde 1996) and recently settled individuals (<50 d) (Rooker et al. 1999), thus caution should be used when interpreting my production calculations for annual estimates since I only used a 61-d period during the late juvenile stage. In addition, mortality estimates for juvenile red snapper in my study were considerably high. Movement and gear avoidance of red snapper may affect the mortality estimates and consequently overestimate total mortality and therefore underestimate production potential. However, results are consistent with the mortality rates estimated by Rooker et al. (2004), where habitat-specific mortality rates of juvenile red snapper ranged from 4 to 12%^{-d} over 47 to 57 days of age. In addition, my comparisons were limited to similar habitat types with the only difference being the presence or absence of shrimp trawling.

Changes in juvenile red snapper vital rates may have repercussions at the sub-adult and adult stages. My study has demonstrated the effects that trawling has on life history parameters of juvenile red snapper, while others have observed demographic differences in adult populations of red snapper. Fischer et al. (2004) found adult red snapper off Texas reached smaller maximum sizes at a faster rate, and had smaller

weight-at-age than red snapper collected off of Louisiana and Alabama. In addition, Woods et al. (2003) reported female red snapper off Alabama reached sexual maturity at smaller sizes and at earlier ages than conspecifics off Louisiana. It has been suggested that fishing pressure may select for phenotypic traits of fishes, such as reduced size-at-maturity and size-at-age, in addition to changes in growth rates (Law 2000). For example, the North Sea plaice (*Pleuronectes platessa*) has decreased in both length and age-at-maturity since 1900 due to fishing pressure (Rijnsdorp 1993). In addition, Kamukuru et al. (2005) reported blackspot snapper (*Lutjanus fulvivflamma*) collected in intensively fished areas off Tanzania had higher total and fishing mortality rates, lower maximum and average ages, and smaller sizes than conspecifics in an adjacent marine reserve. Diamond et al. (1999) found severe declines in the abundances of both Atlantic ocean and GOM Atlantic croaker, but only the Atlantic fish demonstrated changes in vital rates and demographics. These changes were attributed to the fishing pressure on both juveniles (as bycatch in shrimp trawls) and adults (recreational and commercial catch). Similar selective pressures appear to be occurring on GOM red snapper. Therefore, demographic differences in GOM red snapper may be driven by fishing practices at the early life stages when fishing mortality rates are highest.

Age-specific habitat use of red snapper, specifically an ontogenetic shift from low relief to higher relief habitats with increasing size and age, in my study was similar to findings from other studies. Studies characterizing juvenile red snapper habitat use have found juveniles in association with a variety of habitats, including mud, sand, relict shell-rubble, low-relief microhabitats (sponges, rubble patches, debris), and artificial structures with vertical relief (Moseley 1966, Bradley and Bryan 1975, Workman and Foster 1994, Szedlmayer and Howe 1997, Lee 1998, Szedlmayer and Conti 1999, Rooker et al. 2004,

Patterson et al. 2005). In contrast to juveniles, both sub-adult (age 1) and adult (age 2+) red snapper have been shown to occupy habitats such as gravel bottoms, coral reefs, rock outcrops, as well as artificial reefs, petroleum platforms, and submerged wreckage (Moseley 1966, Bradley and Bryan 1975, Moran 1988, Szedlmayer and Shipp 1994, Gledhill 2001). Differences in age-specific habitat use may be attributed to the agonistic behavior by adults toward younger conspecifics (Bailey et al. 2001), but later occupation of offshore reef structures occurs as these younger fish reach a size refuge and recruit into the adult population generally at or around age 2 (Nieland and Wilson 2003). Results from my study suggest juvenile red snapper begin recruiting to the reef structure as early as age 0, but are primarily found over these natural hard bottom reefs at age 1 and above.

To date, studies have been equivocal with respect to the habitat-specific enhancement of early life survival of red snapper. Rooker et al. (2004) found higher growth rates and lower mortality rates of age 0 red snapper over an inshore mud habitat than at a shell bank in the NW GOM. They found no density differences in the first year of the study, but found juvenile red snapper densities were higher over shell substrates during a limited survey the following year. Patterson et al. (2005) found no differences in red snapper densities between sand and shell substrates over study sites within the trawled area of my study region. Other studies investigating density differences have found that age 0 red snapper have an affinity for shell-rubble over sand habitat (Szedlmayer and Howe 1997, Szedlmayer and Conti 1999). In contrast, my results highlight the benefits of occupying sand habitat due to faster daily growth rates over sand than other habitats. In addition, both G:Z and P:B ratios indicated that higher production occurred on the sand habitat, which may be due to prey availability and feeding habits of age 0 red snapper. Age 0 red snapper have been shown to feed on prey associated with

open sand and mud habitats (Bradley and Bryan 1975, Szedlmayer and Lee 2004), and my feeding data suggests the same (Chapter 5). Nagelkerken and van der Velde (2004) found the majority of fishes utilizing both seagrass beds and mangrove habitats obtained most of their food sources from seagrass beds and attributed these habitat-specific feeding differences to the greater food availability in seagrass beds. My study suggests that red snapper rely on sand and mud associated prey, regardless of the habitat from which the red snapper were collected (Chapter 5), suggesting shell-rubble may be more important for providing refuge than additional prey resources.

This study was unique in that I addressed the four levels of information needed to identify and evaluate essential fish habitat (EFH) for red snapper. Based upon the four habitat-specific levels; 1) presence-absence, 2) density, 3) growth, reproduction, or survival, and 4) production (Minello 1999), it appears that all habitats (sand, shell-rubble, reefs) in my study may be essential for particular life stages. Other studies that have attempted to delineate EFH for federally managed fish species have found similar results, identifying almost all waters and habitats encountered over the life history of a species as EFH (Packer and Hoff 1999, Roni et al. 1999). Thus, if management strategies such as shrimp closures are implemented in the GOM to enhance survival of age 0 and age 1 red snapper, then all habitat types in this study will be needed to be protected, which is consistent with an ecosystem-based approach.

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CHAPTER 5: THE ROLES OF ONTOGENY, HABITAT, AND TRAWLING IN THE FEEDING ECOLOGY OF RED SNAPPER, *LUTJANUS CAMPECHANUS*: A COMBINED STABLE ISOTOPE AND STOMACH CONTENTS APPROACH

Introduction

Habitat selection processes for many species are tied to foraging success, and optimal habitat may afford an increase in feeding opportunities (Burke 1995, Eklov 1997). Recent studies have identified the importance of different habitats as feeding grounds to fishes that display ontogenetic dietary shifts (Cocheret de la Moriniere et al. 2003, Nagelkerken and van der Velde 2004). Thus, understanding the mechanisms responsible for habitat selection may identify those factors that are most important to early life survival, and ultimately to increased biomass production.

The impacts of some fishing activities on ecosystems are known to be negative (NRC 2002), but few studies have addressed the direct impact on the feeding patterns of commercially and recreationally important species (Kaiser and Spencer 1994). Indirect effects of trawling and dredging include the alteration of trophic linkages and predator-prey dynamics, which can produce cascading changes on other species from both bottom-up and top-down processes (NRC 2002). Jennings et al. (2001) reported trawling led to significant decreases in total infaunal biomass and productivity over a trawled area in the North Sea. Additionally, declines in numbers of pelagic sharks have been documented in the Gulf of Mexico (GOM) and may have cascading top-down effects on the food web (Baum and Myers 2004).

Red snapper (*Lutjanus campechanus*) is an opportunistic feeder that consumes a suite of different prey such as fishes, benthic crustaceans, squids, and pelagic zooplankton (Moseley 1966, Bradley and Bryan 1975, McCawley 2003, Ouzts and Szedlmayer 2003, Szedlmayer and Lee 2004). Juvenile diets are composed primarily of

shrimp and other crustaceans; fishes, squid, pelagic zooplankton, and other benthic crustaceans are consumed by adults (Bradley and Bryan 1975, McCawley 2003, Szedlmayer and Lee 2004). Several studies have suggested that adult red snapper feed adjacent to reefs over sand and mud bottoms (Moseley 1966, Bradley and Bryan 1975, McCawley 2003). However, other studies focusing on red snapper (70-399 mm SL) have reported diets that consist of reef-associated prey (Ouzts and Szedlmayer 2003, Szedlmayer and Lee 2004). To date, no studies have attempted to evaluate red snapper feeding on low-relief natural reefs and shell-rubble features on the northern GOM shelf, nor has the effect of trawling on red snapper been evaluated.

The combination of stomach content and stable isotope analyses has been used successfully to interpret feeding studies in fishes (Cocheret de la Moriniere et al. 2003). Stomach content analysis provides information about feeding based upon recently ingested prey, thereby serving as an indicator of short-term (hours to days) feeding (Bowen 1996). However, problems associated with prey identification, regurgitation, and the large number of samples necessary to understand feeding patterns means additional techniques are needed to understand trophic dynamics.

Naturally occurring stable isotopes have been widely used in feeding ecology studies (DeNiro and Epstein 1976, Fry et al. 1984, Peterson and Fry 1987, Litvin and Weinstein 2004). In contrast to stomach contents, stable isotopes in animal tissues derive from assimilated food, thus are indicative of long-term (weeks to months) feeding patterns. Comparisons of isotope values of carbon, nitrogen, and sulfur between consumers and their prey provide information on nutrient sources and trophic relationships. Levels of carbon isotopes ($\delta^{13}\text{C}$) in the tissues of predators directly reflect those of their prey, changing only 0.7‰ per trophic level, thus are useful for providing

information on organic source materials (Fry and Sherr 1984). In contrast, nitrogen values ($\delta^{15}\text{N}$) increase an average of 3.4‰ per trophic level between the animal and its diet, and are used to infer trophic relationships (Peterson and Fry 1987). Sulfur isotopes ($\delta^{34}\text{S}$) also are useful for clarifying feeding habits because they change only slightly with increasing trophic level and are useful for identifying food sources (Peterson and Fry 1987). Thus, the combination of stomach content and stable isotope analyses can provide detailed insight into dietary changes and feeding preferences for red snapper.

The goals of this study were to investigate the role of ontogeny, habitat, and the habitats exposure to commercial shrimp trawling on the feeding habits of red snapper. The specific research questions in this study were: 1) Do feeding patterns of red snapper change with respect to ontogeny; if so, do the stable isotope ratios change abruptly or gradually with respect to the associated habitat shifts? 2) Can diets of red snapper be used to infer possible mechanisms of red snapper habitat shifts? 3) Does exposure of habitat to commercial shrimp trawling affect red snapper feeding patterns?

Methods and Materials

Study Site and Sample Collections

Red snapper were collected quarterly during 2004 and 2005 over four distinct habitat types; sand, low shell-rubble (<40% CaCO_3 , 0.5 to 2 m relief), high shell-rubble (>40% CaCO_3 , 1 to 3 m relief), and natural hard bottom reefs (2 to 4 m relief). Study sites were located on the northern GOM continental shelf off Alabama (Figure 5.1). One of each habitat type was assumed to be exposed to commercial shrimp trawling (trawled sites) and one of each habitat type was enclosed in an artificial reef permit area (non-trawled sites), which served as a *de facto* non-trawl area. Trawled and non-trawled areas were ground-truthed with digital sidescan sonar and boxcore sediment analysis to verify

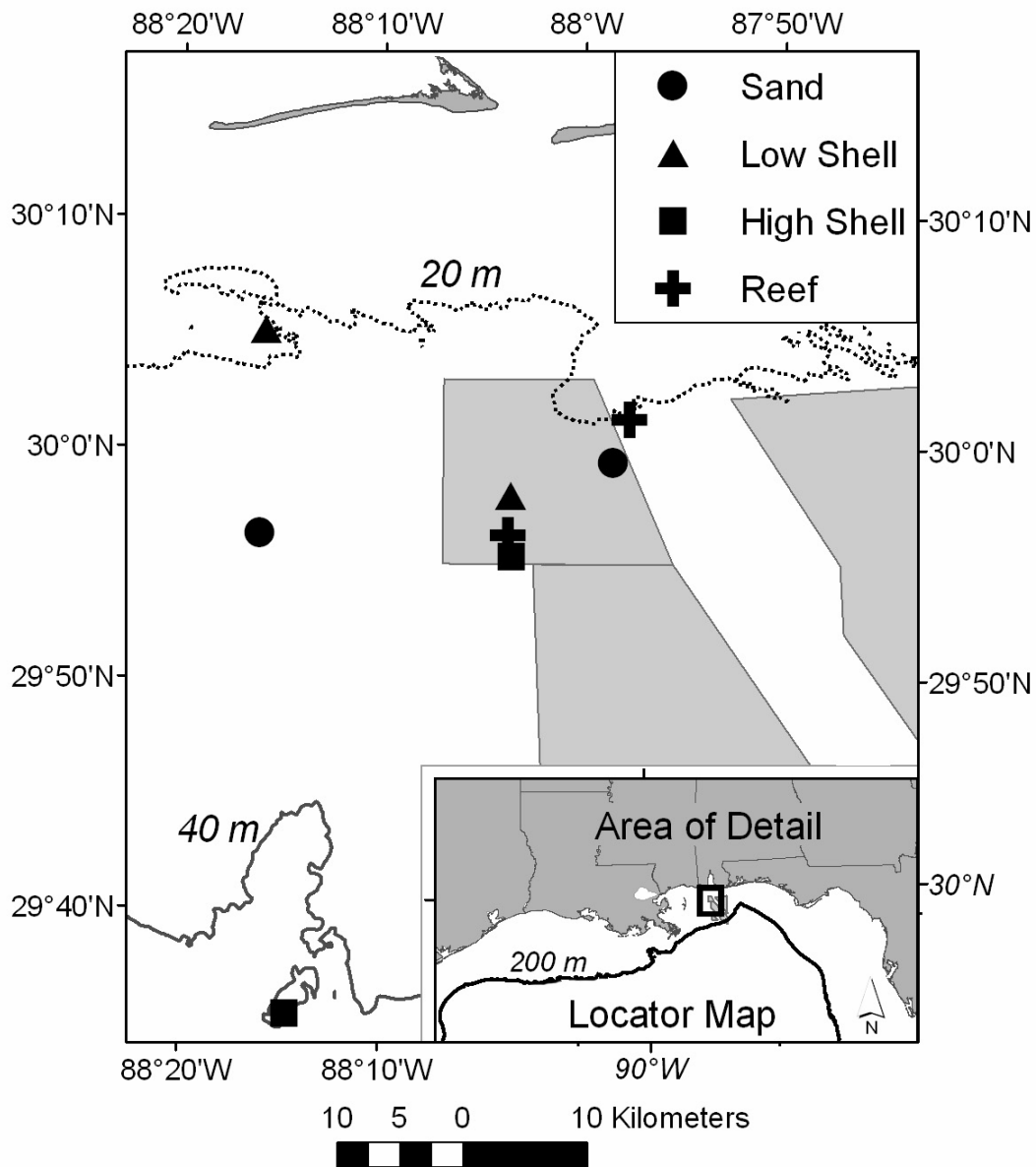


Figure 5.1. Map of the study site locations in the northcentral GOM off Alabama. The 20- and 40-m depth contours are shown with the 200-m depth contour representing the shelf edge. Enclosed shaded regions indicate the *de facto* non-trawl areas inside the Hugh Swingle Artificial Reef Permit Area.

that similar habitat types existed within each area (Dufrene 2005). Red snapper were collected with both otter trawls and fish traps over each habitat type. Trawl gear included a single 12.8 m wide net with 4 cm mesh size and a 0.7 cm cod end lining and was towed at approximately 4.6 km h⁻¹ for 10 min. Three replicate trawl tows were performed at each site. Traps were deployed adjacent to the trawl locations and were used due to the difficulty in trawling directly over reef structure, and to collect larger red snapper that are relatively invulnerable to trawling. A chevron trap (dimensions: 150 cm width x 180 cm length x 60 cm height, opening: 10 cm x 5 cm, mesh: 3.8 cm plastic coated wire) designed to capture large individuals and two small fish traps (dimensions: 64 cm width x 60 cm length x 43 cm height, mesh: 2.2 cm plastic coated wire) that targeted juveniles were soaked at a fixed location for a two hour period. Traps were baited with a single Atlantic menhaden (*Brevoortia tyrannus*) inside a non-accessible bait container; the bait was replaced after each deployment. All sampling was performed during daylight hours. Salinity, temperature, depth, and dissolved oxygen content were taken with a SeaBird SBE-25 conductivity-temperature-depth (CTD) instrument at each sample location.

Red snapper larvae were collected in the study region during a 2002 plankton survey using a 1 x 1.5 m multiple opening/closing net and environmental sensing system (MOCNESS) or with a Tucker trawl with 335 µm mesh towed obliquely for 5 min intervals. Particulate organic matter (POM) was used as a proxy for phytoplankton and was collected by filtering seawater from the sampling area with 47 mm GF/F filters with an effective pore size of 0.8 µm. In addition, benthic microalgae (BMA) (e.g., diatoms) were collected over the same time and area using a benthic grab sampler. Benthic microalgae were isolated with a modification of the vertical migration technique (Eaton and Moss 1966) (lens tissue was replaced with Nytex mesh) and identified to confirm that

sufficient numbers were collected for isotopic analysis. Identification also confirmed that benthic diatom species were successfully isolated. Pennate diatoms, including species from the genera *Tryblionella*, *Pinnularia*, *Nitzschia*, and *Navicula*, were identified from the samples collected.

Stomach Content and Stable Isotope Procedures

All red snapper were immediately frozen before being transported to the laboratory for storage at -80°C. In the laboratory, fish were measured to the nearest mm total length (TL) and weighed to the nearest g. Stomachs were dissected, weighed to the nearest g, slit open and fixed in 10% formalin for 48 h. Stomachs then were preserved in 70% ethyl alcohol until analyzed for stomach contents. All items in the gut were identified to the lowest possible taxon, sorted, counted, dried at 60°C for 24 h, and weighed to the nearest 0.0001 g.

Red snapper epaxial muscle tissue was dissected from the left side and dried in a Yamato DX 600 drying oven at 60°C for 24 h or until the sample reached a constant weight, after which the tissue was homogenized with a ball-mill grinder (Dentsply International, York, PA). Four to five mg of ground tissue was placed in a tin boat with 10 mg of precombusted Vanadium pentoxide (V_2O_5). Five small holes were punched from each POM and BMA filter and were placed in a tin boat. The isotopic composition of carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$), and sulfur ($\delta^{34}S$) were determined from the tissue and plant materials with a Finnigan MAT DeltaPlus continuous-flow stable isotope mass spectrometer attached to a Carlo Erba elemental analyzer at the Louisiana State University (Fry 2007). Isotopic values are reported relative to Vienna PeeDee belemnite for carbon, atmospheric N_2 for nitrogen, and Vienna Canyon Diablo troilite for sulfur with the standard equation:

$$\delta_{\text{sample}}(\text{‰}) = (R_{\text{sample}} / R_{\text{standard}} - 1) * 1000$$

where R represents the ratio of the heavy to light isotope ($^{13}\text{C}/^{12}\text{C}$, $^{15}\text{N}/^{14}\text{N}$, $^{34}\text{S}/^{32}\text{S}$).

Stable isotopes were only analyzed for a subset of fish collected over all habitats in 2004 (n=298), 18 red snapper larvae, and POM (n=3) and BMA (n=2) samples.

Data Analysis

Ten general prey categories were used to analyze the stomach content data: amphipods, copepods, crabs, euphausiids, fish, mysids, polychaetes, shrimp, squid, and stomatopods (mantis shrimp). Red snapper were grouped into five age bins based upon a von Bertalanffy size-at-age model (Chapter 4). These included age 0 (≤ 100 mm TL), age 0.5+ (101-179 mm TL), age 1 (180-279 mm TL), age 2 (280-336 mm TL), and age 3+ (≥ 337 mm TL). Differences in red snapper feeding were investigated by age, habitat type, exposure to trawling, and season. Differences between years were investigated within size x habitat x trawl; no significant differences were detected, I therefore combined years.

Importance of prey type was analyzed with three methods: frequency of occurrence, percent composition by number, and percent composition by weight (Bowen 1996). The percent composition by weight was the primary method chosen to analyze the stomach content data because this metric best assesses the nutritional contribution of prey type (Rooker 1995, Bowen 1996). In addition, a percent index of relative importance (% IRI) was computed to assess prey contribution to red snapper diet (McCawley 2003):

$$\text{IRI} = (\% \text{ number} + \% \text{ weight}) \times \% \text{ frequency of occurrence}$$

$$\% \text{ IRI} = (\text{IRI}_{\text{prey item}} / \text{IRI}_{\text{total}}) \times 100$$

Percent composition by weight of each prey category was computed for each individual. Percent composition for all prey types then was square root transformed to reduce the importance of the most abundant prey. Differences among factors were investigated with the analysis of similarity (ANOSIM) procedure in PRIMER (Plymouth Routines in Multivariate Ecological Research; Warwick et al. 1990). The similarity percentages (SIMPER) procedure was used to assess which prey categories were the most important in discriminating among levels of size, habitat, trawling, and seasonal feeding differences (Clarke 1993).

Stable isotopes of red snapper were compared with multiple analysis of covariance (MANCOVA) with carbon, nitrogen, and sulfur as the dependent variables (Litvin and Weinstein 2004). Independent variables included age class, habitat type, exposure to trawling, and season, with length as the covariate to control for size related differences in stable isotope levels in red snapper tissue. Univariate analysis of covariance (ANCOVA) models were used to identify individual dependent variable responses. Lastly, to further investigate the effects of trawling on stable isotopes in red snapper muscle tissue, a comparison was made only with fish collected on sand and shell-rubble habitats because trawling does not likely occur on the reef (Link 1997). These results did not change the effects of habitat and season; therefore, only the effects of trawling were interpreted.

Red snapper trophic level was calculated following Hobson and Welch (1992):

$$\text{Trophic level} = 1 + (\delta^{15}\text{N}_{\text{consumer}} - 6.56) / 3$$

where 6.56 was the average $\delta^{15}\text{N}$ value of the POM and BMA, and 3.0 ‰ was used as the $\delta^{15}\text{N}$ enrichment value per trophic level (Rooker et al. 2006).

The potential carbon contribution of planktonic sources (POM) versus benthic sources (BMA) to both pre- and post-settled red snapper diets was estimated with the 2-source mixing model of Fredriksen (2003) and Rooker et al. (2006):

$$\%C_{\text{benthic}} = \frac{(\delta^{13}\text{C}_{\text{consumer}} - \delta^{13}\text{C}_{\text{planktonic}} - I)}{\delta^{13}\text{C}_{\text{benthic}} - \delta^{13}\text{C}_{\text{planktonic}}} \times 100$$

where I is the average fractionation value of $\delta^{13}\text{C}$ per trophic level. A carbon enrichment value of 1.0 ‰ was used, thus I was equal to the estimated trophic level (Rooker et al. 2006).

Prey Habitat Selection

Habitat use by the most abundant prey (fish and crabs) found in sub-adult (age 1) and adult (age 2+) red snapper stomachs was characterized to investigate whether habitat-specific prey resources were unique to red snapper collected from that habitat. I included only the percentage of prey that was identified to family or greater, thus general fish or crab material was not included in calculations. Prey habitats were classified according to previous studies that have investigated red snapper prey habitat associations (McCawley 2003, Szedlmayer and Lee 2004). Fish prey in the families Bothidae, Ogcocephalidae, Sparidae, Synodontidae, and Triglidae were classified as sand and mud associated. Open water prey fishes included only Engraulidae and reef-associated prey fishes included both Haemulidae and Serranidae. Crab prey items in the families Calappidae and Portunidae were classified as sand and mud associated, while families Porcellanidae, Pseudorhombilidae, Raninidae, and Xanthidae were assumed to be reef-associated.

Results

A total of 936 red snapper was analyzed for stomach contents; 795 red snapper (85%) contained prey items and were used for statistical comparisons. In addition, 316

red snapper were analyzed for stable isotope composition. A large size and age range was analyzed; post-settled red snapper sizes ranged from 23 to 435 mm TL and ages ranged between 28 days and 5 years. Pre-settled red snapper larvae were between 3 and 18 mm TL.

Effects of Size on Stomach and Stable Isotopic Contents

Red snapper displayed ontogenetic shifts in their diets from the planktonic larval stage, to settlement and into juvenile and adult stages. Red snapper stomach contents and % IRI corresponded well with stable isotope trends and also showed an ontogenetic dietary shift (Table 5.1, Figure 5.2). A general trend of increasing crab and fish with a corresponding decrease in squid and mysid shrimp was observed in red snapper stomachs with increasing age. Age 0 red snapper fed primarily upon mysid shrimp, squid, and copepods and began consuming euphausiids by age 0.5+. Age 1 red snapper primarily ate fish, crab, and squid, while age 2 fish consumed mantis shrimp, fish, crab, and shrimp. Age 3+ red snapper primarily consumed fish and crab.

Red snapper became more enriched in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, while $\delta^{34}\text{S}$ values became depleted with increasing age (Figure 5.3). In addition, stable isotope levels changed abruptly between larval and early juvenile stages, while showing a gradual change during later juvenile and adult stages (Figure 5.3). Pre-settled red snapper initially decreased in $\delta^{15}\text{N}$, but then began to increase in $\delta^{15}\text{N}$ by 10 mm TL (Figure 5.3B). Red snapper $\delta^{15}\text{N}$ increased by nearly two trophic levels, from a low of 8.2 ‰ as larvae, to 11.3 ‰ at the early juvenile stage (age 0), and to 14.8 ‰ at sub-adult (age 1) and adult stages (age 2+). Red snapper increased in carbon by approximately 4 ‰ from the smallest larvae (-22.9 ‰) to recently settled fish (-19.1 ‰), and by 3 ‰ from recently settled to ages 2+ (-16.1 ‰) (Figure 5.3A). Sulfur values were more variable, but

Table 5.1. Percent index of relative importance (% IRI) of the most important prey groups in red snapper diets, by age class.

	Amphipod	Copepod	Euphausiid	Mysid	Crab	Shrimp	Mantis shrimp	Fish	Polychaete	Squid
Age 0	0.24	22.16	0.13	53.40	1.25	0.36	0.02	4.53	0.00	17.91
Age 0.5+	0.30	0.66	4.17	12.93	5.25	5.02	0.31	26.42	0.04	44.91
Age 1	0.01	0.00	0.37	0.46	6.60	3.90	0.77	72.18	0.05	15.65
Age 2	0.00	0.00	0.00	0.09	5.27	2.76	2.04	89.85	0.00	0.00
Age 3+	0.03	0.00	0.00	0.00	25.02	0.00	0.05	73.06	0.00	1.84

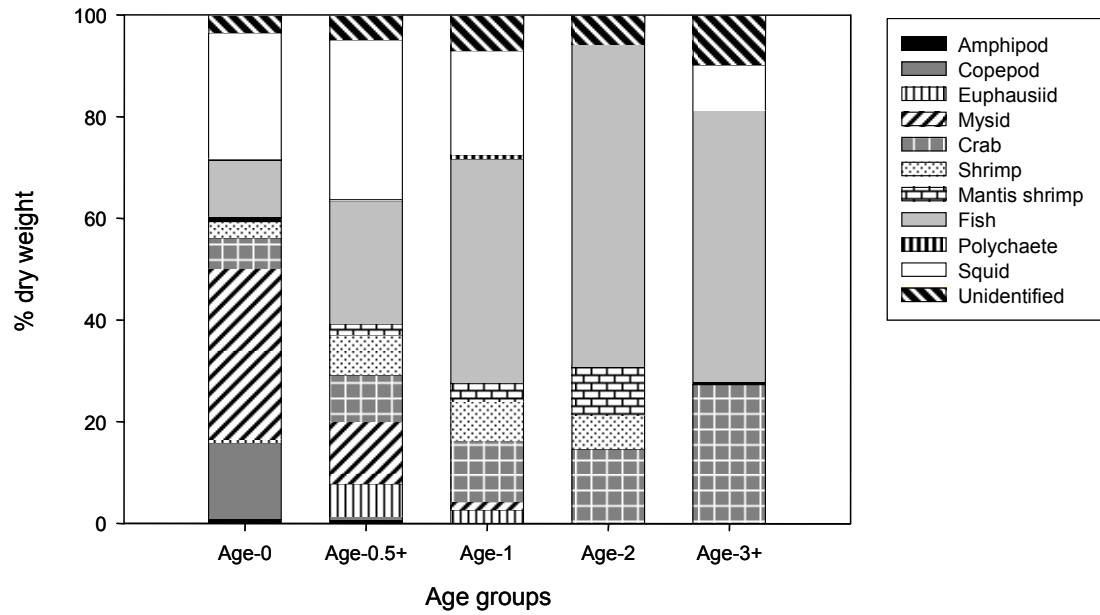


Figure 5.2. Stomach contents of red snapper by age based upon the percent by dry weight of the most abundant food items.

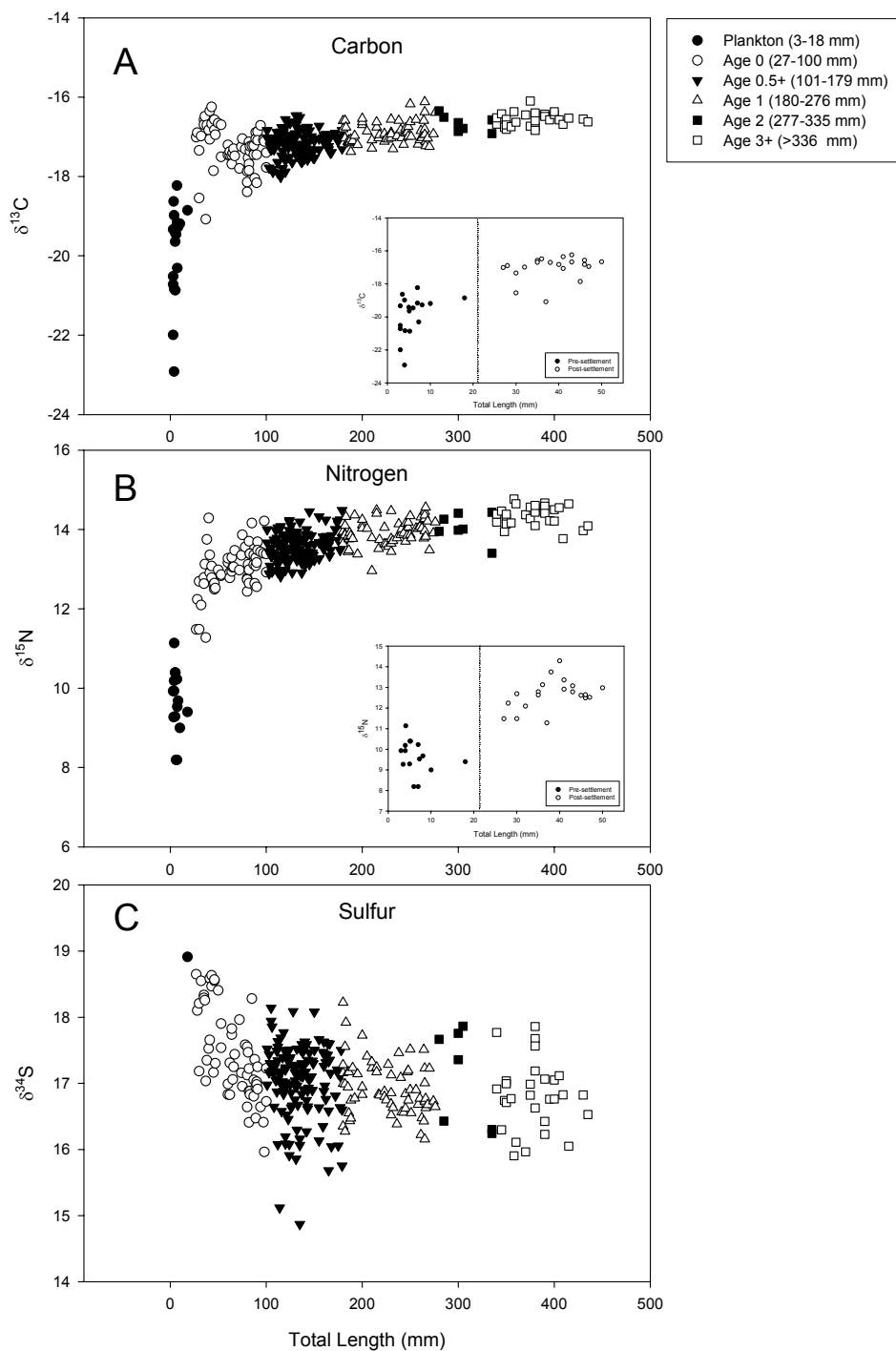


Figure 5.3. (A) Carbon ($\delta^{13}\text{C}$), (B) Nitrogen ($\delta^{15}\text{N}$), (C) and Sulfur ($\delta^{34}\text{S}$) as a function of red snapper total length (TL). Specific age groups of red snapper are shown based upon a von Bertalanffy size-at-age model. Inset figures show the size relationship with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for both pre- and post-settled red snapper, with vertical dotted line showing the size-at-settlement (~21 mm TL).

decreased by almost 3 ‰ from recent settlement (18.7 ‰) to ages 2+ (16.0 ‰) (Figure 5.3C). Sulfur values were not determined for red snapper less than 18 mm TL due to the limited amount of tissue that was available for analysis.

Effects of Habitat on Stomach and Stable Isotopic Contents

Habitat-specific feeding differences were less pronounced than ontogenetic feeding differences of red snapper (Table 5.2 and Figure 5.4). Overall, 71.4% of all pairwise differences were significantly different when analyzing red snapper stomach contents of different age groups, collected over similar habitats (Table 5.2). In contrast, only 44.6% of all pairwise differences were significantly different for similar aged red snapper collected over different habitats (Table 5.2). Stomach contents of red snapper residing on different habitats across similar ages showed an inverse relationship between dietary separation and age with significant differences observed in age 0, age 0.5+, and age 1 fish ($P < 0.01$) (Figure 5.4); however, the dominance of both fish and crab material in the stomachs of age 2 and age 3+ red snapper precluded any statistical differences (age 2: $P = 0.051$, age 3+: $P = 0.457$). Results of the SIMPER analysis indicated mysid shrimp, fish, and squid were the most important prey items differentiating habitat-specific diets of age 0, age 0.5+, and age 1 red snapper, but no consistent trends were observed (Figure 5.4).

Red snapper stable isotope values were significantly different for red snapper collected over different habitats. Specifically, both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of red snapper were significantly different among habitats (Table 5.3), with the most distinct separation among stable isotope values at the youngest age analyzed (Figure 5.5A). Among age 0 red snapper, those collected over sand had the most enriched $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$ along with depleted $\delta^{15}\text{N}$ (Figure 5.5A-C). In contrast, age 0 red snapper collected over reef had the

Table 5.2. The percent of pairwise comparisons of red snapper stomach contents that were significantly different ($P < 0.05$), based upon ontogeny and habitat. Ontogenetic comparisons were made among age 0, age 0.5+, and age 1 groups over the same habitat. Habitat comparisons were made among different habitats over similar age groups. NA represents not applicable due to a low sample size.

		Sand-T	Sand-NT	Low Shell-T	Low Shell-NT	High Shell-T	High Shell-NT	Reef-T	Reef-NT	Total Average
Age 0	Ontogeny	100	100	100	50	na	50	100	100	85.7
	Habitat	50	33	100	33	na	33	50	0	42.7
Age 0.5+	Ontogeny	50	100	50	0	na	50	100	100	64.3
	Habitat	50	100	50	67	na	67	0	100	62.0
Age 1	Ontogeny	50	100	50	50	na	0	100	100	64.3
	Habitat	0	67	33	33	0	33	33	0	24.9
Total	Ontogeny	66.7	100	66.7	33.3	na	33.3	100	100	71.4
Average	Habitat	33.3	66.7	61.0	44.3	na	44.3	29.3	33.3	44.6

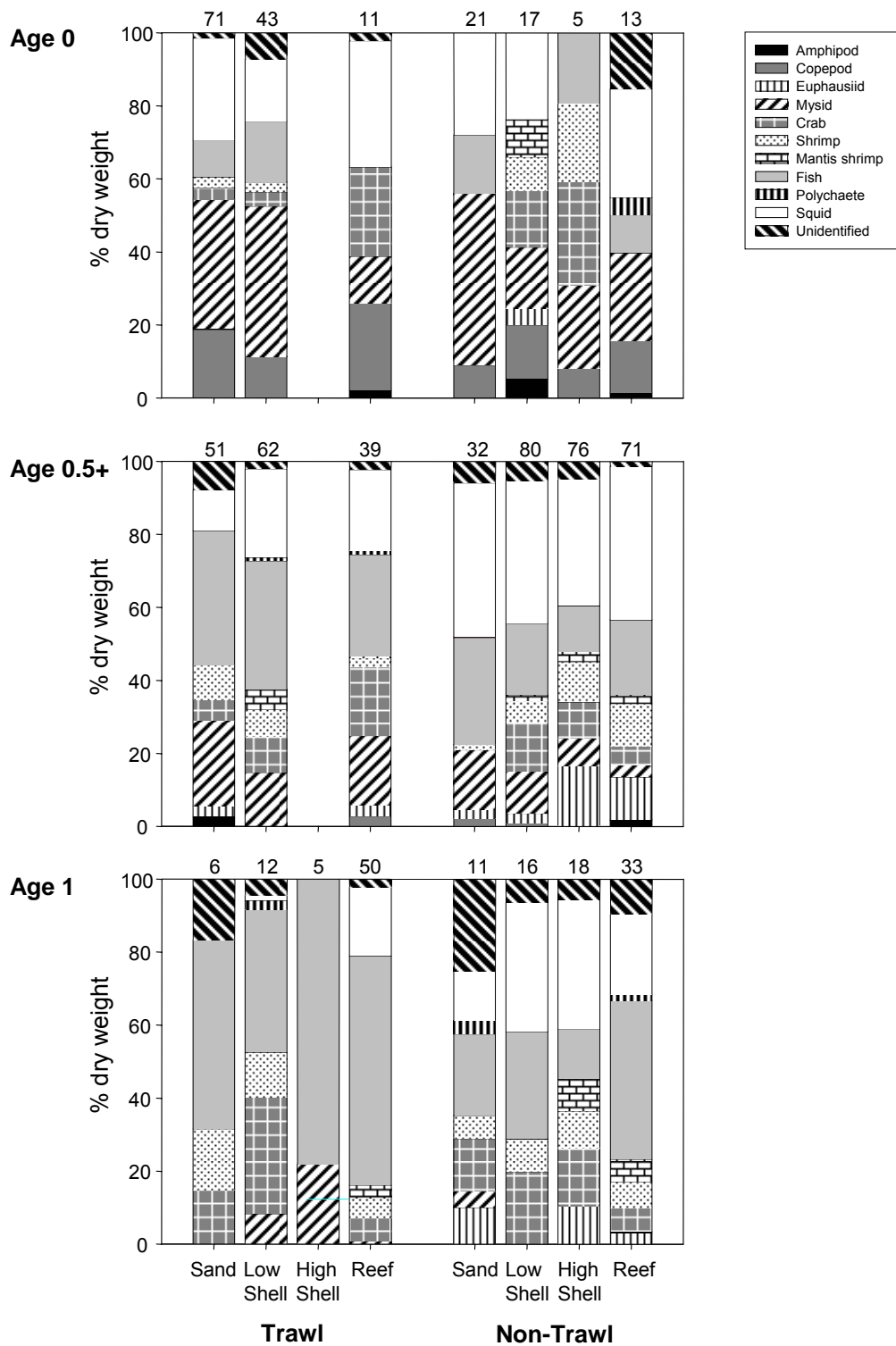


Figure 5.4. Stomach contents of age 0, age 0.5+, and age 1 red snapper by habitat type and the habitats exposure to commercial shrimp trawling (based upon the percent by dry weight). Numbers above the upper abscissa represent the number of red snapper containing prey that were analyzed.

Table 5.3. Multiple analysis of covariance and univariate analyses of covariance models for each factor adjusted for length (covariate: length). Pillai's trace statistic represents calculated p-values.

A. Multiple analysis of covariance (C, N, & S)		
Factor	F value	P value
Habitat	$F_{(9, 798)}=2.03$	0.0333
Trawl	$F_{(3, 264)}=0.48$	0.6935
Season	$F_{(9, 798)}=2.85$	0.0026
B. Analysis of covariance: Habitat		
Isotope	F value (3, 266)	P value
$\delta^{13}\text{C}$	3.95	0.0089
$\delta^{15}\text{N}$	3.64	0.0134
$\delta^{34}\text{S}$	0.31	0.8161
C. Analysis of covariance: Trawl		
Isotope	F value (1, 266)	P value
$\delta^{13}\text{C}$	0.02	0.8803
$\delta^{15}\text{N}$	0.33	0.5665
$\delta^{34}\text{S}$	0.72	0.3972
D. Analysis of covariance: Season		
Isotope	F value (3, 266)	P value
$\delta^{13}\text{C}$	4.93	0.0024
$\delta^{15}\text{N}$	2.47	0.0621
$\delta^{34}\text{S}$	2.26	0.0821

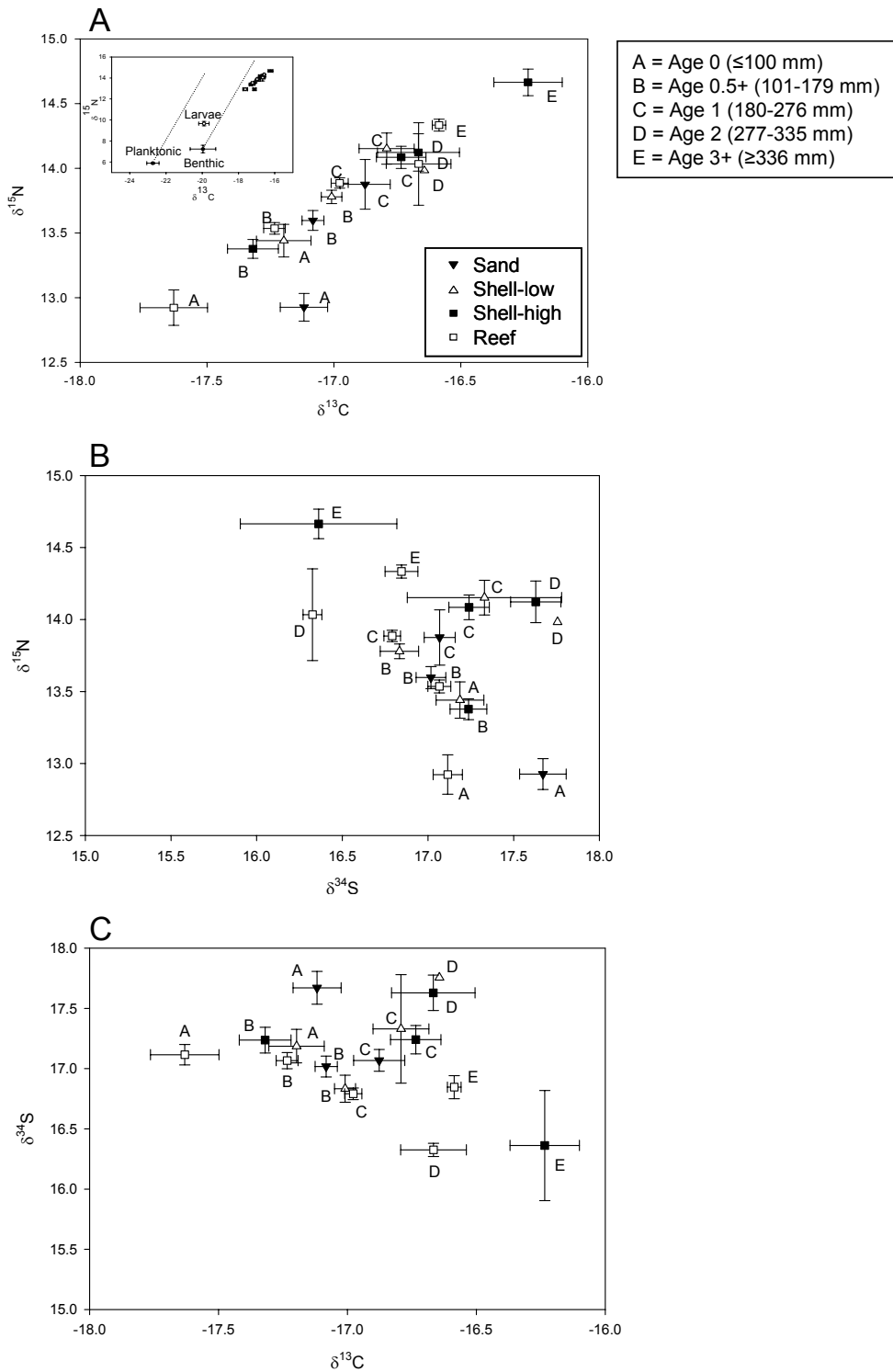


Figure 5.5. Stable isotope plots of carbon ($\delta^{13}\text{C}$), nitrogen ($\delta^{15}\text{N}$), and sulfur ($\delta^{34}\text{S}$) with respect to size (letters A through E) and habitat type red snapper were collected on (symbols). Inset figure in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ biplot shows the plankton and benthic source values and predicted enrichment pathways using 1‰ $\delta^{13}\text{C}$ and 3‰ $\delta^{15}\text{N}$ enrichment per trophic level.

most depleted $\delta^{13}\text{C}$ and $\delta^{34}\text{S}$, while $\delta^{15}\text{N}$ was highest for age 0 red snapper on low shell-rubble (Figure 5.5A-C). Red snapper collected on low shell-rubble continued to exhibit the most enriched $\delta^{15}\text{N}$ for both age 0.5+ and age 1 fish compared to similar size fish collected over different habitats. Three of the four age groups (age 0, age 1, age 2, age 3+) collected over the reef exhibited the most depleted $\delta^{13}\text{C}$. Lastly, a general trend of decreasing separation among red snapper stable isotopes was observed with increasing age (Figure 5.5).

Effects of Trawling on Stomach and Stable Isotopic Contents

Stomach contents of red snapper collected from similar habitats exposed and not exposed to trawling were age and habitat-specific. Age 0 red snapper collected over non-trawled low shell-rubble had different diets than individuals collected over trawled areas of similar habitat ($P=0.043$). More amphipods, euphausiids, crabs, and mantis shrimp were found in the diets of fish collected in the non-trawled area (Figure 5.4). Older age groups (age 2 and age 3+) showed no difference in stomach contents; in addition, red snapper had similar diets over sand trawled and non-trawled areas regardless of age. No significant differences in $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, or $\delta^{34}\text{S}$ were detected in red snapper collected in trawled and non-trawled areas of similar habitats when red snapper collected on the reef were included (Table 5.3). However, when excluding red snapper collected on the reef, a significant trawl effect was observed (MANCOVA: $F_{(3,129)}=6.82$, $P=0.0003$). Further, univariate analyses show that significant trawl effects were found for $\delta^{13}\text{C}$ (ANCOVA: $F_{(1,131)}=17.55$, $P<0.0001$), $\delta^{15}\text{N}$ (ANCOVA: $F_{(1,131)}=12.14$, $P=0.0007$), and $\delta^{34}\text{S}$ (ANCOVA: $F_{(1,131)}=6.25$, $P=0.0137$). Specifically, red snapper $\delta^{13}\text{C}$ was enriched on trawled sand and high shell-rubble, while depleted on trawled low shell-rubble when compared to similar non-trawled habitats; however, differences were not significant

($P > 0.05$). Red snapper $\delta^{15}\text{N}$ values were enriched over all trawled habitats when compared to similar non-trawled habitats. Red snapper occupying trawled sand had significantly higher values for $\delta^{15}\text{N}$ (13.86 ‰) than conspecifics on non-trawled sand (13.41 ‰) ($P = 0.0122$). Lastly, $\delta^{34}\text{S}$ values were depleted in fish collected over trawled habitats, with significantly depleted $\delta^{34}\text{S}$ values in red snapper collected over trawled sand (16.55 ‰) and low shell-rubble (16.74 ‰) compared to those over similar non-trawled sand (17.15 ‰) and low shell-rubble (17.37 ‰) habitats (sand: $P = 0.0248$, shell: $P = 0.0014$).

Effects of Season on Stomach and Stable Isotopic Contents

Seasonal differences in stomach contents were most common among the youngest age groups, but no differences were detected for older red snapper (age 2 and age 3+). Age 0 red snapper showed differences among all seasons ($P < 0.01$), except between winter and fall ($P = 0.270$), when mysid shrimp, fish, squid, and copepods (in descending order of importance) were the most important prey items in red snapper winter diets. Squid and copepods were the most important prey items in age 0 red snapper diets during the spring and summer, and both mysid shrimp and squid contributed most to the red snapper diets in fall. Age 0.5+ red snapper showed differences among all seasons ($P < 0.05$), but squid was the most important by percent weight during the winter, spring, and fall, while fish material dominated the diets in the summer. Winter diets of age 1 red snapper were different when compared to all other seasons due to the abundance of crab material in stomachs ($P < 0.01$).

Seasonal differences in red snapper $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ were negligible; however, $\delta^{13}\text{C}$ of red snapper showed a significant difference among seasons (Table 5.3). Results indicate that red snapper most depleted in $\delta^{13}\text{C}$ (-17.26 ‰) were collected in winter,

slightly increasing into spring (-17.24 ‰), and the most enriched $\delta^{13}\text{C}$ values of red snapper were observed in summer (-16.91 ‰) and fall (-16.95 ‰).

Prey Habitat Selection

The majority of fish and crab prey items found in adult red snapper were sand and mud associated organisms (Table 5.4). The most abundant sand and mud associated fish prey item was the largescale lizardfish (*Saurida brasiliensis*), accounting for 37.1%, 31.8%, and 39.1% of the total dry weight of age 1, age 2, and age 3+ red snapper stomach contents, respectively. The striped anchovy (*Anchoa hepsetus*) was the lone open water fish species and sand perch (*Diplectrum formosum*) and tomtate (*Haemulon aurolineatum*) represented reef-associated fish prey identified to species. The dominant crab prey items associated with sand and mud were *Callinectes* spp. accounting for 22.8%, 96.8%, and 100% of the total dry weight of age 1, age 2, and age 3+ red snapper stomach contents, respectively.

Similar patterns of prey habitat use were seen when investigating stomach contents of all red snapper age groups combined. The total percentage of all fish prey taxa that was classified as reef associated represented 1.73% of total fish prey by dry weight. *Saurida brasiliensis* represented 39.6% of total dry weight of fish material in red snapper stomachs, followed by *A. hepsetus*, with 36.7%. The total dry weight percentage of all reef-associated crab material in red snapper stomachs was 8.3%, while 89.4% was represented by family Portunidae, of which 55.0% was *Callinectes* spp.

Planktonic versus Benthic Carbon Contribution

The average $\delta^{13}\text{C}$ value of POM, which served as a proxy for the planktonic organic contribution to red snapper, was -22.7 ‰ (± 0.98 SE). In contrast, the average $\delta^{13}\text{C}$ value of BMA, which served as the benthic contribution to red snapper, was

Table 5.4. Percentages of crab and fish prey items collected in age 1+ red snapper stomachs according to prey habitat preference. Percentages are calculated for prey items identified to family or greater. The percent of red snapper collected on the reef by age group is also included.

	Crab		Fish			
Habitat	Sand/Mud	Reef	Sand/Mud	Open water	Reef	% of red snapper collected on reef
Age 1	96.2	3.8	40.9	58.5	0.6	56.1
Age 2	100.0	0.0	100.0	0.0	0.0	85.0
Age 3+	100.0	0.0	99.1	0.9	0.0	90.6

-19.9 ‰ (± 0.70 SE). Average $\delta^{15}\text{N}$ values of POM and BMA were 5.9 ‰ (± 0.06 SE) and 7.2 ‰ (± 0.36 SE), respectively.

Results of the 2-source mixing model indicate that benthic carbon contributions are potentially important contributors to the food web of red snapper (Figure 5.5A). Initially, planktonic sources are important for larval red snapper, accounting for 80% of the total carbon contribution, but by the late larval stage (18 mm TL) the planktonic contribution decreases to less than 10%. Based upon the average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for age 0 red snapper, the calculated potential benthic production exceeded 100% over sand and low shell-rubble, and was 95% of the total organic material provided to red snapper over reefs. A majority of the age 0 red snapper with enriched $\delta^{13}\text{C}$ values were collected during the summer of 2004, but when endpoints of the most depleted $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ post-settled individuals collected over other seasons are used, potential benthic production accounts for 66% of the organic material to age 0 red snapper. Nevertheless, benthic production accounted for all the organic material provided to age 0.5+ and older red snapper.

Discussion

The use of both stomach content and stable isotope analyses proved useful in delineating dietary shifts of red snapper from larval to juvenile and adult stages. The rapid isotopic changes in early life stages were likely attributed to a diet switch accompanied by fast tissue turnover time, which is common during the early life stages of fishes (Fry and Arnold 1982, Herzka and Holt 2000). The initial decrease in $\delta^{15}\text{N}$ of pre-settled red snapper followed by a rapid increase in $\delta^{15}\text{N}$ likely resulted from the transition from endogenous to exogenous feeding. Vander Zanden et al. (1998) found the same pattern for age 0 smallmouth bass (*Micropterus dolomieu*) and attributed the change to

the transition from a parental nitrogen source to one dominated by exogenous nitrogen sources. A settlement signal was also observed between pre- and post-settled red snapper stable isotope values as the post-settled fish had enriched $\delta^{13}\text{C}$ (+1.5 ‰) and $\delta^{15}\text{N}$ (+3.0 ‰) values relative to pre-settled conspecifics.

The enrichment of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in red snapper tissues with increasing size and age is consistent with other studies that have investigated ontogenetic diet shifts from juveniles to adults (Fry et al. 1984, Beaudoin et al. 1999, Fry et al. 1999, Cocheret de la Moriniere et al. 2003). The large $\delta^{15}\text{N}$ difference of 3.5 ‰ combined with a major change in stomach contents from juvenile to adult red snapper indicates a trophic level difference. The decrease in $\delta^{34}\text{S}$ values of red snapper were consistent with a seawater-sulfate importance at smaller sizes, and an increasing importance of sediment-sulfides for older red snapper feeding on benthic species (Moncreiff and Sullivan 2001). Stomach contents corroborated stable isotope results by showing the transition of red snapper feeding on low trophic level prey items commonly occupying the water column (i.e. zooplankton) to one dominated by benthic feeding at higher trophic levels (i.e. benthic crustaceans and fishes).

Ontogenetic feeding shifts in red snapper appeared to be more important than the habitat-specific feeding patterns observed in my study. Results show differences in stomach contents were more common among different age groups over the same habitat than among similarly-aged red snapper collected over different habitats. Cocheret de la Moriniere et al. (2003) reported spatial separation of stable isotopes for adult and juvenile fishes are based upon the nursery and adult habitats from which the fishes were collected. Adult fishes collected over coral reefs retained isotopic values characteristic of a reef diet, while juveniles collected in seagrass and mangroves had diets corresponding to

those habitats. I found decreasing separation of stomach contents and stable isotopes with increasing age, suggesting considerable movement among habitats by adults. The shell-rubble features in this study are approximately 100 to 200 m in width (Dufrene 2005) and the nearby reefs are relatively small and patchy, covering no more than several km² (Schroeder et al. 1988); thus, red snapper would not need to move long distances to encounter all habitats in this study.

The ability to discriminate habitat shifts attributable primarily to feeding opportunities provided by habitat-specific resources was minimal. In addition, seasonal feeding differences were minimal in this study. Diet shifts, along with associated habitat shifts have been seen in other studies (Rooker 1995, Cocheret de la Moriniere et al. 2003, Andersen et al. 2005). Szedlmayer and Lee (2004) found unique habitat-specific prey resources in red snapper diets over sand and artificial reef habitats, and attributed the associated habitat shift to available prey resources. This study showed habitat-specific differences, but indicated red snapper were primarily eating prey associated with sand and mud substrates, despite a sand-shell-reef habitat preference continuum by red snapper with increasing age. Differences may be attributed to the function of natural reefs in this study versus the artificial reefs studied by Szedlmayer and Lee (2004). However, McCawley (2003) performed a diet study on red snapper collected on artificial reefs and found stomach contents contained only 1.26% of reef-associated prey, by dry weight. Nagelkerken and van der Velde (2004) found the majority of fishes utilizing both seagrass beds and mangrove habitats obtained most of their food sources from seagrass beds and attributed these habitat-specific feeding differences to greater food availability in seagrass beds. My study has demonstrated red snapper rely on sand and mud associated prey regardless of the habitat from which red snapper were collected,

suggesting the structural importance of shell and natural reef habitats may be more important for red snapper survival than additional prey resources.

Habitat use of red snapper is age-specific; older individuals recruit to more structured habitats (Bradley and Bryan 1975, Rooker et al. 2004, Patterson et al. 2005). However, Szedlmayer and Lee (2004) found no red snapper <70 mm standard length (SL) on artificial reefs and no red snapper >160 mm SL on open sand habitat. They attributed these distinct habitat shifts to the availability of prey resources. My trawl and trap collections provided red snapper of all age groups at each habitat, thus enabling me to determine whether feeding differences were due to ontogeny, habitat, or a combination of both. Gear differences exist between studies, but the otter trawl and fish traps used in this study appear to sample a more complete age spectrum of red snapper occupying sand, shell, and natural reef habitats on the northern GOM shelf.

The shell-rubble habitat may be important for juvenile red snapper by providing protection from predators; however, the sand habitat appears to be the most important for production and enhancing early life survival. Habitat selection has been shown to be a function of predation pressure and prey availability (Auster et al. 1997). Small-scale biogenic and physical habitat features (e.g. shells, cobbles, sand waves) have been shown to be important for demersal fishes and have been suggested to increase juvenile survivorship (Lindholm et al. 1999, Thrush et al. 2002). An assumption in my approach is that natural mortality is growth rate-dependent and faster growing juveniles have lower mortality rates due to reduced exposure time to predators (Sogard 1997, Cowan et al. 1996). Therefore, it is advantageous to utilize high quality habitats that convey greater foraging and growth opportunities, resulting in an enhanced probability of survival. Growth rates and production (G:Z and P:B ratios) of age 0 red snapper were higher over

sand habitats in my study (Chapter 4), but it was difficult to identify any consistent feeding patterns among similar sized red snapper over different habitats. However, the low shell-rubble provided the most enriched $\delta^{15}\text{N}$ values for all age groups that showed feeding differences (age 0, 0.5+, and 1) and the most important prey items for these red snapper age groups typically included fish material. Thus, juvenile red snapper occupying sand and mud may recruit to structured habitats, such as shell rubble, at a size refuge from predators, while obtaining prey items, such as fish, from the adjacent sand and mud areas.

The presence of commercial shrimp trawling was associated with changes in red snapper stable isotopes regardless of habitat type, but had little effect on the prey items identified in stomach content analysis. The depleted $\delta^{34}\text{S}$ values found over the trawled sand and low shell-rubble were likely a result of sediment re-suspension events following trawl disturbances. Habitat disturbance by trawling has been shown to influence the dynamics of trace and heavy metals, nutrient fluxes, and chemistry in marine sediments (Warnken et al. 2003, Eggleton and Thomas 2004). Additionally, reductions in habitat productivity, alterations of the habitat structure and the associated biological community, and negative impacts to infaunal and epifaunal organisms or those that depend on these species for food resources have been observed over disturbed areas (Auster et al. 1996, Auster 1998, Freese et al. 1999, NRC 2002). The enriched $\delta^{15}\text{N}$ values observed in red snapper collected over trawled areas may be attributed to an increase in the opportunity for red snapper to prey upon benthic organisms that have been injured or killed by trawling. Kenchington et al. (2005) found changes in the diets of demersal fishes were caused by changes in the prey availability brought about by trawling disturbances. An increase in foraging opportunities for large fish predators has been demonstrated in

recently trawled areas where the fish predators rapidly moved to the trawled areas to feed (Wassenberg and Hill 1987, Kaiser and Spencer 1994). Similar processes have been observed in the GOM by bottlenose dolphin (*Tursiops truncatus*) responding to the trawls and preying on fishes exiting trawl openings (UGA Marine Extension Service and NMFS Harvesting Branch 2003). Nevertheless, the increased feeding opportunities over trawled areas may not outweigh the negative effects that commercial shrimp trawling has on vital rates of age 0 red snapper, such as slower growth rates, higher mortality rates, and trawl-induced size truncation (Chapter 4).

Isotope values for both POM and BMA, proxies for planktonic and benthic contributors respectively, were similar to those found in other studies. Sauriau and Kang (2000) found average POM $\delta^{13}\text{C}$ values of -22.2‰ and $\delta^{15}\text{N}$ of 5.0‰. Litvin and Weinstein (2004) found that BMA $\delta^{13}\text{C}$ values ranged between -21 and -14‰, and $\delta^{15}\text{N}$ ranged from 7 to 11‰. In addition, Nadon and Himmelman (2006) found $\delta^{13}\text{C}$ values of POM ranging from -25‰ to -22‰ and BMA averaging -19.4‰, quite similar to my values of -22.7‰ and -19.9‰ for POM and BMA, respectively. Benthic $\delta^{13}\text{C}$ values were also similar to sediment organic matter collected by Kang et al. (2003) that averaged -19.5‰ in three different bay systems in Korea. Thus, my benthic collections may contain a mixture of pennate diatoms, bacteria, sediment, or POM that settled on the bottom. A recent review of $\delta^{13}\text{C}$ enrichment in benthic consumers with increasing depth found that factors other than the ingestion of enriched primary producers may account for the $\delta^{13}\text{C}$ enrichment in the consumers (Nadon and Himmelman 2006). Thus, I cannot completely eliminate other factors such as seasonal pulses of heavy ^{13}C enriched POM or enrichment of POM as particles sink in the water column and become degraded by bacteria and consumers.

The importance of benthic primary production has been demonstrated in this study as well as in other studies investigating the importance of benthic autotrophs to coastal food webs (Herman et al. 2000, Sauriau and Kang 2000, Kang et al. 2003). Benthic consumers have been shown to derive most organic material from benthic contributions, such as BMA, while pelagic consumers rely more on planktonic contributions (Kang et al. 2003). Sauriau and Kang (2000) estimated over 70% of the total cockle production in a European Atlantic coastal bay system was produced from microphytobenthos. While a more detailed isotopic construction of the food web needs to be performed, this is the first study to suggest the importance of a benthic contribution to red snapper on the shallow (<20 m depth) northern GOM shelf.

In summary, the combination of both stomach contents and stable isotopes were useful in determining the importance of ontogeny, habitat type, and the exposure to commercial shrimp trawling to red snapper diet. Results indicate red snapper exhibit distinct ontogenetic feeding shifts; however, sand and mud habitats appear to provide prey resources while more structured habitats (i.e. shell-rubble, natural reefs) may act as a refuge from predators. Seasonal feeding differences were found, but were minimal, while the effects of shrimp trawling over sand and low shell-rubble habitats appear to alter the biogeochemistry of the benthos as well as the feeding dynamics of red snapper as revealed by differences in $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$. Given the importance of a benthic contribution to red snapper identified in this study, the effects of trawling may have strong impacts on trophic interactions on the northern GOM shelf.

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GENERAL SUMMARY AND CONCLUSIONS

My two overall goals consisted of identifying essential fish habitat (EFH) of red snapper, *Lutjanus campechanus*, and evaluating the effects of shrimp trawling on juvenile red snapper life history parameters over the northern Gulf of Mexico (GOM) continental shelf. In addition, I incorporated the impacts of shrimp trawling on benthic fish and invertebrate communities and on the associated habitat features to better understand the ecosystem effects of fishing. The use of multiple gear types (otter trawl, fish traps, a baited underwater video camera array, and a video-equipped remotely operated vehicle (ROV)) in this study has provided a more complete image of red snapper life history than previous studies that have used only one or two gear types. The use of multiple gear types is therefore essential to understand life histories of species that utilize different habitats of varying complexity.

Chapter 1 shows that trawls numerically sample the most red snapper per unit area on natural reefs when compared to the small fish trap, chevron trap, and underwater video array. However, each gear type is size-selective, with the trawl targeting the smallest red snapper and the chevron trap targeting the largest red snapper. Thus, the overall effectiveness of a gear for collecting red snapper is size dependent. Trawling has the highest catchability for sampling juvenile red snapper, while the chevron trap best estimates the relative abundance of larger red snapper.

Chapter 2 highlights the efficacy of using video methodology to assess habitat use by larger red snapper and associated fish assemblages. This method has its inherent biases (e.g., larger fishes were observed while smaller cryptic fishes were likely missed, effect of bait plume on abundance estimates); however, it appears to be both a non-destructive and a practical method to characterize red snapper habitat use over a variety

of substrate types. Structurally complex habitat types with high relief, such as natural and artificial reefs, rock outcrops, and petroleum platforms, should be sampled with non-invasive sampling techniques to avoid habitat destruction. In addition, the logistical simplicity of dropping the camera array for a 30 min period makes this an appropriate method if multiple deployments over distant sites are needed, as was the case in this study.

Chapter 3 describes differences among sand, shell, and reef communities over the inner continental shelf. In addition, differences in biotic communities, diversity indices, size structure, and habitat features between similar habitats in trawled versus non-trawled areas indicate the presence of trawling significantly impacts the benthic ecosystem. Benthic communities respond according to disturbance theory: fishes that share similar life history characteristics of small sizes, short life spans, high mortalities, and rapid biomass turnover (opportunistic strategists) are abundant over trawled habitats. In contrast, larger, longer lived, slower growing, and later reproducing species (periodic strategists) with structural affinities are common life history characteristics for several of the abundant fishes over non-trawled habitats. My results suggest that trawling also is size-selective, which could further exacerbate negative impacts on the GOM fish community. Truncated size distributions and reduced median sizes of the most common bycatch fish species suggest differential mortality of larger individuals due to the size selectivity of the fishing gear.

Chapter 4 illustrates an ontogenetic habitat shift of red snapper from low to higher relief habitats with increasing size and age. Specifically, recently settled red snapper primarily utilize sand and mud habitats, moving to low-relief shell-rubble ridges at several months of age and to higher relief natural reef habitats at age 1 and older. These

habitat shifts appear to be more a function of predator avoidance than prey availability based upon stomach content and stable isotope results from Chapter 5.

Post-settlement processes acting on age 0 red snapper are presumed to be negatively affected by trawling. Results from Chapter 4 highlight the apparent effects of shrimp trawls on red snapper density and associated life history parameters. Higher densities of age 0.5+, combined with larger sizes, faster growth rates in the fall, lower mortality estimates, and higher G:Z and P:B ratios, suggest juvenile red snapper residing over non-trawled areas may have a higher probability of survival than juvenile red snapper in areas exposed to shrimp trawling. These changes in life history parameters of red snapper at the juvenile stage also may have repercussions at the sub-adult and adult stages.

Chapter 5 shows that the combination of both stomach contents and stable isotopes are useful in determining the importance of ontogeny, habitat type, and the exposure to commercial shrimp trawling to red snapper diet. Results indicate red snapper exhibit distinct ontogenetic feeding shifts; however, sand and mud habitats appear primarily to provide prey resources while more structured habitats (i.e., shell-rubble, natural reefs) may act as refugia from predators. Seasonal feeding differences were found, but were minimal, while the effects of shrimp trawling over sand and shell-rubble habitats appear to alter the biogeochemistry of the benthos as well as the feeding dynamics of red snapper as revealed by differences in $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$. Given the importance of a benthic contribution to red snapper identified in this study (i.e., benthic microalgae), the effects of trawling may have strong impacts on trophic interactions on the northern GOM shelf.

This study was unique in that I addressed the four levels of information needed to identify and evaluate EFH for red snapper with multiple gear types, over a large spatial scale (100s km²). Based upon the four habitat-specific levels 1) presence-absence, 2) density, 3) growth, reproduction, or survival, and 4) production, it appears that all habitats (sand, shell-rubble, reefs) in this study are essential to some particular life stage. The shell-rubble and reef habitats may be important for red snapper by providing protection from predators; however, the sand habitat appears to be the most important for production and enhancing early life survival of age 0 fish based upon faster daily growth rates and higher production potential (higher G:Z and P:B ratios). Thus, if management strategies such as shrimp closures are implemented in the GOM to enhance survival of age 0 and age 1 red snapper, then all habitat types in this study will need to be protected.

Results from my study also indicate that commercial shrimp trawling on the GOM shelf negatively impacts red snapper, the fish and invertebrate community, and the associated habitats. Bycatch of age 0 and age 1 red snapper in shrimp trawls may be a bottleneck to rebuilding the GOM red snapper population. This study highlights the notion that significant changes in bycatch of the GOM shrimp fishery will need to be made to rebuild the red snapper population and to preserve ecosystem integrity.

VITA

Robert Joseph David Wells was born on April 29th, 1976, in Palm Springs, California. He grew up in Reno, Nevada, and graduated from Reed High School in 1994. He attended Oregon State University and earned his Bachelor of Science degree in biology in 1998. His growing interest in marine ecology enabled him to work as a research assistant for the University of Maine studying the ecology of lobsters, crabs, urchins, and kelp in the Gulf of Maine. David later moved to Texas, and earned his Master of Science in Wildlife and Fisheries Sciences degree at Texas A&M University in 2002. There he studied the importance of pelagic *Sargassum* as nursery habitat to fishes, with an emphasis on the early life history of greater amberjack. Next, David and his wife spent a year overseas in Kobe, Japan, as English teachers. They then moved to Concepcion, Chile, where David worked for the Catholic University of Concepcion, Chile, studying the recruitment and population dynamics of marine decapods. In the fall of 2003, he entered the doctoral program in the Department of Oceanography and Coastal Sciences at Louisiana State University as a Board of Regents fellow under the supervision of Dr. James H. Cowan, Jr. He will earn a Doctor of Philosophy degree from the Louisiana State University in May of 2007. David has accepted a post-doctoral researcher position at Texas A&M University at Galveston under Dr. Jay Rooker.